Adaptive exponential integrate-and-fire model

Wulfram Gerstner and Romain Brette (2009), Scholarpedia, 4(6):8427. doi:10.4249/scholarpedia.8427 revision #90944 [link to/cite this article]

- **Dr. Wulfram Gerstner**, EPFL, Lausanne, Switzerland
- **Romain Brette**, Ecole Normale Supérieure, Paris, France

The **Adaptive exponential integrate-and-fire model**, also called **AdEx**, is a spiking neuron model with two variables. The first equation describes the dynamics of the membrane potential and includes an activation term with an exponential voltage dependence. Voltage is coupled to a second equation which describes adaptation. Both variables are reset if an action potential has been triggered. The combination of adaptation and exponential voltage dependence gives rise to the name Adaptive Exponential Integrate-and-Fire model. The adaptive exponential integrate-and-fire model is capable of describing known neuronal firing patterns, e.g., adapting, bursting, delayed spike initiation, initial bursting, fast spiking, and regular spiking. Introduced by Brette and Gerstner in 2005, the Adaptive exponential integrate-and-fire model AdEx builds on features of the exponential integrate-and-fire model (Fourcaud et al, 2003) and the 2-variable model of Izhikevich (Izhikevich, 2003).

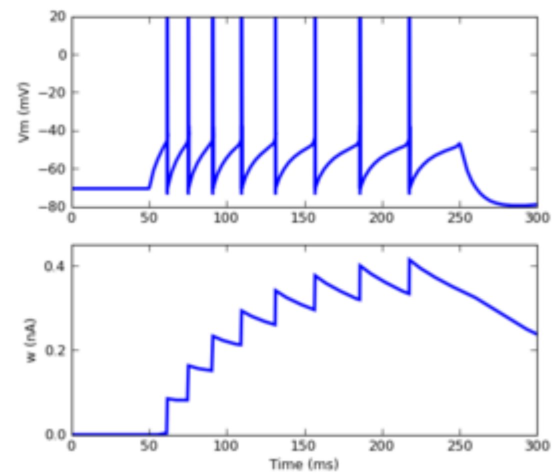

Figure 1: Adaptation and regular firing of the AdEx model in response to a current step; voltage (top) and adaptation variable (bottom); parameters from Brette and Gerstner (2005).

Contents

Definition

The model is described by two differential equations:

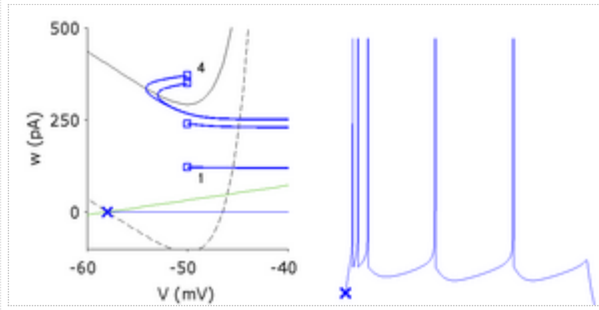

Figure 2: Initial bursting as response of the AdEx model to a current step; right - voltage as a function of time; left - trajectories in the 2-dimensional space of voltage (horizontal axis) and adaptation variable (vertical axis). Resting potential marked by cross; sequence of reset values marked by squares. Nullclines $dw/dt = 0$ (green line) and $dV/dt = 0$ before (black dashed line) and after the current step (black line).

$$C\,\frac{dV}{dt} = -g_L(V-E_L) + g_L\Delta_T \exp\left(\frac{V-V_T}{\Delta_T}\right) - w + I \qquad (1)$$

$$\tau_w\,\frac{dw}{dt} = a(V-E_L) - w \qquad (2)$$

where V is the membrane potential, w the adaptation variable, I the input current, C the membrane capacitance, g_L the leak conductance, E_L the leak reversal potential, V_T the threshold, Δ_T the slope factor, a the adaptation coupling parameter and τ_w is the adaptation time constant.

