Simplified neuron models I:

Integrate-and-fire models

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Outline

Reminder: Ionic currents, conductances, equivalent circuit

The leaky integrate-and-fire (LIF) neuron

Non-linear integrate-and-fire (NIF) models

Multi-timescale adaptive threshold (MAT) model

Literature

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Literature

Ionic currents and conductances

- ionic currents $I_x = I_x(V)$ are voltage (V) dependent
- currents vanish at equilibrium potentials E_x, i.e. $I_x(E_x) = 0 \Rightarrow$

$$I_x(V) = g_x \cdot (V - E_x) \qquad (x \in \{\mathrm{Na}^+, \mathrm{K}^+, \mathrm{Ca}^{2+}, \mathrm{Cl}^-\})$$

with *conductance* g_x and *driving force* $V - E_x$

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  with *conductance* g_x and *driving force* $V - E_x$
- $I_x(V) = g_x \cdot (V - E_x)$ is "Ohmic" if g_x is constant
- conductances $g_x = g_x(V, t)$ are typically *time and voltage dependent* (reflects dynamics of ion channel opening and closing or time dependence of neurotransmitter concentration, etc.), i.e.

$$I_x(V, t) = g_x(V, t) \cdot (V - E_x)$$

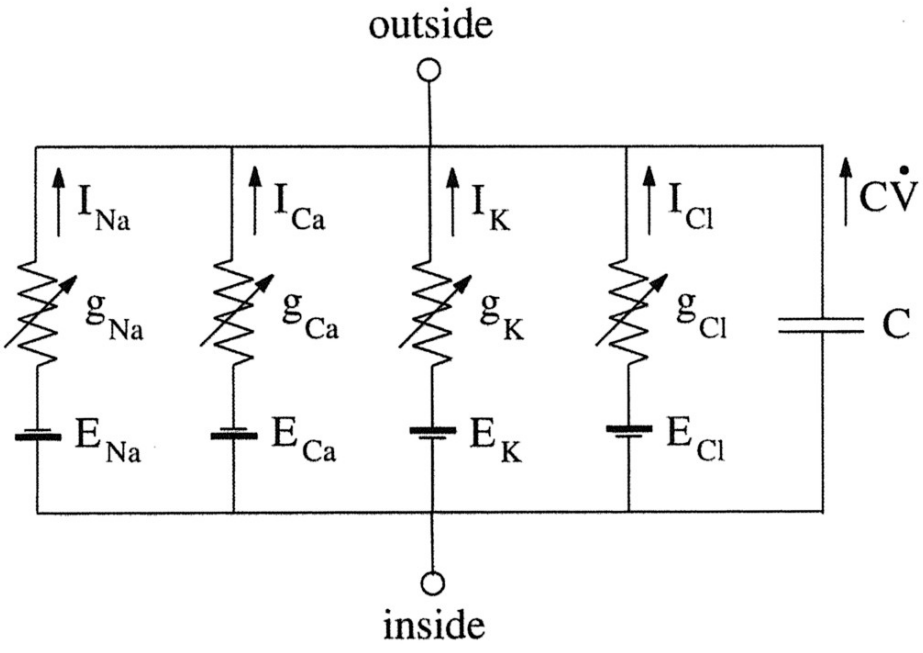
Equivalent circuit of a patch of membrane

- total *membrane current* I given by sum of ionic currents and capacitive current $I_C = C\dot{V}$ caused by the membrane capacitance

$$I = C\dot{V} + I_{\text{Na}^+} + I_{\text{Ca}^{2+}} + I_{\text{K}^+} + I_{\text{Cl}^-}$$

with *membrane capacity* C and $\dot{V} := \frac{\mathrm{d}V}{\mathrm{d}t}$

$$\left(C := \frac{Q}{V} \Rightarrow I_C := \dot{Q} = C\dot{V} \right)$$



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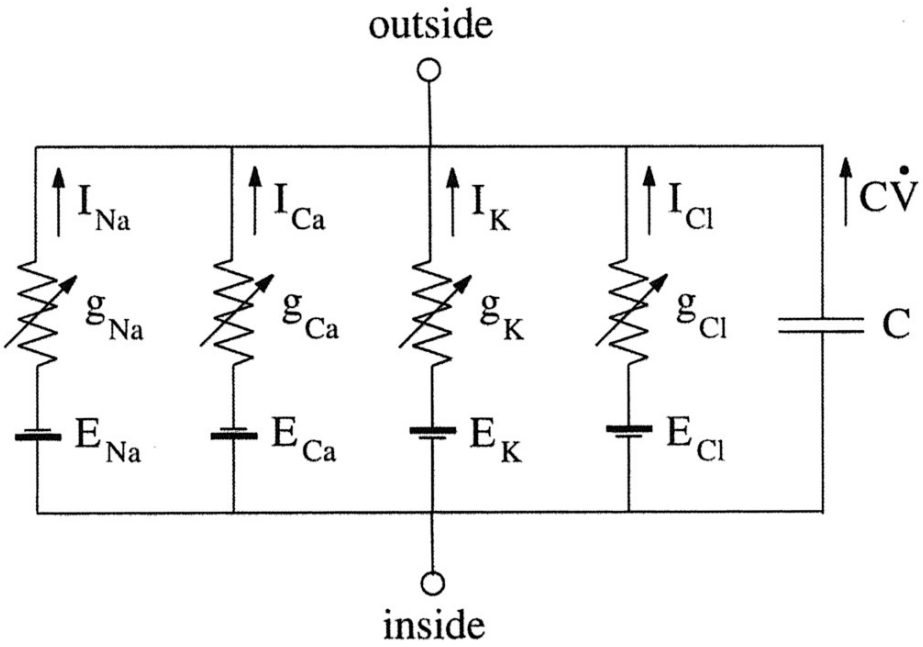

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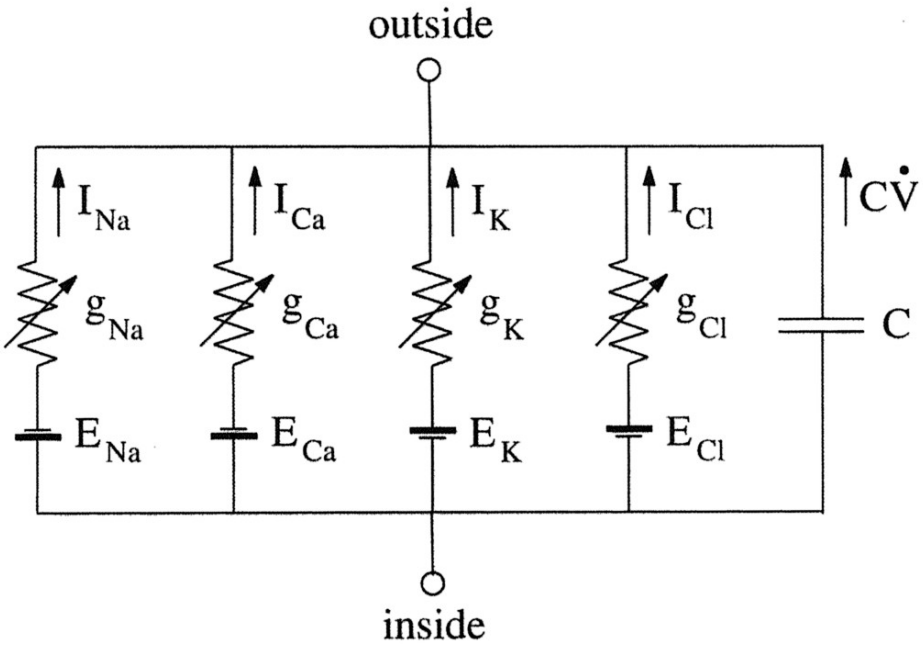

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- note: at rest and in the absence of further (e.g. injected) currents

$$E_{\text{K}^+} < E_{\text{Cl}^-} < V_{\text{rest}} < E_{\text{Na}^+} < E_{\text{Ca}^{2+}}$$

$\Rightarrow \quad I_{\text{Na}^+}, I_{\text{Ca}^{2+}} < 0$ (inward currents) $\quad , \quad I_{\text{K}^+}, I_{\text{Cl}^-} > 0$ (outward currents)

Resting potential and input resistance

- $C\dot{V} = I - g_{\mathrm{Na}^+}(V - E_{\mathrm{Na}^+}) - g_{\mathrm{Ca}^{2+}}(V - E_{\mathrm{Ca}^{2+}}) - g_{\mathrm{K}^+}(V - E_{\mathrm{K}^+}) - g_{\mathrm{Cl}^-}(V - E_{\mathrm{Cl}^-})$

  resting potential V_{rest} determined by stationary state, i.e. $\dot{V} = 0$, for $I = 0$

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with *total input conductance* $g_{\text{inp}} := g_{\text{Na}^+} + g_{\text{Ca}^{2+}} + g_{\text{K}^+} + g_{\text{Cl}^-}$

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  $$V \to V_{\text{rest}} + R_{\text{inp}} \cdot I$$

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- reminder: g_{inp}, R_{inp} and τ_{m} are in general time and voltage dependent

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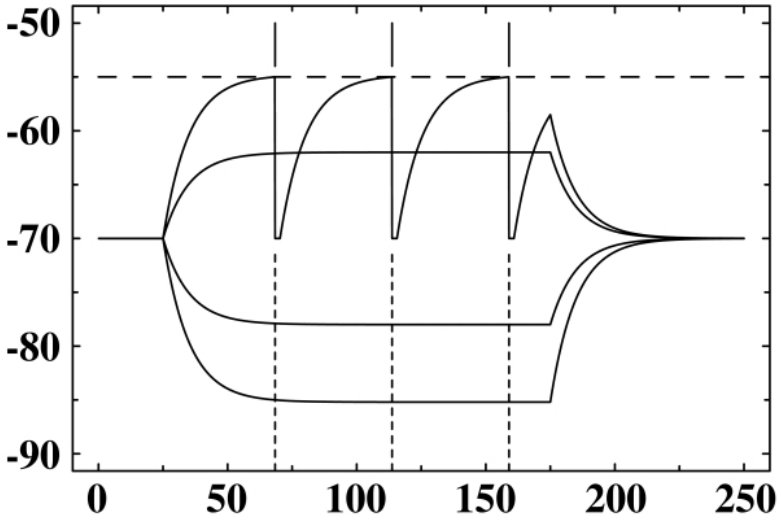

