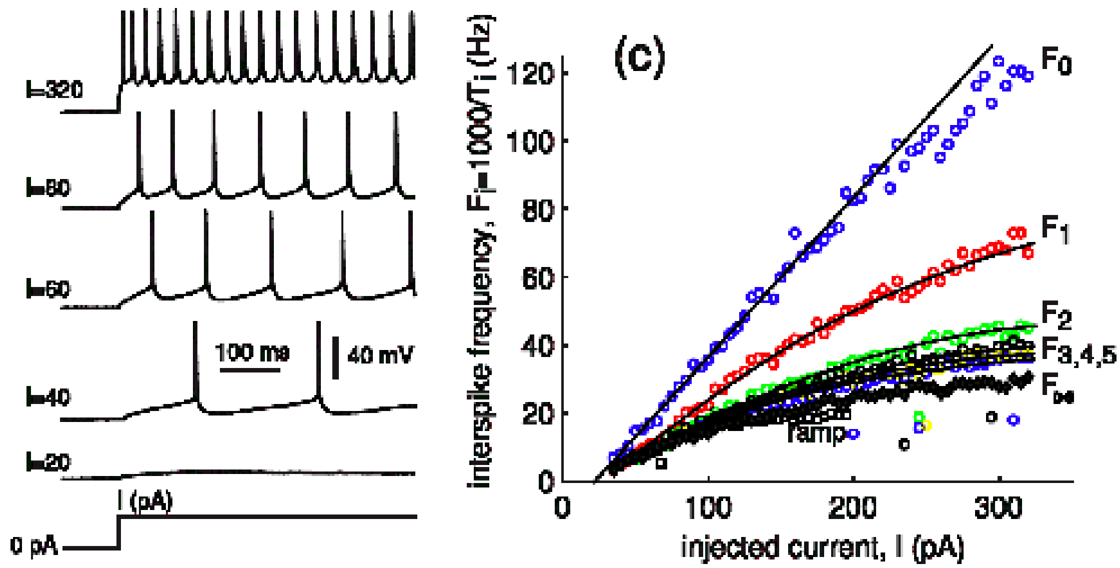
Adaptive Neuron

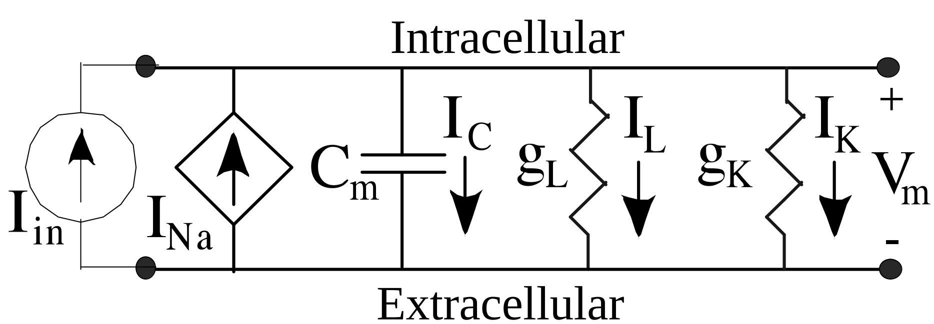


Interspike intervals (T_i) get longer and frequency drops (F_i) (rat L5 pyramidal cell) [Izhikevich07]

Adaptation has a divisive effect on $F(I)$-curve (F_∞ versus F_0 curve)

Makes cell less sensitive to constant current

Membrane-voltage equation



Adaptation can arise from a voltage-dependent K^+-conductance (M-current, I_K)

We add a conductance g_K in parallel with the leak:

$$C_m \frac{dV_m}{dt} + g_{lk} V_m + g_K V_m = I_{in} + \frac{1}{3} \left(\frac{V_m}{V_{th}}\right)^2 g_{lk} V_m$$

This K^+-channel has a high threshold (-44mV) and therefore turns on only during a spike; it decays between spikes.