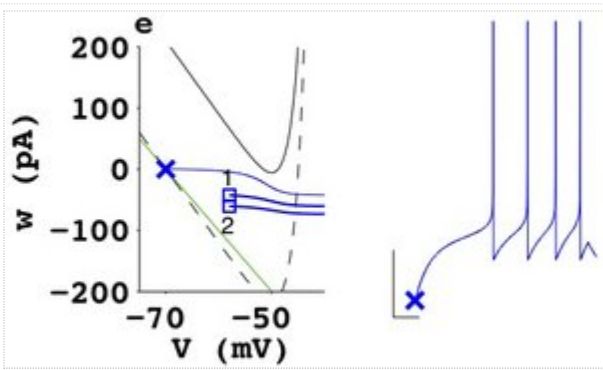

Figure 4: Delayed spiking as response of the AdEx model to a current step; right - voltage as a function of time; left - trajectories in the 2-dimensional space of voltage (horizontal axis) and adaptation variable (vertical axis).

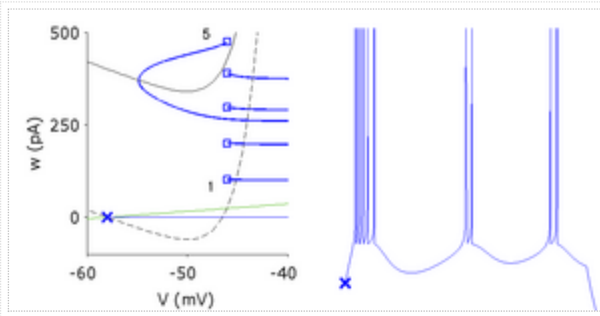

Figure 3: Regular bursting as response of the AdEx model to a current step; right - voltage as a function of time; left - trajectories in the 2-dimensional space of voltage (horizontal axis) and adaptation variable (vertical axis).

The exponential nonlinearity describes the process of spike generation and the upswing of the action potential. In the mathematical definition of the model, a spike is said to occur at the time t^f when the membrane potential V diverges towards infinity. In practice, integration of the model equations is usually stopped and the firing time t^f recorded when the membrane potential reaches a finite value (e.g. 0 mV or +30mV). The downswing of the action potential is not described by the model but replaced by a reset of the voltage to a fixed V_r

$$at \quad t = t^f \quad reset \qquad V \to V_r$$

At the same time, the adaption value is also changed by an amount b

$$at \quad t = t^f \quad reset \qquad w \to w + b$$

The interaction of the discrete resets with the differential equations results in a rich dynamical behavior.Figure 1 shows spike-frequency adaptation in the response of an AdEx model to a current step.Figure 2 -- Figure 5 show some other firing patterns.

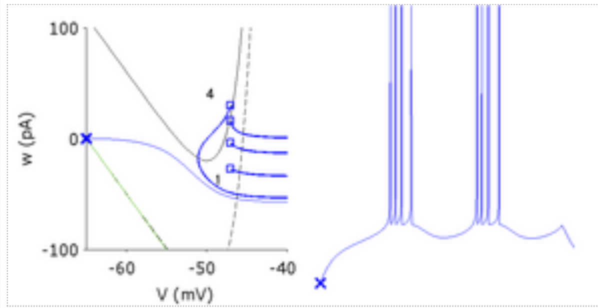

Figure 5: Delayed bursting as response of the AdEx model to a current step; right - voltage as a function of time; left - trajectories in the 2-dimensional space of voltage (horizontal axis) and adaptation variable (vertical axis).

Physiological interpretation

The differential equation (1) for the voltage expresses the conservation of currents across the membrane. The capacitive current CdV/dt must be balanced by the injected current I and (the negative of) the membrane currents. In contrast to detailed Hodgkin-Huxley type models, the membrane currents are compressed into three terms. First, a leak current that is linear in the voltage and increases with distances from the resting potential E_L . Second, an exponential term that describes the voltage dependent activation of the sodium channel under the assumption that activation is instantaneous. The third term on the right-hand side of eq. (1) is an adaptation current w .

The differential equation for the second variable w (equation (2) describes the evolution of the adaptation current with time constant τ_w . It includes both spike-triggered adaptation, through the reset $w \to w + b$, and a linear coupling of the second variable with the voltage (via the parameter a). If the coupling via the parameter b is called spike-triggered adaptation, the coupling via a could be called subthreshold adaptation, even though this terminology is not standard. The parameter a may model ionic channels (e.g. potassium for $a > 0$) that tend to hyperpolarize the membrane or, for $a < 0$, a depolarizing current (e.g., low-threshold calcium current) or coupling to a dendritic compartment. Quantitatively, the coupling parameter a can be derived from detailed models from a linearization of the dynamics of an ionic channel (Richardson et al. 2003), or from the axial conductance in the case of a dendritic compartment.