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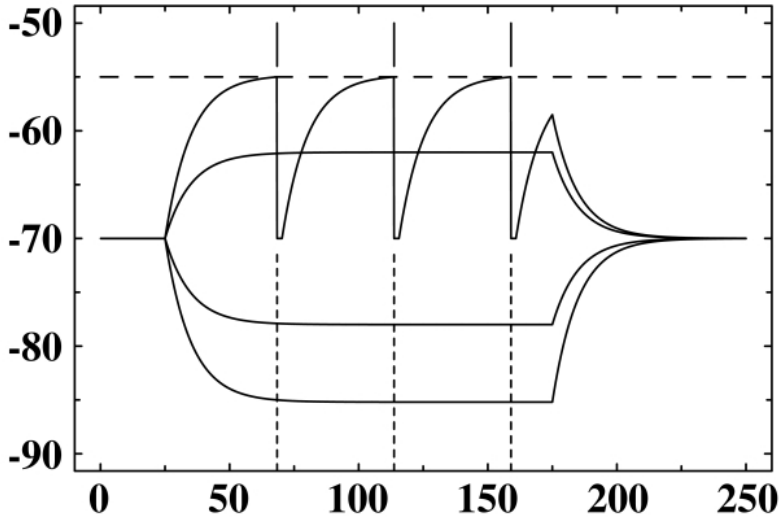

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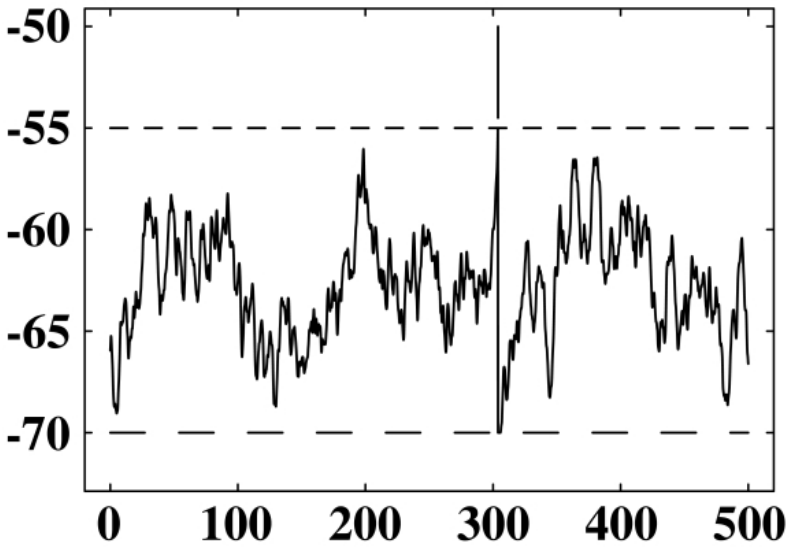

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  with $V(0) = V_{\mathrm{rest}} + V_0$
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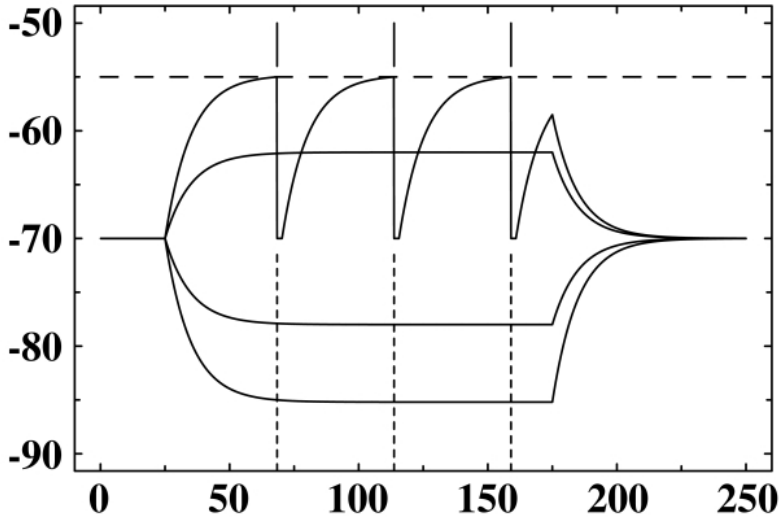

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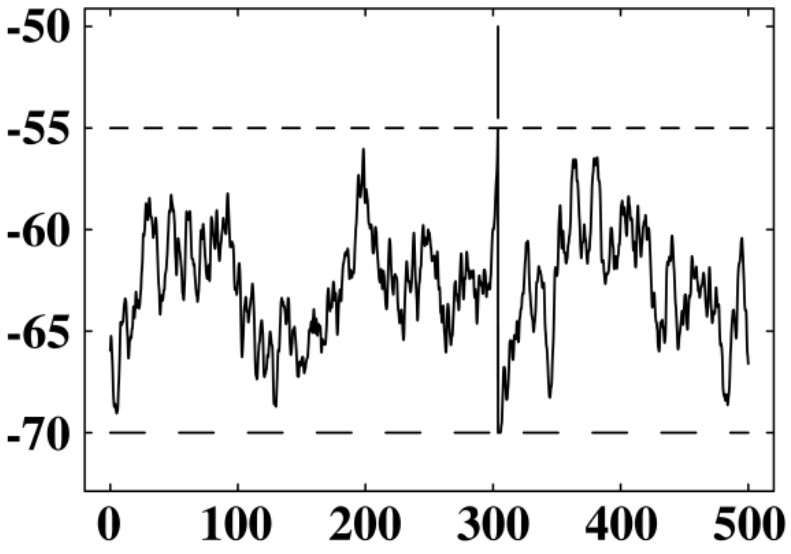

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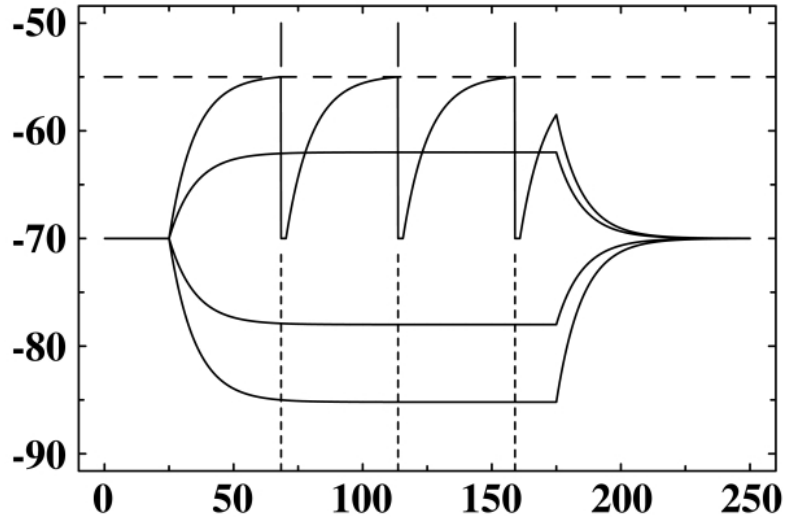

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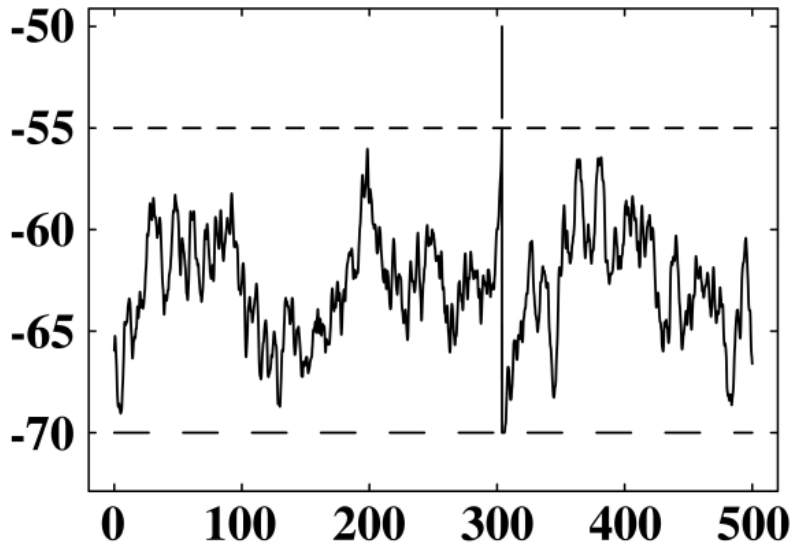

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- *refractoriness* often modelled by $V(t) = V_{\mathrm{reset}}$ for all $t \in (t_s, t_s + \tau_{\mathrm{ref}}]$
- note: – model is one-dimensional
  – subthreshold dynamics is linear, i.e. $V(t) = V_{\mathrm{rest}} + (I * h)(t)$

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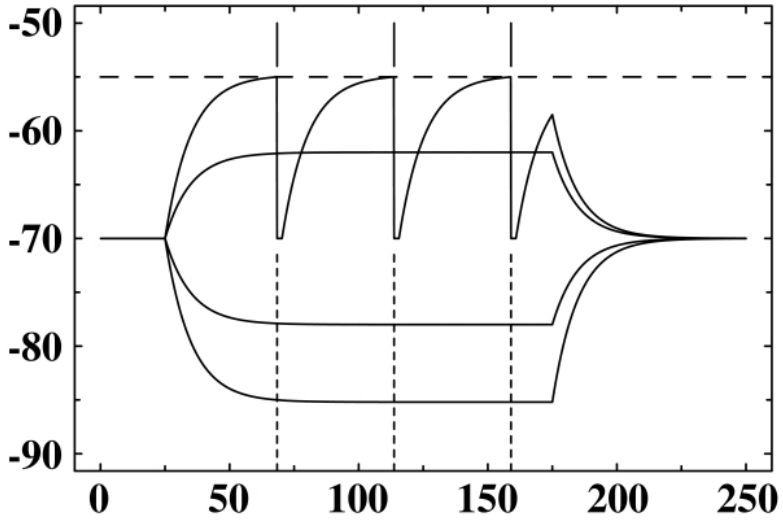

