Spike-Frequency Adaptation in Early Sensory Processing

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Neural Systems
Neural Systems

Sensory input

Environment
Neural Systems

Sensory input

Environment

Motor output

Behavior
Neural Systems

Sensory input

Environment

Neuron

Behavior

Motor output
Neural Systems

Sensory input

Environment

Neuron

Motor output

Behavior

Membrane potential $V$
Phenomenon Spike-Frequency Adaptation

![Graph showing Spike-Frequency Adaptation](image-url)
Phenomenon Spike-Frequency Adaptation

- Steady-state response $f_{\infty}$
- Onset response $f_0$

$V$ [mV]

$f$ [Hz]

Stimulus
Content

Theory: Spike-frequency adaptation

- Biophysical mechanisms
Content

Theory: Spike-frequency adaptation

- Biophysical mechanisms
- General model, filter properties
Content

**Theory:** Spike-frequency adaptation

- Biophysical mechanisms
- General model, filter properties

**Experiments I:** Grasshopper auditory receptor

- Pause detection
Content

Theory: Spike-frequency adaptation
- Biophysical mechanisms
- General model, filter properties

Experiments I: Grasshopper auditory receptor
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Experiments II: Cricket auditory interneuron
- Intensity invariance
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- Biophysical mechanisms
- General model, filter properties

Experiments I: Grasshopper auditory receptor
- Pause detection

Experiments II: Cricket auditory interneuron
- Intensity invariance

Experiments III: Weakly electric fish
- Timescale separation
Theory:
A Universal Model for Spike-Frequency Adaptation

M-type Currents

![Graph showing M-type currents with voltage (V) in mV and time (t) in ms.](image-url)
M-type Currents

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

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

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

\[ \tau \alpha \dot{a} = a_\infty(V) - a \]
M-type Currents

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M-type Currents

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

\[ A = \langle I_M \rangle \]
\[ \tau \dot{A} = A_\infty (f) - A \]

time average!

Graphs showing the relationships between various parameters such as frequency, current, and time.
AHP-type Currents

\[ I_{AHP} = \tilde{g}_{AHP} q_\infty ([Ca^{2+}]) (V - E_K) \]

\[ \tau_{Ca}[Ca^{2+}] = \beta I_{Ca}(V) - [Ca^{2+}] \]
AHP-type Currents

\[
I_{AHP} = \bar{g}_{AHP} q_\infty ([Ca^{2+}]) (V - E_K)
\]

\[
\tau_{Ca}[Ca^{2+}] = \beta I_{Ca}(V) - [Ca^{2+}]
\]
Adaptation currents \((I_M, I_{AHP}, \ldots)\) are ionic currents.

Ionic currents flow in parallel over the cell membrane:

\[ I \rightarrow \text{Adaptation currents } A \text{ act } \text{subtractively} \text{ on input current } I: \]

\[ I - A \]
Spike Generator and $f$-$I$ Curve

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

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

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

Spike generator

$f(t)$  spike frequency

$f_0(I)$  onset $f$-$I$ curve

$f_\infty(I)$  steady-state $f$-$I$ curve

$A$  adaptation current

$I_{th}$  threshold of $f_0$
General Phenomenological Model

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
- $f_\infty(I)$: steady-state $f$-$I$ curve
- $A$: adaptation current
- $I_{th}$: threshold of $f_0$
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
- $f_\infty(I)$: steady-state $f$-$I$ curve
- $A$: adaptation current
- $I_{th}$: threshold of $f_0$
- $\tau$: adaptation time-constant
General Phenomenological Model

Biophysics of slow ionic currents $\Rightarrow$ 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

$f_\infty(I)$ steady-state $f$-$I$ curve

$A$ adaptation current

$I_{th}$ threshold of $f_0$

$\tau$ adaptation time-constant
How does it work?

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

\[ A = 0 \]

\[ f(t) = f_0(I) \]
How does it work?