All parameters of the Adaptive Exponential Integrate-and-Fire model have a biological interpretation:

- In the absence of adaptation, V_T is the maximum voltage that can be reached under constant current injection without generating a spike (rheobase current). In the presence of adaptation the voltage corresponding to the rheobase current is shifted.
- The slope factor Δ_T quantifies the sharpness of spikes. It can be related to the sharpness of the sodium activation curve, when one neglects the activation time constant. In the limit of zero slope factor, the model becomes an integrate-and-fire model with a fixed threshold V_T .
- Spike triggered adaptation (the parameter b) summarizes the effect of calcium dependent potassium channels under the assumption that calcium influx occurs mainly during an action potential. Note that the coupling of voltage and adaptation via the parameter a also contributes to spike-triggered adaptation because of the sharp rise of the voltage during the upswing of an action potential.
- Parameters V_T and Δ_T in Equation (1) can be extracted from experiments using the technique of dynamic I-V curves (Badel et al, 2008). The subthreshold parameters can be extracted from experiments by standard linear identification methods.

Reset parameters have to be fitted.

Electrophysiological features

As shown in Figure 2 - Figure 6, the AdEx model can reproduce many known electrophysiological features:

- spike-frequency adaptation (Figure 1)
- regular and fast spiking (Figure 1)
- phasic spiking (Figure 6A)
- phasic and tonic bursting (Figure 6B and C)
- post-inhibitory spiking and bursting (Figure 6D)
- delayed spike initiation and delayed burst initiation (Figure 4 and Figure 5)
- damped oscillations (Figure 7C)
- overshoot or undershoot of the voltage in response to a subthreshold current step (Figure 7B and Figure 6D)
- type I and type II excitability (see below: Analysis)

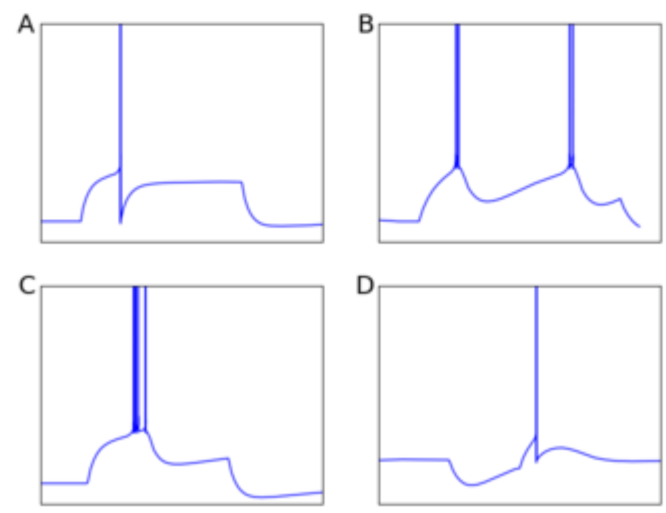

Figure 6: Response of 4 AdEx models with different parameter values to current steps: A) phasic spiking, B) tonic bursting, C) phasic bursting, D) post-inhibitory rebound.

Limitations and Extensions of the AdEx model

The Adaptive Exponential Integrate-and-fire model relies on certain assumptions and simplifications:

- It is a single-compartment model. However, it is straightforward to couple the spike generation mechanism of the adaptive exponential integrate-and-fire model with passive dendritic compartments.
- Sodium channel activation is instantaneous. In a Hodgkin-Huxley model activation of the sodium current (via the m variable) is rapid, but lags the evolution of the voltage by a short time in the millisecond range.
- Downswing of action potential controlled by rapid potassium currents and (also partially by) sodium channel inactivation is neglected. Instead the voltage is reset to a fixed value after the spike.
- Refractoriness is only represented by the reset of voltage and adaptation variables, whereas in real neurons refractoriness shows up as an increase in the firing threshold and conductance after a spike as well as a change in the momentary equilibrium potential (Badel et al. 2008). In particular, effects of inactivation of the sodium channel is ignored.
- There is a single adaptation time constant. This is a strong simplification because in reality adaptation occurs on several time scales ranging from tens of milliseconds to seconds. However, it is straightforward to extend the model so as to include several equations of the form of Eq. (2) for adaptation currents with different time constants.
- Conductance effects are ignored, because the adaptation variable enters as a current rather than as a conductance.
- Effects of pharmacological manipulations (e.g. blocking of specific ion channels) cannot be predicted.
- The AdEx with a fixed set of parameters is supposed to represent neurons in a 'typical' regime. However, a neuron may behave quite differently when studied in a regime of hyperpolarization from the regime just below threshold (because channels that are inactivated and hence invisible below the threshold could be very relevant in a hyperpolarized state. Hence we cannot expect an AdEx model with a single set of parameters to describe both regimes correctly.