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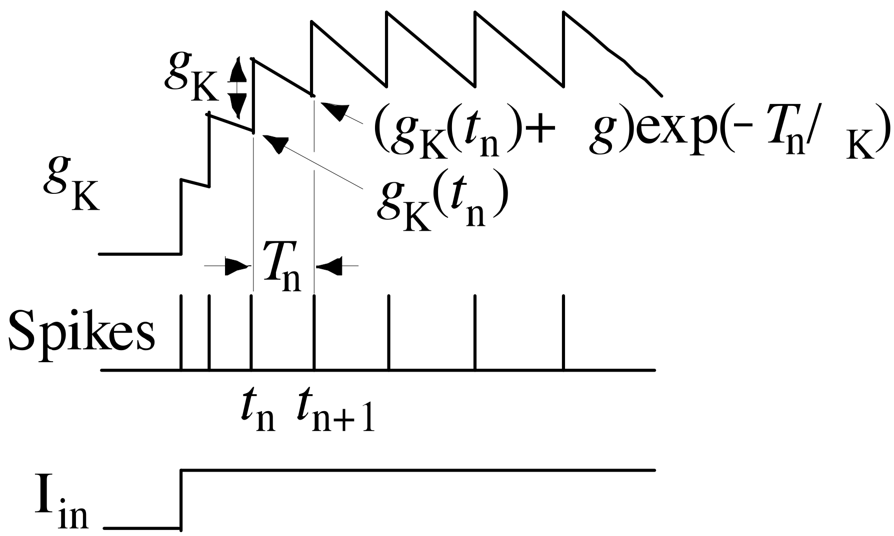
M-Current model (g_K)



Each spike increases g_K by Δg_K; g_K decreases exponentially between spikes

If τ_K is the K^+-channel's time-constant, we have

$$g_K[t - t_n] = (g_K[t_n] + \Delta g_K)\, e^{-(t-t_n)/\tau_K} \quad \text{for} \quad t_n < t < t_{n+1}$$

where $g_K(t_n)$ is the value just before the n^{th} spike occurs.

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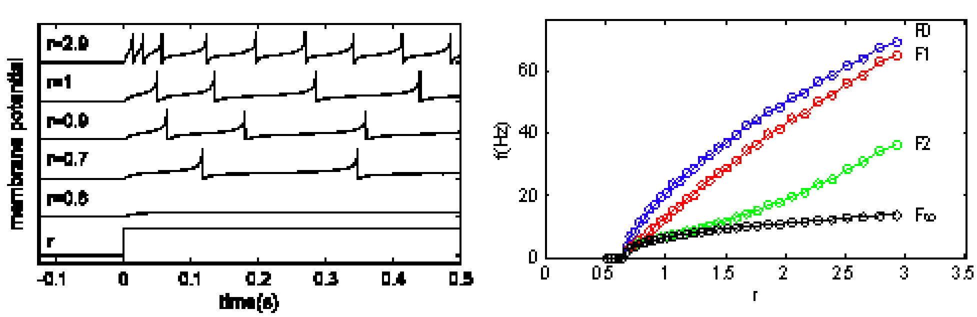
Model's V_m traces and $F(I)$ curves



Interspike intervals lengthen (left) and sensitivity decreases (right)

This simple model displays behavior qualitatively similar to the cortical cell.

We use it to explore the role of the biophysical parameters Δg_K and τ_K.

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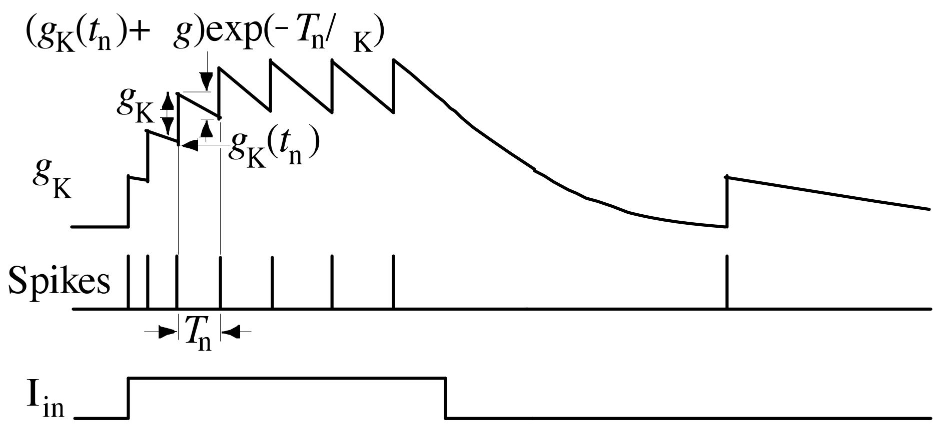
M-current dynamics



