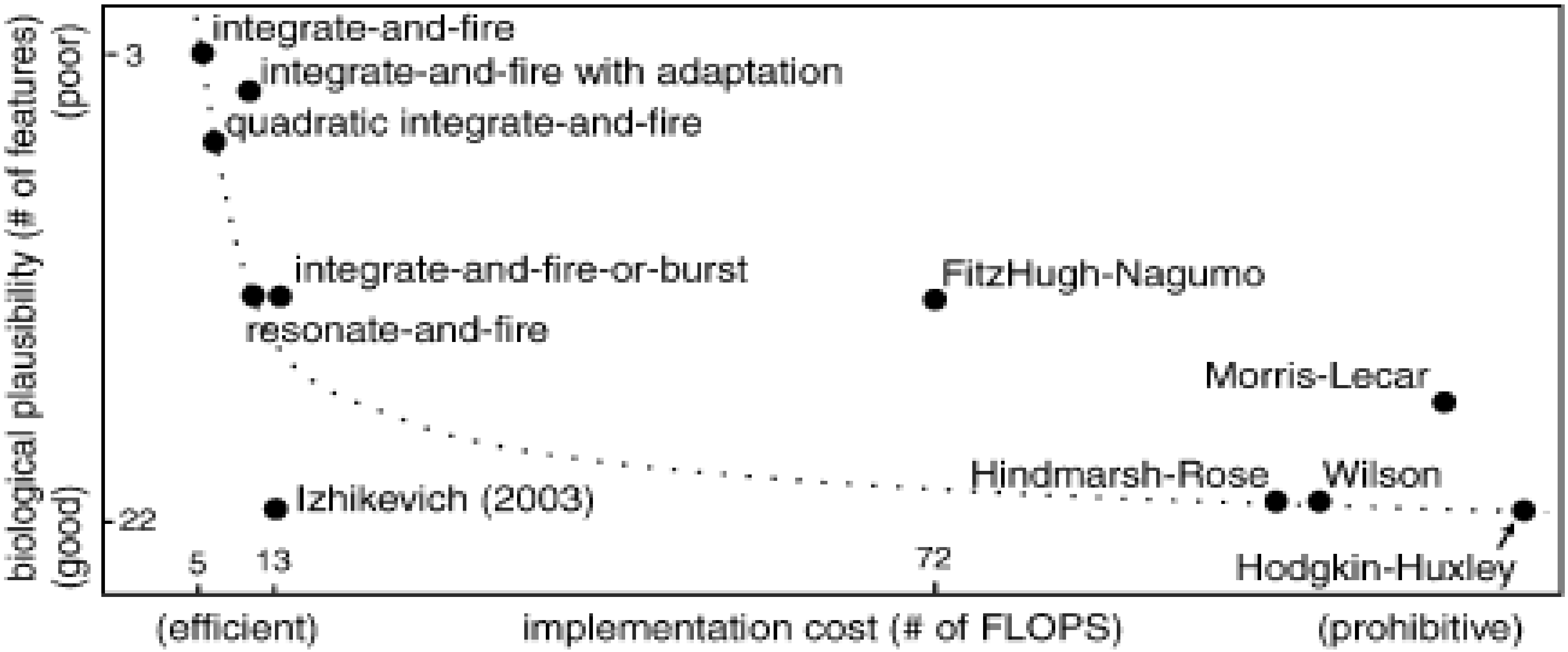
A Generalized Linear Integrate-And-Fire Neural Model Produces Diverse Spiking Behaviors

Stefan Mihalas
Ernst Niebur

Krieger Mind/Brain Institute and
Department of Neuroscience
Johns Hopkins University

The world according to Izkhikevich (2004)



(Izhikevich 2004)

