Simplified neuron models II:

Izhikevich model & Firing-rate models

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slides contributed by Tom Tetzlaff

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Outline

Izhikevich model

From spiking neurons to firing-rate models

Rate dynamics of LIF neurons with strong synapses

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Rate dynamics of LIF neurons with strong synapses

2D reduction of the Hodgkin-Huxley model

- different reductions of the HH model

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\begin{aligned}
C\dot{V} &= I - \bar{g}_{\mathsf{K}^+} n^4 (V - E_{\mathsf{K}^+}) - \bar{g}_{\mathsf{Na}^+} m^3 h (V - E_{\mathsf{Na}^+}) - g_{\mathsf{L}} (V - E_{\mathsf{L}}) \\
\dot{n} &= (n_\infty(V) - n) / \tau_n(V) \\
\dot{m} &= (m_\infty(V) - m) / \tau_m(V) \\
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to 2-dimensional systems of the form

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\dot{x} &= f(x, y) \\
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  - removal of Na^+ inactivation, i.e. $h = 1$
  - assuming instantaneous Na^+ activation, i.e. $m = m_\infty$

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- Many reductions have in common that x is a *fast* voltage (V) and y a slow *recovery* variable (e.g. n or h).

Phase plane

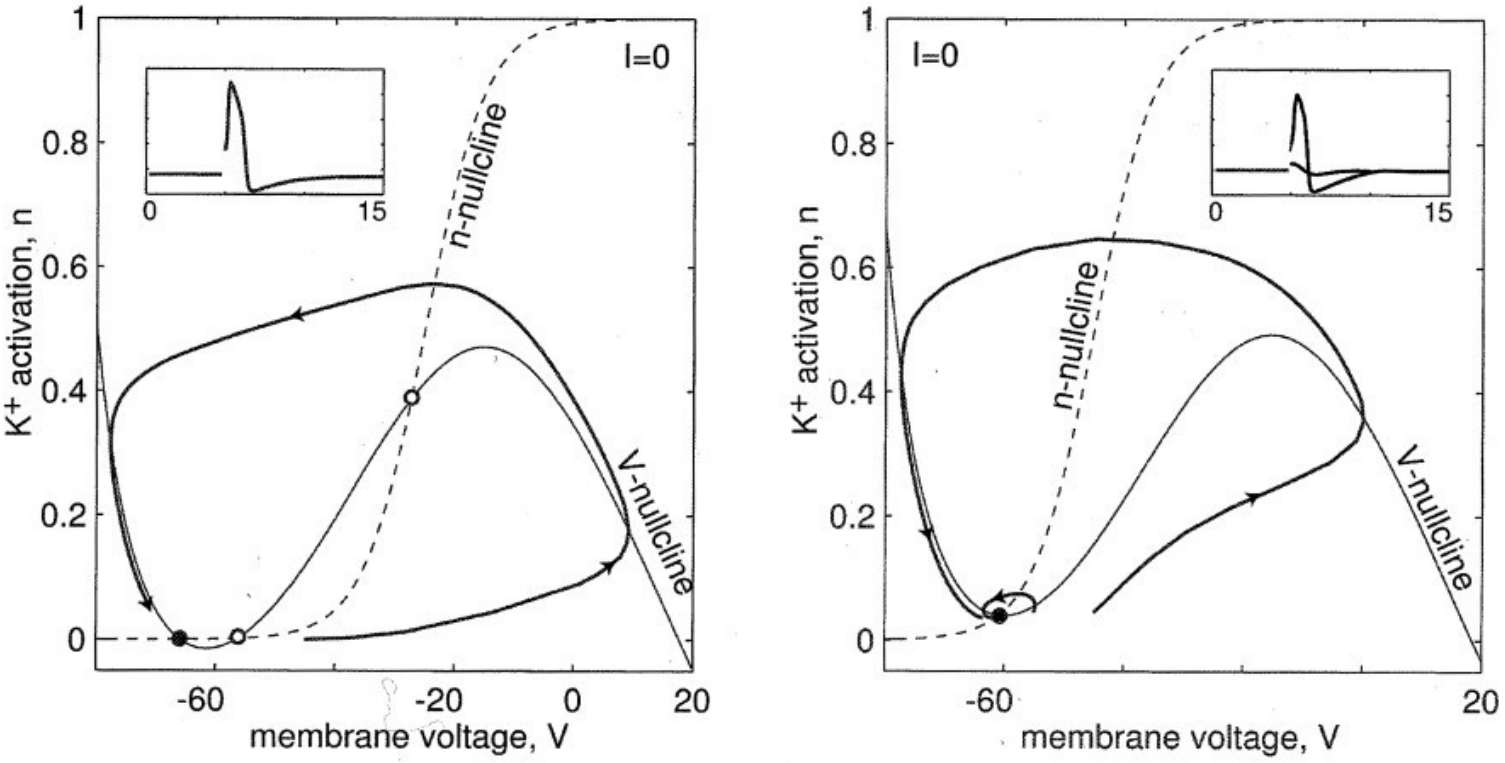
- V-nullcline: curve defined by $\dot{V} = 0 = f(V_0, n_0)$

$$0 = I - \bar{g}_{\mathsf{K}+} n_0^4 (V_0 - E_{\mathsf{K}+}) - \bar{g}_{\mathsf{Na}+} m_\infty^3 (V_0 - E_{\mathsf{Na}+}) - g_{\mathsf{L}} (V_0 - E_{\mathsf{L}})$$

$$\curvearrowright \quad n_0 = \left(\frac{I - \bar{g}_{\mathsf{Na}+} m_\infty^3 (V_0 - E_{\mathsf{Na}+}) - g_{\mathsf{L}} (V_0 - E_{\mathsf{L}})}{\bar{g}_{\mathsf{K}+} (V_0 - E_{\mathsf{K}+})} \right)^{1/4}$$

- n-nullcline: curve defined by $\dot{n} = 0 = g(V_0, n_0)$

$$0 = (n_\infty(V_0) - n_0) / \tau_n(V_0) \quad \curvearrowright \quad n_0 = n_\infty(V_0)$$



Izhikevich model

- decision *"to spike or not to spike"* is made close to left minimum of V-nullcline (resting state)
- approximation of dynamics in the vicinity of the resting state

$$\dot{V} = \tau_{\text{fast}} \left(p \left(V - V_{\text{min}} \right)^2 - \left(u - u_{\text{min}} \right) \right)$$
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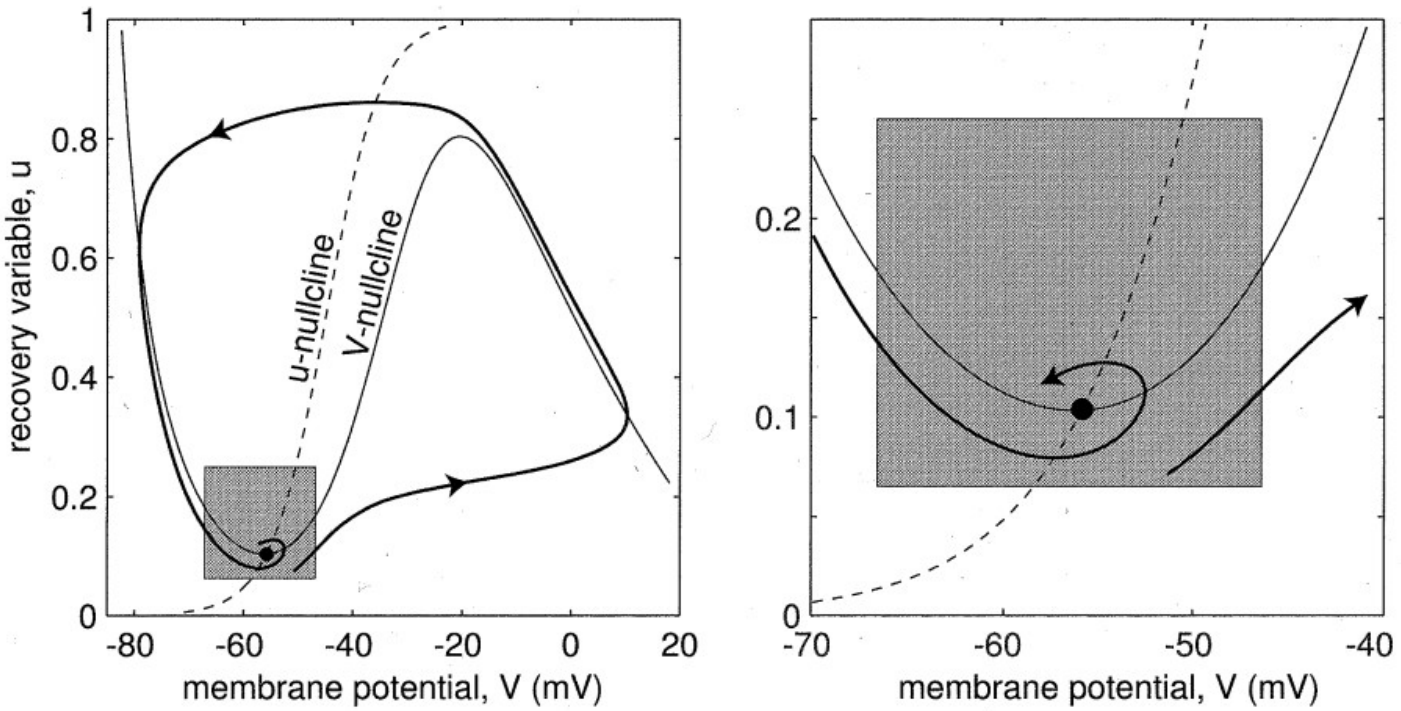

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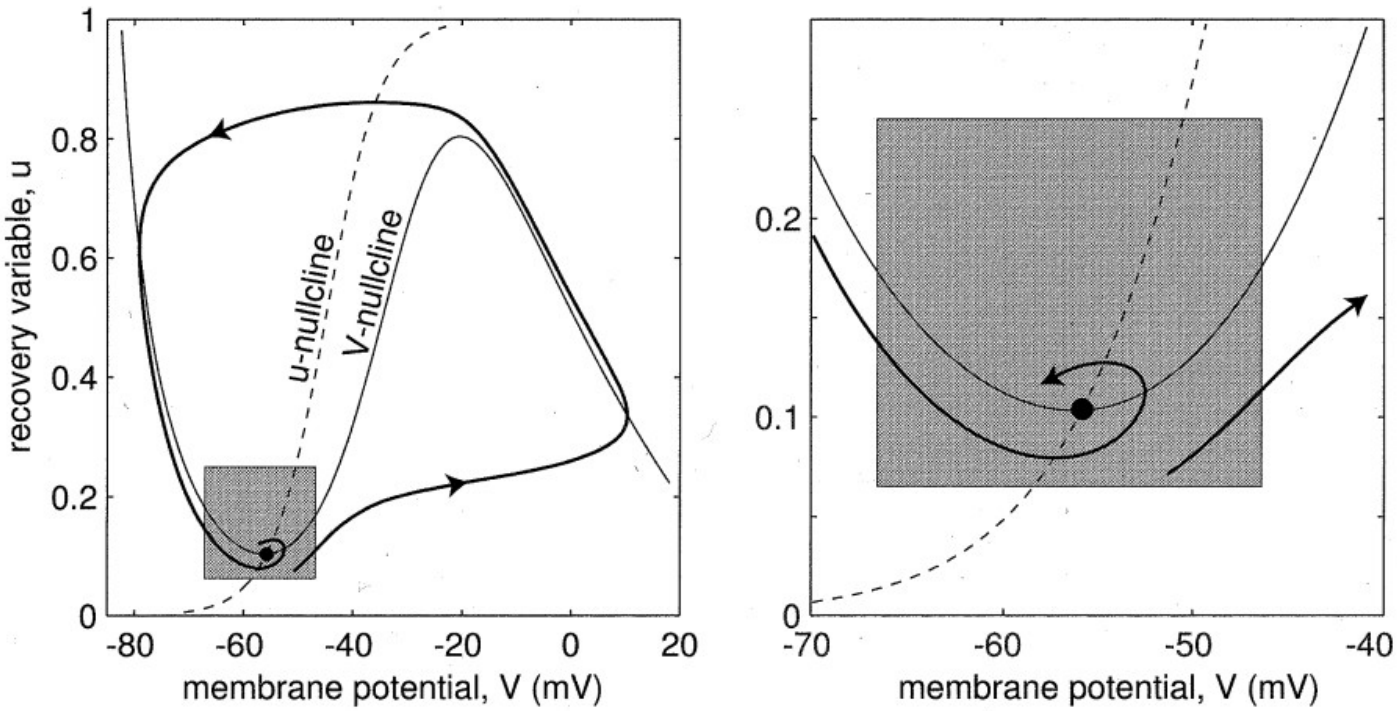