Fitting to real neurons

The parameters of the AdEx model can be fit to match the response of neurons using simple electrophysiological protocols (current pulses, steps and ramps) as described in (Brette and Gerstner, 2005). With the appropriate parameter values, the AdEx model can reproduce up to 96% of the spike times of a regular-spiking Hodgkin–Huxley-type model with an I_m current for adaptation in response to fluctuating synaptic inputs (see Figure 8 and Brette and Gerstner, 2005). Excellent spike timing predictions were also found for real cortical neurons, using genetic algorithms for parameter optimization (Jolivet et al, 2008).

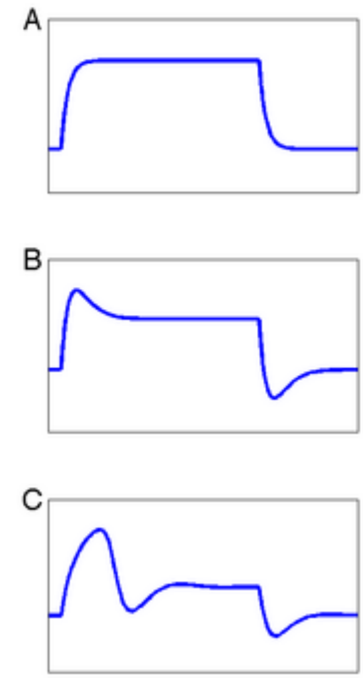

Figure 7: Response of 3 AdEx models to a subthreshold current step. Top: monotonic approach to the new voltage; Middle: sag; Bottom: damped oscillations

Relation to other models

Introduced by Brette and Gerstner in 2005, the Adaptive exponential integrate-and-fire model AdEx combines features of the the exponential integrate-and-fire model (Fourcaud et al, 2003) with the 2-variable model of Izhikevich (Izhikevich, 2003). It also shares features with the leaky integrate-and-fire model and the two-dimensional integrate-and-fire models of Richardson et al. (2003) and Treves et al. (1993)

- The leaky integrate-and-fire model can be obtained from the AdEx by taking the limit $\Delta_T \to 0$ and removing the adaptation current w ;
- The leaky integrate-and-fire model with Spike-Triggered adaptation (Treves et al., 1993) can be obtained from the AdEx by taking the limit $\Delta_T \to 0$ and setting the voltage-adaptation parameter to zero ($a = 0$);
- The leaky integrate-and-fire model with subthreshold adaptation (Richardson et al., 2003) can be obtained from the AdEx by taking the limit $\Delta_T \to 0$ and setting the spike-triggered adaptation parameter to zero ($b = 0$);
- The exponential integrate-and-fire model (Fourcaud et al, 2003) is obtained from the AdEx by removing the adaptation current (w);
- The Izhikevich model (Izhikevich 2001) is obtained by replacing the linear leak current and the exponential nonlinearity in Eq. (1) by a quadratic function of the voltage.

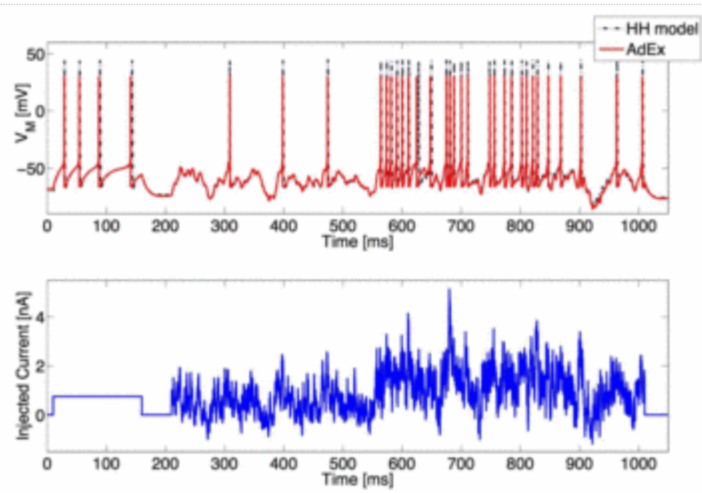

Figure 8: Voltage trace of a Hodgkin-Huxley type model of regular spiking cell with M-current and of an AdEx model with appropriate parameters (as described in Brette and Gerstner, J Neurophysiol 2005), in response to the input shown at the bottom. Adaptation to the step current is visible. With the same set of parameters, the AdEx reproduces spikes of the Hodgkin-Huxley model for various firing rates. The fluctuating input switches at t=550ms

