Linear Filters in Sensory Processing

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Tutorial  Linear systems
Theory  Spike-frequency adaptation
Experiment  Electrosensory system
Tutorial
Linear Systems

$s(t)$ → linear system $H$ → $r(t)$
Fourier Series: Saw-tooth

\[ f(t) = 1 - \frac{x}{\pi} \]
Fourier Series: Saw-tooth

\[ g_1(t) = \frac{2}{\pi} \sin(t) \]

\[ f(t) = 1 - \frac{x}{\pi} \]
Fourier Series: Saw-tooth

\[ f(t) = 1 - \frac{x}{\pi} \]

\[ g_2(t) = \frac{2}{2\pi} \sin(2t) \]

\[ g_1 + g_2 \]
Fourier Series: Saw-tooth

\[ f(t) = 1 - \frac{x}{\pi} \]

\[ g_3(t) = \frac{2}{3\pi} \sin(3t) \]

\[ g_1 + g_2 + g_3 \]
Fourier Series: Saw-tooth

\[ f(t) = 1 - \frac{x}{\pi} \]

\[ g_4(t) = \frac{2}{4\pi} \sin(4t) \]

\[ g_1 + g_2 + g_3 + g_4 \]
Fourier Series: Saw-tooth

\[ \sum_{k=1}^{10} g_k(t) = \frac{2}{10\pi} \sin(10t) \]

\[ f(t) = 1 - x/\pi \]

Graph showing the functions: blue line for \( f(t) \), orange line for \( g_{10}(t) \), and red line for \( \sum_{k=1}^{10} g_k(t) \) over the range of \( 0 \) to \( 5\pi \).
Fourier Series: Saw-tooth

\[ f(t) = 1 - x / \pi \]

\[ g_{20}(t) = \frac{2}{20\pi} \sin(20t) \]

\[ \sum_{k=1}^{20} g_k \]
Each odd function \( f(t) \) with period \( T \) can be decomposed into a sum of sine functions:

\[
f(t) = \sum_{k=1}^{\infty} A_k \sin\left(\frac{2k\pi t}{T}\right)
\]
Time and Frequency Domain

\[ f(t) = 1 - \frac{x}{\pi} \]
Time and Frequency Domain

\[ f(t) = 1 - \frac{x}{\pi} \]

\[ f(t) = \sum_{k=1}^{\infty} A_k \sin(kt) \]
Time and Frequency Domain

Time Domain

\[ f(t) = 1 - \frac{x}{\pi} \]

Frequency Domain

\[ f(t) = \sum_{k=1}^{\infty} A_k \sin(kt) \]
Linear System

\[ s(t) \xrightarrow{H} r(t) \]

Linear system \( H \) transforms signal \( s(t) \) into response \( r(t) \)
Frequency of sine wave is not changed
Linear System and Sine Waves

- Frequency of sine wave is **not** changed
- Amplitude can be changed
Linear System and Sine Waves

- Frequency of sine wave is not changed
- Amplitude can be changed
- Phase can be changed
Linear System Definition

\[ s(t) \xrightarrow{H} r(t) \]

Linear system \( H \) transforms signal \( s(t) \) into response \( r(t) \):

\[ r(t) = H\{s(t)\} \]

The system is **linear**, if

- \( H\{\alpha s(t)\} = \alpha H\{s(t)\} \) (scaling)

- \( H\{s_1(t) + s_2(t)\} = H\{s_1(t)\} + H\{s_2(t)\} \) (superposition)
Superposition and Sine-Waves

\[ s_1(t) \xrightarrow{A_1 \mapsto 0.8 \cdot A_1, \varphi_1 \mapsto \varphi_1} r_1(t) \]
Superposition and Sine-Waves

\[ s_1(t) + s_2(t) \rightarrow A_1 \mapsto 0.8 \cdot A_1 \]

\[ r_1(t) \]

\[ \varphi_1 \mapsto \varphi_1 \]

\[ A_2 \mapsto 0.5 \cdot A_2 \]

\[ \varphi_2 \mapsto \varphi_2 - \pi/2 \]

\[ r_2(t) \]
Superposition and Sine-Waves

\[ r(t) = r_1(t) + r_2(t) \]

\[ s(t) = s_1(t) + s_2(t) \]
Linear Filter Defines Linear System

\[ s(t) \xrightarrow{\text{Filter}} H(\omega) \xrightarrow{} r(t) \]
Linear Filter Defines Linear System

\[ H(\omega) \]

\[ s(t) \xrightarrow{\text{Filter}} r(t) \]
Linear Filter Defines Linear System

\[ s(t) \xrightarrow{\text{Filter}} H(\omega) \xrightarrow{\text{Filter}} r(t) \]

