



## Spike-frequency adaptation: Phenomenological model and experimental tests

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### Abstract

Spike-frequency adaptation is a common feature of neural dynamics. Here we present a low-dimensional phenomenological model whose parameters can be easily determined from experimental data. We test the model on intracellular recordings from auditory receptor neurons of locusts and demonstrate that the temporal variation of discharge rate is predicted with high accuracy. We relate the model to biophysical descriptions of adaptation in conductance-based models and analyze its implications for neural computation. © 2001 Elsevier Science B.V. All rights reserved.

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### 1. Introduction

Neural activity results from a large number of interacting ionic currents across the cell membrane. Biophysically motivated neuron models such as the Hodgkin–Huxley model may reproduce the membrane potential with high precision. For theoretical investigations, however, abstract models, like integrate-and-fire neurons, have the advantage that they do not depend on a large number of parameters. Here we present a low-dimensional neuron model which can be related directly to experimental data.

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At the same time, it is amenable to theoretical analysis. To apply the model to a particular neuron one only has to measure its transient and steady state  $f$ - $I$ -curves.

## 2. The model

In systems with spiking neurons, the timing of action potentials constitutes the elementary neural signal. The underlying intrinsic dynamics of a single neuron can be described as the time evolution of a non-linear oscillator.

For sufficiently strong constant stimuli, neurons exhibit oscillations with period  $T = 1/f$ . The dependence of  $f$  on the input current  $I$  is given by the neuron's  $f$ - $I$ -curve, which can be easily determined in experiments (Fig. 1B). The oscillations correspond to stable limit cycles. On these trajectories the phase-velocity  $d\Phi/dt$  in general is a function of the phase  $\Phi$  and the input  $I$ :

$$\frac{d\Phi}{dt} = h(\Phi, I(t)). \quad (1)$$

For the upper part of the neuron's  $f$ - $I$ -curve this function can approximately be factorized:  $h(\Phi, I) = g(\Phi)f(I)$ . Introducing another phase variable  $\varphi \in [0, 1)$  via  $d\varphi/d\Phi = 1/g(\Phi)$  Eq. (1) can be transformed into the evolution equation of a non-leaky integrator

$$\begin{cases} \frac{d\varphi}{dt} = f(I(t)), & \varphi < 1, \\ \varphi = 0, & \varphi = 1 \Rightarrow \text{spike}. \end{cases} \quad (2)$$

The condition that  $f$  depends exclusively on  $I(t)$  is, however, not fulfilled for real neurons. In particular, spike-frequency adaptation is exhibited by many types of neurons [3–5] and leads to large transients as can be seen in the response to a step

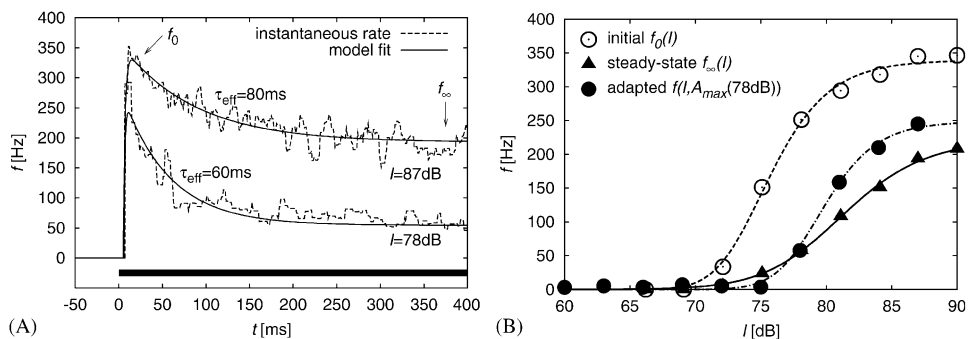


Fig. 1. Response properties of a locust auditory receptor neuron. A. Step responses (dashed lines) to constant stimuli (bottom bar) with different intensities as indicated by the labels. Note that the observed time constant  $\tau_{\text{eff}}$  depends on input intensity. B. The initial  $f$ - $I$ -curve ( $f_0$ , open circles) and the steady-state  $f$ - $I$ -curve ( $f_\infty(I)$ , filled circles) determined from the measurements shown in A. The triangles display the  $f$ - $I$ -curve for a fixed adaptation state ( $A = \text{constant}$ ) corresponding to  $I = 78 \text{ dB}$ .