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

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

\[ A = 0 \]

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

\[ \tau \dot{A} = f_\infty^{-1}(f) - f_0^{-1}(f) - A \]}
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 $\rightarrow$ 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 $H_f(\omega)$

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

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

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

Cutoff frequency $\omega_{\text{cutoff}} \tau_{\text{eff}} \approx 1$
• 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
Experiments I:
Locust Auditory Receptors
Onset & Steady-State $f-I$ Curve

$I = 52$ dB

$I = 63$ dB

$I = 79$ dB
Onset & Steady-State $f-I$ Curve

\[ f(I) = \text{dB} \]

$f_I = \text{Hz}$

\[ f_I = \text{Hz} \]

\[ f_I = 52 \text{ dB} \]

\[ f_I = 63 \text{ dB} \]

\[ f_I = 79 \text{ dB} \]

\[ f_I = 50 \text{ Hz} \]

\[ f_I = 40 \text{ Hz} \]

\[ f_I = 30 \text{ Hz} \]

\[ f_I = 20 \text{ Hz} \]

\[ f_I = 10 \text{ Hz} \]

\[ f_I = 0 \text{ Hz} \]

\[ t = \text{ms} \]

\[ t = 200 \text{ ms} \]

\[ t = 100 \text{ ms} \]

\[ t = 0 \text{ ms} \]

\[ f_I = 500 \text{ Hz} \]

\[ f_I = 400 \text{ Hz} \]

\[ f_I = 300 \text{ Hz} \]

\[ f_I = 200 \text{ Hz} \]

\[ f_I = 100 \text{ Hz} \]

\[ f_I = 0 \text{ Hz} \]

\[ I = 52 \text{ dB} \]

\[ I = 63 \text{ dB} \]

\[ I = 79 \text{ dB} \]
Onset & Steady-State $f$-$I$ Curve

\[ f = \frac{I - I_0}{I - I_{\infty}} \]

- \( f_0(I) \) (green line)
- \( f_\infty(I) \) (red line)
Adapted $f-I$ Curve

$f_0(I)$
$f_\infty(I)$
$f(I,A)$

$I_b = 47 \text{ dB}$
Adapted $f$-$I$ Curves

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

Adaptation shifts $f$-$I$ curve
Adapted $f$-$I$ Curves

Adaptation shifts $f$-$I$ curve

\[ f(I,A) = f_0(I - A) \]
Grasshopper Song

stimulus

$I$ = dB SPL

$800$ $1000$ $1200$ $1400$ $1600$

$t$ = ms

$100$ $90$ $80$ $70$ $60$ $50$

$\text{stimulus}$

$t$/ms
Grasshopper Song

- $I = \text{dB SPL}$
- $t = \text{ms}$
- Spike frequency: experiment
- Stimulus
Grasshopper Song

- $I = \text{dB SPL}$
- $t = \text{ms}$
- $f = \text{Hz}$

- Spike frequency: adaptation model
- Spike frequency: experiment
- Stimulus
Grasshopper Song

\[ I = \text{dB SPL} \]

\[ t = \text{ms} \]

\[ f = \text{Hz} \]

\[ A \]

Firing rate

\[ I_{th} \]

\[ I_{th} + A \]
Grasshopper Song

\[ f_0(I - A) \]

\[ f_0(I) \]

\[ f = \text{Hz} \]

\[ I_{\text{th}} + A \]

\[ I_{\text{th}} \]

\[ I_{\text{dB SPL}} \]

\[ t / \text{ms} \]

\[ I_{\text{th}} \text{ Firing rate} \]
Conclusion Grasshopper Auditory Receptor

- Spike-frequency adaptation $\Rightarrow$ Pause-detection
- Adapts threshold to stimulus intensity
Experiments II:
Cricket Auditory Interneuron
Cricket Auditory System

- Receptor cells
- Connectives
- Prothoracic ganglion
- "Brain"
- Extracellular recording
- Intracellular recording
- AN1
- AN2
Spike-Frequency Adaptation

\[ f_f \]

\[ I = 78 \text{ dB SPL} \]

\begin{align*}
\text{Spike frequency [Hz]} \\
\text{Time [ms]} \\
\end{align*}

\begin{align*}
\text{Trial} \\
\text{0} & \quad \text{10} & \quad \text{20} & \quad \text{30} & \quad \text{40} & \quad \text{50} \\
\end{align*}
Onset & Steady-State $f-I$ Curve