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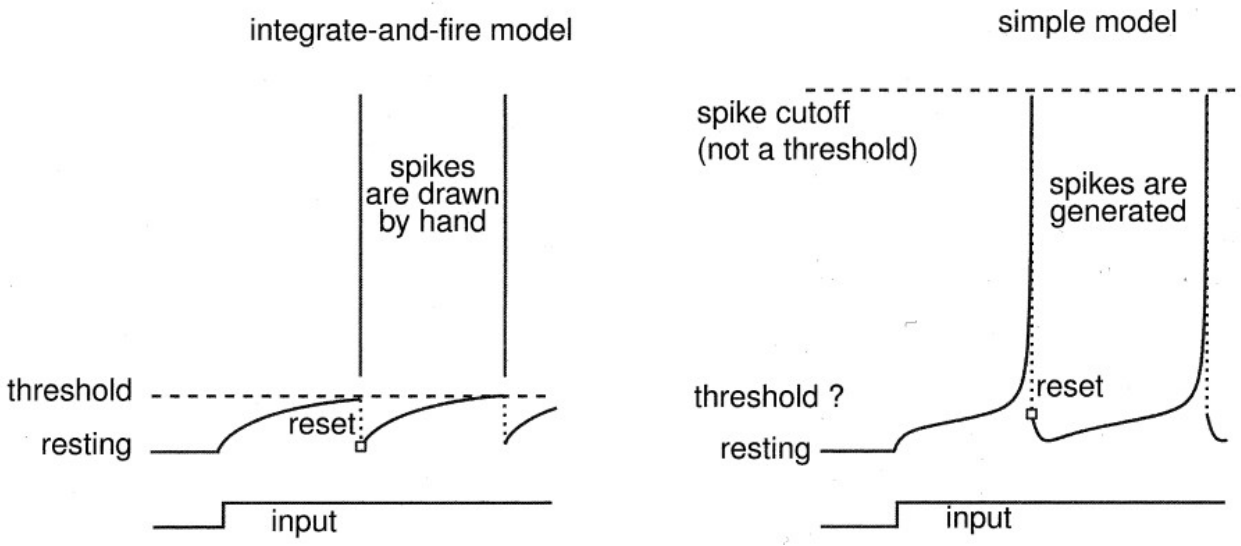

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- note: only 4 dimensionless parameters a, b, c, d

Izhikevich model

- model can mimic both
  integrators and *resonators*
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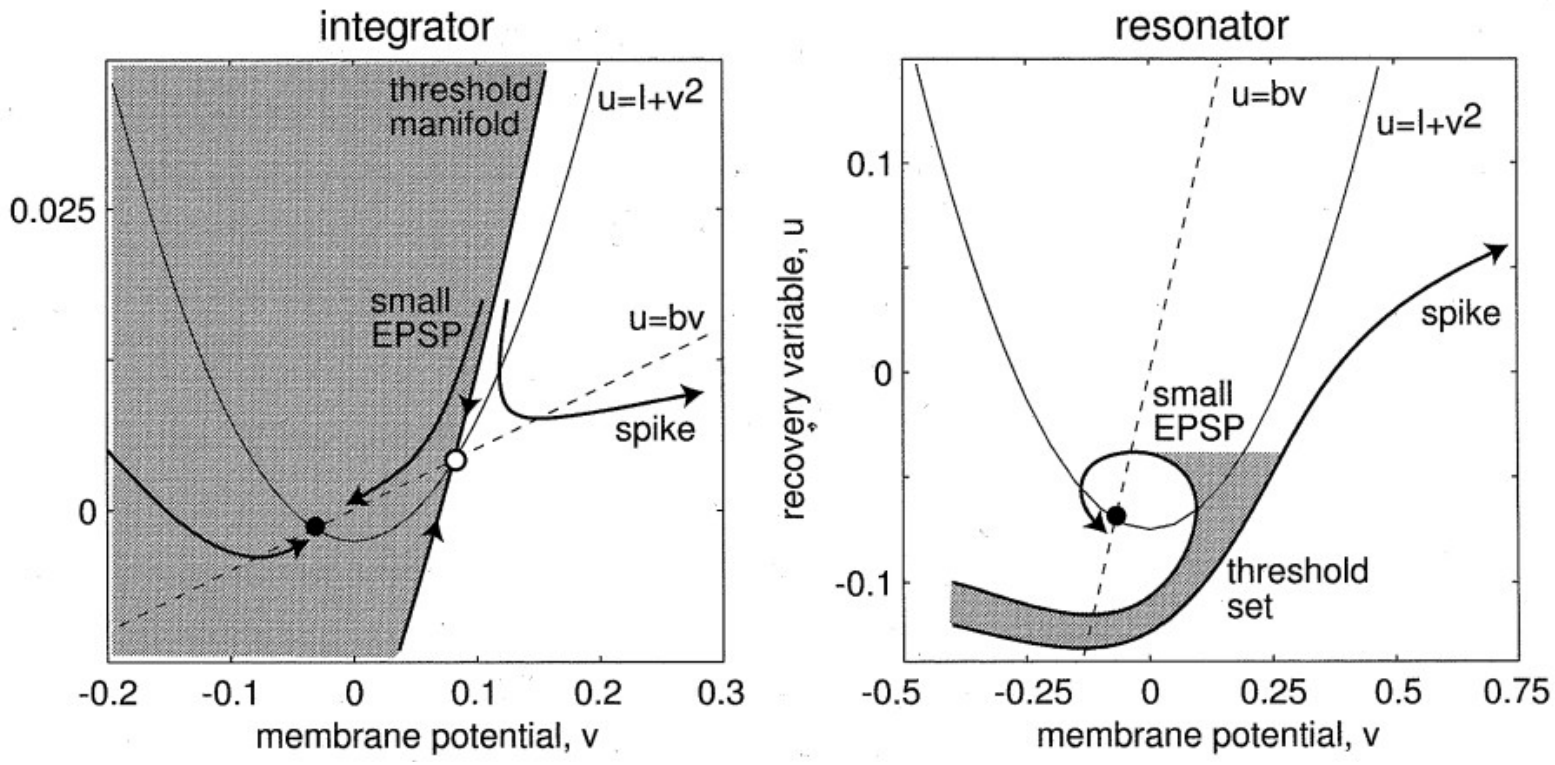
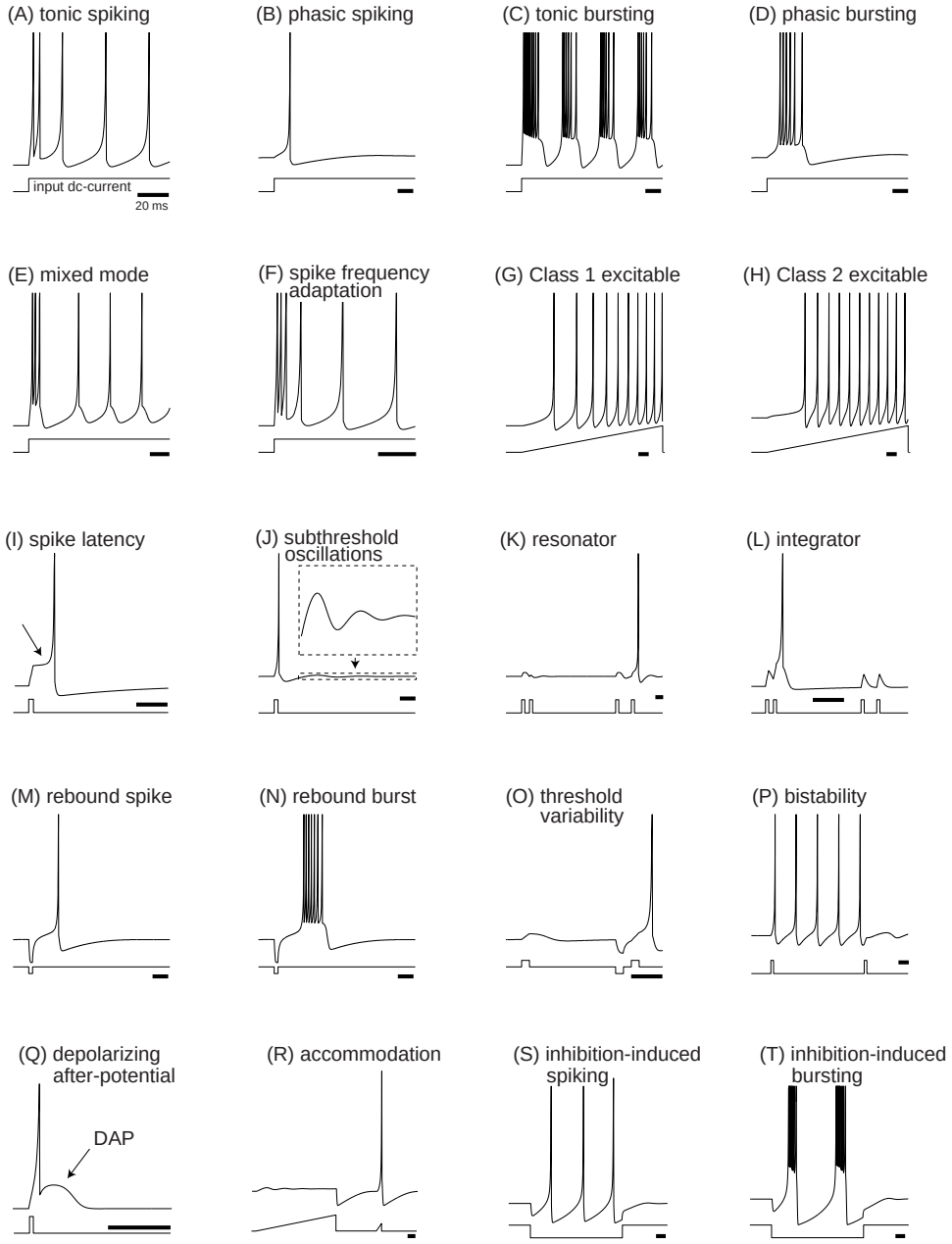


Izhikevich model

- model can mimic both *integrators* and *resonators* (by appropriate choices of parameters)