The main similarities between the Izhikevich model and the AdEx model are:

- both models have the same bifurcation patterns;
- both models can account for a large variety of neuronal firing patterns;
- both models are easy to implement and rapid to simulate;

The main differences of the Izhikevich model and the AdEx model are:

- quadratic voltage dependence in the voltage equation of the Izhikevich model versus exponential dependence in the AdEx model;
- upswing of the action potential is too slow in the Izhikevich model (Izhikevich 2007) compared to real neurons and more realistic in the AdEx model because of the exponential voltage dependence (Badel et al. 2008);
- the Izhikevich model shows unrealistic nonlinearities in the subthreshold regime, whereas the AdEx model is linear in agreement with experiments (Badel et al. 2008);
- attenuation of high frequency inputs as $1/f^2$ for a model with quadratic voltage dependence like in the Izhikevich model vs. $1/f$ for models with exponential voltage dependence (Fourcaud et al, 2003);
- the choice of the voltage cut-off value for spikes is critical in the Izhikevich model but less so in the AdEx model (In the absence of a cut-off the adaptation variable w diverges in the Izhikevich model during the upswing of the action potential but does not diverge in the AdEx model.);
- extraction of the voltage dependence from experiments suggests a combination of linear and exponential terms as in the AdEx model (Badel et al. 2008), rather than a quadratic dependence as in the Izhikevich model;
- while qualitative fits to firing patterns are possible with both models, the AdEx model allows better quantitative fits to voltage traces (Naud et al. 2008).

The quartic model (Touboul, 2008) is another bidimensional model but the voltage equation is a polynomial of order 4 (the exponential term is replaced by V^4). The main difference with the AdEx model is that the quartic model can exhibit sustained subthreshold oscillations.

Analysis of the Model

Rescaling

The equations can be written in dimensionless units by expressing time in units of the membrane time constant $\tau_m = C/g_L$, voltage in units of the slope factor Δ_T and with reference potential V_T , and rewriting both the adaptation variable w and the input current I in voltage units. With this change of units, it appears that the model has only four free parameters (plus the input current).

Slow ramp currents and Bifurcations

When the input current I is very negative, the AdEx model has two equilibria, one of which is stable (the resting potential). When increasing I (slow ramp current), the stable equilibrium can disappear through either

- a saddle-node bifurcation if $\frac{a}{g_L} < \frac{\tau_m}{\tau_w}$ (ratio of conductances and ratio of time constants, where $\tau_m = C/g_L$): the stable and unstable equilibria merge and disappear. (The saddle-node bifurcation can be a simple one, or a saddle-node on invariant circle.)
- or a subcritical Andronov-Hopf bifurcation if $\frac{a}{g_L} > \frac{\tau_m}{\tau_w}$: the stable equilibrium first becomes unstable.

See Figure 9 for an illustration of these conditions.

Type I and Type II in frequency-current curves

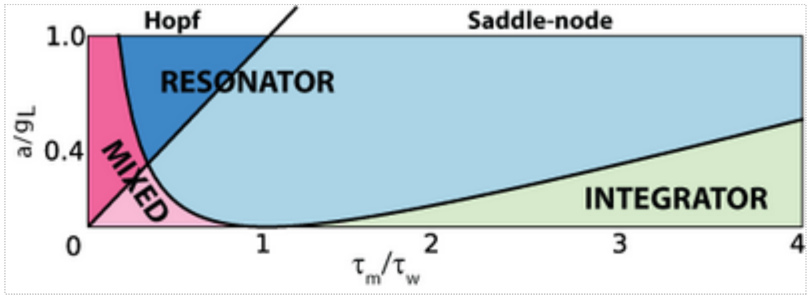

Figure 9: Behavior of the AdEx model as a function of a/g_L and τ_m/τ_w (where $\tau_m = C/g_L$). Light colors indicate loss of stability via saddle-node bifurcation and dark colors via subcritical Andronov-Hopf bifurcation. Subcritical Andronov-Hopf corresponds to f-I curves of type II, whereas saddle-node bifurcations can lead to type I or II (see Figure 9). Blue: resonator mode (oscillations for any or almost any input current I). Green: integrator mode (no oscillation for any I). Pink: mixed mode (resonator if I is large enough, otherwise integrator).