Spike frequency [Hz]

Intensity [dB SPL]
Adapted $f$-$I$ Curves

\[ f(I, A) \approx f_0(I - A) \]

Adaptation shifts $f$-$I$ curve
Adapted $f-I$ Curves

Flat steady-state $f-I$ curve

**Hypothesis:** Intensity invariance for $I > 60$ dB SPL
Intensity Invariance

$I = 62 \text{ dB}$
Intensity Invariance

$I = 52\,\text{dB}$

$I = 62\,\text{dB}$
Intensity Invariance

Spike frequency [Hz]

Stimulus [dB SPL]

Time [ms]

$I = 62 \text{ dB}$

$I = 72 \text{ dB}$
**Intensity Invariance**

Stimulus (dB SPL) vs. Time (ms) for three different intensities:
- $I = 52$ dB
- $I = 62$ dB
- $I = 72$ dB

Spike frequency (Hz) is plotted against Time (ms) for each intensity level.
Adaptation Model

\[ I = 62 \text{ dB SPL} \]

---

**Stimulus [dB SPL]**

**Spike frequency [Hz]**

**Time [ms]**

---

Experiment line

Stimulus line
Adaptation Model

$I = 62$ dB SPL

Spike frequency [Hz]

Stimulus [dB SPL]

Time [ms]
Adaptation Model

$I = 62$ dB SPL

Spike frequency [Hz]

Stimulus [dB SPL]

Time [ms]
Adaptation Model

$I = 72 \text{ dB SPL}$
- Spike-frequency adaptation $\Rightarrow$ Intensity Invariance
- Flat steady-state $f$-$I$ curve for $I > 60$ dB SPL
Experiments III: Weakly Electric Fish

Weakly Electric Fish (*Apteronotus leptorhynchus*)

Electric Organ Discharge (EOD)

600–1100 Hz

mV/cm

time [ms]
Weakly Electric Fish (*Apteronotus leptorhynchus*)

Electric Organ Discharge (EOD)

600–1100 Hz

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

Electric Organ Discharge (EOD)

- 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 $f_2$

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

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

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

Male – Male

$|\Delta f| < 30$ Hz
Communication II: Small Chirps

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

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

short (14 ms) increase in EOD frequency (30–150 Hz)

---

<table>
<thead>
<tr>
<th>Time [ms]</th>
<th>Frequency [Hz]</th>
<th>mV/cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1040</td>
<td>-0.2</td>
</tr>
<tr>
<td>11</td>
<td>1080</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td>1120</td>
<td>0.2</td>
</tr>
</tbody>
</table>

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76 Hz

11 ms
Communication II: Small Chirps

EOD Fish 1 (male)
Communication II: Small Chirps

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

Chirp
Communication II: Small Chirps

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

EOD Amplitude Modulation Fish 1

Amplitude [mV/cm]

0
0.5
1

Time [ms]

−200 −100 0 100 200

Beat 5 Hz

Chirp
Communication II: Small Chirps

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

EOD Amplitude Modulation Fish 1

Amplitude [mV/cm]

Beat 5 Hz

Time [ms]

Chirp
Communication II: Small Chirps

$\Delta f = 5 \text{ Hz}$

EOD Amplitude

Time [ms]

-200 0 200
Communication II: Small Chirps

Two stimulus timescales: (slow) beat and fast chirp.
Communication II: Small Chirps

⇒ Two stimulus timescales: (slow) beat and fast chirp.
In vivo recording of electroreceptor afferents (P-units)

Response

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

\[ \Delta f = 10 \text{ Hz} \]
Spike-Frequency Adaptation!