How the model ranking was obtained

Models	biophysically meaningful	tonic spiking	phasic spiking	tonic bursting	phasic bursting	mixed mode	spike frequency adaptation	class 1 excitable	class 2 excitable	spike latency	subthreshold oscillations	resonator	integrator	rebound spike	rebound burst	threshold variability	bistability	DAP	accommodation	inhibition-indiced spiking	inhibition-induced bursting	chaos	# of FLOPS
integrate-and-fire	-	+	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	5
integrate-and-fire with adapt.	-	+	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	-	10
integrate-and-fire-or-burst	-	+	+		+	-	+	+	-	-	-	-	+	+	+	-	+	+	-	-	-		13
resonate-and-fire	-	+	+	-	-	-	-	+	+	-	+	+	+	+	-	-	+	+	+	-	-	+	10
quadratic integrate-and-fire	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	+	+	-	-	-	-	-	7
Izhikevich (2003)	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	13
FitzHugh-Nagumo	-	+	+	-		-	-	+	-	+	+	+	-	+	-	+	+	-	+	+	-	-	72
Hindmarsh-Rose	-	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	120
Morris-Lecar	+	+	+	-		-	-	+	+	+	+	+	+	+		+	+	-	+	+	-	-	600
Wilson	-	+	+	+			+	+	+	+	+	+	+	+	+	+		+	+				180
Hodgkin-Huxley	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	1200

(Izhikevich 2004)

How the model ranking was obtained

Models	biophysically meaningful	tonic spiking	phasic spiking	tonic bursting	phasic bursting	mixed mode	spike frequency adaptation	class 1 excitable	class 2 excitable	spike latency	subthreshold oscillations	resonator	integrator	rebound spike	rebound burst	threshold variability	bistability	DAP	accommodation	inhibition-indiced spiking	inhibition-induced bursting	chaos	# of FLOPS
integrate-and-fire	-	+	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	5
integrate-and-fire with adapt.	-	+	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	-	10
integrate-and-fire-or-burst	-	+	+		+	-	+	+	-	-	-	-	+	+	+	-	+	+	-	-	-		13
resonate-and-fire	-	+	+	-	-	-	-	+	+	-	+	+	+	+	-	-	+	+	+	-	-	+	10
quadratic integrate-and-fire	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	+	+	-	-	-	-	-	7
Izhikevich (2003)	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	13
FitzHugh-Nagumo	-	+	+	-		-	-	+	-	+	+	+	-	+	-	+	+	-	+	+	-	-	72
Hindmarsh-Rose	-	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	120
Morris-Lecar	+	+	+	-		-	-	+	+	+	+	+	+	+		+	+	-	+	+	-	-	600
Wilson	-	+	+	+			+	+	+	+	+	+	+	+	+	+		+	+				180
Hodgkin-Huxley	+	+	+	+	O	O	+	+	+	+	+	+	+	+	+	+	+	+	+	+	O	+	1200

NB: Model is more 'biologically plausible' than the real thing!

How the model ranking was obtained

Models	biophysically meaningful	tonic spiking	phasic spiking	tonic bursting	phasic bursting	mixed mode	spike frequency adaptation	class 1 excitable	class 2 excitable	spike latency	subthreshold oscillations	resonator	integrator	rebound spike	rebound burst	threshold variability	bistability	DAP	accommodation	inhibition-indiced spiking	inhibition-induced bursting	chaos	# of FLOPS
integrate-and-fire	-	+	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	5
integrate-and-fire with adapt.	-	+	-	-	-	-	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	-	10
integrate-and-fire-or-burst	-	+	+		+	-	+	+	-	-	-	-	+	+	+	-	+	+	-	-	-		13
resonate-and-fire	-	+	+	-	-	-	-	+	+	-	+	+	+	+	-	-	+	+	+	-	-	+	10
quadratic integrate-and-fire	-	+	-	-	-	-	-	+	-	+	-	-	+	-	-	+	+	-	-	-	-	-	7
Izhikevich (2003)	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	13
FitzHugh-Nagumo	-	+	+	-		-	-	+	-	+	+	+	-	+	-	+	+	-	+	+	-	-	72
Hindmarsh-Rose	-	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	120
Morris-Lecar	+	+	+	-		-	-	+	+	+	+	+	+	+		+	+	-	+	+	-	-	600
Wilson	-	+	+	+			+	+	+	+	+	+	+	+	+	+		+	+				180
Hodgkin-Huxley	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	1200

... except it isn't!!!