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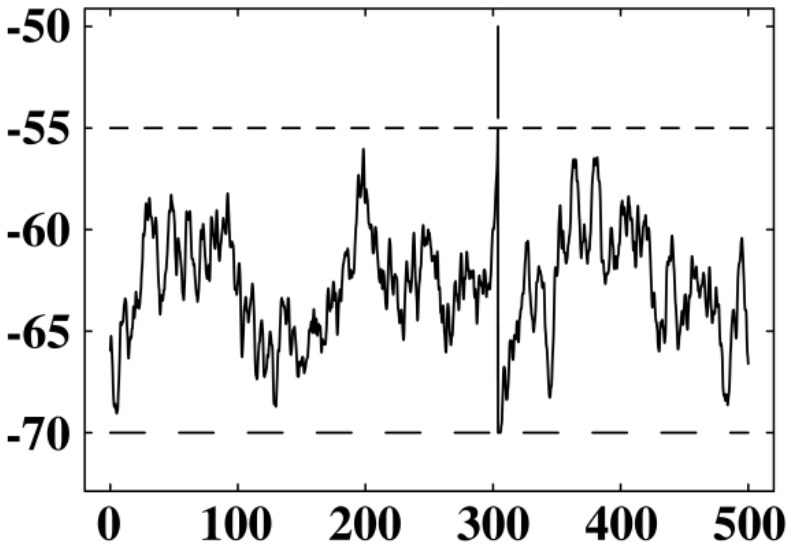

Dynamics of the LIF neuron

- rescaling of $\tau_{\mathsf{m}}\dot{V} = -(V - V_{\mathsf{rest}}) + R_{\mathsf{inp}} \cdot I$

$$v := \frac{V - V_{\mathsf{rest}}}{\vartheta - V_{\mathsf{rest}}} \quad , \quad i := \frac{R_{\mathsf{inp}} I}{\vartheta - V_{\mathsf{rest}}} \quad , \quad t' := t/\tau_{\mathsf{m}}$$

$$\Rightarrow \quad \boxed{\dot{v} = -v + i}$$

with $\dot{v} := \mathrm{d}v/\mathrm{d}t'$, $v := v(t')$
threshold at $v = 1$,
reset potential $v_{\mathsf{reset}} = (V_{\mathsf{reset}} - V_{\mathsf{rest}})/(\vartheta - V_{\mathsf{rest}})$,
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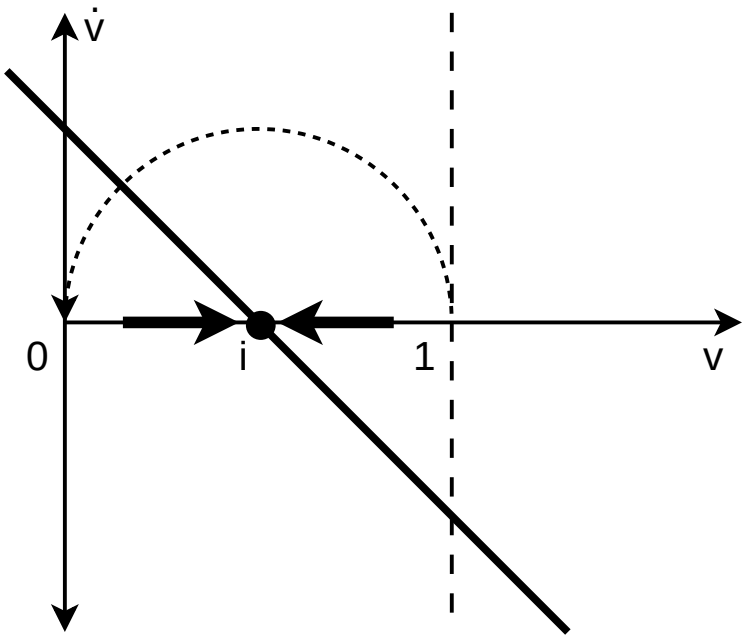
"instability" at threshold $v = 1$



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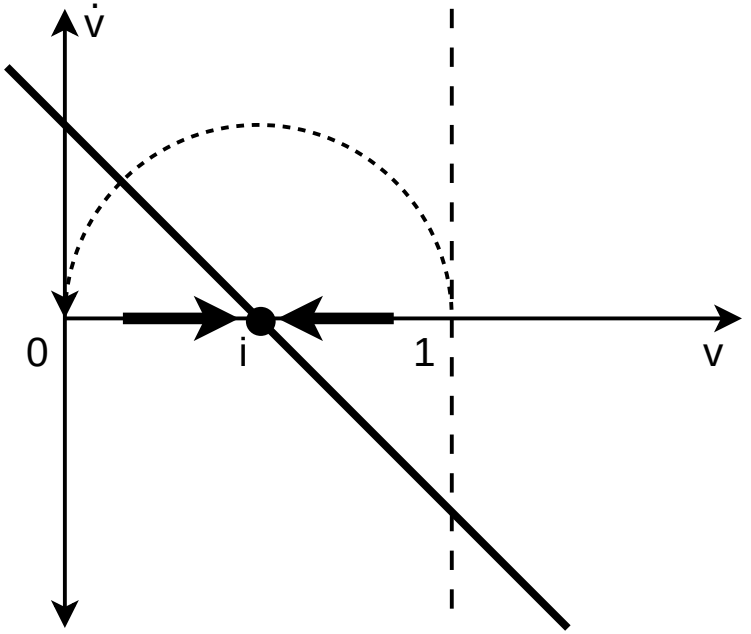

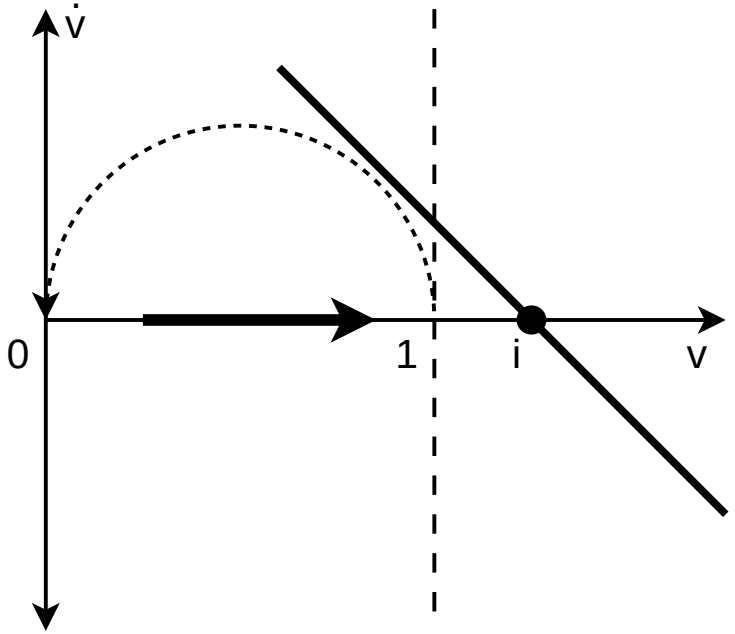

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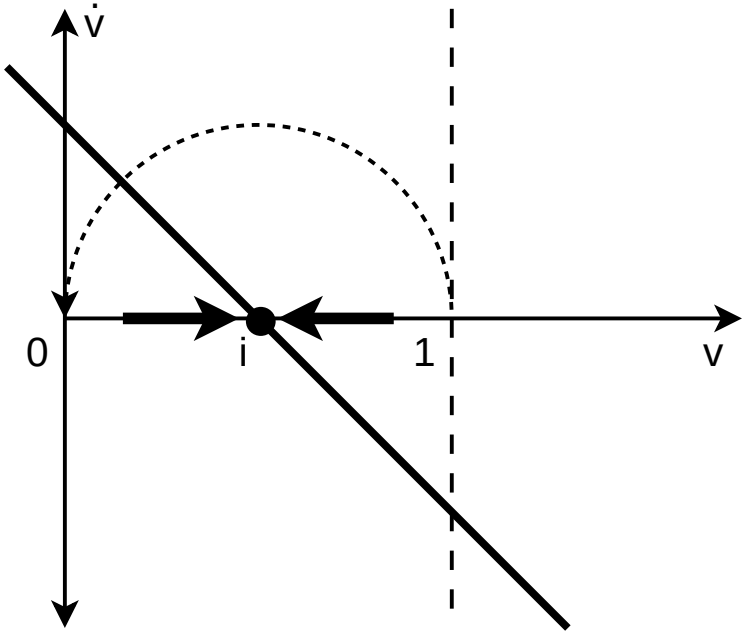
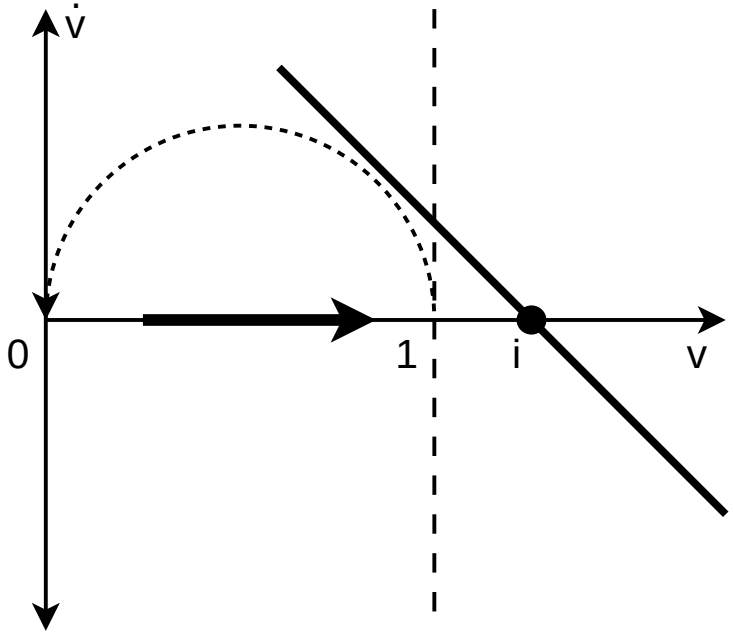
with $\dot{v} := \mathrm{d}v/\mathrm{d}t'$, $v := v(t')$
threshold at $v = 1$,
reset potential $v_\mathrm{reset} = (V_\mathrm{reset} - V_\mathrm{rest})/(\vartheta - V_\mathrm{rest})$,
refractory period $\tau_\mathrm{ref} = \tau_\mathrm{ref}/\tau_\mathrm{m}$

- stable fixed point at $v = i$,
  "instability" at threshold $v = 1$
- sharp voltage threshold doesn't exist in real neurons

  non-continous dynamics at threshold
  (infinitely "fast" action potential onset)





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The leaky integrate-and-fire (LIF) neuron

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Non-linear integrate-and-fire (NIF) models

- extensions of the LIF model to account for the instability generating action potentials

$$\boxed{\dot{v} = -v + \psi(v) + i}$$

e.g.