- Gain
- Phase
- Frequency
Low-pass Filter

Filter $H(\omega)$
Low-pass Filter

\[ H(\omega) \]

\[ s(t) \rightarrow \text{Filter} \rightarrow r(t) \]
High-pass Filter

\[ H(\omega) \]

Frequency
Gain

\( s(t) \)

Filter

?
High-pass Filter

\[ H(\omega) \]

\[ s(t) \rightarrow H(\omega) \rightarrow r(t) \]
A Model for Spike-Frequency Adaptation

Phenomenon: Spike-Frequency Adaptation

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>Stimulus</th>
</tr>
</thead>
<tbody>
<tr>
<td>300</td>
<td>50</td>
</tr>
<tr>
<td>250</td>
<td>100</td>
</tr>
<tr>
<td>200</td>
<td>150</td>
</tr>
<tr>
<td>150</td>
<td>200</td>
</tr>
<tr>
<td>100</td>
<td>250</td>
</tr>
<tr>
<td>50</td>
<td>300</td>
</tr>
</tbody>
</table>

Onset response $f_0$

Steady-state response $f_\infty$
Mechanism: Encoder Adaptation

- M-type currents
- AHP-currents
- Slow recovery from inactivation

Input Current $I$

$g(J)$

$I-A$

Subtractive

Spike frequency $f(t)$
• Adaptation currents \( I_M, I_{AHP}, \ldots \) are ionic currents.
• Ionic currents flow in parallel over the cell membrane \( \Rightarrow \) Adaptation currents \( A \) act **subtractively** on input current \( I \):
  \[ I - A \]
M-type Currents

\[ I_M = \bar{g}_M a (V - E_K) \]
\[ \tau_a \dot{a} = a_\infty (V) - a \]
M-type Currents

\[ I_M = \bar{g}_M a (V - E_K) \]

\[ \tau_a \dot{a} = a_\infty (V) - a \]

\[ f_0(I) \quad \tau_{\text{eff}} \]

\[ f_\infty(I) \]

\[ I \]

\[ I_M \quad [\mu A/cm^2] \]

Time [ms]
M-type Currents

\[ I_M = \bar{g}_M a (V - E_K) \]
\[ \tau_a \dot{a} = a_\infty (V) - a \]
\[ \Rightarrow \quad A = \langle I_M \rangle \]
\[ \tau \dot{A} = A_\infty (f) - A \]

time average!
Spike Generator and $f$-$I$ Curve

Spike frequency $f$ [Hz]

Input current $I$ [$\mu$A/cm$^2$]

$f(I) = f_0(I)$
General Phenomenological Model

Biophysics of slow ionic currents ⇒ model for spike frequency:

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

Spike generator

- \( f(t) \) spike frequency
- \( f_0(I) \) onset \( f\text{-}I \) curve
- \( I_{th} \) threshold of \( f_0 \)
Biophysics of slow ionic currents $\Rightarrow$ model for spike frequency:

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

**Subtractiveness**

- $f(t)$: spike frequency
- $f_0(I)$: onset $f$-$I$ curve
- $I_{th}$: threshold of $f_0$
- $A$: averaged adaptation current

![Diagram showing the relationship between injected current and spike frequency](chart.png)
General Phenomenological Model

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

\[
f(t) = f_0(I - A)
\]
\[
\tau \dot{A} = A_\infty(f) - A
\]

Adaptation dynamics

- $f(t)$: spike frequency
- $f_0(I)$: onset $f$-$I$ curve
- $I_{th}$: threshold of $f_0$
- $A$: averaged adaptation current
- $\tau$: adaptation time-constant
General Phenomenological Model

Biophysics of slow ionic currents ⇒ model for spike frequency:

\[ f(t) = f_0(I - A) \]
\[ \tau \dot{A} = f_\infty^{-1}(f) - f_0^{-1}(f) - A \]

Steady-state

- \( f(t) \) spike frequency
- \( f_0(I) \) onset \( f-I \) curve
- \( I_{th} \) threshold of \( f_0 \)
- \( A \) averaged adaptation current
- \( \tau \) adaptation time-constant
- \( f_\infty(I) \) steady-state \( f-I \) curve
How does it work?

