Functional Aspects of Spike-Frequency Adaptation

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Neural Systems
Neural Systems

Sensory input

Environment
Data-Processing Inequality

Sensory input

Environment

$X \rightarrow Y \rightarrow Z$

$I(X; Y) \geq I(X; Z)$

Motor output

Behavior
Data-Processing Inequality

\[ I(X;Y) \geq I(X;Z) \]

Signal processing = information destruction
Neural Computation

Sensory input

Environment

Motor output

Behavior

Neuron
Neural Computation

Sensory input

Environment

Neuron

Motor output

Behavior

Membrane potential V
Phenomenon Spike-Frequency Adaptation

Steady-state response \( f_\infty \)

Onset response \( f_0 \)

Voltage \( V \) [mV]

Frequency \( f \) [Hz]

Stimulus

Time [ms]
Content

Theory: Spike-frequency adaptation

- Biophysical mechanisms
Content

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- Biophysical mechanisms
- General model, filter properties
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Experiments I: Weakly electric fish
- High-pass filter
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- Intensity invariance
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Experiments I: Weakly electric fish
- High-pass filter

Experiments II: Cricket auditory interneuron
- Intensity invariance

Experiments III: Grasshopper auditory receptor
- Pause detection
Theory:

A Universal Model for Spike-Frequency Adaptation

Mechanism: Encoder Adaptation

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

Input Current $I$

Spike frequency $f(t)$

$g(J)$

$I - A$ subtractive
Adaptation currents ($I_M$, $I_{AHP}$, ...) 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
M-type Currents

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

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

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

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

\[ \tau_0 \dot{a} = a_\infty(V) - a \]
M-type Currents

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

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

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

\[ A = \langle I_M \rangle \]

\[ f_\infty (I) \]

\[ f_0 (I) \]

\[ \tau_{\text{eff}} \]

\[ f_\text{eff} \]

\[ I \]

\[ \text{time average!} \]

\[ I_M \text{ [\( \mu A/cm^2 \)]} \]

\[ a \text{ [Hz]} \]

\[ L \text{ [ms]} \]

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

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AHP-type Currents

\[ I_{Ca}(V) = \bar{g}_{Ca} s_{\infty}(V) (V - E_{Ca}) \]
AHP-type Currents

\[ I_{Ca}(V) = \bar{g}_{Ca} s_\infty(V)(V - E_{Ca}) \]

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

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

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

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

\[ \tau_{Ca}[Ca^{2+}] = \beta I_C(V) - [Ca^{2+}] \]

\[ A = \langle I_{AHP} \rangle \]

\[ \tau \dot{A} = A_\infty (f) - A \]
Spike Generator and $f-I$ Curve

Spike frequency $f = f_0(I)$

Input current $I$ [μA/cm²]

Spike frequency $f$ [Hz]
General Phenomenological Model

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

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

Spike generator

J. Benda & A. Herz (2003), *Neural Computation* 15, 2523–2564
General Phenomenological Model

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

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

Subtractiveness

Injected current $I$

Spike frequency $f$ [Hz]

$J. Benda & A. Herz (2003), Neural Computation 15, 2523–2564$
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

J. Benda & A. Herz (2003), *Neural Computation* 15, 2523–2564
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

J. Benda & A. Herz (2003), *Neural Computation* 15, 2523–2564
How does it work?

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

\[ A = 0 \]

\[ f_0(I) \]

\[ f_\infty(I) \]
How does it work?

\[ A = 0 \]

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

\[ A = 0 \]

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

\[ \tau \dot{A} = f_\infty^{-1}(f) - f_0^{-1}(f) - A \]
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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 → Linear adaptation → Transfer function $H_f(\omega)$

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

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 $H_f(\omega)$

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

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

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

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
Experiments I: Weakly Electric Fish

Weakly Electric Fish (*Apteronotus leptorhynchos*)

Electric Organ Discharge (EOD)

- **mV/cm**
- **Time [ms]**
- **Frequency range**: 600–1100 Hz
Weakly Electric Fish (*Apteronotus leptorhynchos*)

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 $f_2$
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 $f_2$

$\Rightarrow$ 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 ($\Delta f < 30 \text{ Hz}$)
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)

![Graph showing frequency and time variations with a short chirp pattern. The graph displays a blue line representing frequency in Hz and an orange line representing time in ms. The frequency increases from 1040 Hz to 1120 Hz over 11 ms, then returns to 1040 Hz. The graph also shows a voltage in mV/cm, where the voltage fluctuates between -0.2 mV/cm and 0.2 mV/cm.]

