Two Population Codes for Two Types of Communication Signals in Weakly-Electric Fish: Firing Rate and Spike Desynchronization.

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University of Ottawa, Ontario, Canada 🇨🇦
1 Introduction: Communication signals in weakly electric fish:
1 **Introduction:** Communication signals in weakly electric fish:

- Small chirps
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- Small chirps
- Large chirps
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   - Small chirps
   - Large chirps

2 **Results I:** Encoding of chirps in electroreceptor afferents.
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2 Results I: Encoding of chirps in electroreceptor afferents.
   - Small chirps
   - Large chirps
Content

1 **Introduction:** Communication signals in weakly electric fish:
   - Small chirps
   - Large chirps

2 **Results I:** Encoding of chirps in electroreceptor afferents.
   - Small chirps
   - Large chirps

3 **Results II:** Population rate code.
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   - Small chirps
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2 **Results I**: Encoding of chirps in electroreceptor afferents.
   - Small chirps
   - Large chirps

3 **Results II**: Population rate code.

4 **Summary**
1 Communication Signals in Weakly Electric Fish
Weakly Electric Fish (*Apteronotus leptorhynchus*)

Electric Organ Discharge (EOD)

- Frequency: 600–1100 Hz

Graph showing EOD waveform with time in milliseconds (ms) and voltage in mV/cm.
Weakly Electric Fish \textit{(Apteronotus leptorhynchus)}

Electric Organ Discharge (EOD)

600–1100 Hz

- Prey detection
Weakly Electric Fish (*Apteronotus leptorhynchus*)

Electric Organ Discharge (EOD)

- Frequency: 600–1100 Hz
  - Prey detection
  - Communication
Communication I: Two Fish

Fish 1: EOD frequency $f_1$
Fish 2: EOD frequency $f_2$
Communication I: Two Fish

Fish 1: EOD frequency $f_1$
Fish 2: EOD frequency $f_2$

$\Rightarrow$ Beat with frequency $\Delta f = f_2 - f_1$
Communication I: Two Fish

Fish 1: EOD frequency \( f_1 \)
Fish 2: EOD frequency \( f_2 \)

\[ \Rightarrow \text{Beat with frequency} \; \Delta f = f_2 - f_1 \]

Male – Male
\[ |\Delta f| < 30 \text{ Hz} \]

Male – Female
\[ |\Delta f| > 100 \text{ Hz} \]
Communication II: Small Chirps

Agonistic signals emitted during male – male interaction ($\Delta f < 30$ Hz)
Communication II: Small Chirps

Agonistic signals: short (14 ms) increase in EOD frequency (30–150 Hz)
Communication II: Small Chirps

Agonistic signals: short (14 ms) increase in EOD frequency (30–150 Hz)
Communication II: Small Chirps

EOD Fish 1 (male)
Communication II: Small Chirps

EOD Fish 1 (male) + EOD Fish 2 (male)
Communication II: Small Chirps

EOD Fish 1 (male) + EOD Fish 2 (male)

EOD Amplitude Modulation Fish 2

Amplitude [mV/cm]

-200 -100 0 100 200

Time [ms]

Beat 5 Hz
Chirp
Communication II: Small Chirps

\[ \Delta f = 5 \text{ Hz} \]

\[ \Delta f = 10 \text{ Hz} \]

\[ \Delta f = 30 \text{ Hz} \]

EOD Amplitude vs. Time [ms]
Two stimulus timescales: beat and chirp.

A small chirp is a small but fast stimulus interrupting a beat.
Communication III: Large Chirps

Courtship signals emitted during male – female interaction ($\Delta f > 100$ Hz)
Communication III: Large Chirps

Courtship signals: short (24 ms) increase in EOD frequency (500 Hz)
Courtship signals: short (24 ms) increase in EOD frequency (500 Hz)

**Frequency [Hz]**

**Amplitude [mV/cm]**

**Time [ms]**
Communication III: Large Chirps

EOD Fish 1 (female)
Communication III: Large Chirps

EOD Fish 1 (female)

EOD Fish 2 (male)

Chirp
Communication III: Large Chirps

EOD Fish 1 (female)

EOD Fish 2 (male)

Chirp

Amplitude [mV/cm]

Time [ms]

Beat 130 Hz

Chirp

EOD Amplitude Modulation Fish 1 (female)
Summary Communication Signals

Small Chirps

Transient signals on low beat frequencies ($\Delta f < 30$ Hz).
Summary Communication Signals

Small Chirps

Transient signals on low beat frequencies ($\Delta f < 30$ Hz).