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

\[ A = 0 \]
How does it work?

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

\[ A = 0 \]
How does it work?

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

\[ \tau \dot{A} = f_\infty^{-1}(f) - f_0^{-1}(f) - A \]
How does it work?

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

\[ \tau \dot{A} = f_{\infty}^{-1}(f) - f_0^{-1}(f) - A \]
How does it work?

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

\[ \tau \dot{A} = f_\infty^{-1}(f) - f_0^{-1}(f) - A \]
How does it work?

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

\[ \tau \dot{A} = f_\infty^{-1}(f) - f_0^{-1}(f) - A \]
Highpass Filter

Linearized $f$-$I$ curves → Linear adaptation

$$\tau \frac{f_\infty'}{f_0'} \dot{f} = f'_\infty I + \tau f'_\infty \dot{I} - f$$

Slopes of onset and steady-state $f$-$I$ curve: $f'_0$ and $f'_\infty$
Highpass Filter

Linearized $f$-$I$ curves $\rightarrow$ Linear adaptation $\rightarrow$ Transfer function $H_f(\omega)$

$$\tau \frac{f'_\infty}{f'_0} \dot{f} = f'_\infty I + \tau f'_\infty \dot{I} - f$$

Slopes of onset and steady-state $f$-$I$ curve: $f'_0$ and $f'_\infty$

Effective time constant of adaptation: $\tau_{\text{eff}} \approx \tau \frac{f'_\infty}{f'_0}$

Cutoff frequency $\omega_{\text{cutoff}} \tau_{\text{eff}} \approx 1$
Highpass Filter

Linearized $f$-$I$ curves $\rightarrow$ Linear adaptation $\rightarrow$ Transfer function $H_f(\omega)$

\[ \tau \frac{f'_\infty}{f'_0} \dot{f} = f'_\infty I + \tau f'_\infty \dot{I} - f \]

Slopes of onset and steady-state $f$-$I$ curve: $f'_0$ and $f'_\infty$

Effective time constant of adaptation: $\tau_{\text{eff}} \approx \tau \frac{f'_\infty}{f'_0}$

Cutoff frequency $\omega_{\text{cutoff}} \tau_{\text{eff}} \approx 1$
Conclusion Spike-Frequency Adaptation

- Slow, inhibitory ionic currents ($I_M, I_{AHP}, \ldots$)
- Act subtractively on input: $I - A$
- Model for spike frequency: $f_0(I)$, $f_\infty(I)$, $\tau$
- Highpass filter
Encoding of Communication Signals in Weakly Electric Fish

Weakly Electric Fish (*Apteronotus leptorhynchos*)

Electric Organ Discharge (EOD)

- Frequency: 600–1100 Hz
Weakly Electric Fish (*Apteronotus leptorhynchus*)

Electric Organ Discharge (EOD)

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

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

$\Rightarrow$ Beat with frequency $\Delta f = f_2 - f_1$

Male – Male
$|\Delta f| < 30\,\text{Hz}$
Communication II: Small Chirps

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

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

EOD Male 1
Communication II: Small Chirps

EOD Male 1

EOD Male 2

Chirp
Communication II: Small Chirps

EOD Male 1 + EOD Male 2

EOD Amplitude Modulation Male 1

Amplitude [mV/cm]

Time [ms]

Beat 5 Hz

Chirp
Communication II: Small Chirps

EOD Male 1

EOD Male 2

Chirp

EOD Amplitude Modulation Male 1

Amplitude [mV/cm]

Beat 5 Hz

Chirp

Time [ms]
In vivo recording of electoreceptor afferents (P-units)

Stimulus $\Delta f = 10$ Hz

Response
In vivo recording of electroreceptor afferents (P-units)

Stimulus $\Delta f = 10$ Hz
In vivo recording of electroreceptor afferents (P-units)

Stimulus $\Delta f = 10$ Hz

Response
In vivo recording of electroreceptor afferents (P-units)

Stimulus $\Delta f = 10$ Hz

Response
Spike-Frequency Adaptation!