$\dot{v} = a \cdot (v - b)^2 + i$ (quadratic IF neuron, QIF)
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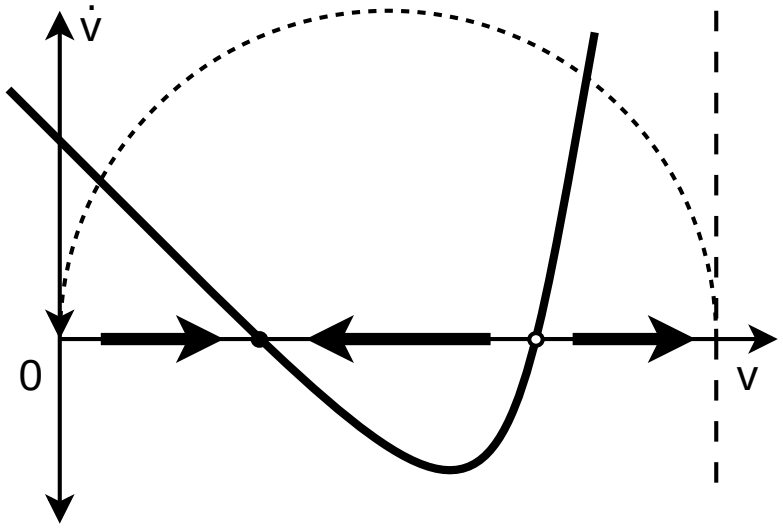

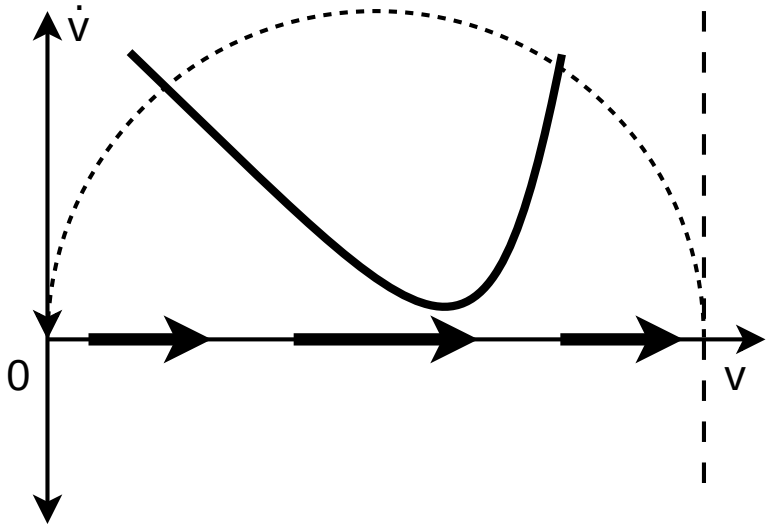

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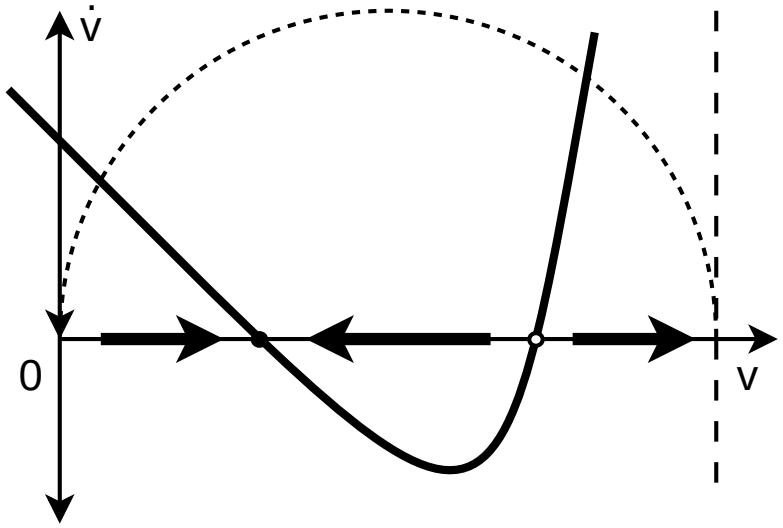

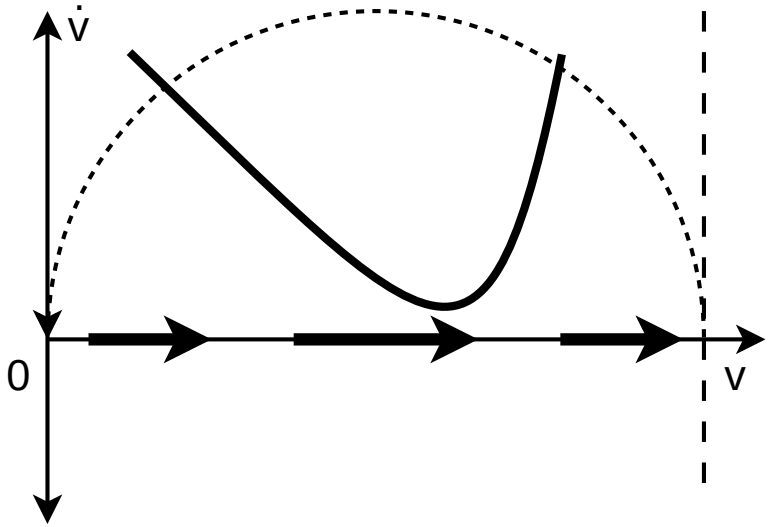

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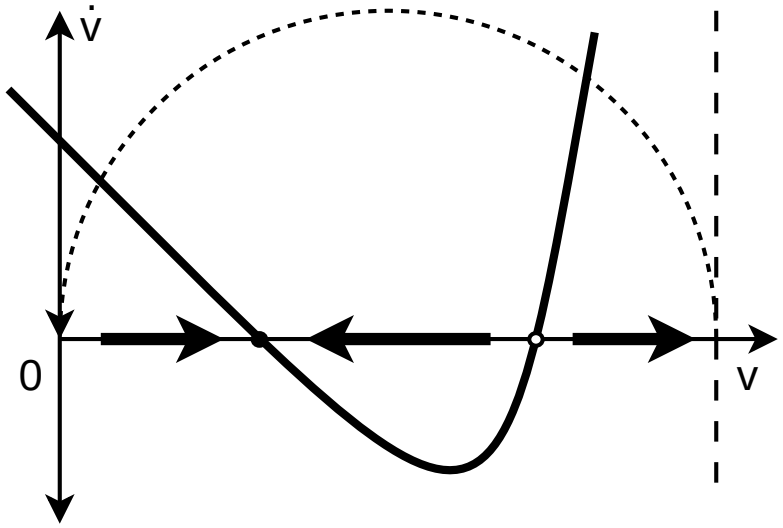

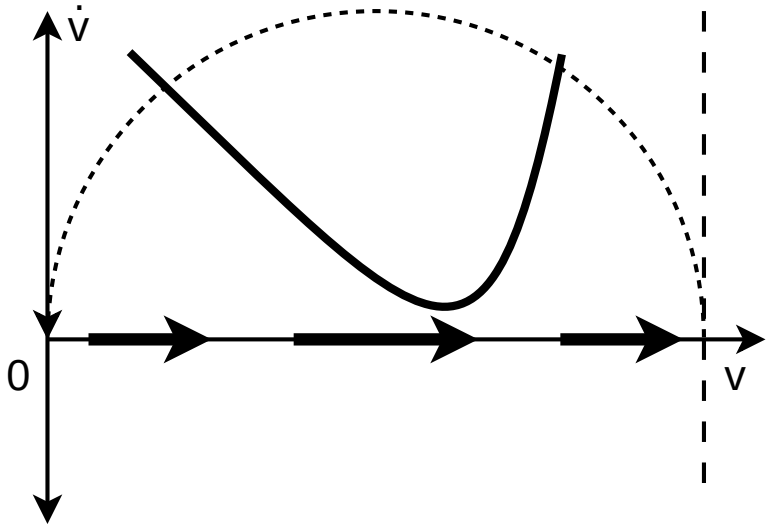

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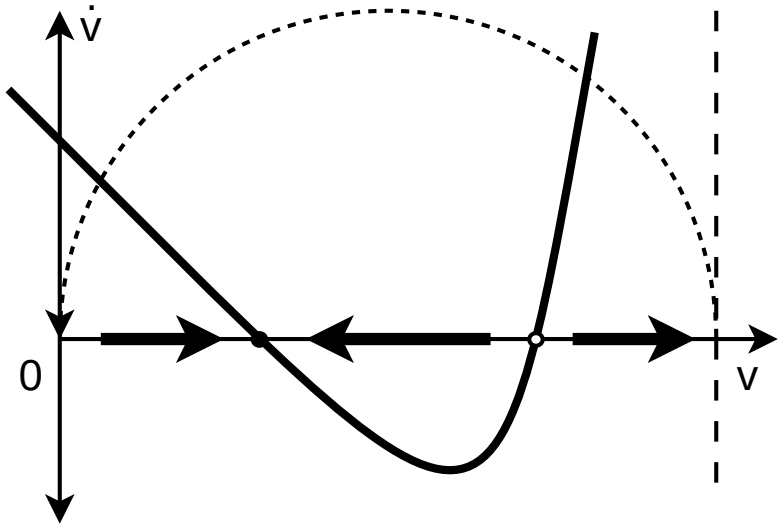
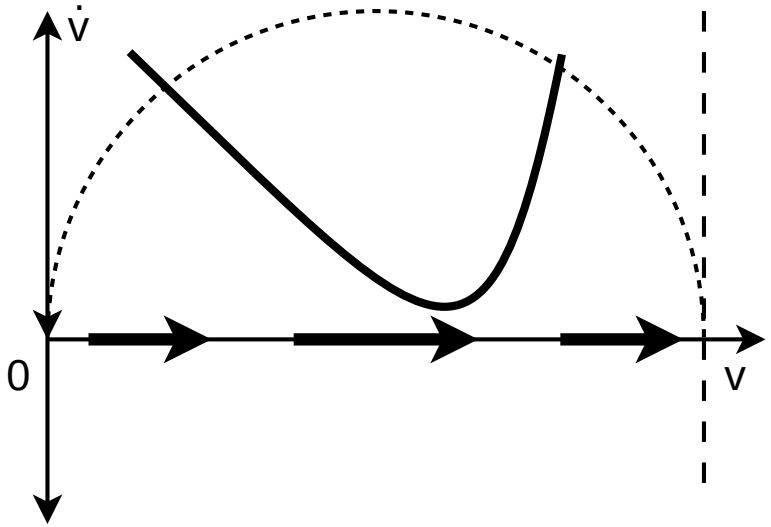
- note: QIF model constitutes *normal form* of EIF model (*topological equivalence*)





