L20. The Jamming Avoidance Response (J.A.R.) of Electric Fish (1: Behavior)

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Outline

1) Electroreception and electrogenesis.
   - Electroreception arose as a 6th sense in aquatic vertebrates as a means for detecting bioelectric current arising from muscles and epithelial tissues of prey.
   - Several clades of fishes generate weak electric discharges from e-organs; the e-organs are used for communication or object detection.
   - Powerful electric discharges evolved later for predation or defense.
2) Independently, 2 large clades of e-fish evolved elaborate e-communication.
   - Some species have pulse discharges others have wave discharges.
3) Wave fish jam each other when the discharges have the same frequency.
   - Can’t e-locate when jammed.
4) The jamming avoidance response (JAR) shifts the discharge frequency away from the jamming frequency.
   - JAR restores electrolocation.
5) The JAR is an ideal sensory/motor system for tracing out the entire neural circuit of a complex behavior.

"Passive" electroreception is electrical listening

AMPULLARY

Electroreception is present in many aquatic vertebrates

“Passive” electroreception is electrical listening

Electric Fishes

Electric organs arose independently in 6 lineages of fishes.

Elasmobranchs
- Torpedo rays
- Skates (Raja) (Ray-finned fishes)

Actinopterygii (ray-finned fishes)
- Mormyrids
  - Gymnarchus (1 family, 1 species)
  - Mormyridae (1 family, 200+ species)
- Siluriformes
  - Malapteruridae (1 family, 3-10 species?)
- Gymnotiformes (7 families, 150+ species)
- Perciformes: Uranoscopidae (stargazers)

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Electric fish produce either "pulsed" discharges or "wave" discharges.

"Active" Electrolocation

Resistive object (glass rod).

Discovered using training paradigm (Lissmann, 1958).
Swinging fish quantifies electrolocation performance

Heiligenberg, 1974

Conclusion: Eigenmannia is unable to electrolocate when external stimulus is similar in frequency to its own discharge.
**THE JAR = jamming avoidance response**

![Graph](image1)

**Frequency Clamp**

- Stimulus frequency "tracks" the fish's EOD frequency.
- Moves up or down until asymptote (takes 20 seconds).
- Switch stimulus from \( +\delta F \) to \( -\delta F \).

**Key Stimuli**

Q: What are the essential conditions needed to evoke a JAR?

<table>
<thead>
<tr>
<th>Condition</th>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silence F. Stimulus = ( S_1 ) + ( S_2 ) (same geometry)</td>
<td>no JAR</td>
</tr>
<tr>
<td>Stimulus: ( S_1 ) ( + S_2 ) (differential geometry)</td>
<td>JAR</td>
</tr>
<tr>
<td>( S_1 ) (tail only) ( + S_2 ) (head only)</td>
<td>JAR</td>
</tr>
</tbody>
</table>

Thus: NO apparent connection between pacemaker and sensory areas. (No corollary discharge)

**“Key” Stimuli for JAR**

1. \( |S-F| < 4 \text{ Hz} \).
2. Two signals:
   - \( S \) (stimulus) + \( F \) (fish),
   - or
   - \( S_1 \) (artificial EOD) \( + S_2 \) (artificial jamming stimulus)
     - \( F \) is silenced with curare.
     - Fish's pacemaker is monitored in tail.
     - \( S_1 \) (if substitute) delivered between gut and tail.
     - \( S_2 \) delivered through external electrodes.
3. Geometry for two signals.
The Stimulus

sine wave 1
sine wave 2

amplitude envelope is identical for +df and -df
Interval between zero crossings
phase of S1+S2 relative to S1 alone

What is the stimulus?

both fish generate EODs
Fish 1, senses self plus fish 2

strong S1
moderate S2

beat

Strong S1
Zero S2
Very small beat

What is the nature of the real stimulus?

Mixing of Two Signals

The mixing of two signals is modulated both in amplitude and in phase.

Summed signals

phase, plotted against amplitude.

What differs between +ΔF and -ΔF?

JAR Video
Clever Experiment Shows Need for both phase and amplitude information

A gets both phase and amplitude modulated signal, B gets pure sine wave.
A gets amplitude modulated, B gets phase modulated.

Electroreceptors

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TUBEROUS

Ampullary Electroreceptors Code for D.C. stimuli.
Tonic activity in absence of stimulus.
Increase firing rate on D.C. +ve outside.
Decrease firing rate on D.C. –ve outside.
‘Frequency code’

Peripheral Receptors

T-unit: fires on zero-crossing (every cycle) of stim.
P-unit: probability codes amplitude of stimulus;
P(spike) ~ amplitude of stimulus.

Neuronal responses are close match to phase/amplitude plots

Neuroanatomy of JAR

Overview of entire pathway
Torus semicellularis
Electrosensory Lateral Line Lobe (ELL)
3 ‘redundant’ maps of skin
Lessons from JAR

1. Electric fish use EOD for electrolocation of objects: active location of objects.
2. Eigenmannia (a wave species) is jammed by sinusoidal stimuli near their own frequency (electrolocation performance deteriorates when $\Delta F < 4$ Hz).
3. Eigenmannia performs JAR to avoid jamming. Both $F^+$ and $F^-$ JAR is a model for understanding decision making.
4. JAR depends on two inputs, $S_1 + S_2$ (no reference to pacemaker)
5. JAR depends on differential geometry.
6. Two cues: amplitude modulation + phase modulation
7. Counter clockwise rotation if $+\Delta F$, clockwise rotation if $-\Delta F$
8. Two sensory cues: $AM$, $PM$
9. Two receptor types: amplitude coder ($P$), phase coder ($T$)

References