Spike frequency [Hz]

Time [ms]

Stimulus \( I \)
Spike-Frequency Adaptation!

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

\[
f_0(I) \quad f_\infty(I)
\]

Stimulus $I$

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>Spike frequency [Hz]</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>20</td>
<td>800</td>
</tr>
<tr>
<td>40</td>
<td>600</td>
</tr>
<tr>
<td>60</td>
<td>400</td>
</tr>
<tr>
<td>80</td>
<td>200</td>
</tr>
<tr>
<td>100</td>
<td>0</td>
</tr>
</tbody>
</table>
$F-I$ Curves

<table>
<thead>
<tr>
<th>Spike Frequency [Hz]</th>
<th>EOD Amplitude $I$ [mV/cm]</th>
</tr>
</thead>
<tbody>
<tr>
<td>32.82</td>
<td>0</td>
</tr>
<tr>
<td>39.62</td>
<td>1.8</td>
</tr>
<tr>
<td>46.42</td>
<td>2</td>
</tr>
<tr>
<td>53.22</td>
<td>2.2</td>
</tr>
<tr>
<td>60.02</td>
<td>2.4</td>
</tr>
<tr>
<td>66.82</td>
<td>2.6</td>
</tr>
<tr>
<td>73.62</td>
<td>2.8</td>
</tr>
<tr>
<td>80.42</td>
<td>3.0</td>
</tr>
</tbody>
</table>

- baseline
- steady-state $f_\infty(I)$
- onset $f_0(I)$
$F-I$ Curves

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

Spike Frequency [Hz] vs. EOD Amplitude $I$ [mV/cm]

<table>
<thead>
<tr>
<th>EOD Amplitude $I$ [mV/cm]</th>
<th>Spike Frequency [Hz]</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.8</td>
<td>0</td>
</tr>
<tr>
<td>2.0</td>
<td>100</td>
</tr>
<tr>
<td>2.2</td>
<td>200</td>
</tr>
<tr>
<td>2.4</td>
<td>300</td>
</tr>
<tr>
<td>2.6</td>
<td>400</td>
</tr>
<tr>
<td>2.8</td>
<td>500</td>
</tr>
<tr>
<td>3.0</td>
<td>600</td>
</tr>
</tbody>
</table>

Legend:
- Teal line: baseline
- Red circle: steady-state $f_\infty(I)$
- Green square: onset $f_0(I)$
\[ F - I \text{ Curves} \Rightarrow f(I) = f_0(I - A) \]
Model Prediction

Stimulus $\Delta f = 5$ Hz

Response

Spike frequency [Hz]

Amplitude

Time [ms]
Model Prediction

Stimulus $\Delta f = 5$ Hz

Data model

Spike frequency [Hz]

Amplitude

Time [ms]

Response
Model Prediction

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

Response

Spike frequency [Hz]

Amplitude

Stimulus \( \Delta f = 5 \text{ Hz} \)

Time [ms]
Model Prediction

Stimulus $\Delta f = 30$ Hz

Response

Spike frequency [Hz]

Amplitude

Stimulus $\Delta f = 30$ Hz

Time [ms]
Highpass Filter of Adaptation

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

![Graph showing the relationship between stimulus frequency and gain](image)
Highpass Filter of Adaptation

Linear $f-I$ curves $\rightarrow$ Linear adaptation: $\tau_{\text{eff}} \approx 7$ ms, $f_0'/f_\infty' \approx 6$

$\Rightarrow$ The high-pass filter’s cutoff frequency separates slow beats from fast chirps.
Summary

- Linear systems and filter
- Spike-frequency adaptation and high-pass filtering
- Encoding of communication signals in the electrosensory system
Thanks to

Andreas Herz

Len Maler & André Longtin

Apteronotus leptorhynchus