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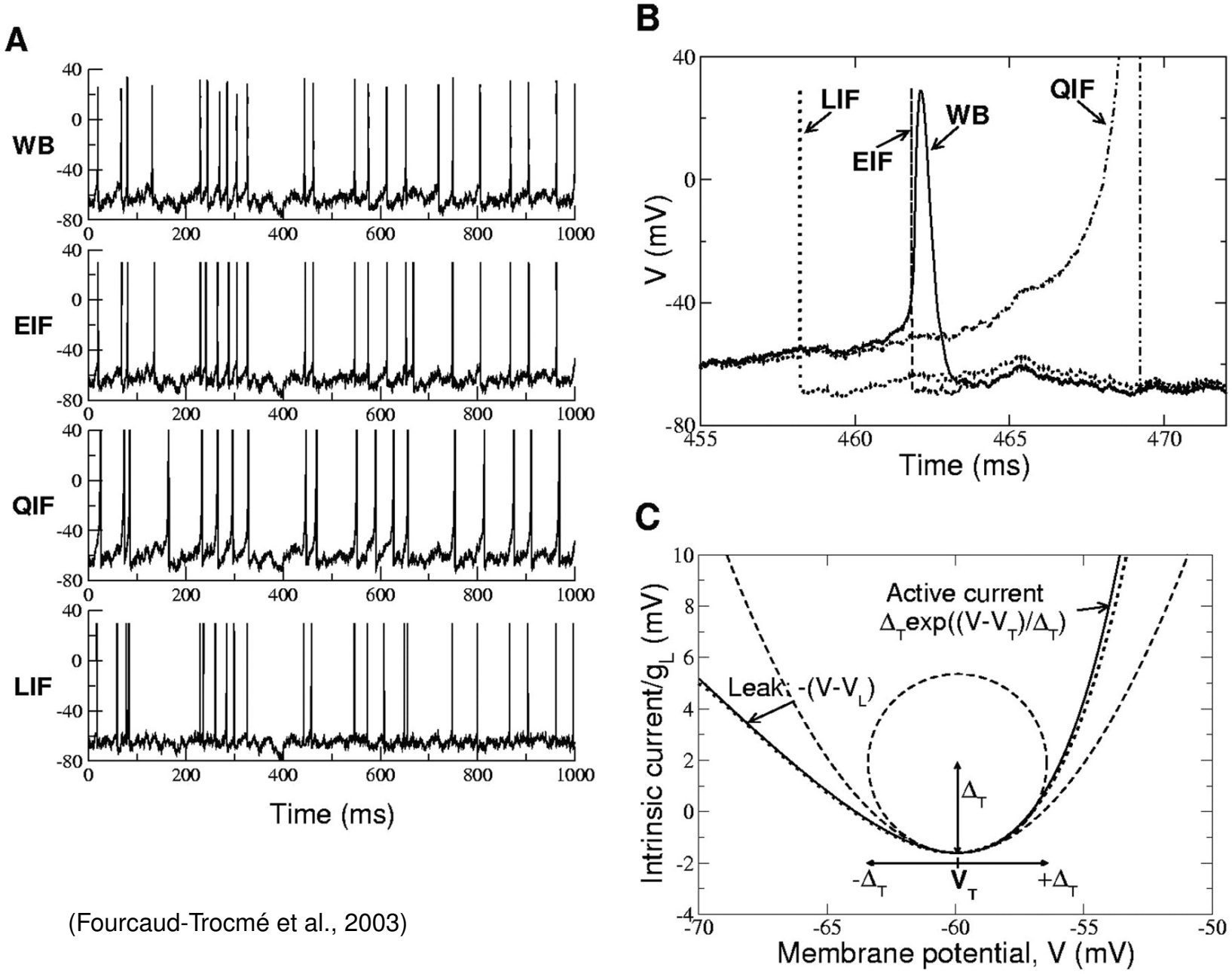


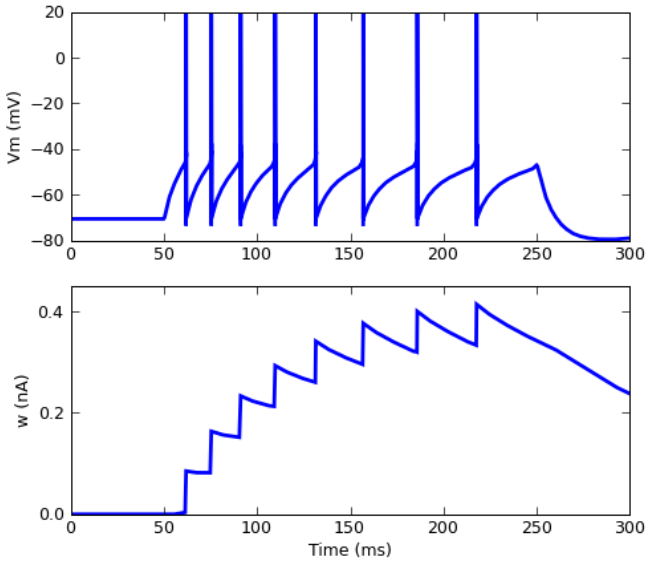
(Fourcaud-Trocmé et al., 2003)

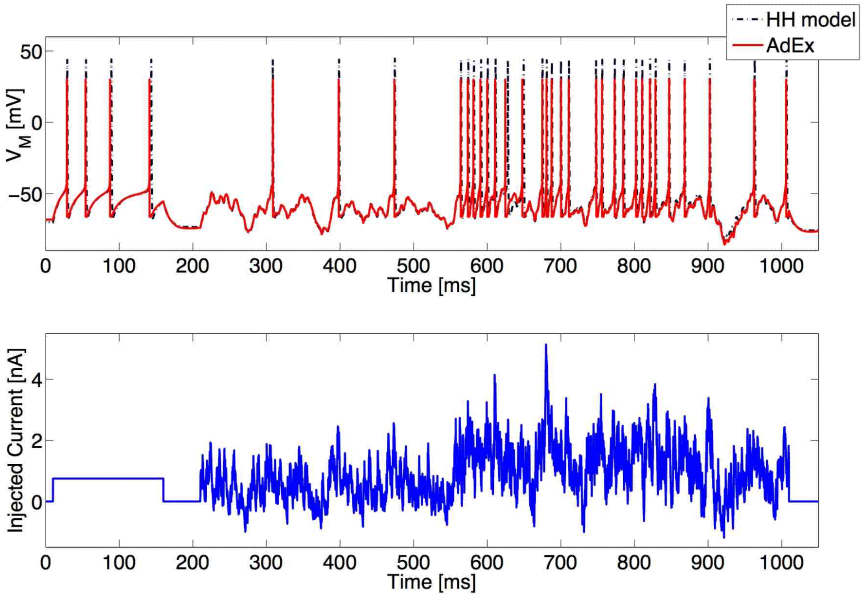
Adaptive exponential integrate-and-fire model

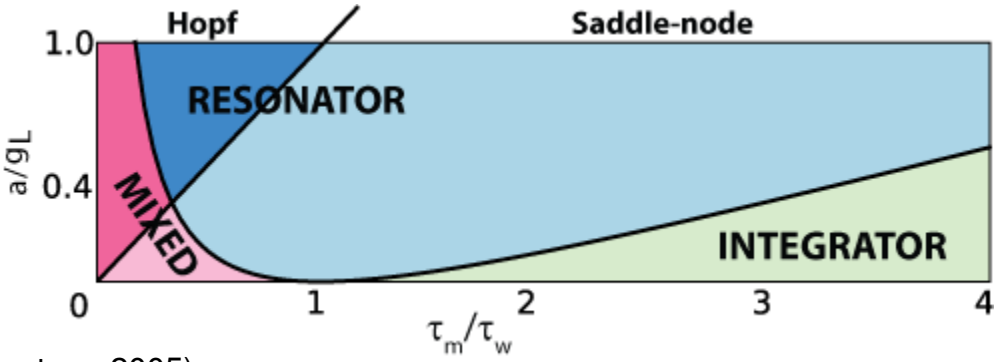
$$C\frac{dV}{dt} = -g_L(V - E_L) + g_L \Delta_T \exp\left(\frac{V - V_T}{\Delta_T}\right) - w + I$$

$$\tau_w \frac{dw}{dt} = a(V - E_L) - w$$

at spike: $V \to V_r$, adaptation variable $w \to w + b$







(Brette and Gerstner, 2005)