Spike frequency [Hz]

Stimulus $I$

$f_0(I)$

$f_\infty(I)$

time [ms]
$F-I$ Curves

Spike frequency [Hz]

EOD Amplitude $I$ [mV/cm]

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

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

- **Baseline**: Blue line
- **Steady-state $f_\infty(I)$**: Red dots
- **Onset $f_0(I)$**: Green triangles

Data points:
- 32: 82
- 62: 42
- 82: 62
- 100: 8
- 321: 221
$F-I$ Curves $\Rightarrow f(t) = f_0(I - A)$
\( \Delta f = 5 \text{ Hz} \)
Model Prediction

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

![Graph showing model prediction for response and stimulus over time in ms with spike frequency and amplitude axes.](image)
$\Delta f = 5\,\text{Hz}$

Model Prediction

- **Time [ms]**
- **Amplitude**
- **Spike frequency**

- **Stimulus**
- **Response**

Data vs. Model
Model Prediction

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

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

- $\tau_{\text{eff}} \approx 7$ ms
- $f_0'/f_\infty' \approx 6$

![Diagram showing gain $|H_f|/f_\infty$ versus stimulus frequency $[\text{Hz}]$.](image)
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 $|H_f|/f_\infty$ vs stimulus frequency in Hz, with $f_c$ as the cutoff frequency and the range from 1 to 100 chucks marked on the x-axis.](image-url)
Conclusion Electroreceptors

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

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

Theory: Spike-frequency adaptation

- Slow, inhibitory ionic currents
Summary

Theory: Spike-frequency adaptation

- Slow, inhibitory ionic currents
- Model: shift of the neuron’s $f-I$ curve, highpass filter
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Experiments I: Grasshopper auditory receptor
- Adapting threshold: Pause detection
Summary

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Experiments I: Grasshopper auditory receptor
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Experiments II: Cricket auditory interneuron
- Flat steady-state $f-I$ curve: Intensity invariance
Summary

Theory: Spike-frequency adaptation
- Slow, inhibitory ionic currents
- Model: shift of the neuron’s $f$-$I$ curve, highpass filter

Experiments I: Grasshopper auditory receptor
- Adapting threshold: Pause detection

Experiments II: Cricket auditory interneuron
- Flat steady-state $f$-$I$ curve: Intensity invariance

Experiments III: Weakly electric fish
- Timescale separation by highpass filter enhances response to chirps relative to slow beats
The Team

Theory:
- Matthias Bethge
- Martin Nawrot
- Andreas V. M. Herz

Grasshopper:
- Astrid Vogel
- Hartmut Schütze
- Tim Gollisch
- Olga Kolesnikova

Crickets:
- Matthias Hennig

Weakly Electric Fish:
University of Ottawa, Canada
- Leonard Maler
- André Longtin
Mechanism: Encoder Adaptation

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

Input Current $I$

Firing Frequency $f(t)$
Noise Stimulus

- **I (dB SPL)**
- **t (ms)**
- **spike frequency: experiment**
- **f (Hz)**
- **I/dB SPL**

Graph showing:
- Red line: spike frequency experimental data
- Orange line: stimulus data
Noise Stimulus

- Stimulus: $I = \text{dB SPL}$
- Frequency: $f = \text{Hz}$
- Time: $t = \text{ms}$

Graph showing:
- Spike frequency: adaptation model (blue)
- Spike frequency: experiment (red)
- Stimulus (orange)

Time range: 800 ms to 1600 ms
Noise Stimulus

Noise Stimulus

The graph shows the relationship between time (t) and stimulus intensity (I) in dB SPL. The x-axis represents time in milliseconds (ms), while the y-axis represents intensity in dB SPL. The graph includes three curves:

1. Blue line: Spike frequency of the adaptation model.
2. Red line: Spike frequency of the experiment.
3. Orange line: Stimulus intensity and threshold $I_{th} + A$.

The spike frequencies are plotted against time, with the threshold intensity also shown for comparison. The graph illustrates how the spike frequency changes with time and intensity, demonstrating the effect of the noise stimulus on neural activity.
Noise Stimulus

- Stimulus levels: 800, 1000, 1200, 1400, 1600 dB SPL
- Time: 0 to 1800 ms

Spike frequency:
- No adaptation: $f_0(I)$
- Adaptation model: $f_0(I - A)$

Thresholds:
- $I_{th} + A$
- $I_{th}$
Grasshopper: Stimulus Distribution

**Distribution**

- Normal distribution with threshold
- $f_0(I)$
- Original distribution

**Cumulative**

- Cumulative distribution with threshold
- $f_0(I)$
- Original cumulative distribution
- 50% threshold
Grasshopper: Stimulus Distribution

⇒ Adapted $f$-$I$ curves do not match stimulus distribution.