The drop in g_K depends on its initial level ($g_K(t_n) + \Delta g$) as well as the interspike interval (T_n)

The net change in g_K from spike to spike is:

$$g_K[t_{n+1}] - g_K[t_n] = (g_K[t_n] + \Delta g_K)\, e^{-T_n/\tau_K} - g_K[t_n]$$

$$= \Delta g_K\, e^{-T_n/\tau_K} - g_K[t_n]\left(1 - e^{-T_n/\tau_K}\right)$$

$$\Longleftrightarrow \frac{g_K[t_{n+1}] - g_K[t_n]}{1 - e^{-T_n/\tau_K}} = g_{K\infty}[T_n] - g_K[t_n] \quad \text{where} \quad g_{K\infty}[T_n] \equiv \frac{e^{-T_n/\tau_K}}{1 - e^{-T_n/\tau_K}}\, \Delta g_K$$

Thus, during interspike interval T_n, g_K rises if it is smaller than $g_{K\infty}(T_n)$, falls if it is greater, and remains unchanged if it is equal (steady-state).

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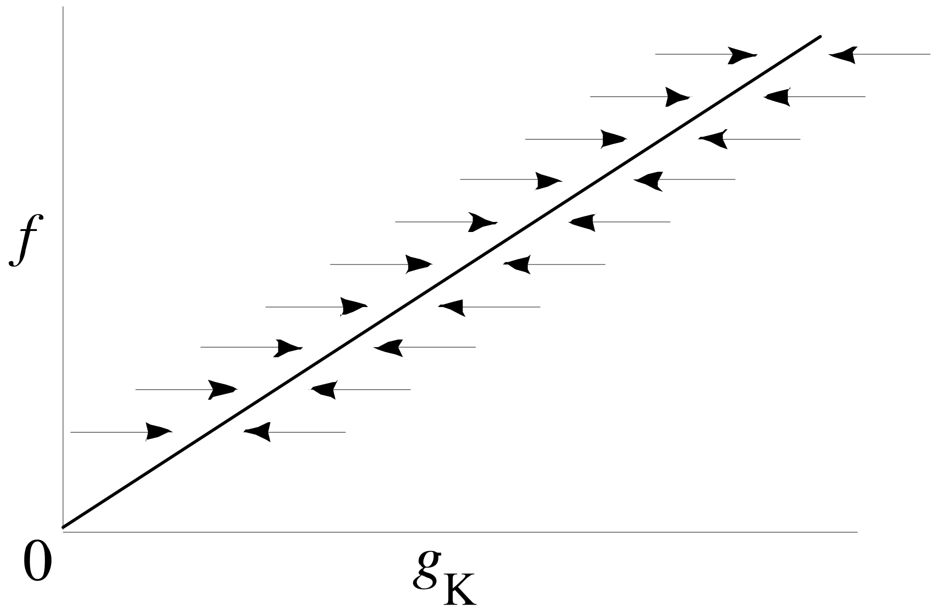
$f_K(g)$ curve



g_K's steady-state value for spike frequency f: increases (→) if it's smaller; decreases (←) if it's greater.