current (Fig. 1A). To account for this effect, we introduce an adaptation variable  $A$  so that the  $f$ - $I$ -curve now reads  $f(I, A)$ . A mathematical analysis of conductance-based models reveals the following dependence of  $f$  upon  $I$ : (1) The current of a potassium adaptation channel acts subtractive on the input current  $I$ , which shifts the  $f$ - $I$ -curve to higher input intensities. (2) The dependence of the adaptation current on the membrane potential leads to a scaling of the  $f$ - $I$ -curve by a factor  $\alpha(A)$ . (3) The adaptation state  $A$  is governed by a first-order relaxation to a maximum value  $A_{\max}$ . This kind of dynamics can be directly derived from the underlying slow mechanism, which may either be the gating process of a voltage-gated potassium current or calcium dynamics [7]. These results suggest the following low-dimensional model:

$$\begin{aligned} f(t) &= f(I, A) = \alpha(A)f_0(I - A), \\ \tau \frac{d}{dt}A &= A_{\max}(f(I, A), I) - A, \end{aligned} \quad (3)$$

where  $f_0(I)$  is the initial  $f$ - $I$ -curve (Fig. 1B) and  $\tau$  denotes the adaptation time constant. The current approach is intended to be as independent from a specific microscopic model as possible. We therefore use the steady-state  $f_\infty(I)$ -curve (Fig. 1B) to determine  $A_{\max}$  instead of deriving it from channel properties. Neglecting the scaling factor  $\alpha(A)$  we obtain:

$$\begin{aligned} f(t) &= f_0(I - A), \\ \tau \frac{d}{dt}A &= \frac{I - f_0^{-1}(f_\infty(I))}{f_\infty(I)} f(t) - A. \end{aligned} \quad (4)$$

It follows that the time constant of the exponential decay of the firing rate observed for constant stimuli  $\tau_{\text{eff}}$  is related to the adaptation time constant  $\tau$  by

$$\tau_{\text{eff}} = \tau \frac{f_\infty(I)}{f_0(I)}. \quad (5)$$

### 3. Results

#### 3.1. Experiments

In order to test the model (Eq. (2) together with Eq. (4)), intracellular recordings in auditory receptor neurons of the Locust (*Locusta migratoria*) were performed. Since the input of these receptors can be reliably controlled without any interfering influences from dendritic processes, synaptic dynamics, or inputs from other neurons, these receptors are ideally suited for this type of investigation. The parameters were determined from two  $f$ - $I$ -curves derived from step inputs. Subsequently, the model behavior was tested on a strongly time-dependent stimulus. As Fig. 2 demonstrates, the model predicts the measured instantaneous rates very well.

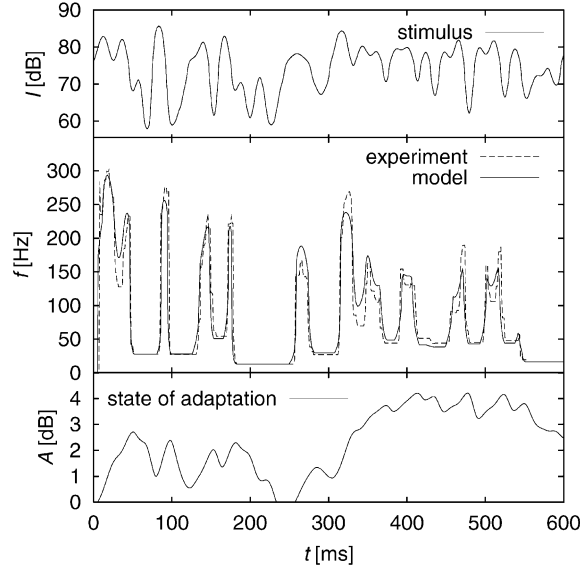


Fig. 2. As an example for the performance of the model, the neuron's response (middle panel, dashed line) to an amplitude-modulated stimulus (carrier frequency: 5 kHz, modulation: broad-band noise with cut-off frequency 50 Hz) is shown (upper panel). The  $f$ - $I$ -curves shown in Fig. 1 and an adaptation time constant  $\tau = 150$  ms resulting from Eq. (5) are used to calculate spike trains with the model. The instantaneous rate of these spike trains (middle panel, solid line) closely follows the experimental data (dashed line). In the middle panel the instantaneous rate  $f$  is the reciprocal value of the inter-spike interval at any time bin. The lower panel shows the value of the adaptation state  $A$ . Note, that a 5 dB shift of the  $f_0(I)$ -curve may alter the output of the model by 150 Hz.