The firing frequency as a function of constant input current (f-I curve) defines two types of excitability: type I is continuous while type II is discontinuous at the threshold (rheobase current). In two-dimensional neuron models the bifurcation patterns influence directly the excitability: a subcritical Andronov-Hopf bifurcation leads to a type II behavior and a saddle-node on invariant circle gives rise to a type I behavior (Izhikevich 2007). However, for saddle-node bifurcations, a limit cycle can exist even before the saddle and node merge. In this case we have a regime of bistability and the saddle-node bifurcation is not linked to the limit cycle. (Hence, a simple saddle node bifurcation as opposed to a saddle-node onto invariant circle, see Izhikevich 2007).

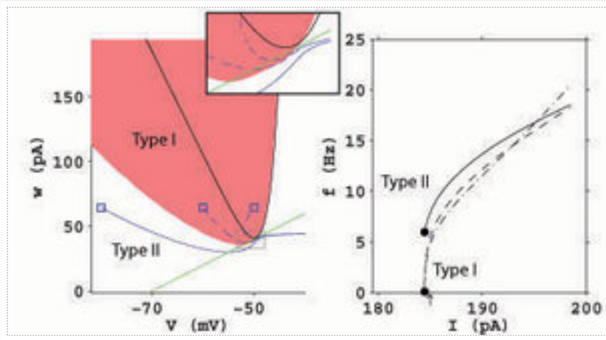

Figure 10: Excitability of type I and type II depends not only on bifurcation parameters but also on choice of reset value. Left: If, during periodic firing, reset falls inside the shaded area, the f-I curves is of type I; outside the shaded area of type II. Right: frequency-current curves. Adapted from Naud et al. 2008

For a fixed set of parameters leading to saddle-node bifurcations, but different choices of voltage reset, the AdEx model can exhibit f-I curves either of type I or type II, as shown in Figure 10. Type I corresponds to saddle-node on invariant circle whereas type II corresponds to a simple saddle-node combined with a bistability between the 'node' (equilibrium corresponding to inactive neuron) and limit cycle (regular firing) for currents just below the rheobase current (Naud et al. 2008, Touboul and Brette, 2008). Hence the voltage reset V_r is an important parameter in the AdEx model.

Oscillations

Because of the coupling between the two variables V and w , there can be damped oscillations near the resting potential. The occurrence of oscillations is summarized in Figure 9 and depends on the bifurcation type, the input current and the following condition (Touboul and Brette, 2008):

$$\frac{a}{g_L} < \frac{\tau_m}{4\tau_w}\left(1 - \frac{\tau_w}{\tau_m}\right)^2 \tag{3}$$

whose border is the curved line in Figure 9. If noise is added to the system, damped oscillations become noisy sustained subthreshold oscillations similar to those recorded in many neurons in vitro.

In the blue parameter region, the AdEx model exhibits oscillations for any or almost any input current I . In the green one, it never oscillates. In the pink one, the model exhibits oscillations for large I but not for small I . The same distinction exists between integrator (green) and oscillator (blue) in linear two-variable models (Richardson et al, 2003; Fig. 2C), but the mixed mode (pink) is specific to the AdEx model.

Bursting and chaos

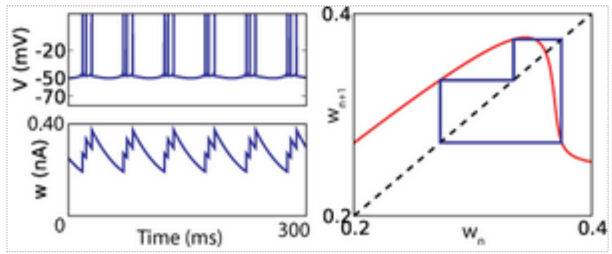

Figure 11: Bursting with 3 spikes per burst in the AdEx model (top: voltage, bottom: adaptation variable), corresponding to a period three cycle of the adaptation map (right).

Because V is always reset to the same value V_r after a spike, interspike intervals are determined by the value of the adaptation variable w at spike time. The sequence (w_n) of those values is the orbit of w_0 under the *adaptation map* Φ , which maps w to the value of $w(t)$ at spike time plus b for a solution starting from (V_r, w) (Touboul and Brette, 2008). Thus, $w_n = \Phi^n(w_0)$. Regular spiking corresponds to a stable equilibrium of Φ while bursting corresponds to cycles of Φ .