  . . . and a large variety of different neuron types



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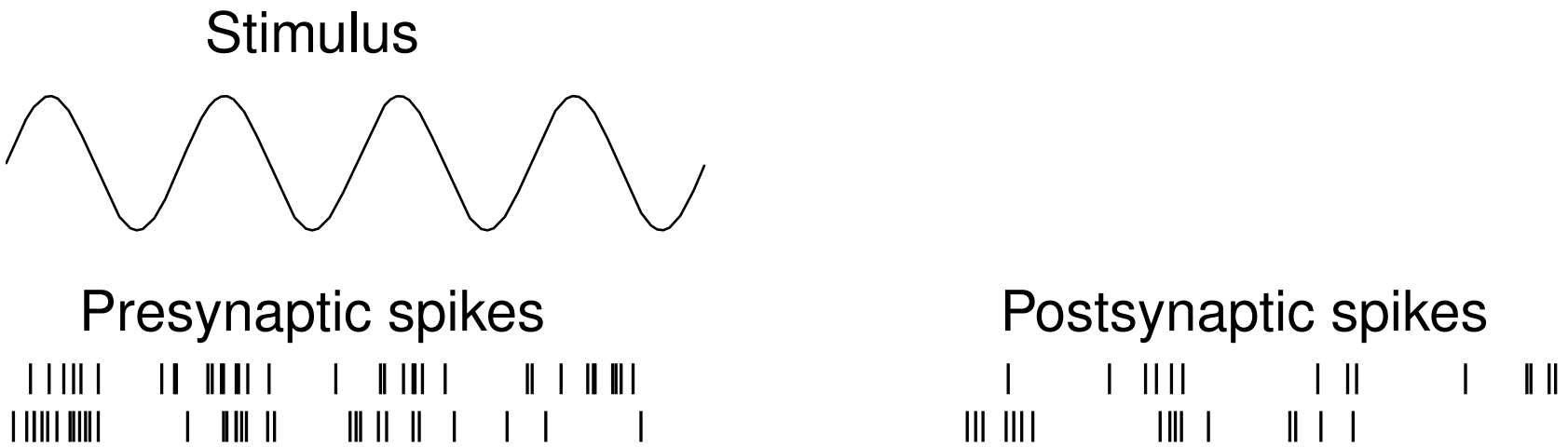
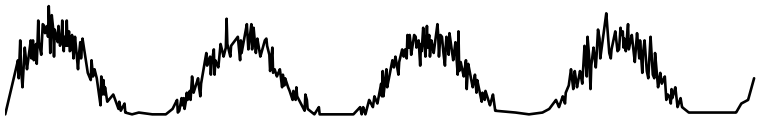


- variable (stochastic) spike times

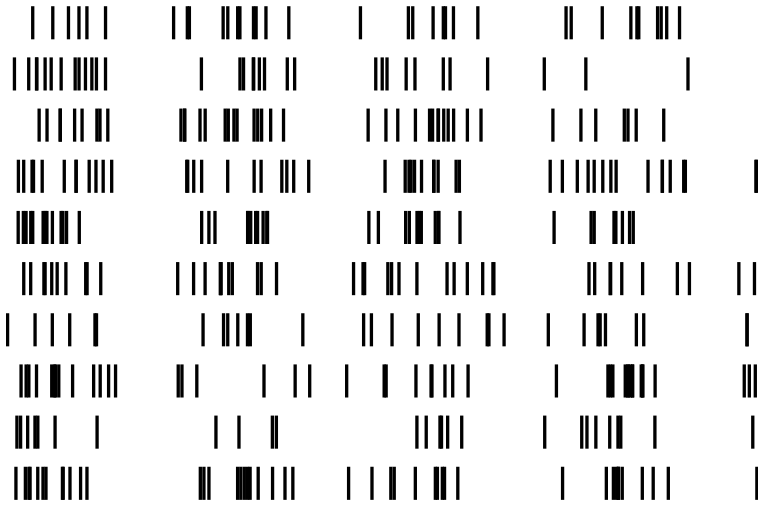
Firing-rate models

Stimulus

Response firing rate



Presynaptic spikes



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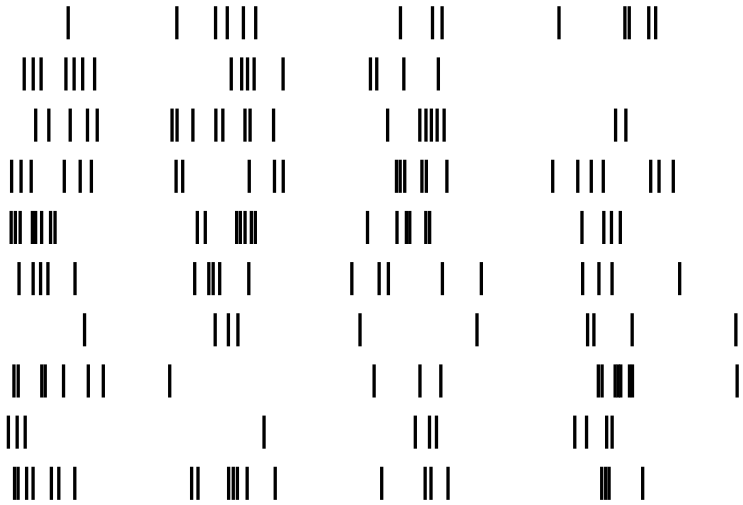

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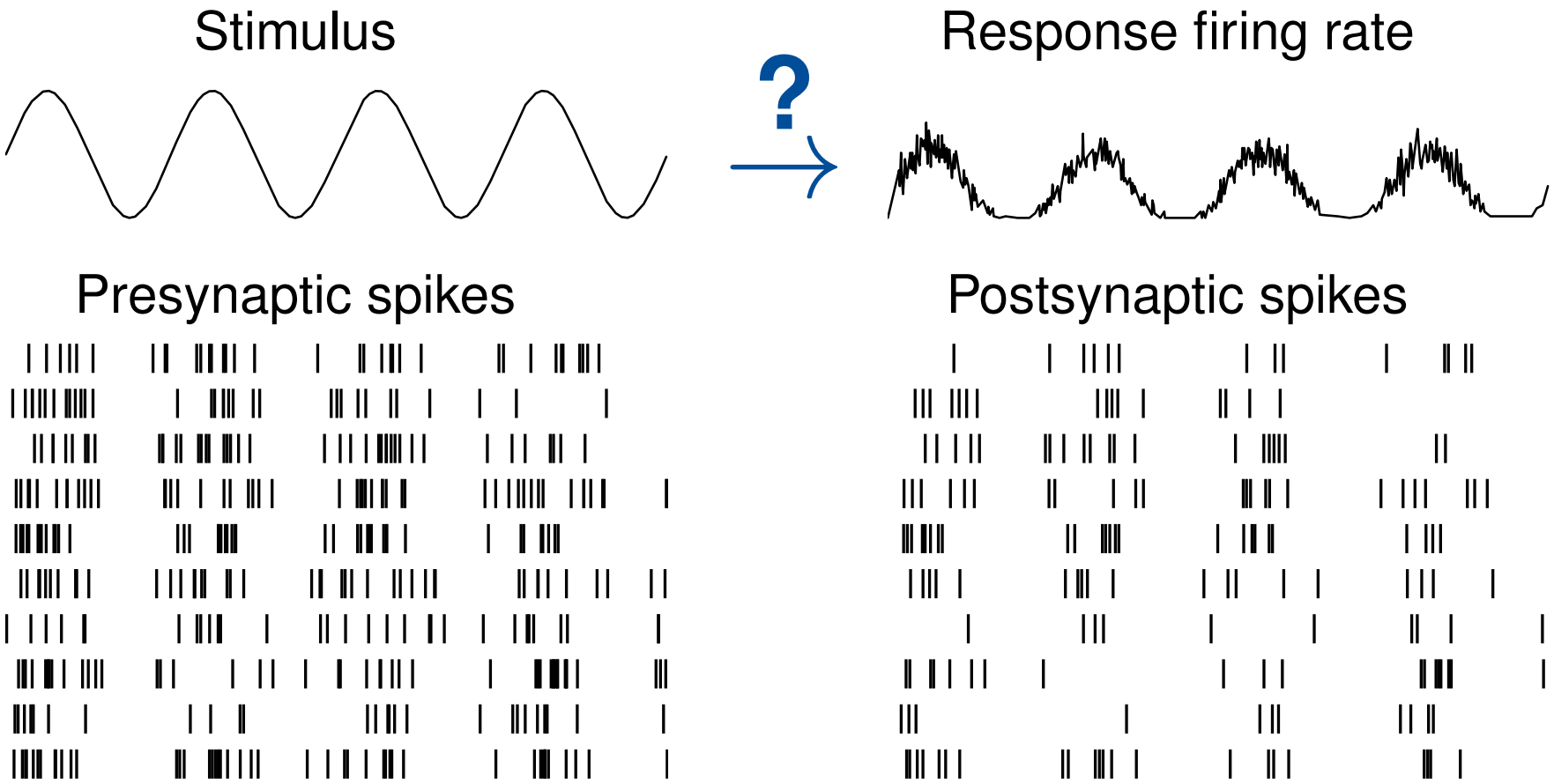
Firing-rate models



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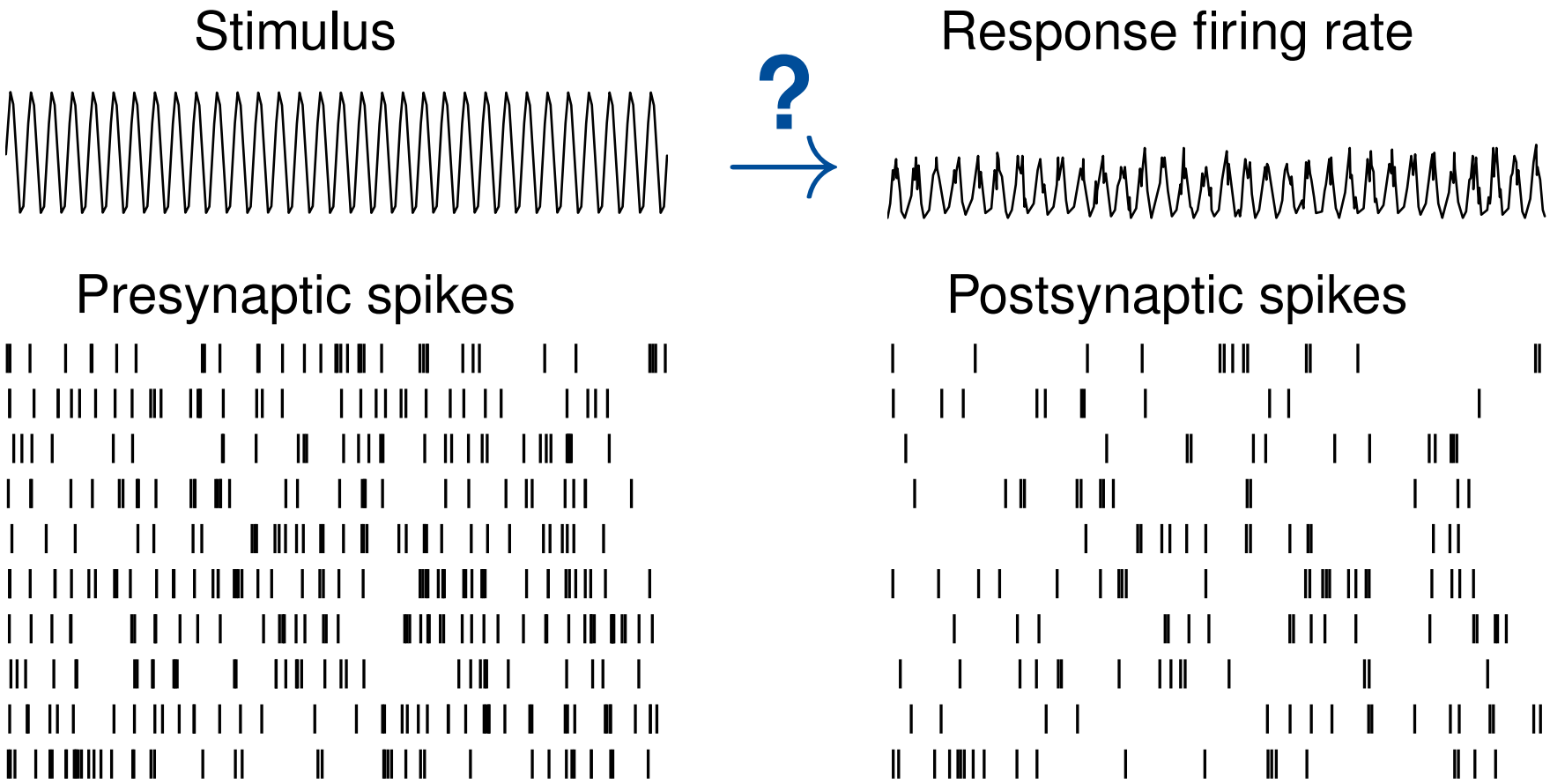