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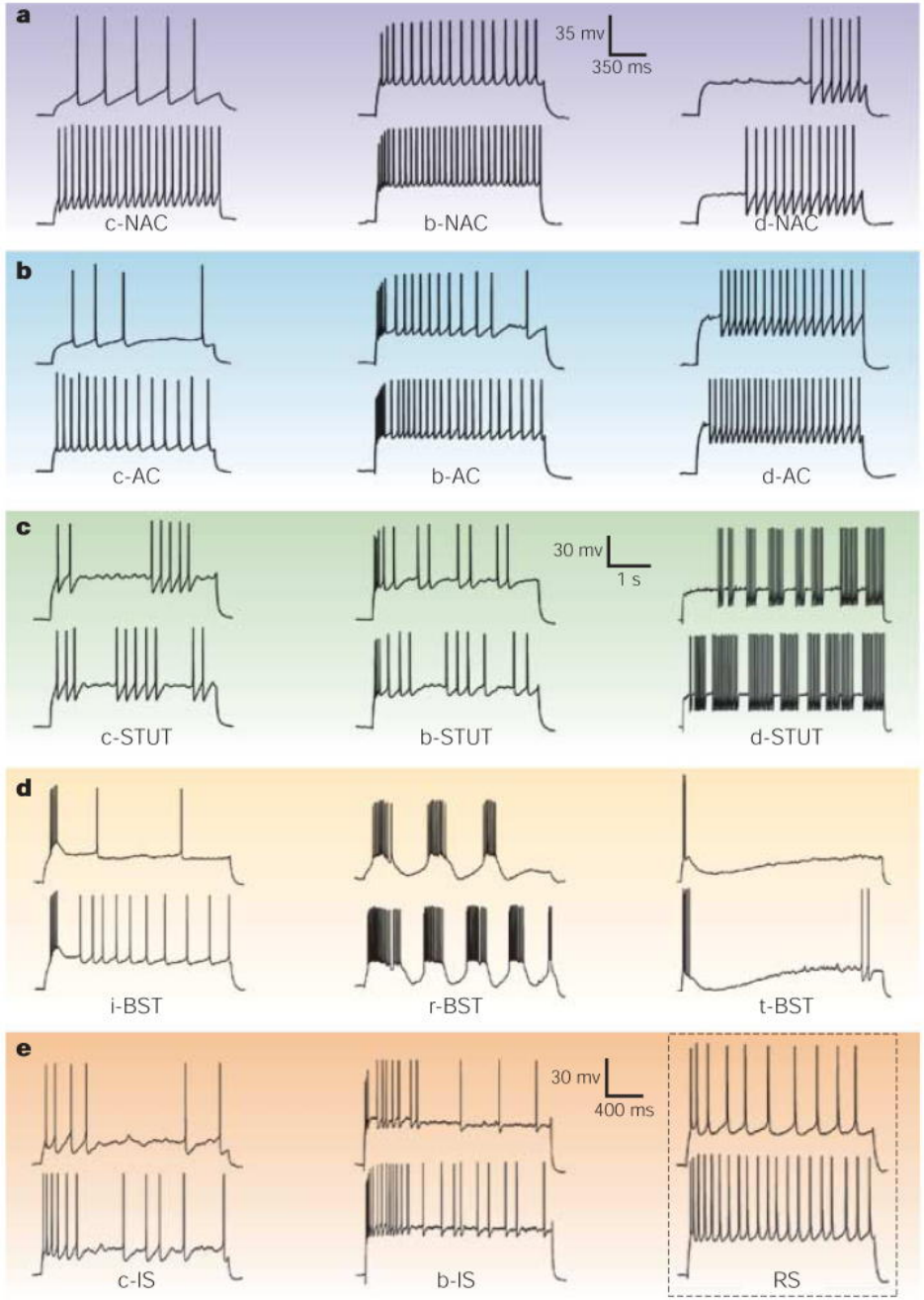
- simple LIF and NIF cannot reproduce response diversity observed in experiments

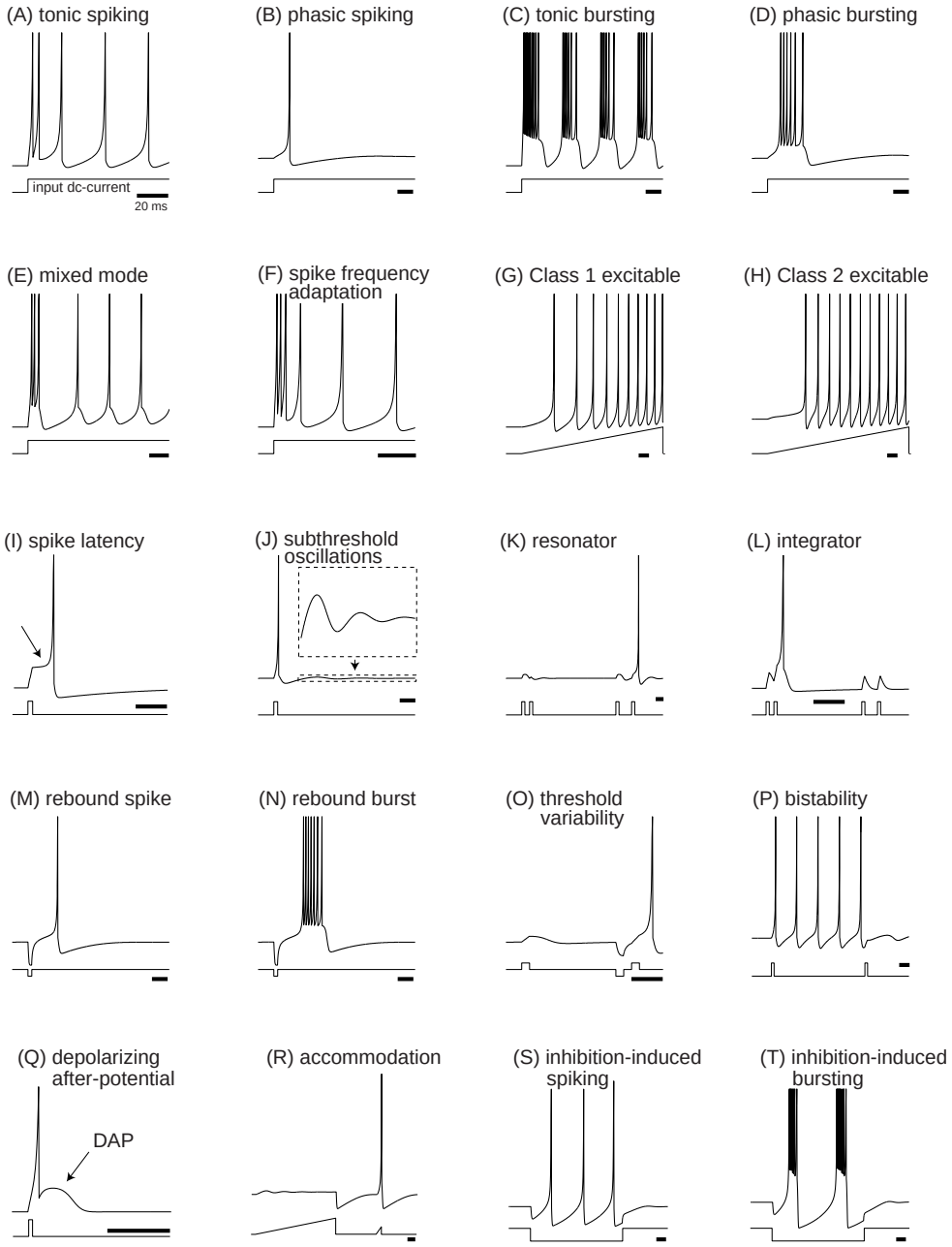


Markram et al. (2004)

Multi-timescale adaptive threshold (MAT) model

- simple LIF and NIF cannot reproduce response diversity observed in experiments
- in contrast to Izhikevich model (Izhikevich, 2007):

  characterisation of 20 different firing modes



Izhikevich (2007)

Multi-timescale adaptive threshold (MAT) model

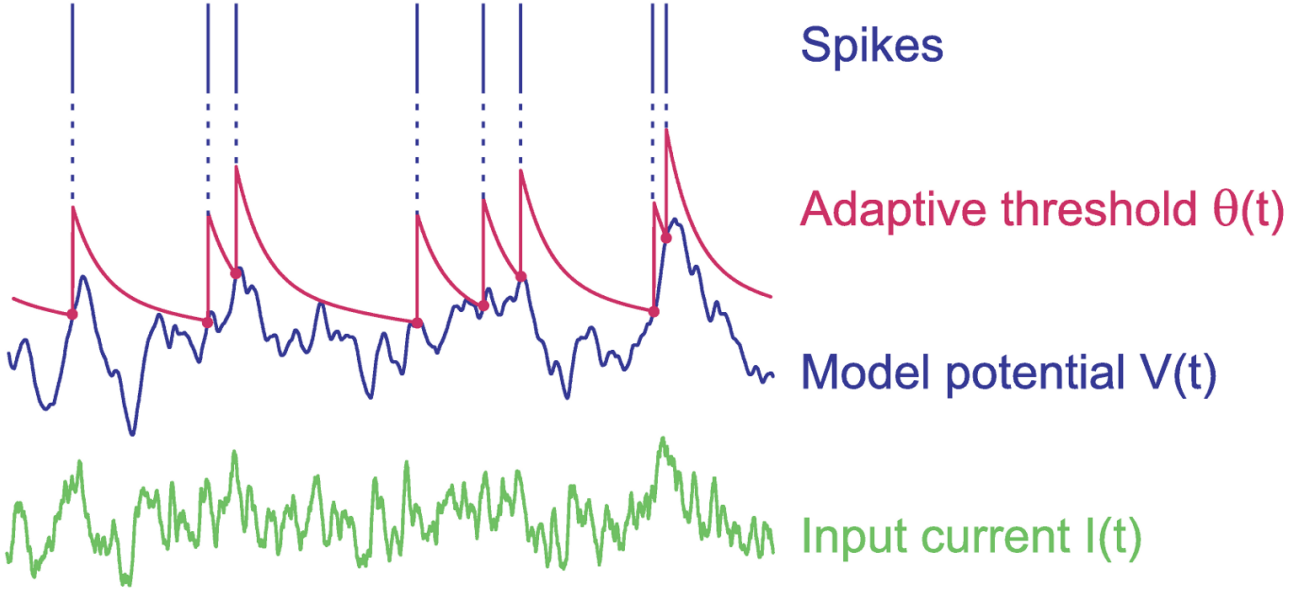
MAT model (Kobayashi et al., 2009):

- subthreshold voltage dynamics as in LIF: $\dot{v} = -v + i$
- spike emission at time t_k if $v(t_k) \geq \vartheta(t_k)$ with *dynamic* threshold

$$\vartheta(t) = \sum_k H(t - t_k) + \omega \quad \text{with} \quad H(t) = \begin{cases} \alpha_1 e^{-t/\tau_1} + \alpha_2 e^{-t/\tau_2} & \text{if } t \geq 0 \\ 0 & \text{if } t < 0 \end{cases}$$

$\tau_{1/2}$ = threshold time constant, $\alpha_{1/2}$ = weights, ω = resting threshold value

- *no* voltage reset after spiking
- refractoriness: no firing in time interval $[t_k, t_k + \tau_{\text{ref}}]$



Yamauchi et al. (2011)