The Izihikevich (2003) phenomenological model

$$v' = 0.04v^2 + 5v + 140 - u + I \quad (1)$$

$$u' = a(bv - u) \quad (2)$$

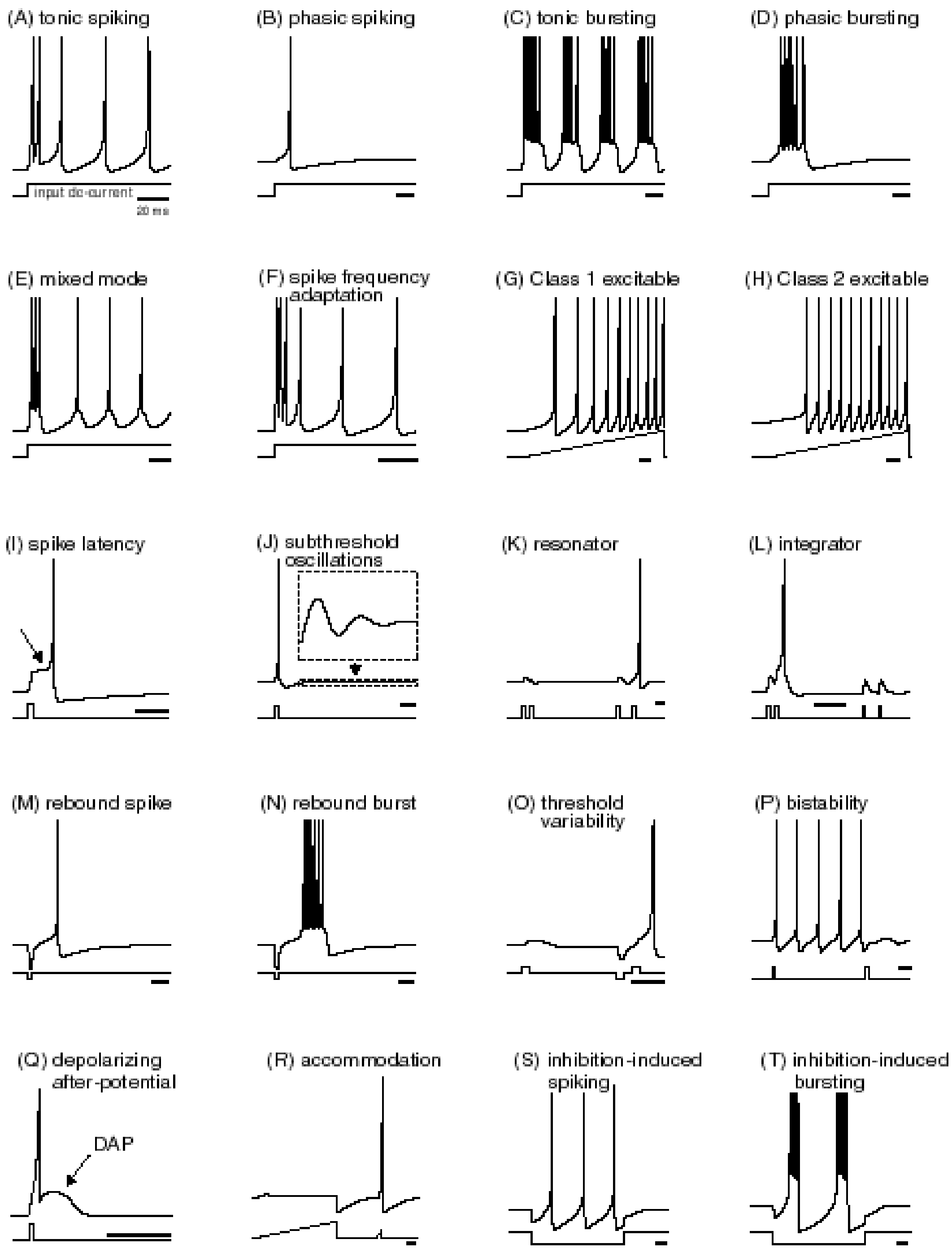
with the auxiliary after-spike resetting

$$\text{if } v \geq 30 \text{ mV, then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d. \end{cases} \quad (3)$$

Here, v and u are dimensionless variables, and a, b, c, and d are dimensionless parameters, and $' = d/dt$, where t is the time.