⇒ Pause detection
Cricket: Stimulus Distribution

Pause detection
Periodic Spiking: Oscillation

Period $T$
\[ \triangleq \text{Interspike interval} \]

Frequency of oscillation
\[ f = \frac{1}{T} \]
\[ \triangleq \text{Firing frequency} \]
**Periodic Spiking: Oscillation**

\[ f = 1/T \]

- **Period** $T$
  - $\triangleq$ Interspike interval
- **Frequency of oscillation**
  - $f = 1/T$
  - $\triangleq$ Firing frequency

---

**Phase-plane**

- $U/mV$
  - $\sim -40$ to $\sim -80$
- $V/mV$
  - $\sim -80$ to $\sim 0$

- $50 mV$
- $10 ms$
Periodic Spiking: Oscillation

Period $T$
\[ \triangleq \text{Interspike interval} \]

Frequency of oscillation
\[ f = \frac{1}{T} \]
\[ \triangleq \text{Firing frequency} \]

Phase-plane
\[ U / \text{mV} \]
\[ V / \text{mV} \]

Limit cycle!
Phase Rotator
"Perfect Integrate-&-Fire" Neuron

\[ \phi = 0 \]

\[ \phi = 1 \]

Spike
Phase Rotator
"Perfect Integrate-&-Fire" Neuron

Phase velocity is given by $f-I$ curve:

$$\dot{\phi} = f(I)$$
Phase Rotator
“Perfect Integrate-&-Fire” Neuron

Phase velocity is given by $f(I(t))$ with time dependent input $I(t)$:

$$\dot{\varphi} = f(I(t))$$

Spike

$\varphi = 0$

$\varphi = 1$
Phase Rotator
"Perfect Integrate-&-Fire" Neuron

Phase velocity is given by $f$-$I$ curve with time dependent input $I(t)$:

$$
\dot{\phi} = f(I(t))
$$

Spike frequency $1/T$:

$$
\frac{1}{T} \int_{t-T/2}^{t+T/2} f(t') \, dt' = 1
$$
Slow Stimulus

Stimulus: “White” noise $f_c = 25$ Hz
Spikes: Connor (1971) - model
Mean firing rate: $\bar{f} \approx 100$ Hz
Slow Stimulus

Stimulus: “White” noise $f_c = 25$ Hz
Spikes: Connor (1971) - model
Mean firing rate: $\bar{f} \approx 100$ Hz
Slow Stimulus

Stimulus: “White” noise $f_c = 25$ Hz

Spikes: Connor (1971) - model

Mean firing rate: $\bar{f} \approx 100$ Hz
Slow Stimulus

Stimulus: "White" noise $f_c = 25$ Hz
Spikes: Connor (1971) - model
Mean firing rate: $\bar{f} \approx 100$ Hz
Stimulus: “White” noise $f_c = 400 \text{ Hz}$

Spikes: Connor (1971) - model

Mean firing rate: $\bar{f} \approx 100 \text{ Hz}$
Fast Stimulus

Stimulus: “White” noise $f_c = 400$ Hz
Spikes: Connor (1971) - model
Mean firing rate: $\bar{f} \approx 100$ Hz
Fast Stimulus

\[ f(t) = \text{measured ring frequency} \]

\[ f(I(t)) \]

\[ f/I = \text{measured firing frequency} \]

\[ f = \text{measured ring frequency} \]

\[ I = \text{Stimulus} \]

\[ t/\text{ms} = 0, 20, 40, 60, 80, 100 \]

\[ f/\text{Hz} = 0, 50, 100, 150 \]
Fast Stimulus

Low-pass filter with cutoff frequency set by spike frequency

Response Gain

Spike frequency difference during chirp divided by difference during beat

![Graph showing response gain against beat frequency Δf [Hz]. The graph includes box plots for different beat frequencies with corresponding numbers of observations (n). The y-axis represents the response gain, ranging from 0.5 to 2.5, and the x-axis represents beat frequencies Δf [Hz] ranging from 5 to 60. There are box plots for n = 505, 251, 73, 247, and 60.]
Behavior: System Output

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