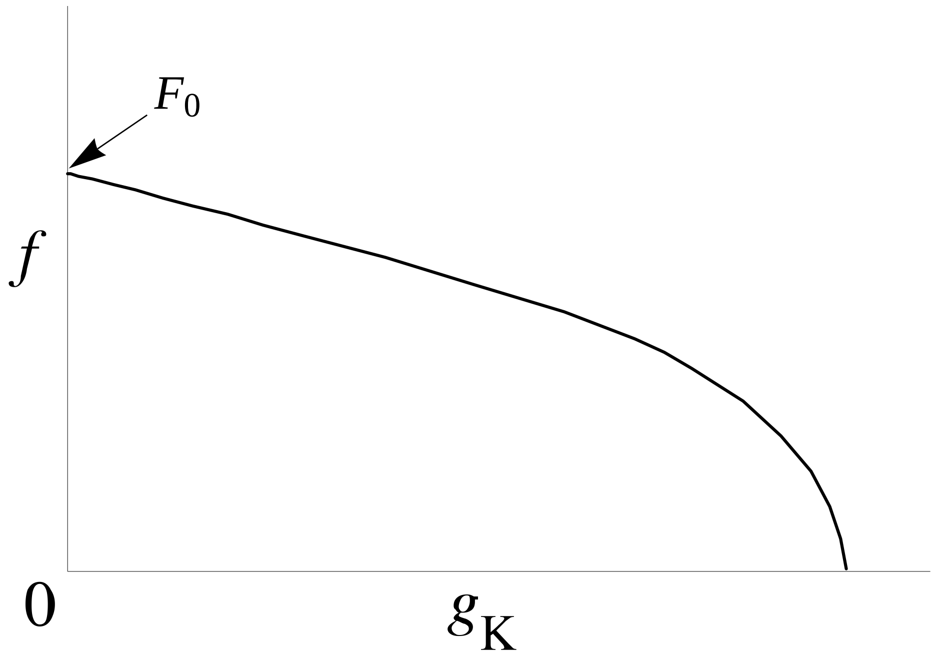
We obtain a plot of frequency $f = 1/T$ versus $g_{K\infty}$ by inverting our expression for $g_{K\infty}(T_n)$:

$$g_{K\infty}[T_n] = \frac{1}{e^{T_n/\tau_K} - 1} \Delta g_K \iff e^{T_n/\tau_K} - 1 = \Delta g_K / g_{K\infty} \iff T_n = \tau_K \, \mathrm{Log}[\Delta g_K / g_{K\infty} + 1]$$

Taking the reciprocal and making the approximation $\frac{1}{\log(1+x)} \approx \frac{1}{x} + \frac{1}{2}$ for $x \ll 1$ yields:

$$f_K[g_{K\infty}] = \frac{1}{\tau_K} \mathrm{Log}\left[\frac{\Delta g_K}{g_{K\infty}} + 1\right]^{-1} \approx \frac{1}{\tau_K}\left(\frac{g_{K\infty}}{\Delta g_K} + \frac{1}{2}\right)$$

$f_{spk}(g)$ curve



The neuron's spike frequency given the potassium conductance g_K is shown ($f(g_K)$ curve)

The neuron's spike frequency is obtained from its membrane-voltage equation (in dimensionless units):

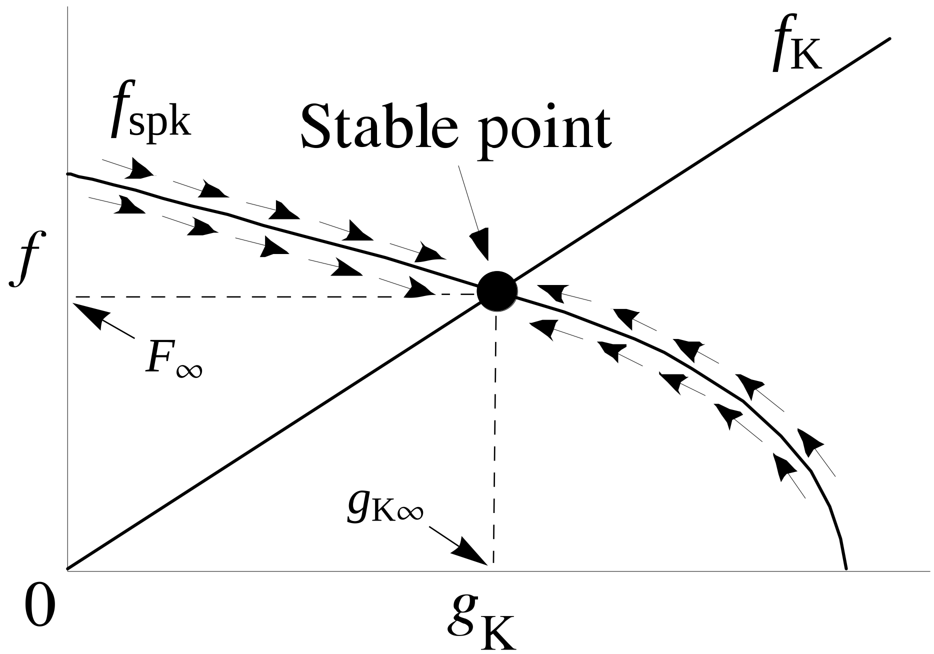
$$\tau_m \frac{dx}{dt} + (1+g)\,x = r + \frac{1}{3}x^3 \quad \text{where} \quad \tau_m = \frac{C_m}{g_{lk}},\; x = \frac{V_m}{V_{th}},\; r = \frac{I_{in}}{g_{lk}\,V_{th}},\; g = \frac{g_K}{g_{lk}}$$