Large Chirps

Interruption of high frequency beats ($\Delta f > 100$ Hz).
2 Chirp Encoding
In vivo recordings of electroreceptor afferents (P-units)

2.1 Small Chirps
\[ \Delta f = 10 \text{ Hz} \]
$\Delta f = 10 \text{ Hz}$
\[ \Delta f = 10 \text{ Hz} \]
Spike-Frequency Adaptation

Firing frequency [Hz]

Time [ms]

Stimulus $I$

$f_0(I)$

$f_\infty(I)$
Spike-Frequency Adaptation

\[ \tau_{\text{eff}} = 5.5 \text{ ms} \]

**Firing frequency [Hz]**

**Time [ms]**

**Stimulus I**

\[ f_0(I) \]

\[ f_\infty(I) \]
$F-I$ Curves

- **Baseline**
- **Steady-state $f_\infty(I)$**
- **Onset $f_0(I)$**
$F-I$ Curves

Baseline

Steady-state $f_\infty(I)$

Onset $f_0(I)$

Firing frequency [Hz]

EOD Amplitude $I$ [mV/cm]
$F-I$ Curves

- Onset $f_0(I)$
- Steady-state $f_\infty(I)$
- Baseline

Firing frequency [Hz]

EOD Amplitude $I$ [mV/cm]

- 32: 82
- 38: 62
- 42: 42
- 49: 221
- 108: 8
- 149: 18
Model for Spike-Frequency Adaptation

Biophysics of slow ionic currents $\Rightarrow$ model for firing frequency:

\[ f(t) = f_0(I) \]

---

Graph:
- $f(t)$: firing frequency
- $f_0(I)$: onset $f$-$I$-curve
- $f_\infty(I)$: steady-state $f$-$I$-curve
- $A$: adaptation current
- $I_{th}$: threshold of $f_0$

Source:
Model for Spike-Frequency Adaptation

Biophysics of slow ionic currents $\Rightarrow$ model for firing frequency:

$$f(t) = f_0(I - A)$$

$\begin{array}{c}
\text{J. Benda & A. Herz (2003), } \textit{Neural Computation} \textbf{15}, \text{ 2523–2564}
\end{array}$
Model for Spike-Frequency Adaptation

Biophysics of slow ionic currents $\Rightarrow$ model for firing frequency:

$$f(t) = f_0(I - A)$$

$$\tau \dot{A} = f_\infty^{-1}(f) - f_0^{-1}(f) - A$$

---

\[ \Delta f = 5 \text{ Hz} \]
Model Prediction

$\Delta f = 5$ Hz

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>Amplitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>200</td>
<td>2</td>
</tr>
<tr>
<td>100</td>
<td>2.4</td>
</tr>
<tr>
<td>0</td>
<td>2.8</td>
</tr>
<tr>
<td>-100</td>
<td>2.4</td>
</tr>
<tr>
<td>-200</td>
<td>2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Firing frequency</th>
<th>Stimulus</th>
</tr>
</thead>
<tbody>
<tr>
<td>1000</td>
<td>2</td>
</tr>
<tr>
<td>800</td>
<td>2.4</td>
</tr>
<tr>
<td>600</td>
<td>2.8</td>
</tr>
<tr>
<td>400</td>
<td>2.4</td>
</tr>
<tr>
<td>200</td>
<td>2</td>
</tr>
<tr>
<td>0</td>
<td>2.8</td>
</tr>
</tbody>
</table>
Model Prediction

$\Delta f = 5$ Hz
Model Prediction

\[ \Delta f = 30 \text{ Hz} \]
Highpass Filter of Adaptation

Linear \( f-I \) curves → Linear adaptation: \( \tau_{\text{eff}} \approx 7 \text{ ms}, \frac{f_0'}{f_\infty'} \approx 6 \)
Highpass Filter of Adaptation

Linear $f$-$I$ curves $\rightarrow$ Linear adaptation: $\tau_{\text{eff}} \approx 7$ ms, $f'_0/f'_\infty \approx 6$

![Graph showing the gain $|H_f|/f'_\infty$ as a function of stimulus frequency $[\text{Hz}]$]
The high-pass filter’s cutoff frequency separates slow beats from fast chirps.
Behavior: System Output

![Graph showing chirp probability vs. beat frequency (Δf) in Hz.]