### 3.2. Theory

Selective filtering of input signals is a key component of neural computation at the single-cell level. The characterization of filter properties is therefore an important issue in theoretical neuroscience. To obtain an analytical expression we focused on linear  $f$ - $I$ -curves  $f_0(I) = m_0(I - I_0)$  and  $f_\infty(I) = m_\infty(I - I_\infty)$ . Eq. (4) implies that  $I_0$  equals  $I_\infty$  so that both these values can be set to zero. In this case Eq. (4) leads to the differential equation

$$\left[1 + \tau \frac{m_\infty}{m_0} \frac{d}{dt}\right] f(t) = m_\infty \left[1 + \tau \frac{d}{dt}\right] I(t). \quad (6)$$

The neural filter properties are then completely characterized by the complex-valued transfer function:

$$H(\omega) = m_\infty \frac{1 + (\tau\omega)^2 m_\infty/m_0 + i\tau\omega(m_\infty/m_0 - 1)}{1 + (\tau\omega m_\infty/m_0)^2}. \quad (7)$$

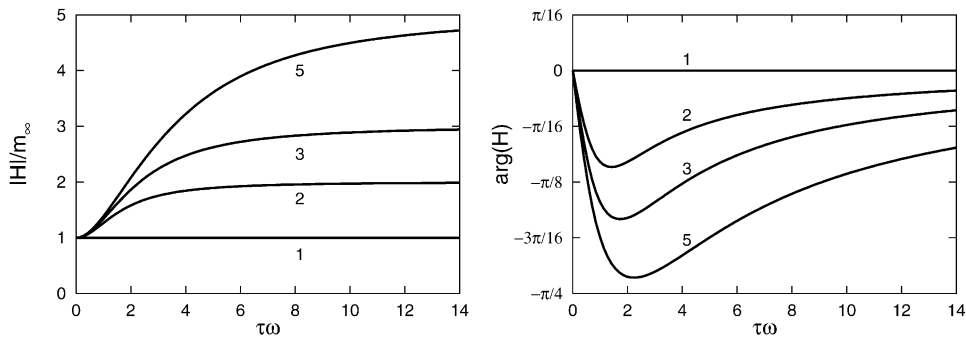


Fig. 3. The amplitude  $|H|$  and the phase  $\arg(H)$  of the transfer function  $H(\omega)$  Eq. (7) plotted for different ratios of  $m_0/m_\infty$  as indicated by the labels.

As can be seen from the amplitude frequency relation  $|H(\omega)|$  in Fig. 3, increasing adaptation (high  $m_0/m_\infty$ -ratios) turns the neuron into a high-pass filter. The phase frequency relation is given by  $\arg(H(\omega))$  and reflects the neuron's tendency to respond with a phase advance (Fig. 3). Note that the transfer function describes the output signal  $f(t)$  before Eq. (2) is used to calculate the model spike trains.

If one compares the above filter properties with those of depressing synapses [1,6] the frequency dependence of both systems is strikingly similar. Brief interruptions of an input signal [2] are transmitted very reliably in both systems. This property strongly enhances the capability to detect behaviorally relevant signals such as brief gaps in acoustic communication signals.

#### 4. Conclusion

The phenomenological model presented here combines three aspects: (1) The model contains few parameters that can be easily measured in experiments. (2) The model can be derived from detailed conductance-based approaches. (3) The simplicity of the model allows detailed theoretical analysis and quantitative predictions. To test the model, intracellular recordings in auditory receptor neurons of the Locust were performed. The time-resolved rates of the predicted spike trains agree well with experimental measurements.

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**References**

- [1] L.F. Abbott, J.A. Varela, K. Sen, S.B. Nelson, Synaptic depression and cortical gain control, *Science* 275 (1997) 220–224.
- [2] M. Bethge, K. Pawelzik, T. Geisel, Brief pauses as signals for depressing synapses, *Neurocomputing* 26–27 (1999) 1–7.
- [3] B.W. Connors, M.J. Gutnick, Intrinsic firing patterns of diverse neocortical neurons, *TINS* 13 (1990) 99–104.
- [4] A. French, Two components of rapid sensory adaptation in a cockroach mechanoreceptor neuron, *J. Neurophysiol.* 62 (3) (1989) 768–777.
- [5] D.A. McCormick, B.W. Connors, J.W. Lighthall, D.A. Prince, Comparative electrophysiology of pyramidal and sparsely stellate neurons of the neocortex, *J. Neurophysiol.* 54 (1985) 782–805.
- [6] M.V. Tsodyks, H. Markram, The neural code between neocortical pyramidal neurons depends on neurotransmitter release probability, *PNAS* 94 (1997) 719–723.
- [7] X.-J. Wang, Calcium coding and adaptive temporal computation in cortical pyramidal neurons, *J. Neurophysiol.* 79 (1998) 1549–1566.



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