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Firing-rate models

Decomposition of stimulus $a(t)$ and response rate $r(t)$ into constant and time-dependent components: $a(t) = a_0 + a_1(t)$ and $r(t) = r_0 + r_1(t)$

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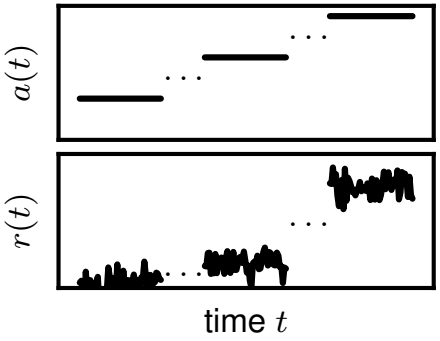
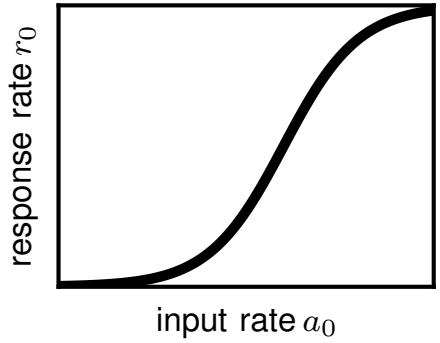


Activation function



$$r_0 = f(a_0)$$

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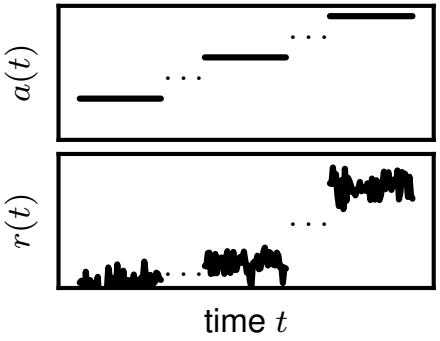
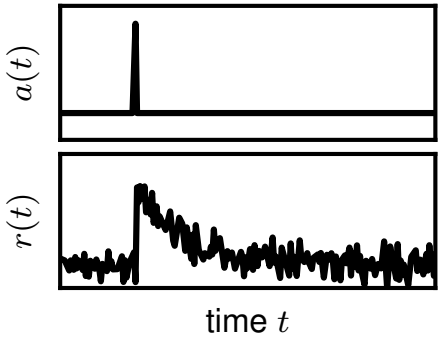


Nonstationary (time-dependent) response



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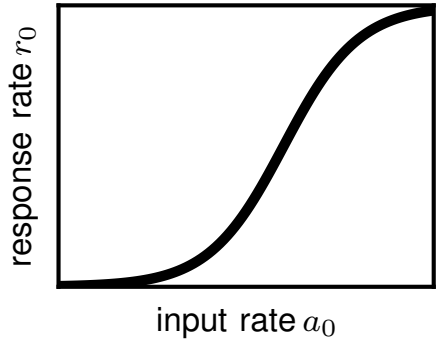

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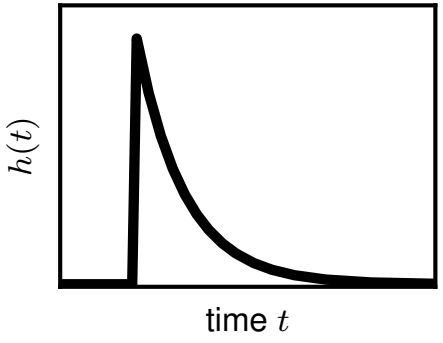
Impulse response



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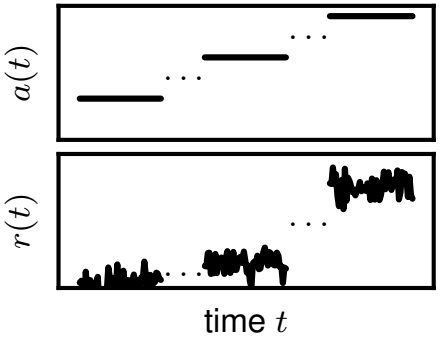

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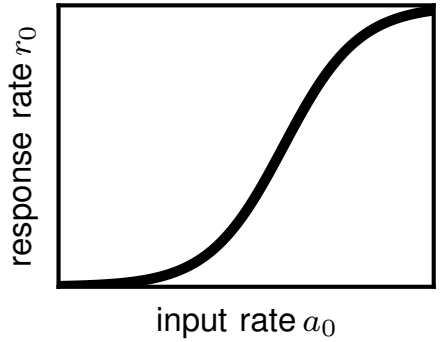

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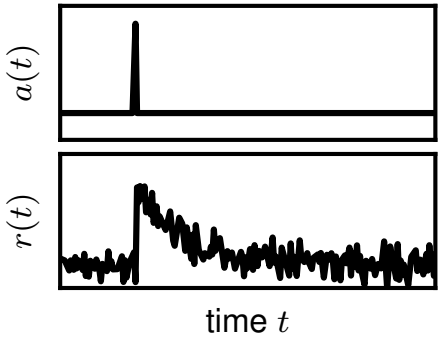

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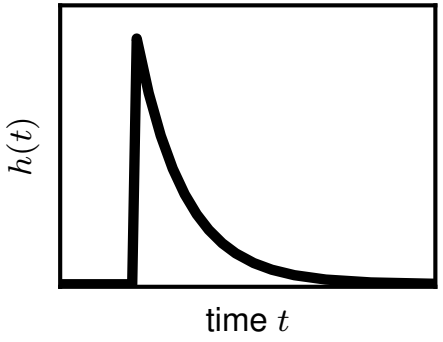

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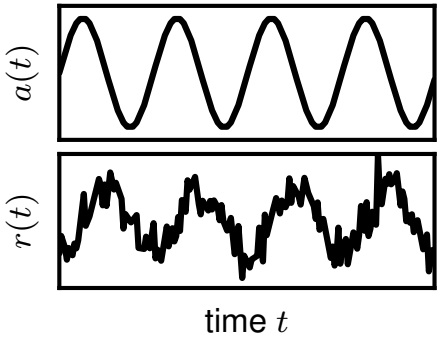
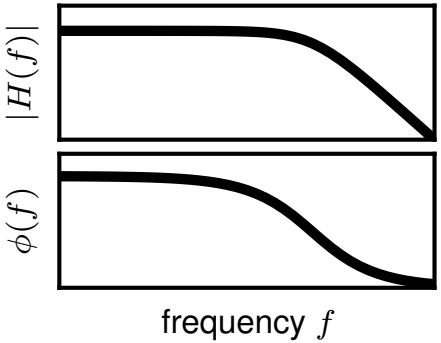


Transfer function



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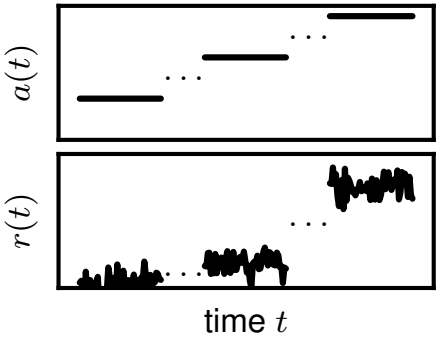

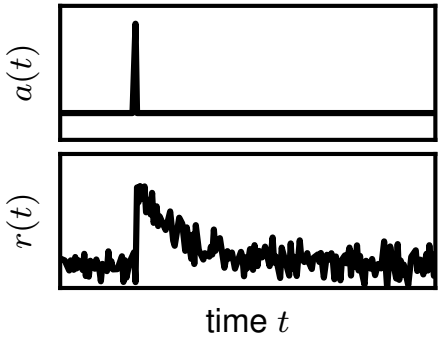

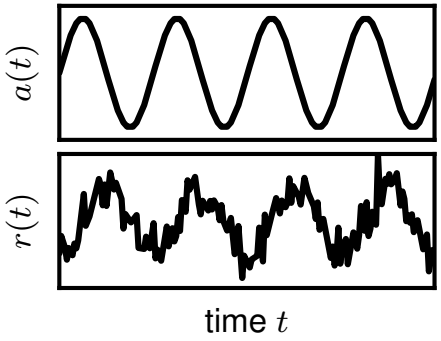

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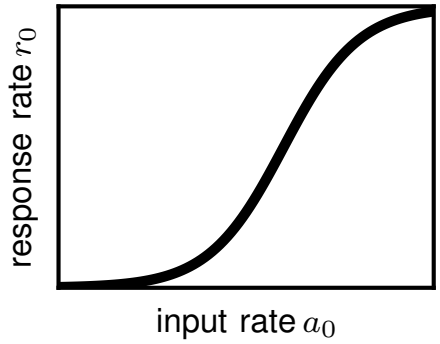

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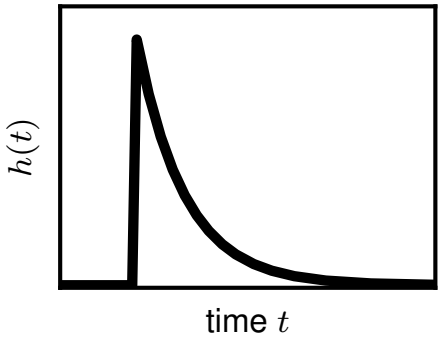

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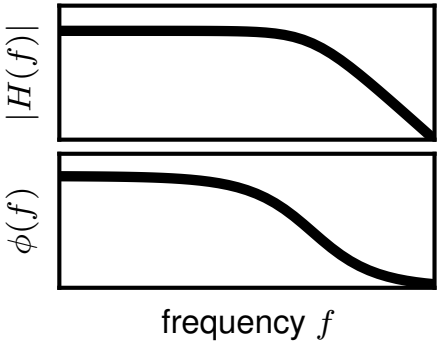

$$R_1(f) = A_1(f)H_0(f)$$

- Combination of stationary and nonstationary response properties:

$$\boxed{r(t) = f\big((a * h)(t)\big)}$$

('linear-nonlinear model')

Rate models in NEST

$$X(t) = X_0 + \int_{t_0}^{t} a(s, X(s))ds + \int_{t_0}^{t} b(s, X(s))dW(s)$$

- more general model:
  - explicit time dependence
  - stochastic input: Wiener process $W(t)$ (Brownian motion)
- second integral defined as Itô integral:

$$\int_{t_0}^{t} Y(s)dW(s) := \lim_{n\to\infty} \sum_{i=1}^{n} Y_{i-1} \cdot (W_i - W_{i-1})$$

with $Y_i = Y(t_0 + i \cdot \frac{t-t_0}{n})$ and $W_i = W(t_0 + i \cdot \frac{t-t_0}{n})$
rather than Stratonovich integral

$$\int_{t_0}^{t} Y(s) \circ dW(s) := \lim_{n\to\infty} \sum_{i=1}^{n} \frac{Y_{i-1} + Y_i}{2} \cdot (W_i - W_{i-1})$$

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- examples:
  - complex single-neuron dynamics