Similar reduction of electroreceptor response and behavior with increasing beat frequency.
Similar reduction of electroreceptor response and behavior with increasing beat frequency.

⇒ Response gain / firing frequency might be the relevant code.
Similar reduction of electroreceptor response and behavior with increasing beat frequency.

⇒ Response gain / firing frequency might be the relevant code.

⇒ The receptors are likely the only bottleneck in detecting chirps.
Conclusion Small Chirps

**Stimuli:** Small chirps are small but fast communication signals on top of slow beats.
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**Recordings:** Firing frequency response of electroreceptor afferents to small chirps is enhanced compared to the response to slow beats.
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Model: Data can be explained by spike-frequency adaptation:
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**Model:** Data can be explained by spike-frequency adaptation:

Timescale separation by highpass filter
In vivo recordings of electroreceptor afferents (P-units)

2.2 Large Chirps
Single Unit Recordings

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat $\Delta f = 100$ Hz

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat $\Delta f = 100$ Hz

Chirp 24 ms 600 Hz

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat $\Delta f = 100$ Hz

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat $\Delta f = 100$ Hz

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat $\Delta f = 100$ Hz

Synchronous

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat $\Delta f = 100$ Hz

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat \( \Delta f = 180 \text{ Hz} \)

EOD: 822 Hz, non-bursting P-unit \( r = 160 \text{ Hz} \), P-value=0.2
Single Unit Recordings

Beat $\Delta f = 180$ Hz

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Single Unit Recordings

Beat Δf = 180 Hz

EOD: 822 Hz, non-bursting P-unit r = 160 Hz, P-value=0.2
Single Unit Recordings

Beat $\Delta f = 260$ Hz

EOD: 822 Hz, non-bursting P-unit $r = 160$ Hz, P-value=0.2
Dual Unit Recordings: Setup
Dual Unit Recordings: Introduction

Cell 1

Spike raster

EOD Amplitude

$EOD = 853 \text{ Hz}, \ \Delta f = 100 \text{ Hz}$

$r_1 = 178 \text{ Hz}, \ \text{P-value}=0.21$

$r_2 = 140 \text{ Hz}, \ \text{P-value}=0.16$
Dual Unit Recordings: Introduction

\[ r_1 = 178 \text{ Hz, P-value}=0.21 \]

EOD: 853 Hz, Beat \( \Delta f = 100 \text{ Hz} \)

\[ r_2 = 140 \text{ Hz, P-value}=0.16 \]
**Dual Unit Recordings: Introduction**

Cell 1 & Cell 2

- **EOD Amplitude**
  - Cell 1: $r_1 = 178$ Hz, P-value=0.21
  - Cell 2: $r_2 = 140$ Hz, P-value=0.16

- **Spike raster**

- **Time [ms]**
  - $r_1$: EOD 853 Hz, Beat $\Delta f = 100$ Hz

---

- **EOD Amplitude**
  - 6
  - 5.5
  - 5
  - 4.5
  - 4

- **Spike raster**
  - 60
  - 40
  - 20
  - 0
  - 20
  - 40
  - 60
Dual Unit Recordings: Introduction

Cell 1 & Cell 2

$EOD: 853\, \text{Hz}, \, \Delta f = 100\, \text{Hz}$

$r_1 = 178\, \text{Hz}, \, \text{P-value}=0.21$

$r_2 = 140\, \text{Hz}, \, \text{P-value}=0.16$
Dual Unit Recordings: Introduction

Cell 1 & Cell 2

EOD Amplitude

Spike raster

$\Delta f = 100$ Hz

$r_1 = 178$ Hz, P-value=0.21

EOD: 853 Hz

$r_2 = 140$ Hz, P-value=0.16
Dual Unit Recordings: Coincidence

Spike raster

Time [ms]

Coincidence probability

Δt [ms]

-60 -40 -20 0 20 40 60

0 0.2 0.4 0.6 0.8 1

Beat

$r_1 = 178 \text{ Hz}, \text{ P-value}=0.21$

EOD: 853 Hz, Beat $\Delta f = 100 \text{ Hz}$

$r_2 = 140 \text{ Hz}, \text{ P-value}=0.16$
Dual Unit Recordings: Coincidence

Spike raster

Coincidence probability

Time [ms]

Δt [ms]