NB: The model is purely phenomenological, with little biophysical meaning of most components (e.g., there is no capacitive current!).
'Highly nonlinear curve fitting'

Model reproduces rich phenomenology



However:

- (nearly) purely phenomenologically (params not given or derived)
- No systematic way of adding more behaviors (requires 'tweaking' of coupled parameters)
- Solution is clock-based (not event-based)

(from Izhikevich 2004)

Desirable properties of a model

(all violated by Izhikevich 2003)

- All terms have biophysical interpretation
  - This implies number of state variables not fixed, as in I&F (N=1) Fitzhugh-Nagumo, Morris-Lecar, Izhikevich (all N=2).
- *Systematic* way of adding arbitrary number of additional mechanisms
- Modular architecture (*i.e.,* minimal interference between mechanisms)
- Analytical solution available
- Event-based (natural for AER!)

New model on the block

(Mihalas & Niebur, Neural Computation, in press)

Neural dynamics:

$$I_j'(t) = -k_j I_j(t);\ j = 1, ..., N$$

$$V'(t) = \frac{1}{C}\left(I_e + \sum_j I_j(t) - G\left(V(t) - E_L\right)\right)$$

$$\Theta'(t) = a(V(t) - E_L) - b(\Theta(t) - \Theta_\infty)$$

- I_j: spiking-related currents (any number; we use ≤2)
- V: membrane voltage
- Θ: adaptive threshold
  - updated continuously, not only at spikes
  - equivalent to voltage-dependent currents

Update rules

- Any update rule can be used provided $\Theta_r > V(t)$ after update.
- We use:

$$I_j(t) \leftarrow R_j \times I_j(t) + A_j$$

$$V(t) \leftarrow V_r$$

$$\Theta(t) \leftarrow \max(\Theta_r, \Theta(t))$$

- R_j, A_j, V_r, Θ_r are free parameters ($\Theta_r > V_r$)
- Special cases for spike-induced currents:
  - R_j=1: additive update
  - R_j=0: constant update (jump independent of $I_j(t)$)

Model properties

- Linear dynamics
- Dynamic matrix is triangular
  → immediately solvable
- Diagonalizable (over reals)
  - Eigenvalues ($-k_j$, $-G/C$, $-b$), all <0
  - One stationary solution; stable; can analyze behavior in phase space
- Exponential decay of all spike-induced currents
- Synapses treated the same way
- Arbitrary number of spike-induced currents
- Analytical solution for voltage between spikes
- Can be solved as zero of polynomial (Brette 2007)