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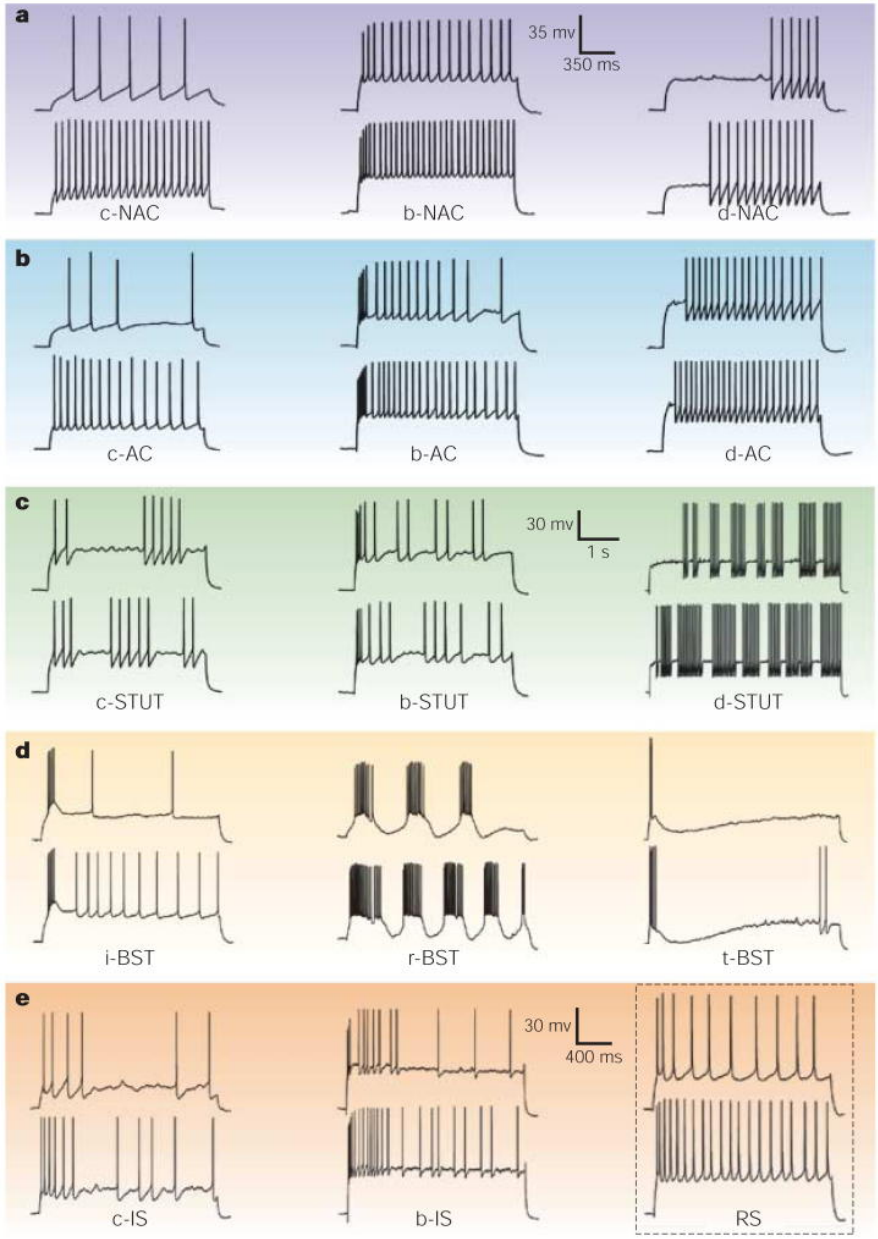
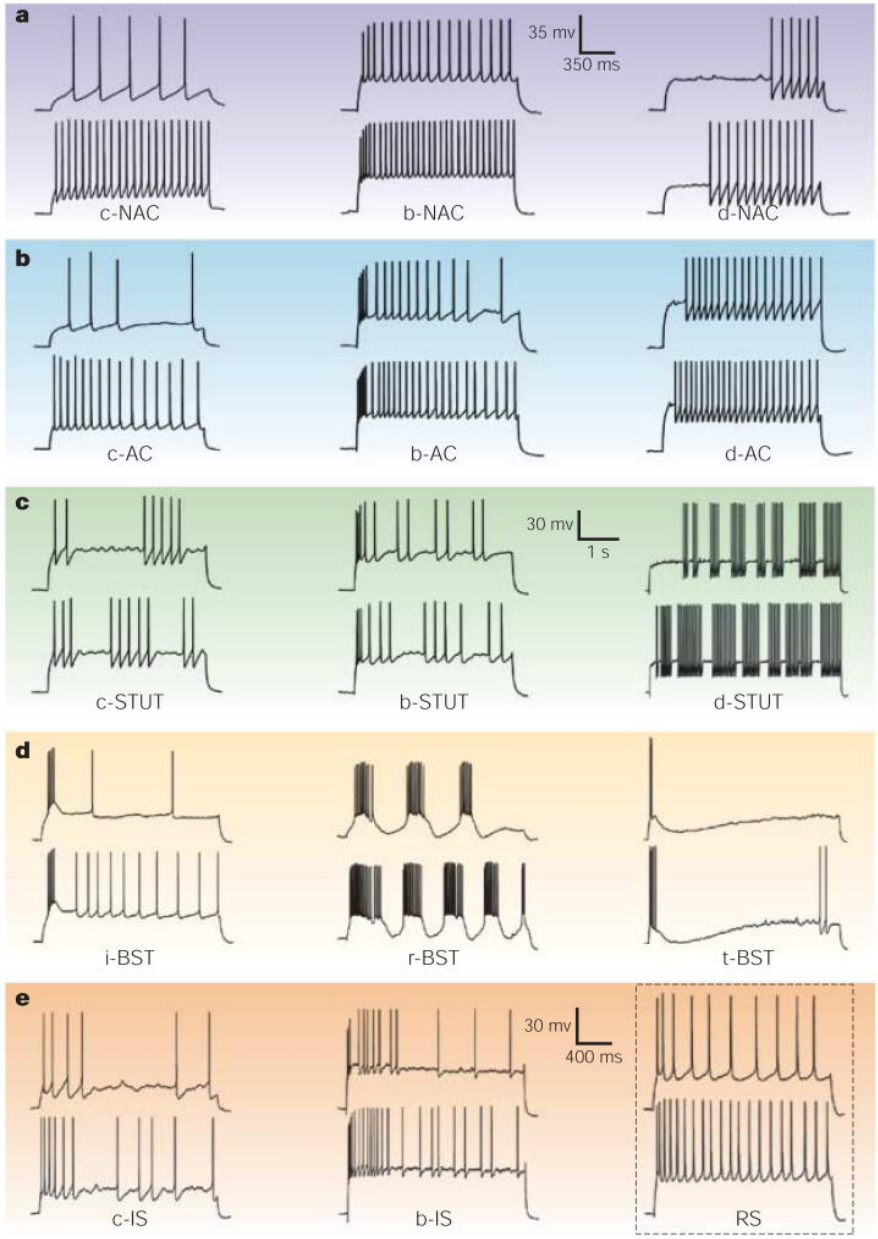


Markram et al. (2004)

Firing-rate models



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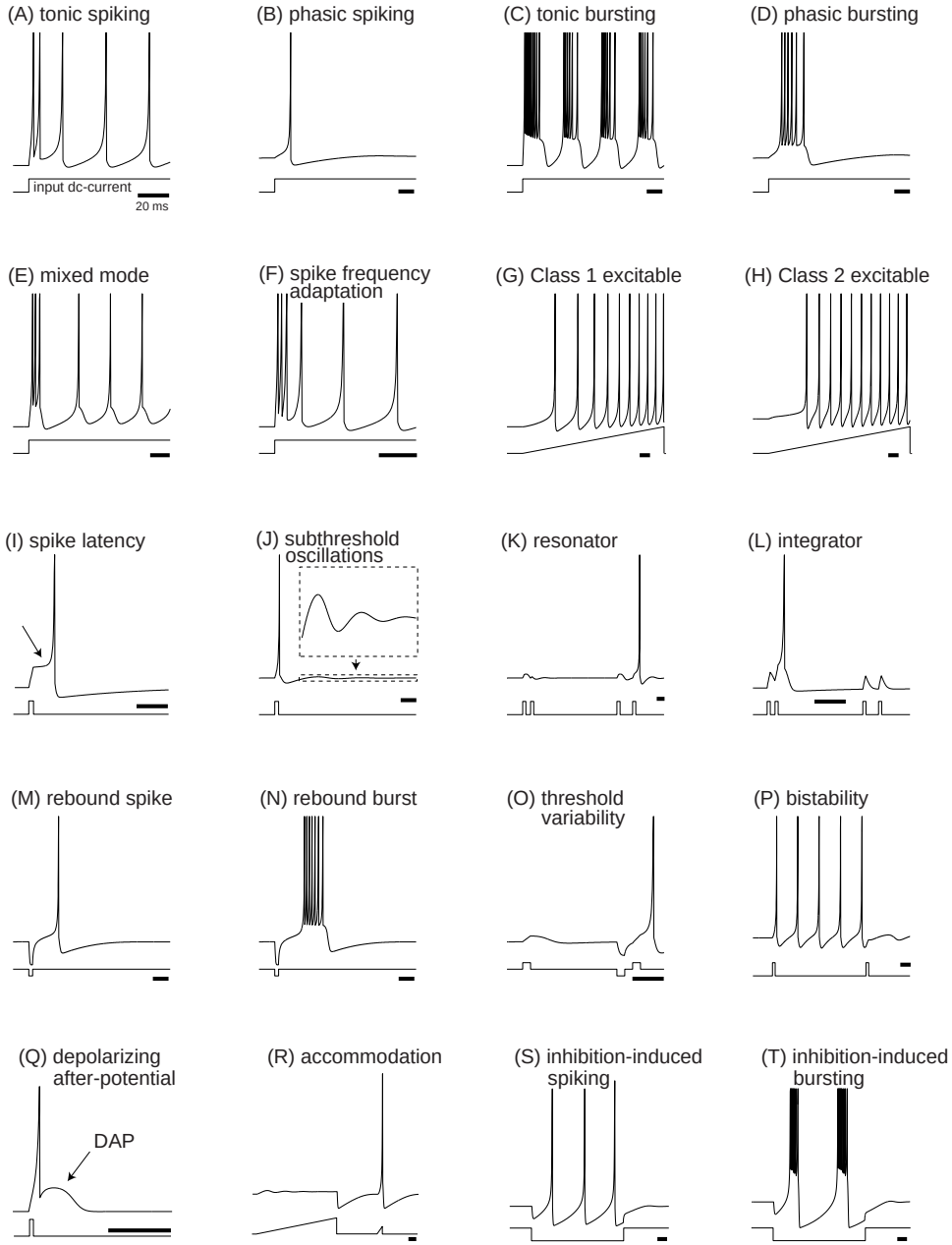

Izhikevich (2004)

Firing-rate models

- can create networks of rate neurons
- often difficult to relate rate model parameters to neuronal and synaptic characteristics
- examples:
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  - synaptic dynamics

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  however,

  a) requires controlled stimulation of synapses
  b) possible only under simplifying assumptions