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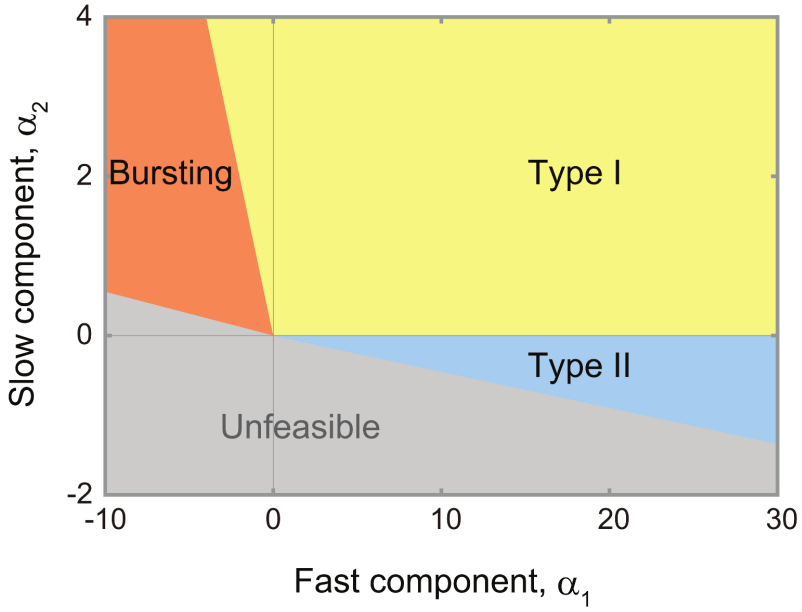
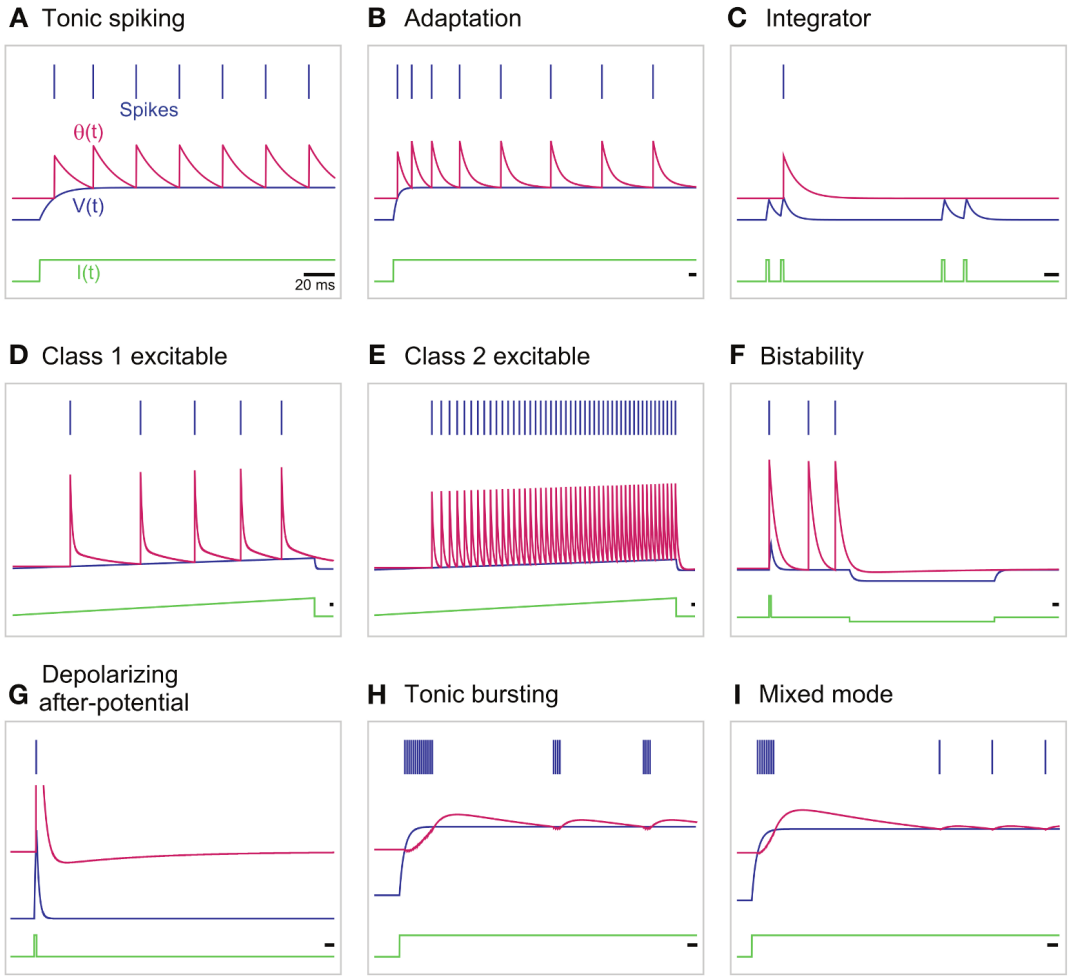
- MAT model by Kobayashi et al. can reproduce 9 out of the 20 firing modes characterised by Izhikevich, incl. type I, type II and bursting behaviour





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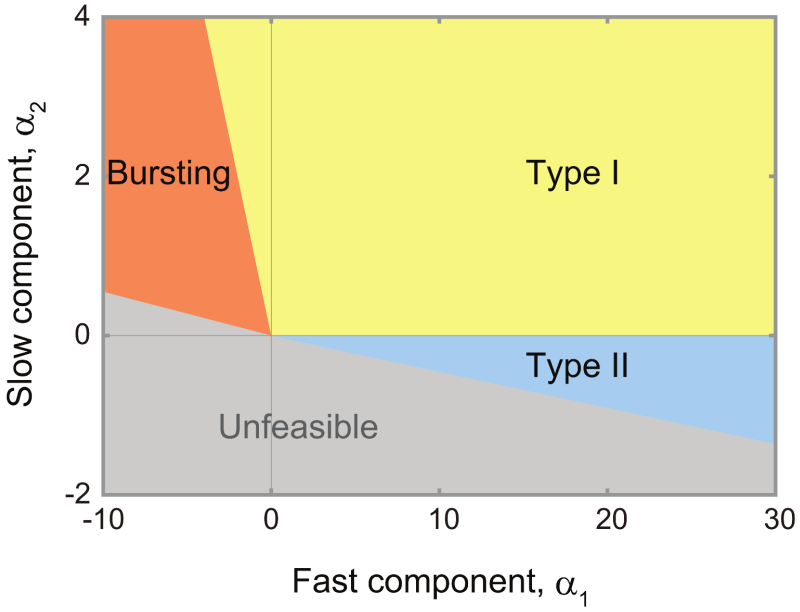
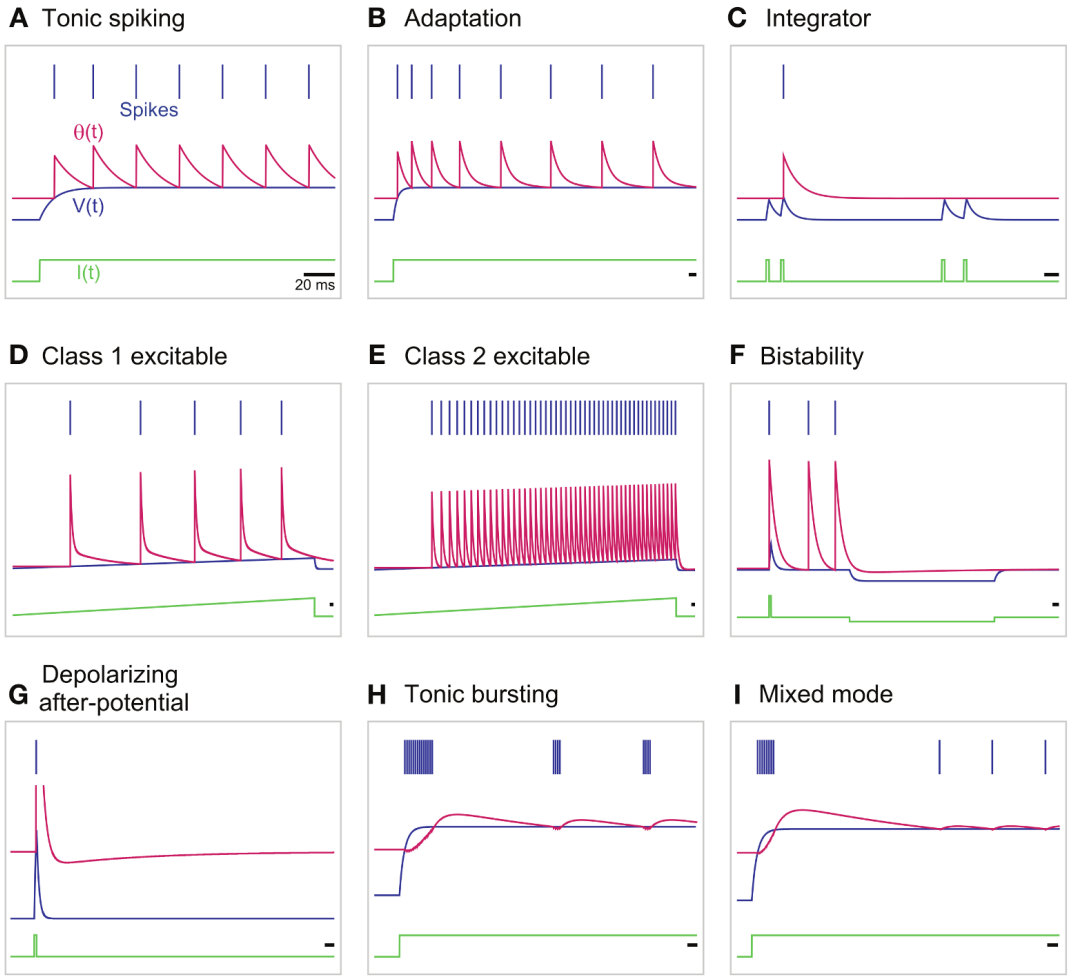
- but not: resonating behaviour, phasic spiking or bursting, spiking and bursting in response to inhibitory input





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Multi-timescale adaptive threshold (MAT) model

Yamauchi et al. (2011):