$ r_1 = 178 \text{ Hz, P-value}=0.21 $  
EOD: 853 Hz, Beat $ \Delta f = 100 \text{ Hz} $  
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Dual Unit Recordings: Coincidence

Spike raster

Time [ms]

Coincidence probability

\[ \Delta t [\text{ms}] \]

\[ r_1 = 178 \text{ Hz}, \text{ P-value}=0.21 \]

EOD: 853 Hz, Beat \( \Delta f = 100 \text{ Hz} \)

\[ r_2 = 140 \text{ Hz}, \text{ P-value}=0.16 \]
Dual Unit Recordings: Synchrony

Spike raster

Time [ms]

Synchrony \( P(A, B) - P(A)P(B) \)

\[ \Delta t [\text{ms}] \]

Beat

\( r_1 = 178 \, \text{Hz}, \, \text{P-value}=0.21 \)  \hspace{1cm} \text{EOD: 853 Hz, Beat } \Delta f = 100 \, \text{Hz} \)  \hspace{1cm} \( r_2 = 140 \, \text{Hz}, \, \text{P-value}=0.16 \)
Dual Unit Recordings: Synchrony

Spike raster

Time [ms]

Synchrony $P(A, B) - P(A)P(B)$

Δt [ms]

$\Delta f = 100$ Hz

$EOD: 853$ Hz

$P_1 = 178$ Hz, $P$-value=0.21

$P_2 = 140$ Hz, $P$-value=0.16
Trunk-Nerve Recordings: Introduction

Beat $\Delta f = 100$ Hz

EOD: 764 Hz
Trunk-Nerve Recordings: Introduction

Beat $\Delta f = 100$ Hz

EOD: 764 Hz
Trunk-Nerve Recordings: Introduction

Beat $\Delta f = 100$ Hz

EOD: 764 Hz
Trunk-Nerve Recordings: Introduction

Beat $\Delta f = 100$ Hz

EOD: 764 Hz
Trunk-Nerve Recordings: Introduction

Beat $\Delta f = 100$ Hz

EOD: 764 Hz
Trunk-Nerve Recordings: Introduction

Beat $\Delta f = 100$ Hz

EOD: 764 Hz
Trunk-Nerve Recordings: Introduction

Beat $\Delta f = 100$ Hz

EOD: 764 Hz
Trunk-Nerve Recordings: Beats

Beat $\Delta f = 100$ Hz

Beat $\Delta f = 200$ Hz

Beat $\Delta f = 150$ Hz

Beat $\Delta f = 300$ Hz
Behavior: System Output

Population synchrony vs. Beat frequency $\Delta f$ [Hz]

- $\Delta f$ values: 300, 250, 200, 150, 100, 50
Behavior: System Output

Population synchrony

Beat frequency $\Delta f$ [Hz]

Behavior: System Output


⇒ Electroreceptor synchrony and behavior peak at similar beat frequencies.
Conclusion Large Chirps

**Stimuli:** Large chirps interrupt high frequency beats.
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**Recordings:**

- High-frequency beats elicit *synchronous* spikes.
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- Large chirps are coded by *desynchronization*. 
Conclusion Large Chirps

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- High-frequency beats elicit *synchronous* spikes.
- Large chirps are coded by *desynchronization*.

⇒ *Desynchronization* of the spike response can be as important as *synchronous* spikes.
Conclusion Large Chirps

**Stimuli:** Large chirps interrupt high frequency beats.

**Recordings:**
- High-frequency beats elicit **synchronous** spikes.
- Large chirps are coded by **desynchronization**.

⇒ **Desynchronization** of the spike response can be as important as **synchronous** spikes.

Any change of the degree of synchrony could code a signal!
Summary Chirp Encoding

Small chirps: Enhancement of spike-frequency response on slow beats ($\Delta f < 30$ Hz)
⇒ high-pass due to spike-frequency adaptation.
Summary Chirp Encoding

**Small chirps:** Enhancement of spike-frequency response on slow beats ($\Delta f < 30$ Hz)
$\Rightarrow$ high-pass due to spike-frequency adaptation.