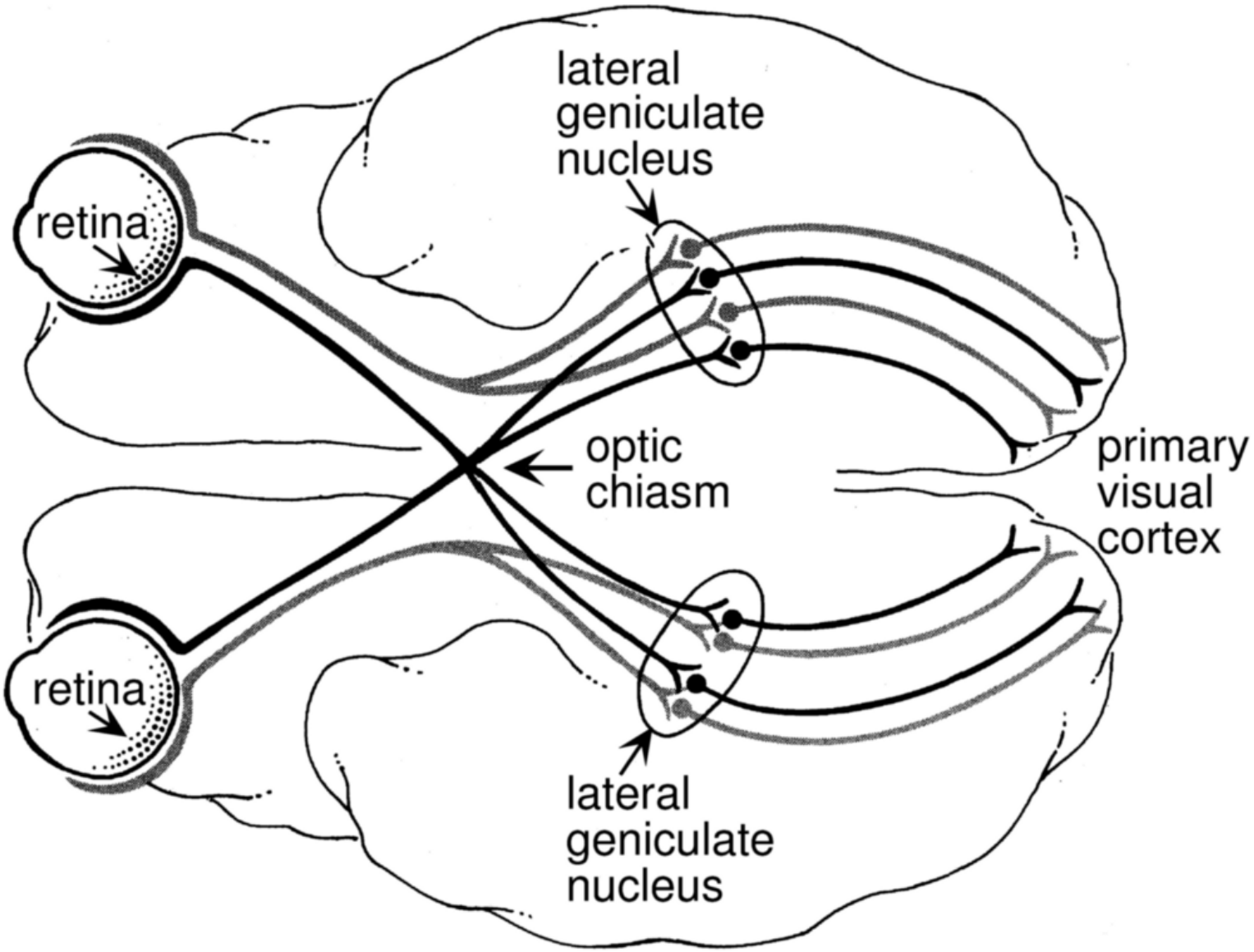
Outline

Izhikevich model

From spiking neurons to firing-rate models

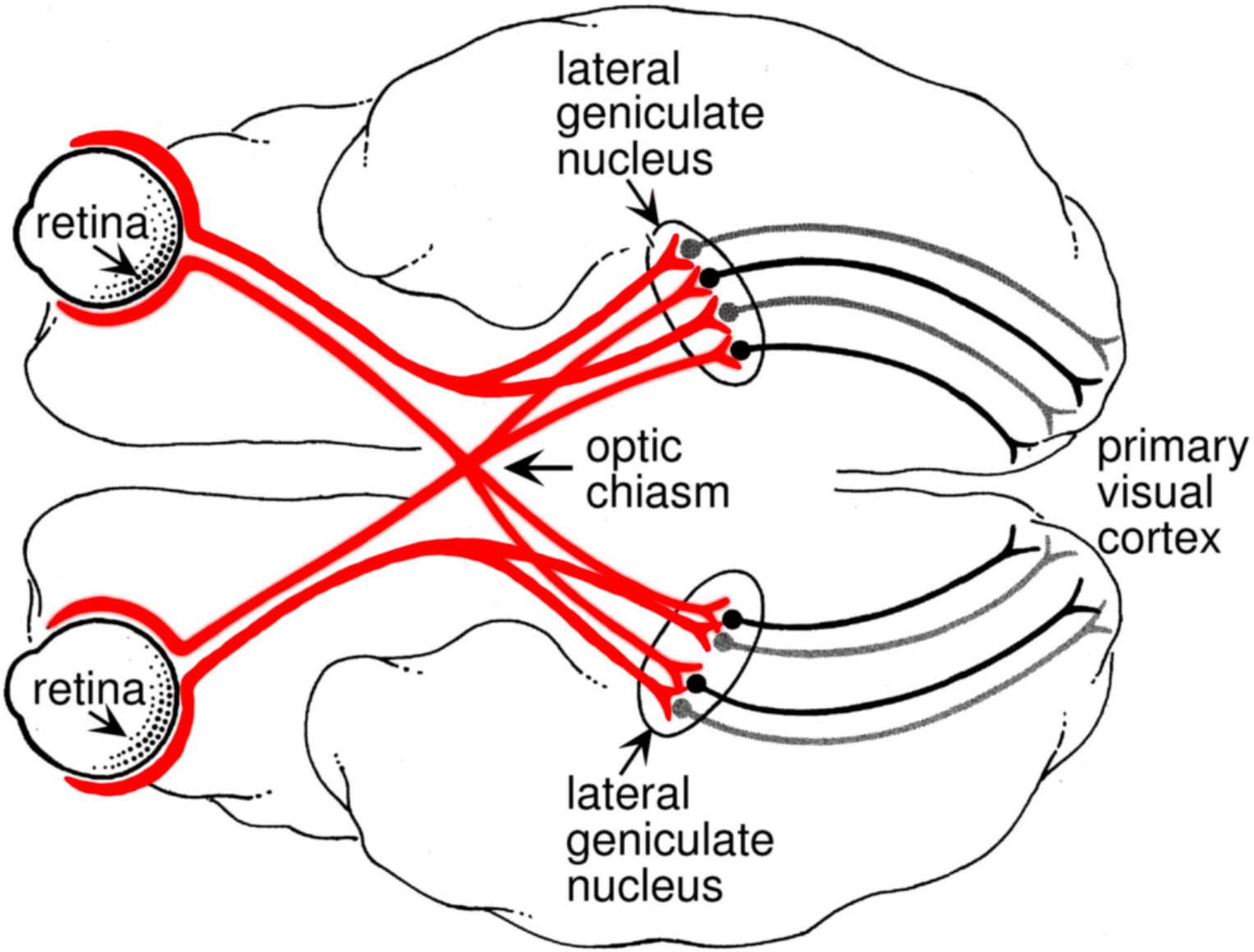
Rate dynamics of LIF neurons with strong synapses

The early visual system



Sketch of the early visual pathway (Dayan & Abbott, 2001)

The early visual system



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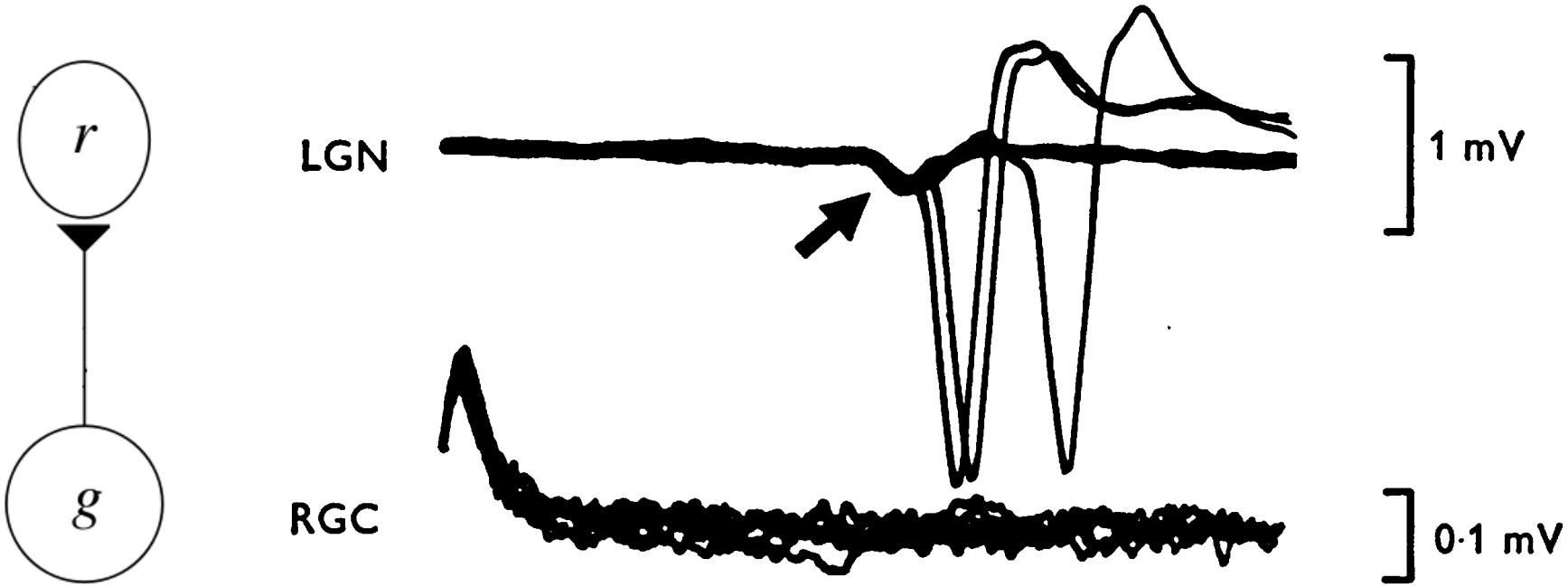

(Cleland et al., 1971)

- single ganglion-cell spikes can elicit spikes in thalamic relay cells
- transfer ratio up to 50% (Ruksenas et al., 2000; Ozaki & Kaplan, 2006)

$\curvearrowright$ connections between ganglion and relay cells are **strong**

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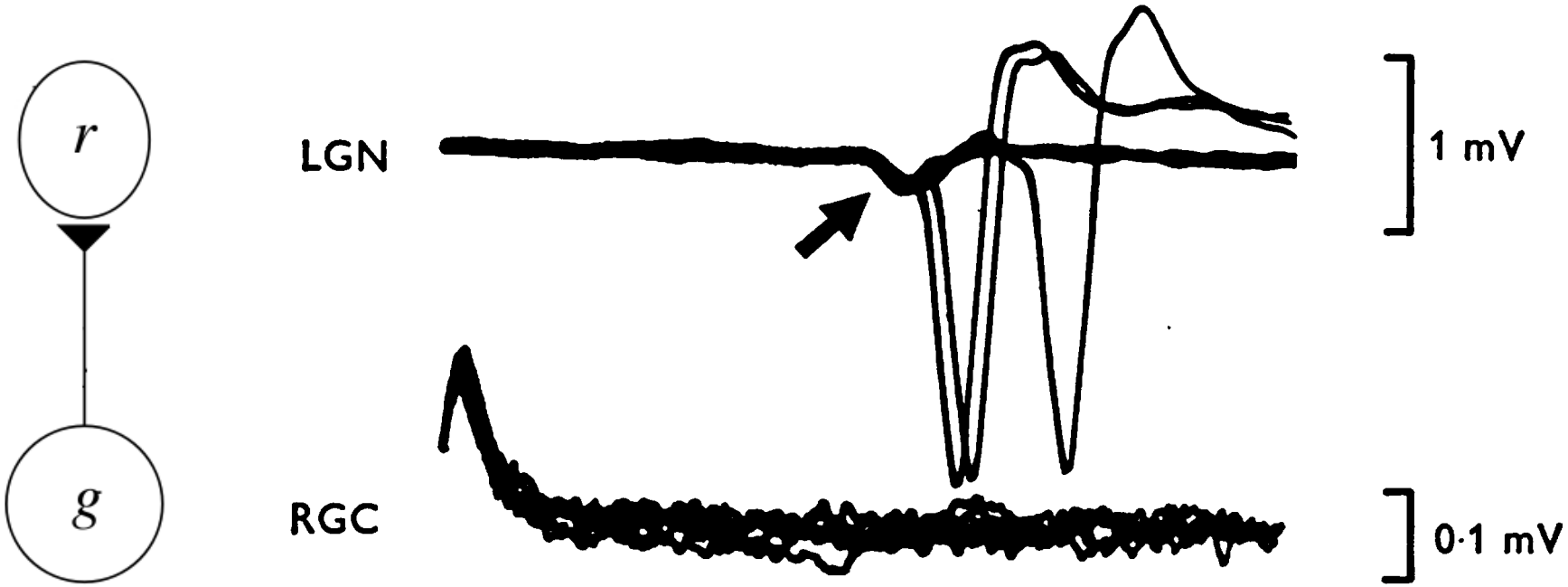