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)

Chirp

EOD Amplitude Modulation Fish 1

Amplitude [mV/cm]

Time [ms]

Beat 5 Hz

Chirp
Communication II: Small Chirps

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

EOD Amplitude Modulation Fish 1

Amplitude [mV/cm]

Time [ms]

Beat 5 Hz

Chirp
Communication II: Small Chirps

Δf = 5 Hz

EOD Amplitude

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

Two stimulus timescales: (slow) beat and fast chirp.
In vivo Recordings of Electroreceptor Afferents
In vivo Recordings of Electroreceptor Afferents

Stimulus

Fish EOD

Fish EOD + Stimulus
Response

\textit{In vivo} recording of electroreceptor afferents (P-units)

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

In vivo recording of electrorreceptor afferents (P-units)

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

Spike frequency [Hz]

Stimulus $I$

$\mathcal{f}_0(I)$

$\mathcal{f}_\infty(I)$

Time [ms]

0 20 40 60 80 100
Spike-Frequency Adaptation!

\[ t = 5.5 \text{ ms} \]

Spike frequency \( [\text{Hz}] \)

\( f_0(I) \)

\( f_\infty(I) \)

\( \tau_{\text{eff}} = 5.5 \text{ ms} \)

Stimulus \( I \)
$F-I$ Curves

**Diagram:**
- **Spike frequency [Hz]** vs. **EOD Amplitude $I$ [mV/cm]**
- Color coding:
  - Blue line: baseline
  - Red circle: steady-state $f_\infty(I)$
  - Green triangle: onset $f_0(I)$

**Data Points:**
- Spike frequency values:
  - Round 1: 82 Hz
  - Round 2: 62 Hz
  - Round 3: 42 Hz
  - Round 4: 22 Hz
- EOD Amplitude $I$ values:
  - Round 1: 8 mV/cm
  - Round 2: 10 mV/cm
  - Round 3: 15 mV/cm
  - Round 4: 20 mV/cm
**F-I Curves**

- **Spike frequency [Hz]**
- **EOD Amplitude $I$ [mV/cm]**

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

- Data points for Spike frequency and EOD Amplitude are shown on the graph. The graph illustrates the relationship between Spike frequency and EOD Amplitude across different values of $I$. The baseline, steady-state, and onset points are indicated with different markers and lines.
\( F-I \) Curves \( \Rightarrow f(t) = f_0(I - A) \)

![Graph showing F-I Curves](image-url)
Model Prediction

Δf = 5 Hz

Diagram showing the response and model comparison with time [ms] and spike frequency on the y-axis, and amplitude on the x-axis.
Model Prediction

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

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

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

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

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

Gain $|H_f|/f^8$

Stimulus frequency [Hz]

$\tau_{\text{eff}}$
Conclusion Electroreceptors

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

- The high-pass filter’s cutoff frequency separates slow beats from fast chirps.
Experiments II: Cricket Auditory Interneuron

J. Benda & M. Hennig (2007), J. Computational Neuroscience online
Cricket Auditory System

extracellular recording
+ -
intracellular recording
receptor cells
prothoracic ganglion
connectives

"brain"
AN1
AN2
Spike-Frequency Adaptation

\[ f(t) = f_0 \] 

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

Trial

Time [ms]

Trial

Spike frequency [Hz]

Time [ms]

Trial

Spike frequency [Hz]
Onset & Steady-State $f-I$ Curve

Spike frequency [Hz] vs. 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
Experiment: Intensity Invariance

- Stimulus [dB SPL]
- Time [ms]

- Spike frequency [Hz]
- Stimulus [dB SPL]

Time [ms]

- $I = 62$ dB
Experiment: Intensity Invariance

- **Stimulus [dB SPL]**
  - I = 62 dB
  - I = 52 dB

- **Spike frequency [Hz]**
  - Time [ms]: 0 to 800

- **Stimulus [dB SPL]**
  - Time [ms]: 0 to 800
Experiment: Intensity Invariance

### Stimulus [dB SPL]

800 - 700 - 600 - 500 - 400 - 300 - 200 - 100 - 0

### Spike frequency [Hz]

800 - 700 - 600 - 500 - 400 - 300 - 200 - 100 - 0

### Stimulus [dB SPL]

800 - 700 - 600 - 500 - 400 - 300 - 200 - 100 - 0

- $I = 62$ dB
- $I = 72$ dB
Adaptation Model

I = 62 dB SPL

Spike frequency [Hz]

Stimulus [dB SPL]

