Conductance-Based Integrate-and-Fire Models

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A conductance-based model of Na\(^+\) and K\(^+\) currents underlying action
An alternative approach was to simplify the process of action potential generation by representing the neuron as an integrate-and-fire (IAF) do
Figure 1: Comparison of action potential generation in Hodgkin-Huxley and pulse-based models. A train of spikes was generated by injecting a depolarizing current pulse (2 nA) in a single compartment model (area of 15,000 μm²;...
given threshold. For example, $\alpha_m$ will be assigned a positive value during the pulse and will be zero otherwise. Generalizing for other rate constants, before and after the pulse, we have:

$$
\begin{align*}
\alpha_m &= 0, & \beta_m &= \beta_M \\
\alpha_h &= \alpha_H, & \beta_h &= 0 \\
\alpha_n &= 0, & \beta_n &= \beta_N
\end{align*}
$$

(2.2)

whereas during the pulse:

$$
\begin{align*}
\alpha_m &= \alpha_M, & \beta_m &= 0 \\
\alpha_h &= 0, & \beta_h &= \beta_H \\
\alpha_n &= \alpha_N, & \beta_n &= 0.
\end{align*}
$$

(2.3)

Here, $\alpha_M$, $\beta_M$, $\alpha_H$, $\beta_H$, $\alpha_N$, and $\beta_N$ are constant values. They are estimated from the value of the voltage-dependent expressions at hyperpolarized and depolarized potentials. Choosing $-70$ mV and $+20$ mV and using Traub and Miles’s formulation gives:

$$
\alpha_m = \alpha_m(20) \simeq 22 \text{ ms}^{-1}
$$
Here, \( t_0 \) is the time at which the pulse began, and \( m_0, h_0, \) and \( n_0 \) are the values of \( m, h, \) and \( n \) at that time.

Using this procedure, the simplified model generated action potentials similar to the HH model (see Fig. 1, right panel). The time course of the activation variables \( m, h, \) and \( n \) was also comparable in both models. The optimal values of parameters were estimated by fitting expressions 2.5 and 2.6 directly to the original HH model. Using a simplex procedure (Press et al., 1986), and starting from different initial values of the parameters, the fitting led to a unique estimate of the pulse duration \((0.6 \pm 0.08 \text{ ms})\) and of the membrane threshold \((-50.1 \pm 0.3 \text{ mV})\); other parameters were as in Fig. 1).

The computational efficiency of the pulse-based mechanism is essentially due to the direct estimation of variables \( m, h, n \) from the membrane potential (see equations 2.5 and 2.6). Another factor providing further acceleration is that outside the pulse, an expression similar to equation 2.5 can be written for \( m^3 \) and \( n^4 \), which greatly reduces the number of multiplications since no exponentiation is calculated.

### 3 Comparison of Pulse-Based Models with Other Mechanisms

The important point of pulse-based (PB) models is that they provide a good approximation of dynamical properties of firing behavior described by the HH mechanism. These properties were tested in three ways: repetitive firing, random firing, and network behavior. First, the optimized PB model was compared to HH and IAF mechanisms following injection of current pulses of increasing amplitudes (see Fig. 2). Pulse-based models gave an excellent approximation of interspike intervals at different firing frequencies, the spike shape, and the rise and decay of the membrane potential. On the other hand, the IAF model taken in the same conditions gave a poor approximation (see Fig. 2). For IAF models, the threshold or the absolute refractory period affected the frequency of firing, but variations of these parameters failed to generate the correct firing frequencies.

Second, PB models were tested in the case of random synaptic bombardment in a single-compartment cell having AMPA and GABA\(_A\) postsynaptic receptors (see Fig. 3). The conductance of synaptic currents was chosen such that most postsynaptic potentials were subthreshold, occasionally leading to firing. This subthreshold dynamics is surprisingly irrelevant for spiking as PB and IAF mechanisms behaved very closely to the HH model (see Fig. 3), with spike timing differences of \(1.1 \pm 1.8 \text{ ms} \) (average ± standard deviation) and near coincidence of correspondingly spiked. The condition in
Hodgkin–Huxley

Pulse–based

Integrate–and–fire

Figure 3: Comparison of pulse-based and original Hodgkin-Huxley models using random synaptic bombardment. Top panel: Single compartment model (same parameters as in equation 1) with 100 excitatory (AMPA-mediated) and 10 inhibitory (GABA_A-mediated) synaptic inputs. Synaptic currents were described by kinetic models (Destexhe et al., 1997) and had maximal conductances of 1.5 and 6 nS for each simulated AMPA- and GABA_A-mediated contact, respectively. Each synaptic input was random (Poisson distributed) with a mean rate of 50 Hz. Middle panel: Same simulation with action potentials generated using pulse-based models. Bottom panel: Same simulation using integrate-and-fire mechanisms.

in vivo and in vitro recordings (Steriade et al., 1993). This behavior was successfully reproduced by the model using either HH equations or PB models (see Fig. 4). As in the case of synaptic bombardment, action potential timing
| Hodgkin-Huxley | Pulse-based | Integrate-and-fire |
Table 1: Computational Performance of Different Methods for Generating Action Potentials.

<table>
<thead>
<tr>
<th>Method</th>
<th>NEURON (relative CPU time)</th>
<th>Minimal C Code (relative CPU time)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DE</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>DEo</td>
<td>0.32</td>
<td>0.45</td>
</tr>
<tr>
<td>PB</td>
<td>0.25</td>
<td>0.17</td>
</tr>
<tr>
<td>IAF</td>
<td>0.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Note: A single-compartment cell comprising passive currents, 1 nA injected current, and a model for action potentials was simulated. Different models for action potentials were: DE: Hodgkin-Huxley model described by differential equations; DEo: same equations solved using optimized algorithms; PB: pulse-based model; IAF: simple integrate-and-fire model. A backward Euler integration scheme was used with a time step of 0.025 ms over a total simulated time of 50 seconds. The equations were solved using either the NEURON simulator (Hines, 1993) or directly in C code (minimal code for solving the equations without graphic interface; the exact same algorithms and optimizations as in NEURON were used). Codes are available on request.
<sup>a</sup> IAF models could not be implemented optimally in NEURON.

4 Discussion

This article has presented a novel method to approximating the dynamics of
differ from IAF models because they take into account the decay of variables $m$, $h$, and $n$ in between spikes, which has a determinant influence on repetitive firing at high frequencies. In IAF models, the membrane is reset instantaneously after a spike to a hyperpolarized level. In PB models, the reset occurs through the activation of the delayed-rectifier current, which has an effect over a longer period of time due to the relatively slow decay of the...
formance of IAF models (see Table 1). However, this increase of efficiency could be minimal in the case of network simulations where action potentials represent only a small fraction of the computation time. On the other hand, if PB models could be used in conjunction with pulse-based mechanisms,