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- remark:
  - in neocortex: wide distribution of synaptic weights
  - considerable fraction of cortical synapses is **not weak** (postsynaptic potentials up to several mV)

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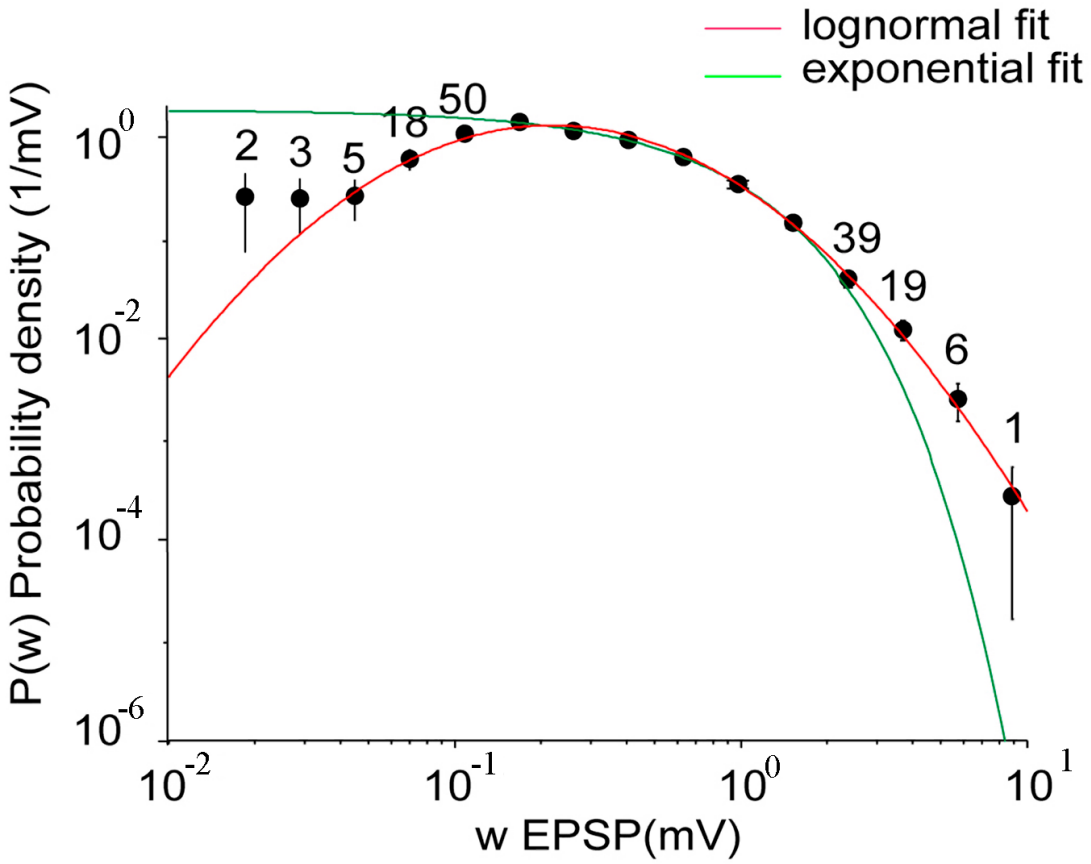


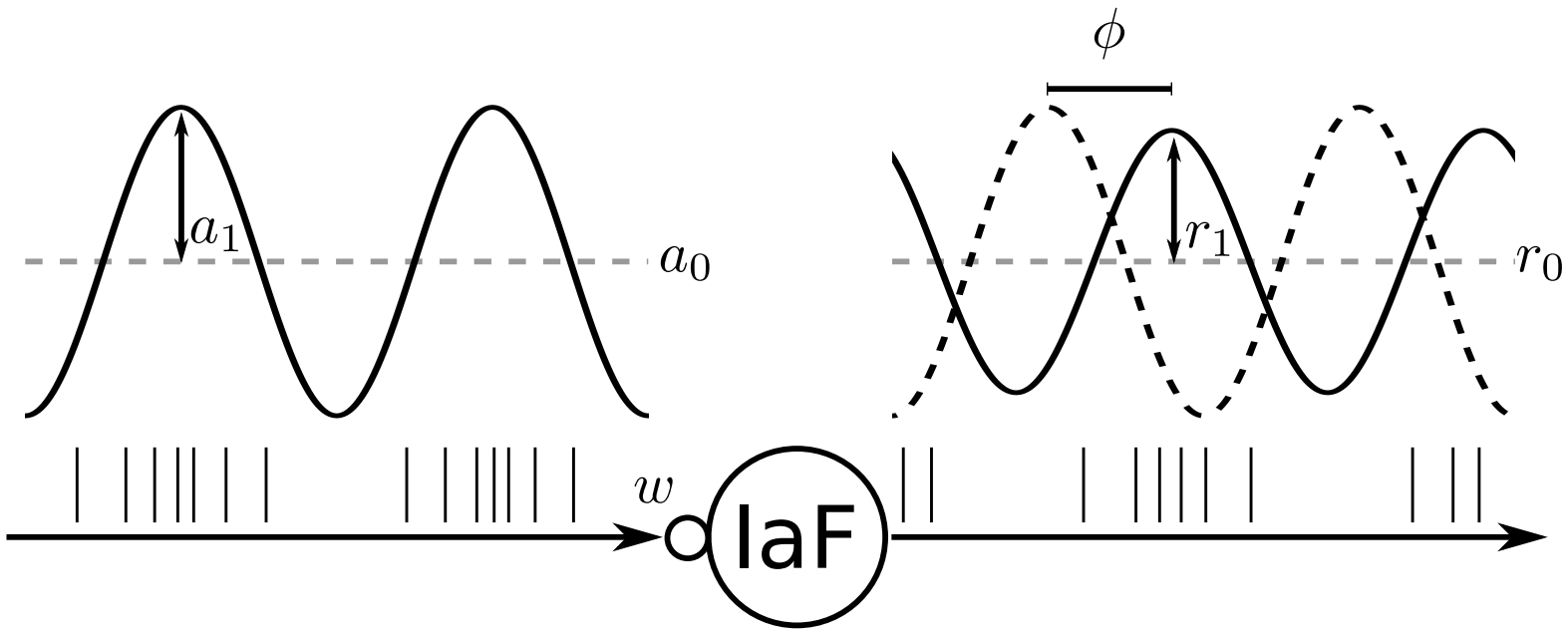
(Song et al., 2005)

- remark:
  - in neocortex: wide distribution of synaptic weights
  - considerable fraction of cortical synapses is **not weak** (postsynaptic potentials up to several mV)

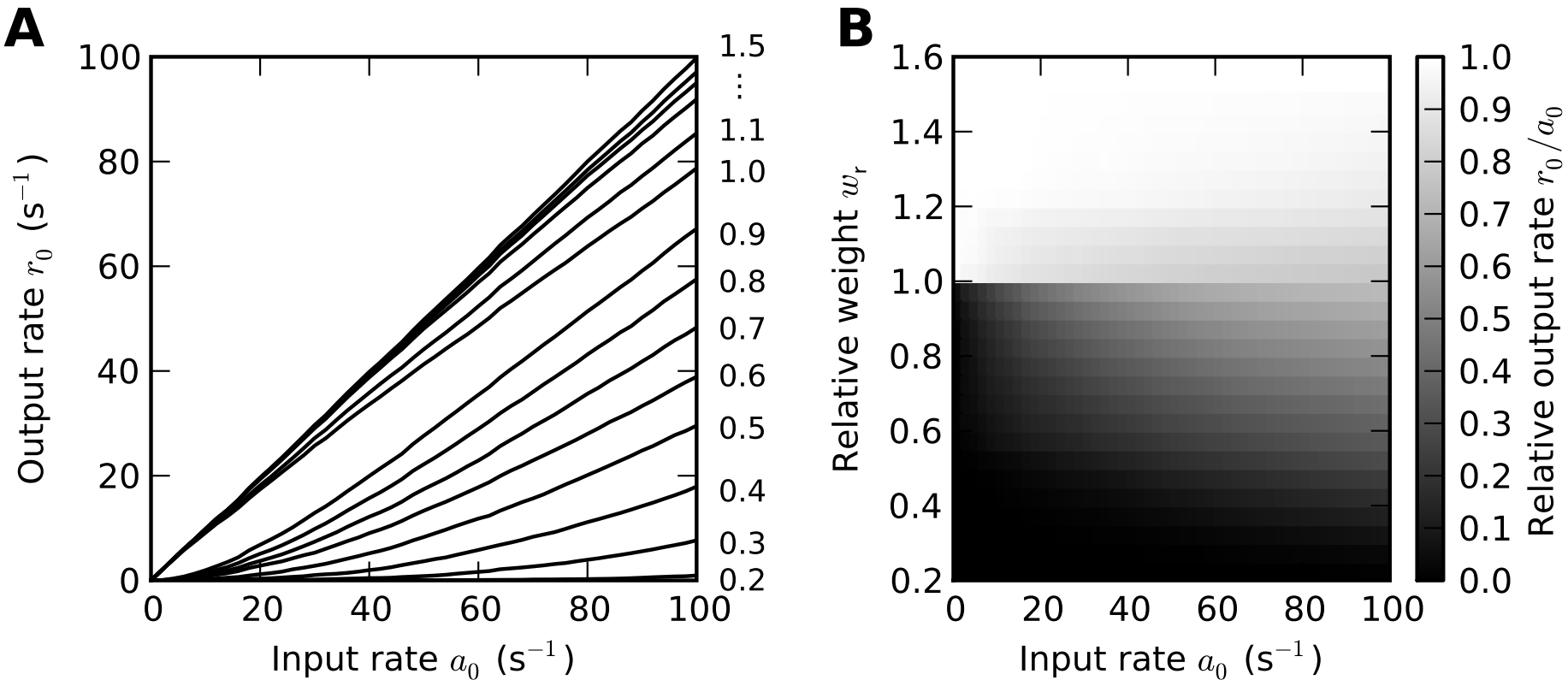
Model and setup

- neuron model: leaky integrate-and-fire
- synapse model: α-function shaped currents with amplitude w
- input: spike trains with sinusoidal firing rate $a(t) = a_0 + a_1 \sin(2\pi f t)$
- response rate fitted by $r(t) = r_0 + r_1 \sin(2\pi f t + \varphi)$

for wide range of
- input parameters: f, a_0, a_1
- neuron and synapse parameters: w, τ_s, τ_m