**Large chirps:** Desynchronization of spike response on fast beats ($\Delta f > 100$ Hz).
3 Population Rate Code
## Single Trial: Small Chirps I

<table>
<thead>
<tr>
<th>Stimulus $\Delta f$</th>
<th>Amplitude</th>
<th>Time [ms]</th>
<th>Spikes</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 Hz</td>
<td></td>
<td></td>
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</table>

<table>
<thead>
<tr>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Firing rate [Hz]</td>
</tr>
<tr>
<td>600</td>
</tr>
<tr>
<td>400</td>
</tr>
<tr>
<td>200</td>
</tr>
<tr>
<td>0</td>
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</table>

<table>
<thead>
<tr>
<th>Stimulus $\Delta f = 5$ Hz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude</td>
</tr>
<tr>
<td>3.0</td>
</tr>
<tr>
<td>2.8</td>
</tr>
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<td>2.4</td>
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<td>1.6</td>
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<tr>
<td>0.4</td>
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<td>0.0</td>
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</tbody>
</table>

Graph showing response and stimulus over time.
Single Trial: Small Chirps I

Stimulus $\Delta f = 5$ Hz

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>200</th>
<th>1000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Firing rate [Hz]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spikes</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

Response

Stimulus $\Delta f = 5$ Hz

Amplitude

Time [ms]
Single Trial: Small Chirps I

Response

Stimulus $\Delta f = 5$ Hz

$\Rightarrow$ Single trial firing rate matches averaged firing rate.
Single Trial: Small Chirps I

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>200</th>
<th>1000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude</td>
<td>10</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>200</th>
<th>1000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude</td>
<td>10</td>
<td>0</td>
</tr>
</tbody>
</table>

Nerve [V]

Stimulus $\Delta f = 5$ Hz
Single Trial: Small Chirps I

Population signal is similar to single trial firing rate of each cell.
Single Trial: Small Chirps II

Stimulus: $\Delta f = 5$ Hz

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>Amplitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>200</td>
<td>2</td>
</tr>
<tr>
<td>1000</td>
<td>4</td>
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Response:

<table>
<thead>
<tr>
<th>Firing rate [Hz]</th>
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<tbody>
<tr>
<td>900</td>
</tr>
<tr>
<td>600</td>
</tr>
<tr>
<td>300</td>
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<tr>
<td>0</td>
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Spikes:

<table>
<thead>
<tr>
<th>Spikes</th>
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<tbody>
<tr>
<td>5</td>
</tr>
<tr>
<td>4</td>
</tr>
<tr>
<td>3</td>
</tr>
<tr>
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<tr>
<td>1</td>
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</table>
Single Trial: Small Chirps II

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>$\Delta f$ = 5 Hz</th>
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</table>

<table>
<thead>
<tr>
<th>Amplitude</th>
<th>Time [ms]</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>2.4</td>
<td>200</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Response</th>
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<tbody>
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<td>Firing rate [Hz]</td>
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<tr>
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<thead>
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<tbody>
<tr>
<td>5</td>
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<td>4</td>
</tr>
<tr>
<td>3</td>
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<tr>
<td>2</td>
</tr>
<tr>
<td>1</td>
</tr>
</tbody>
</table>
Single Trial: Small Chirps II

Stimulus \( \Delta f = 5 \) Hz

Amplitude

Time [ms]

200 1000

2 10

2 2

2 0

Spikes

Firing rate [Hz]

900

600

300

90

5

0

Single trial firing rate matches averaged firing rate.
Single Trial: Small Chirps II

Stimulus $\Delta f = 5$ Hz

<table>
<thead>
<tr>
<th>Nerve [\mu V]</th>
<th>Time [ms]</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>200</td>
</tr>
<tr>
<td></td>
<td>1000</td>
</tr>
<tr>
<td></td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>200</td>
</tr>
</tbody>
</table>

Stimulus $\Delta f = 5$ Hz
Autoencoder unsupervised learning algorithms are used to extract meaningful patterns from raw nerve signal data. The population signal is similar to the single trial firing rate of each cell.

⇒ Population signal is similar to single trial firing rate of each cell.
Conclusion Small Chirps

- Single trial firing rate matches averaged firing rate.
- Population signal is similar to single trial firing rate of each cell.
Conclusion Small Chirps

- Single trial firing rate matches averaged firing rate.
- Population signal is similar to single trial firing rate of each cell.
Conclusion Small Chirps

- Single trial firing rate matches averaged firing rate.
- Population signal is similar to single trial firing rate of each cell.

Redundancy

- Each P-unit carries already most of the information about a small chirp.
Conclusion Small Chirps

- Single trial firing rate matches averaged firing rate.
- Population signal is similar to single trial firing rate of each cell.