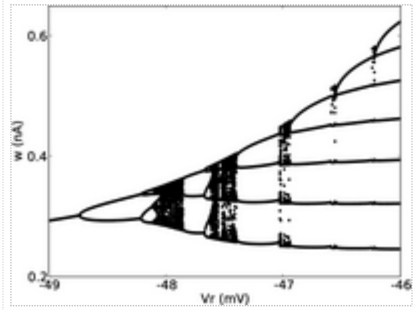

Figure 12: Values of the adaptation variable of a bursting AdEx model at spike times as a function of Vr (reset value), revealing the number of spikes per burst.

An example of a bursting response with 3 spikes per burst is shown in Figure 11, corresponding to a period 3 cycle of the adaptation map. Bursting occurs when the reset value V_r is high, so that spikes are produced quickly after reset, until adaptation builds up and induces a return to hyperpolarized potentials. Figure 12 shows how the number of spikes per burst increases with the reset value. For some parameter values, the dynamics is chaotic, resulting in irregular spike patterns.Figure 13 shows how the choice of reset of voltage (horizontal) and adaptation (vertical) influences firing patterns.

History

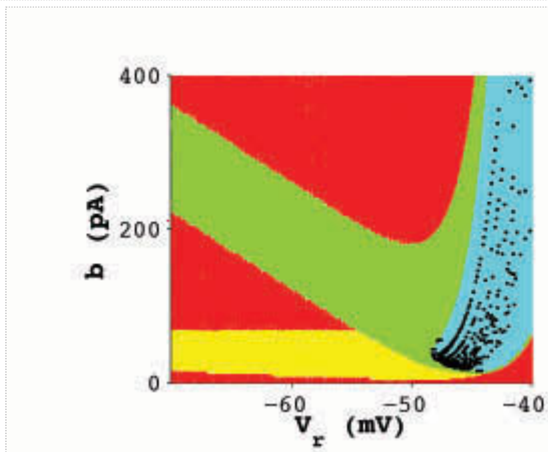

Figure 13: Firing patterns for different choices of reset parameters V_r (horizontal axis) and b (vertical axis). regular firing (red), adaptive (yellow), initial bursting(green), regular bursting (light blue), irregular-chaotic (black dots); Adapted from Naud et al. (2008).

The idea of integrate-and-fire models can be traced back to Lapicque (1907) and was already by Hill in 1936 combined with a second equation in order to describe adaptation (called accommodation at that time and mainly referring to the coupling between threshold and subthreshold voltage). Spike-triggered adaptation (in form of a moving threshold) for an integrate-and-fire mechanism is clearly present in the work of Fuortes and Mantegazzini (1962) and has inspired their experimental work on neuronal refractoriness. The leaky integrate-and-fire model in its modern form was combined with a mechanism for spike-triggered adaptation by Treves (1993) and linearly coupled in the subthreshold regime with a second variable by Izhikevich (2001) and Richardson et al. (2003). If the equation of the leaky integrate-and-fire model (coupled to a second equation) is replaced by a quadratic nonlinearity (known to the experts as the canonical form of a type I neuron model, see Latham et al. 2000) one arrives at the model of Izhikevich (2003). If the leaky integrate-and-fire model (coupled to a second equation) is augmented by an exponential nonlinearity (known to be a good approximation for a Hodgkin-Huxley model, see Fourcaud-Trocme et al. 2003), one arrives at the Adaptive Exponential Integrate-and-Fire model (Brette and Gerstner, 2005). In other words, if one adds to the exponential integrate-and-fire model of Fourcaud-Trocme et al. (2003) a second variable as in the Izhikevich model (2003) one gets the AdEx. Adaptation in simple neuron models has been reviewed by Benda and Herz (2004).