Time [ms]
Adaptation Model

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

**Spike frequency [Hz]**

- Experiment
- Adaptation model

**Stimulus [dB SPL]**

Experiment: 80, 60, 40, 30, 20, 10, 0

Adaptation model: 90, 80, 70, 60, 50, 40, 30

Time [ms]: 300, 400, 500, 600, 700, 800, 900
Adaptation Model

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

<table>
<thead>
<tr>
<th>Stimulus [dB SPL]</th>
<th>Time [ms]</th>
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<tbody>
<tr>
<td>80</td>
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<td>20</td>
<td>600</td>
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<tr>
<td>0</td>
<td>500</td>
</tr>
</tbody>
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Spike frequency [Hz]

stimulus

threshold \( I_{th} + A \)

Time [ms]
Adaptation Model

\[ I = 72 \text{ dB SPL} \]

Experiment: red line
Adaptation model: yellow line

Spike frequency [Hz]

Stimulus [dB SPL]

Threshold \( I_{th} \) + A

Stimulus

Time [ms]
Conclusion Cricket AN1

- Spike-frequency adaptation + flat steady-state $f$-$I$ curve

$\Rightarrow$ Intensity Invariance for $I > 60$ dB SPL
Experiments III:
Locust Auditory Receptors
Onset & Steady-State $f$-$I$ Curve

$I = 52$ dB

$I = 63$ dB

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

- For $I = 52$ dB:
  - Onset: $f_0$
  - Steady-state: $f_\infty$

- For $I = 63$ dB:
  - Onset: $f_0$
  - Steady-state: $f_\infty$

- For $I = 79$ dB:
  - Onset: $f_0$
  - Steady-state: $f_\infty$
Adapted $f$-$I$ Curves

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

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

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

Adaptation shifts $f$-$I$ curve
Grasshopper Song

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**Grasshopper Song**

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**Grasshopper Song**
Grasshopper Song

---

**Grasshopper Song**

![Graph showing the spike frequency and stimulus over time](image)

- **Spike Frequency (f)**: Experiment
- **Stimulus (I)**: dB SPL

- Time [ms]: 800 to 1800
- Frequency [Hz]: 0 to 500
- Intensity [dB SPL]: 50 to 100
Grasshopper Song

Graph showing the relationship between time (in milliseconds) and intensity (in dB SPL) for the Grasshopper Song. The graph includes two lines representing spike frequency: an adaptation model in yellow and an experiment in red. The intensity values range from 50 to 500 Hz on the y-axis and 800 to 1800 ms on the x-axis. The stimulus is represented by a green line with values ranging from 60 to 80 dB SPL.
Grasshopper Song

A stimulus in [dB SPL] affects the firing rate and spike frequency. The graph shows the relationship between the time in milliseconds and the firing rate, as well as the relationship between the stimulus and the threshold $I_{th} + A$. The yellow line represents the spike frequency from the adaptation model, while the red line represents the experiment. The graph also shows the threshold $I_{th}$ and $I_{th} + A$, with an inset diagram illustrating the effect of $A$ on the firing rate.
Grasshopper Song

- Stimulus $I$ [dB SPL]
- Time [ms]
- Spike frequency: no adaptation $f_0(I)$
- Spike frequency: adaptation model $f_0(I - A)$
- Threshold $I_{th} + A$
- Threshold $I_{th}$

Firing rate

$A$
Grasshopper: Stimulus Distribution

Distribution

Cumulative

Stimulus intensity [dB SPL]

Threshold

$\textbf{$f_0(I)$}$

Original

Stimulus intensity [dB SPL]

Threshold

50%

$\textbf{$f_0(I)$}$

Original
Grasshopper: Stimulus Distribution

⇒ Adapted \( f-I \) curves do not match stimulus distribution.

⇒ Pause detection
Conclusion Grasshopper Auditory Receptor

- Spike-frequency adaptation $\Rightarrow$ Pause-detection
- Adapts threshold to stimulus intensity
Summary

**Theory**: Spike-frequency adaptation

- Slow, inhibitory ionic currents
- Model: shift of the neuron’s $f$-$I$ curve
- Highpass filter
Summary

**Theory:** Spike-frequency adaptation

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**Experiments I:** Weakly electric fish

- Timescale separation by highpass filter enhances response to chirps relative to slow beats
Summary

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Experiments I: Weakly electric fish

- Timescale separation by highpass filter enhances response to chirps relative to slow beats

Experiments II: Cricket auditory interneuron

- Flat steady-state $f$-$I$ curve: Intensity invariance
Summary

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Experiments II: Cricket auditory interneuron

- Flat steady-state $f$-$I$ curve: Intensity invariance

Experiments III: Grasshopper auditory receptor

- Adapting threshold: Pause detection
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
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