Exact solution

Assume distinct eigenvalues; initial conditions I_{j0},V_0,Θ_0 -->

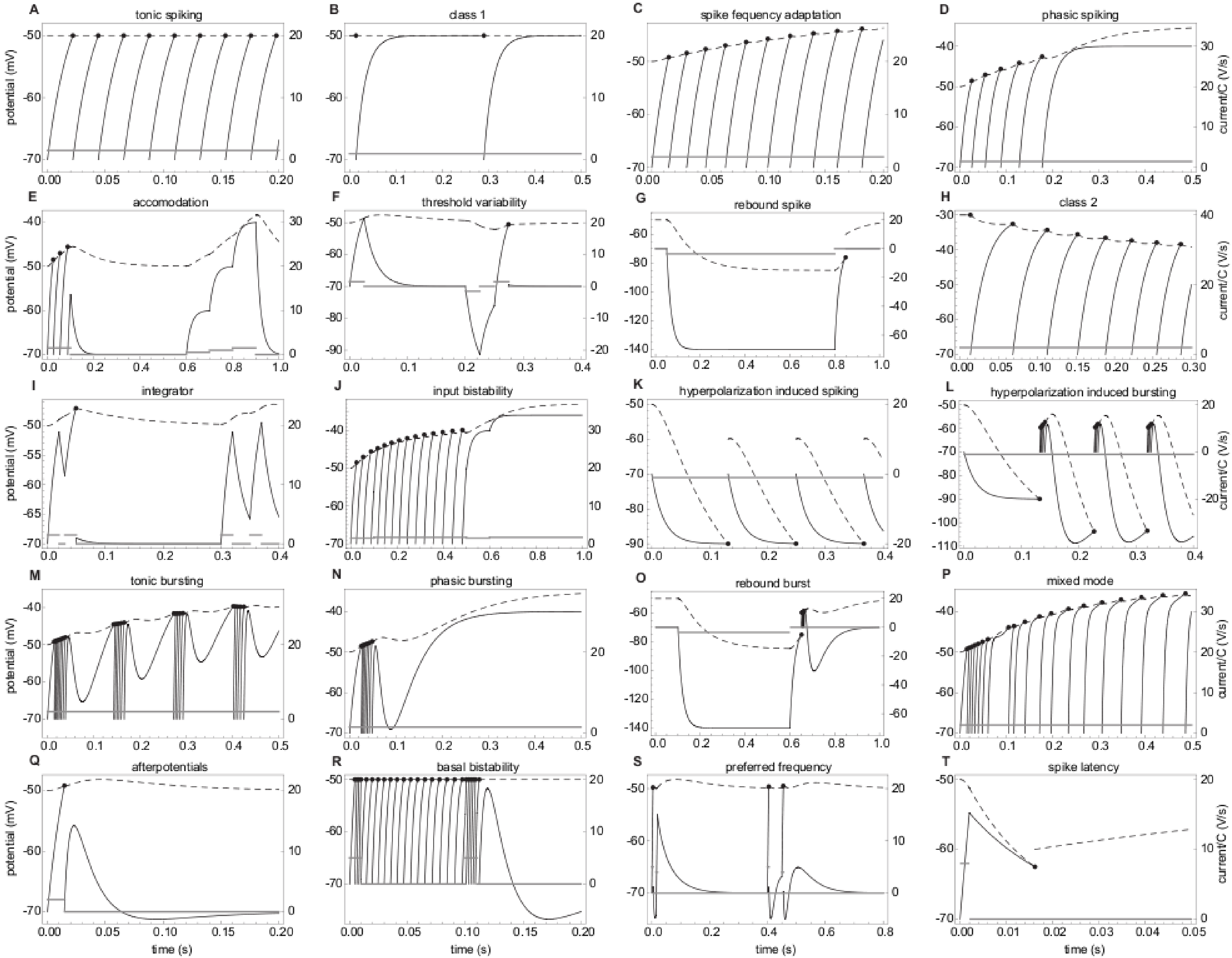
$$
\begin{aligned}
I_j(t) =& I_{j0} \times \exp(-k_j t) \\
V(t) =& E_L + \frac{I_e}{G} + \sum_j \frac{I_{j0} \exp(-k_j t)}{G - k_j C} \\
& + \exp(-Gt/C) \left(V_0 - E_L - \frac{I_e}{G} - \sum_j \frac{I_{j0}}{G - k_j C} \right) \\
\Theta(t) =& \Theta_\infty + \frac{a I_e}{bG} + \sum_j \frac{a I_{j0}}{(G - k_j C)(b - k_j)} \exp(-k_j t) + \qquad (4) \\
& + \frac{a}{b - G/C} \left(V_0 - E_L - \frac{I_e}{G} - \sum_j \frac{I_{j0}}{G - k_j C} \right) \exp(-Gt/C) + \\
& + \left(\Theta_0 - \Theta_\infty - \frac{a}{b - G/C} \left(V_0 - E_L - \frac{I_e}{bC} - \sum_j \frac{I_{j0}}{C(b - k_j)} \right) \right) \exp(-bt)
\end{aligned}
$$