As before, we solve this equation by ignoring the leak and potassium conductances, which we then account for with a subtractive term:

$$f_{spk}[r, g] \approx \frac{3^{7/6}}{2\,\pi\,\tau_m}\left(r^{2/3} - \frac{1+g}{2}\right)$$

(The coefficient 1/2 was determined empirically.)

Phase diagram



The neuron's spike frequency given the potassium conductance g_K is shown ($f(g_K)$ curve)

Setting $f_K(g) = f_{spk}(r, g)$ yields

$$\frac{1}{\tau_K}\left(\frac{g}{\Delta g_K} + \frac{1}{2}\right) = \frac{a}{\tau_m}\left(r^{2/3} - \frac{1+g}{2}\right) \quad \text{where} \quad a = \frac{3^{7/6}}{2\pi} = 0.573$$

Solving for g yields

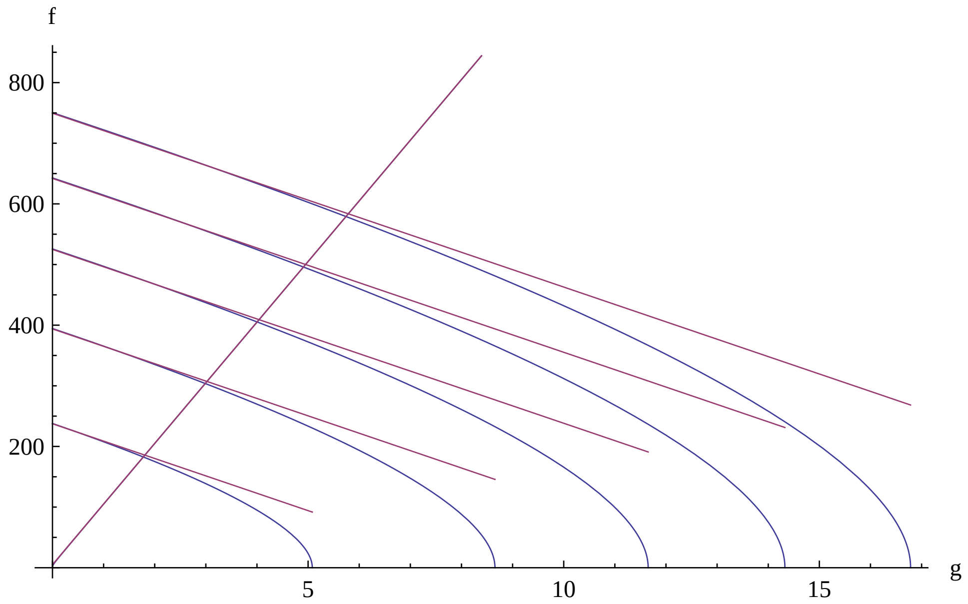
$$g = \frac{f[r, 0] - 1/2\,\tau_K}{a/2\,\tau_m + 1/\Delta g_K\,\tau_K} \quad \text{where} \quad f[r, 0] = \frac{a}{\tau_m}\left(r^{2/3} - \frac{1}{2}\right)$$

Substituting this result back into the $f_K(g)$ formula gives

$$f_\infty = \frac{f[r, 0] + a\,\Delta g_K / 4\,\tau_m}{1 + a\,\tau_K\,\Delta g_K / 2\,\tau_m}$$

Adaptation has a divisive effect on firing rate---because Δg_K appears in the denominator.