Stationary response (constant input)



- increase in stationary response rate r_0 with synaptic weight w
- transfer ratio $r_0/a_0 < 1$ even for strong weights

Nonstationary response (sinusoidal input)

- measured transfer function

$$H(f) = r_1(f)/a_1 \cdot e^{i\varphi(f)}$$

well fitted by a 1st-order low-pass filter

$$\tilde{H}(f) = \frac{\gamma}{1 + if/f_c}$$

with cutoff-frequency f_c and low-frequency gain γ

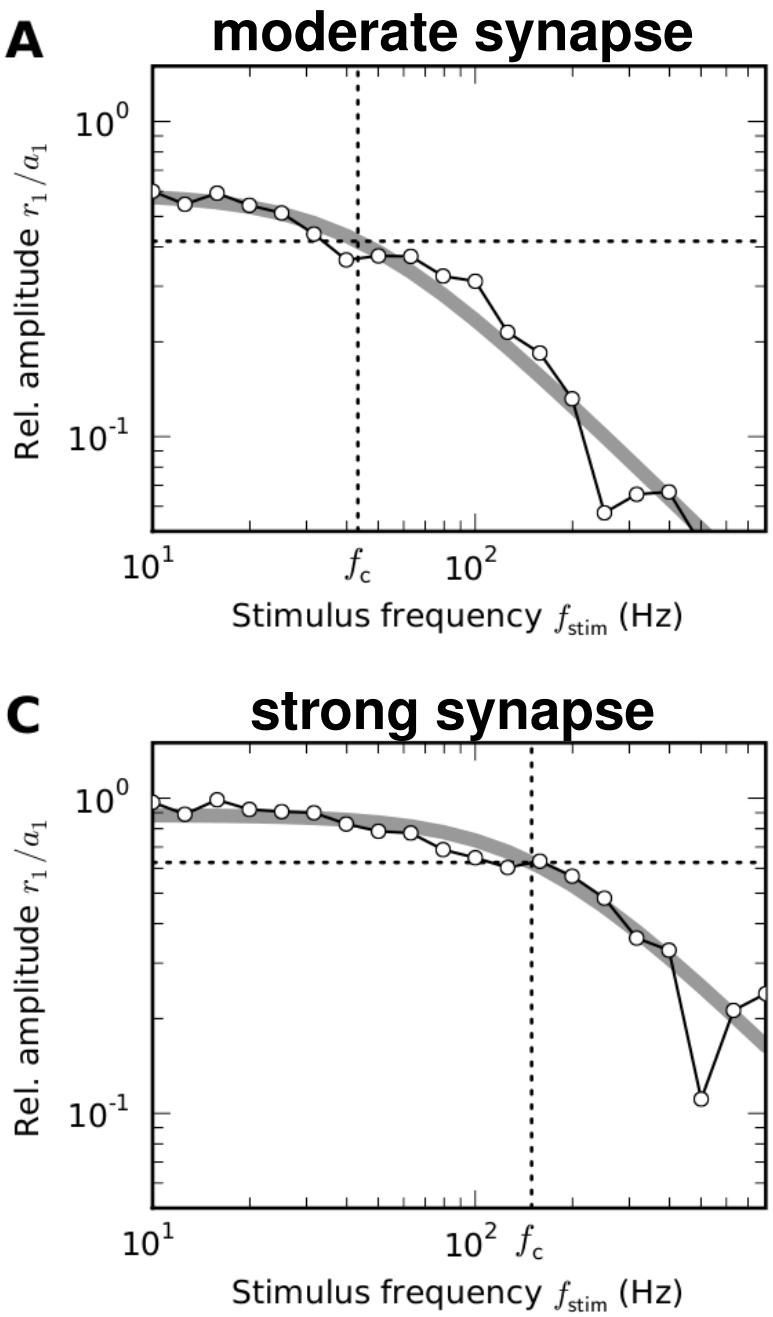
- exponential impulse response

$$h(t) = \gamma/\tau \begin{cases} e^{-t/\tau} & t \geq 0 \\ 0 & t < 0 \end{cases}$$

with time constant $\tau = 1/(2\pi f_c)$

- rate dynamics $r(t) = f((a * h)(t))$ equivalent to

$$\tau \dot{u} = -u(t) + \gamma a(t) \quad , \quad r(t) = f(u(t))$$



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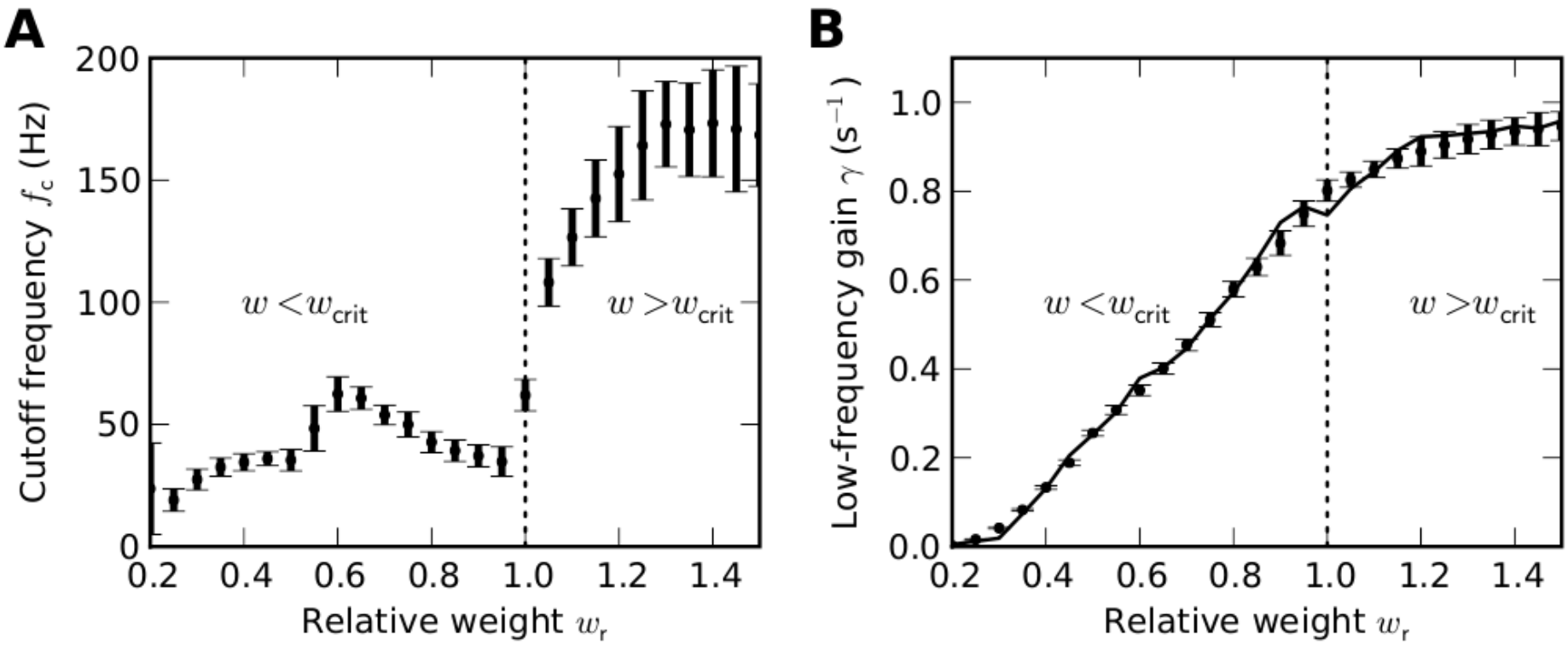
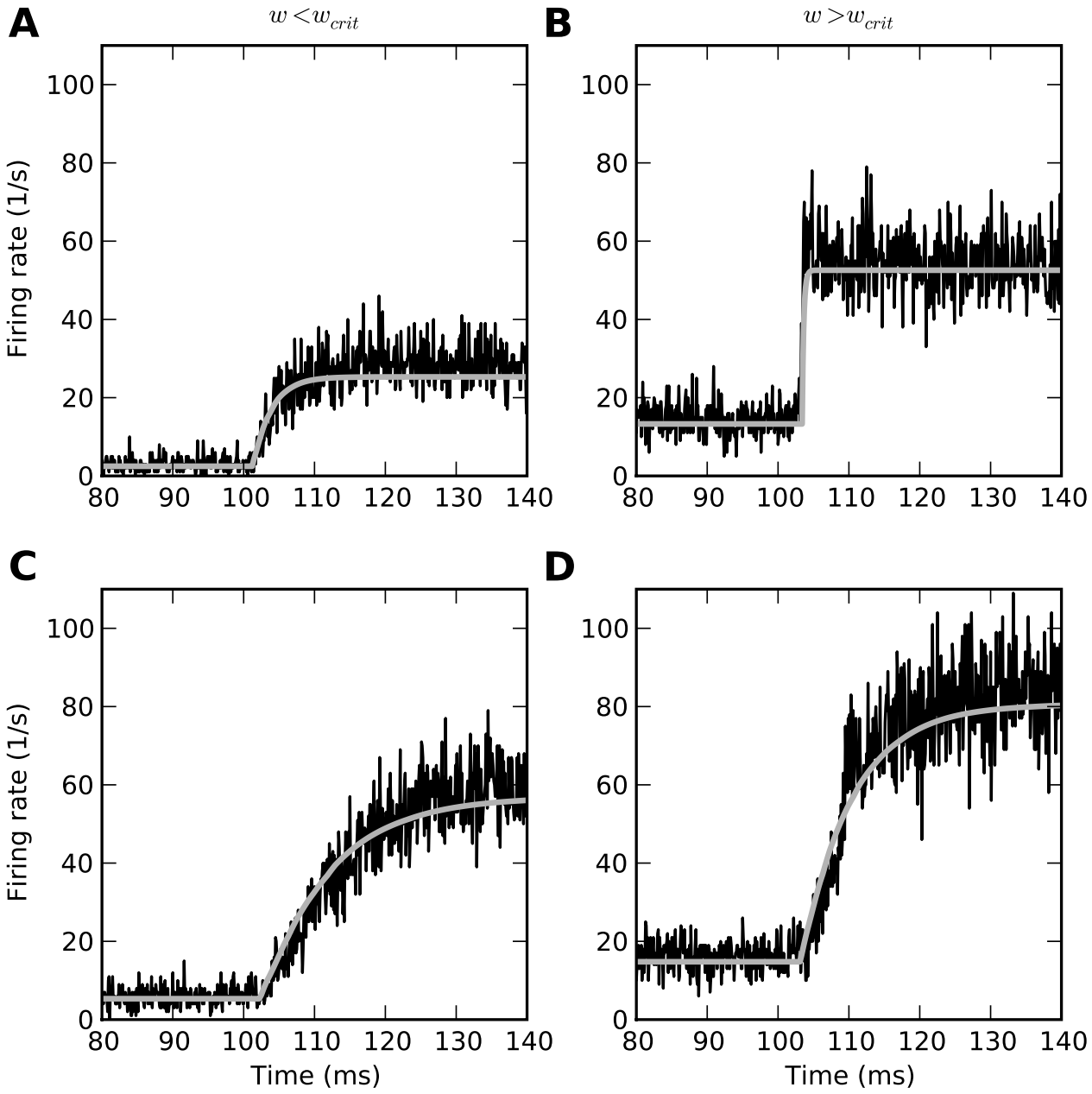


- cutoff frequency f_c
  - slightly increases with synaptic weight w for small to moderate weights
  - jumps to high values at critical weight w_{crit}
- low-frequency gain γ
  - increases with synaptic weight w
  - is fully explained by slope of activation function

Prediction for non-sinusoidal stimuli



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