- augmentation of original MAT model with voltage dependency

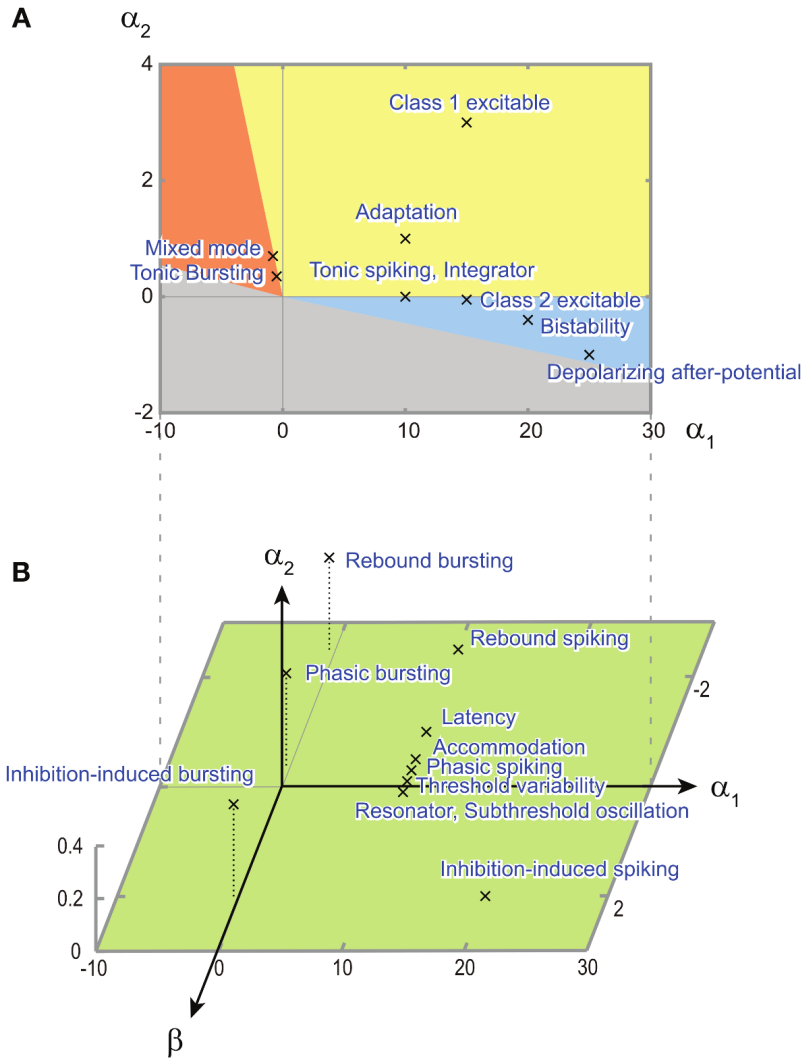
$$\vartheta(t) = \sum_k H(t - t_k) + \beta \int K(s) \frac{dv}{dt}(t - s) ds + \omega$$

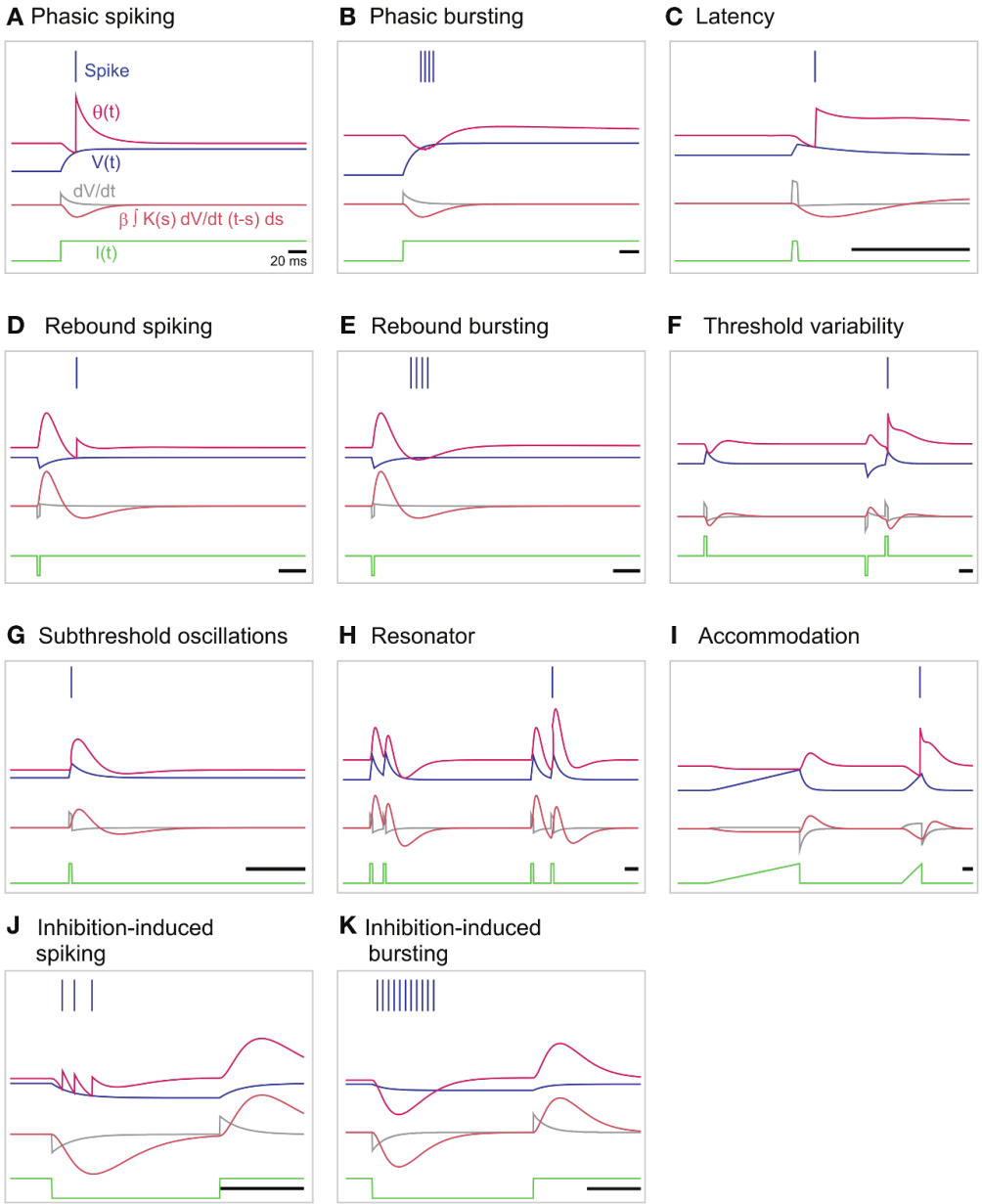
  $\beta =$strength of voltage dependence,
  $K(s) = s \exp(-s/\tau_v)$ alpha-function kernel with time constant τ_v

- note: dependence of threshold on voltage derivative dv/dt is experimentally observed (Azouz & Gray, 2000)

Multi-timescale adaptive threshold (MAT) model

- MAT model with voltage dependent threshold can reproduce all 20 firing patterns (Izhikevich) by variation of only 3 parameters





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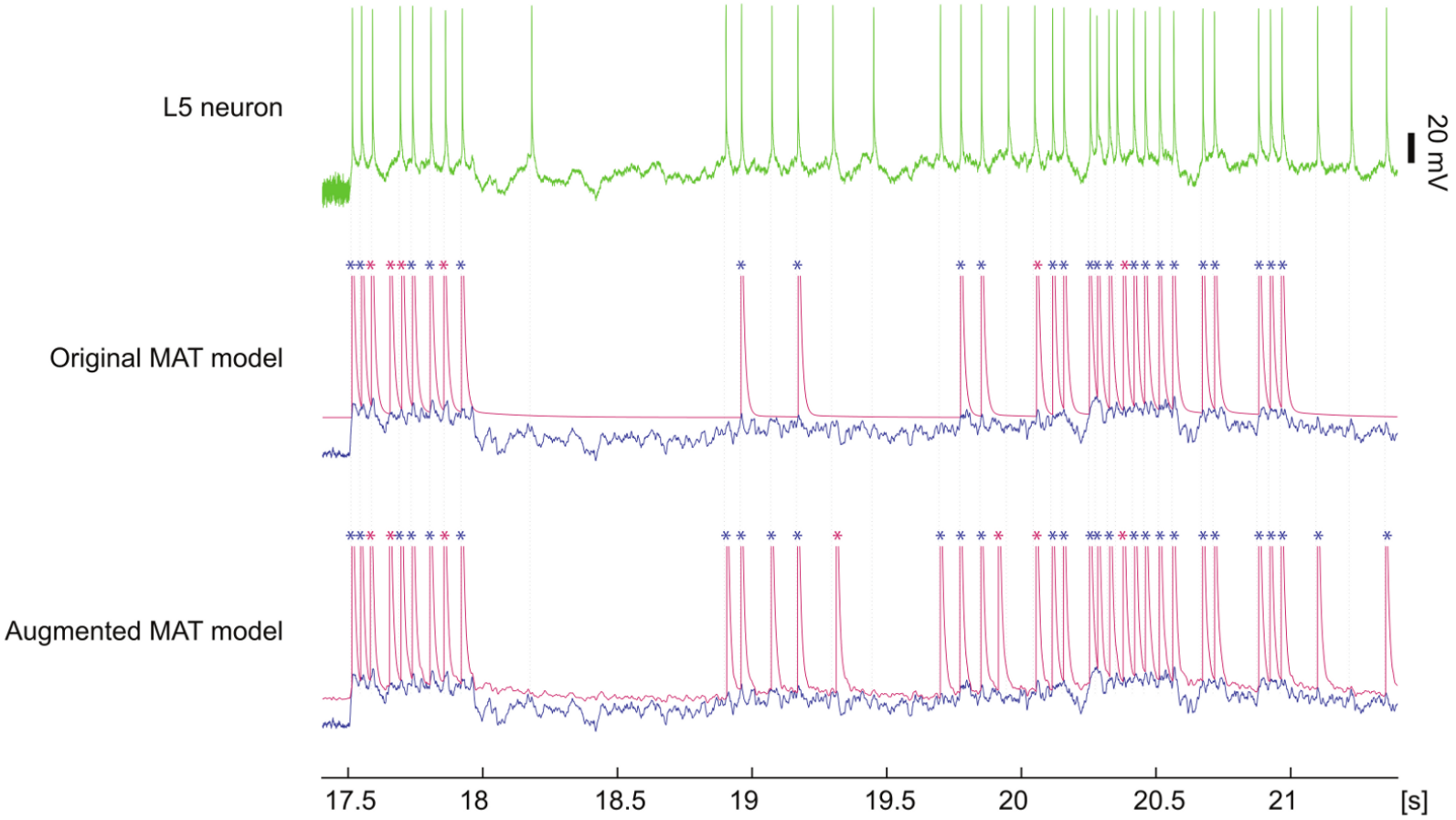

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- Kobayashi model won the *International Competition on Quantitative Single-Neuron Modeling* organised by the INCF (International Neuroinformatics Coordinating Facility) (see Gerstner & Naud, 2009)

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