How good are our approximations?

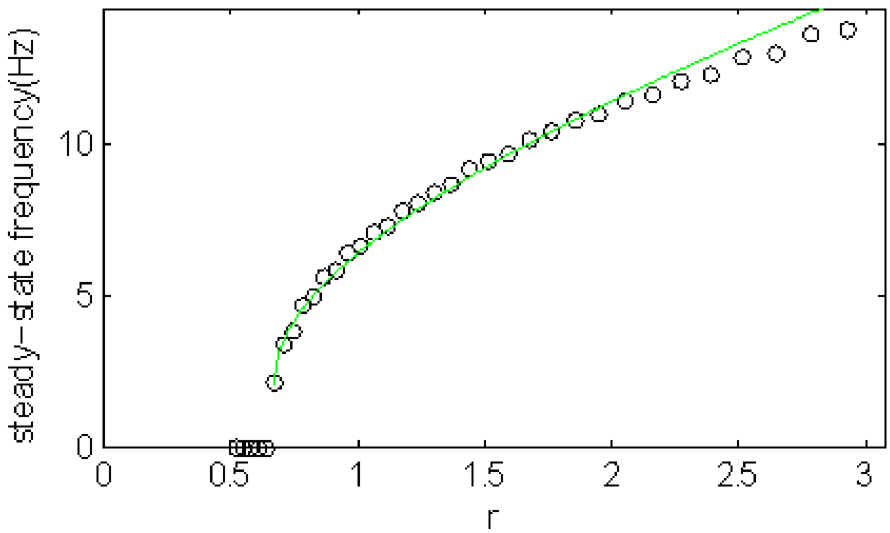


Exact $f_K(g)$ and $f_{spk}(r, g)$ expressions (blue) and their linear approximations (red) for $r = 10, 20, ..., 50$

$f_K(g)$'s approximation is excellent; $f_{spk}(r, g)$'s is good for high firing rates. The parameter values were:

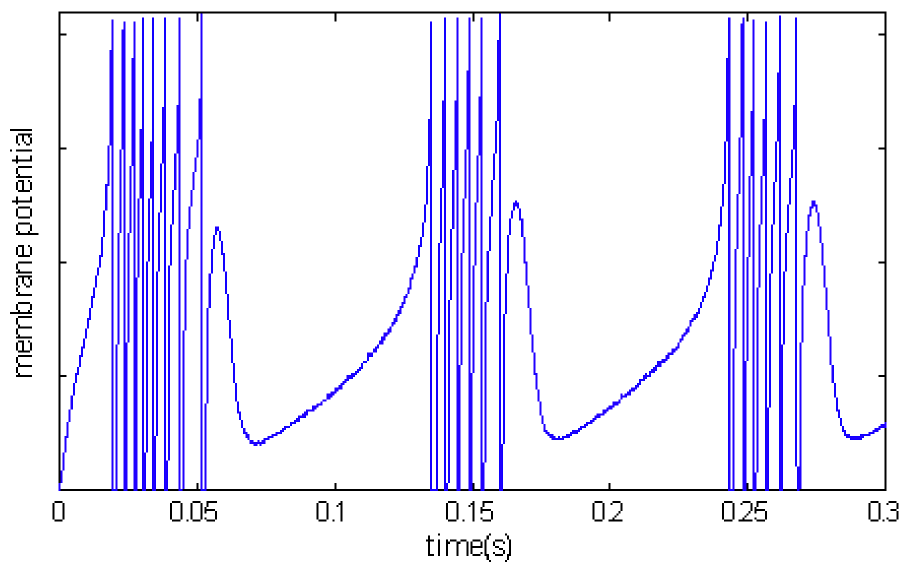
$$\left\{\tau_m \to 10\ \text{ms},\ \tau_k \to 100\ \text{ms},\ \frac{\Delta g_k}{g_{lk}} \to 0.1\right\}$$

Steady-state firing rate (F_∞)



The theory (green) holds for moderate currents (a few times the minimum)

Next Lecture: Bursting



Adding a Ca^{2+} current leads to bursting