Redundancy

- Each P-unit carries already most of the information about a small chirp.
- Averaging over the whole population just improves the signal.
Single Trial: Large Chirps I

Stimulus

$\Delta f = 200$ Hz

Amplitude

Time [Hz]

80 60 40 20 0

4

3.6

3.2

2.8

Spikes

Response

Firing rate [Hz]

600

400

200

0

8

6

4

2

Spike counts

Stimulus $\Delta f = 200$ Hz

Time [Hz]
Single Trial: Large Chirps I

Stimulus

$\Delta f = 200$ Hz

<table>
<thead>
<tr>
<th>Time [Hz]</th>
<th>Amplitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>80</td>
<td>6</td>
</tr>
<tr>
<td>60</td>
<td>4</td>
</tr>
<tr>
<td>40</td>
<td>2</td>
</tr>
<tr>
<td>20</td>
<td>4</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Time [Hz]</th>
<th>Firing rate [Hz]</th>
</tr>
</thead>
<tbody>
<tr>
<td>80</td>
<td>600</td>
</tr>
<tr>
<td>60</td>
<td>400</td>
</tr>
<tr>
<td>40</td>
<td>200</td>
</tr>
<tr>
<td>20</td>
<td>0</td>
</tr>
</tbody>
</table>

Response

Stimulus $\Delta f = 200$ Hz

Time [Hz] range from $-80$ to $80$.
Single Trial: Large Chirps I

Stimulus $\Delta f = 200$ Hz

Amplitude

Time [Hz]

80 60 40 20 0

4 2 0

Spikes

Response

Firing rate [Hz]

600 400 200 0

4 2 0

Singles trial firing rate does NOT match averaged firing rate.
Population signal differs from single trial firing rate of each cell.
Single Trial: Large Chirps II

Stimulus $\Delta f = 100$ Hz

<table>
<thead>
<tr>
<th>Time [Hz]</th>
<th>Amplitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>80</td>
<td>3.8</td>
</tr>
<tr>
<td>60</td>
<td>3.6</td>
</tr>
<tr>
<td>40</td>
<td>3.2</td>
</tr>
<tr>
<td>20</td>
<td>2.8</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Time [Hz]</th>
<th>Firing rate [Hz]</th>
</tr>
</thead>
<tbody>
<tr>
<td>80</td>
<td>600</td>
</tr>
<tr>
<td>60</td>
<td>400</td>
</tr>
<tr>
<td>40</td>
<td>200</td>
</tr>
<tr>
<td>20</td>
<td>0</td>
</tr>
</tbody>
</table>

Response

Stimulus $\Delta f = 100$ Hz

Spikes
Single Trial: Large Chirps II

Stimulus \( \Delta f = 100 \text{ Hz} \)

<table>
<thead>
<tr>
<th>Amplitude</th>
<th>Time [Hz]</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
</tr>
</tbody>
</table>

Response

Firing rate [Hz]

<table>
<thead>
<tr>
<th>Spikes</th>
</tr>
</thead>
<tbody>
<tr>
<td>600</td>
</tr>
<tr>
<td>400</td>
</tr>
<tr>
<td>200</td>
</tr>
</tbody>
</table>

Spikes

Time [Hz]

-80   -60   -40   -20    0    20    40    60    80
Single Trial: Large Chirps II

Stimulus $\Delta f = 100$ Hz

Response

Firing rate [Hz]

Spikes

Amplitude

$\Rightarrow$ Single trial firing rate does NOT match averaged firing rate.
Single Trial: Large Chirps I

[Graph showing time and firing rate with annotations]

⇒ Population signal differs from single trial firing rate of each cell.
Conclusion Large Chirps

- Single trial firing rate does NOT match averaged firing rate.
- Population signal differs from single trial firing rate of each cell.
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Synergy

- A P-unit alone is not sufficient to encode a large chirp.
Conclusion Large Chirps

- Single trial firing rate does NOT match averaged firing rate.

- Population signal differs from single trial firing rate of each cell.

Synergy

- A P-unit alone is not sufficient to encode a large chirp.

- The whole population is needed to encode the signal.
4 Final Summary

**Small chirps:** Enhancement of spike-frequency response on slow beats ($\Delta f < 30$ Hz)

$\Rightarrow$ high-pass due to spike-frequency adaptation.

$\Rightarrow$ redundant population rate code.
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