References

- Badel L., Lefort S., Brette R., Petersen C., Gerstner W. and Richardson M.J.E. (2008), Dynamic I-V Curves Are Reliable Predictors of Naturalistic Pyramidal-Neuron Voltage Traces, J Neurophysiol 99: 656 - 666.
- Benda J, Herz A.V.M. (2003), A universal model for spike-frequency adaptation. Neural Comput. 15:2523-2564.
- Brette R. and Gerstner W. (2005), Adaptive Exponential Integrate-and-Fire Model as an Effective Description of Neuronal Activity, J. Neurophysiol. 94: 3637 - 3642.
- Fourcaud-Trocme N., Hansel D., van Vreeswijk C., and Brunel N. (2003), How spike generation mechanisms determine the neuronal response to fluctuating inputs, J. Neuroscience 23:11628-11640
- Fuortes, M. G. F. and Mantegazzini, F. (1962), Interpretation of the repetitive firing of nerve cells. J. Gen. Physiol., 45:1163-1179.
- Hill, A. V. (1936). Excitation and accommodation in nerve. Proc. R. Soc. B, 119:305-355.
- Izhikevich, E.M. (2001), Resonate-and-fire neurons, Neural Networks, 14:883-894
- Izhikevich E.M. (2003), Simple model of spiking neurons, IEEE Transactions On Neural Networks, 14:1569-1572
- Izhikevich, E.M. (2007), Dynamical systems in neuroscience, MIT Press.
- Jolivet R., Schürmann F., Berger T.K., Naud R., Gerstner W., Roth A. (2008), The quantitative single-neuron modeling competition, Biological Cybernetics 99(4-5):417-26
- Lapicque, L. (1907), Recherches quantitatives sur l'excitation electrique des nerfs traitée comme une polarisation. J. Physiol. Pathol. Gen., 9:620-635.
- Latham, P.E., Richmond, B.J., Nelson, P.G., and Nirenberg, S. (2000), Intrinsic dynamics in neuronal networks. I. Theory. J. Neurophysiol., 83:808-827.
- Naud R., Marcille N., Clopath C. and Gerstner W. (2008), Firing patterns in the adaptive exponential integrate-and-fire model, Biological Cybernetics 99:335-347
- Richardson M.J.E., Brunel N., and Hakim V (2003), From Subthreshold to Firing-Rate Resonance. Journal of Neurophysiology 89:2538-2554
- Touboul J. (2008), Bifurcation Analysis of a General Class of Nonlinear Integrate-and-Fire Neurons, SIAM J. Appl. Math. 68(4):1045-1079
- Touboul J. and Brette R. (2008), Dynamics and bifurcations of the adaptive exponential integrate-and-fire model, Biological Cybernetics, 99(4-5):319-34.
- Treves, A. (1993), Mean-field analysis of neuronal spike dynamics, Network: Computation in Neural Systems, 4(3):259-284

Internal references

- Yuri A. Kuznetsov (2006) Andronov-Hopf bifurcation. Scholarpedia, 1(10):1858.
- John Guckenheimer (2007) Bifurcation. Scholarpedia, 2(6):1517.
- Eugene M. Izhikevich (2006) Bursting. Scholarpedia, 1(3):1300.
- Eugene M. Izhikevich (2007) Equilibrium. Scholarpedia, 2(10):2014.

- Bertil Hille (2008) Ion channels. Scholarpedia, 3(10):6051.
- Rodolfo Llinas (2008) Neuron. Scholarpedia, 3(8):1490.
- Jeff Moehlis, Kresimir Josic, Eric T. Shea-Brown (2006) Periodic orbit. Scholarpedia, 1(7):1358.
- Yuri A. Kuznetsov (2006) Saddle-node bifurcation. Scholarpedia, 1(10):1859.
- Wulfram Gerstner (2008) Spike-response model. Scholarpedia, 3(12):1343.
- Philip Holmes and Eric T. Shea-Brown (2006) Stability. Scholarpedia, 1(10):1838.

See Also

Integrate-and-fire Neuron, Neural Excitability, Quadratic Integrate-and-Fire Neuron, Spike-response model.

Sponsored by: Eugene M. Izhikevich, Editor-in-Chief of Scholarpedia, the peer-reviewed open-access encyclopedia
Reviewed by (http://www.scholarpedia.org/w/index.php?title=Adaptive_exponential_integrate-and-fire_model&oldid=60956) : Anonymous
Reviewed by (http://www.scholarpedia.org/w/index.php?title=Adaptive_exponential_integrate-and-fire_model&oldid=0) : Eugene M. Izhikevich, Editor-in-Chief of Scholarpedia, the peer-reviewed open-access encyclopedia
Accepted on: 2009-04-06 13:09:01 GMT (http://www.scholarpedia.org/w/index.php?title=Adaptive_exponential_integrate-and-fire_model&oldid=60956)

Categories: Computational Neuroscience | Models of Neurons | Multiple Curators