Solution as zero of polynomial

Brette (2007) has pointed out that since the equation $V(t) = \Theta(t)$ is a sum of exponentials in t, it can be reduced to a polynomial equation. Consider k_j, G/C and b to be rational numbers and $k \in \mathbb{Q}$ their greatest common divisor such that $n_j = k_j/k$, $n_g = G/(Ck)$, $n_b = b/k$ which defines n_j, n_g and n_g, all $\in \mathbb{N}$. With the transformation $x = \exp(-kt)$, the time of next spike is obtained by numerically solving the equation $D(x) = 0$, where

$$
\begin{aligned}
D(x) =& E_L - \Theta_\infty + \frac{I_e}{G}\left(1 - \frac{a}{b}\right) + \sum_j \left(1 - \frac{a}{b - k_j}\right)\frac{I_{j0}}{G - k_jC}x^{n_j} + \\
&+ \left(1 - \frac{a}{b - G/C}\right)\left(V_0 - E_L - \frac{I_e}{G} - \sum_j \frac{I_{j0}}{G - k_jC}\right)x^{n_g} \qquad (7) \\
&- \left(\Theta_0 - \Theta_\infty - \frac{a}{b - G/C}\left(V_0 - E_L - \frac{I_e}{bC} - \sum_j \frac{I_{j0}}{C(b - k_j)}\right)\right)x^{n_b}
\end{aligned}
$$

Phenomenology



Parameters

panel	feature	$a[s^{-1}]$	$A_1/C[V/s]$	$A_2/C[V/s]$	$I_e/C[V/s]$
A	tonic spiking	0	0	0	1.5
B	class 1	0	0	0	$1 + 10^{-6}$
C	spike freq. adapt.	5	0	0	2
D	phasic spiking	5	0	0	1.5
E	accommodation	5	0	0	1.5, 0, 0.5, 1, 1.5, 0
F	threshold variability	5	0	0	1.5, 0, -1.5, 0, 1.5, 0
G	rebound spike	5	0	0	0, -3.5, 0
H	class 2	5	0	0	$2(1 + 10^{-6})$
I	integrator	5	0	0	1.5, 0, 1.5, 0, 1.5, 0, 1.5, 0
J	input bistability	5	0	0	1.5, 1.7, 1.5, 1.7
K	hyperpol. spiking	30	0	0	-1
L	hyperpol. bursting	30	10	-0.6	-1
M	tonic bursting	5	10	-0.6	2
N	phasic bursting	5	10	-0.6	1.5
O	rebound burst	5	10	-0.6	0, -3.5, 0
P	mixed mode	5	5	-0.3	2
Q	afterpotentials	5	5	-0.3	2, 0
R	basal bistability	0	8	-0.1	5, 0, 5, 0
S	pref. frequency	5	-3	0.5	5, 0, 4, 0, 5, 0, 4, 0
T	spike latency	80	0	0	8, 0

Fixed parameters: $b = 10s^{-1}$, $G/C = 50s^{-1}$, $k_1 = 200s^{-1}$, $k_2 = 20s^{-1}$, $\Theta_\infty = -0.05V$, $R_1 = 0$, $R_2 = 1$, $E_L = -0.07V$, $V_r = -0.07V$ and $\Theta_r = -0.06V$.

Conclusion

- Our new model has rich phenomenology
- Features constructed *systematically*
- Biophysically plausible terms
- Efficient solution of linear system (triangular)
- Analytical solution of dynamic equations available
- Event-based solution, not clock-based
- Some level of modularity: decoupling of
    - Mechanisms caused by active currents (=adaptive threshold)
    - Spike-induced currents
- Extendable: just add currents...
    - And adding currents is cheap, too!
- Currently implementing large-scale numerical network simulator