Conductance-Based Integrate-and-Fire Models

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An alternative approach was to simplify the process of action potential
generation by representing the neuron as an integrate-and-fire (IAF) de-
vice (see Arbib, 1995). In this case, the neuron produces a spike when its
membrane potential crosses a given threshold value and the membrane is
instantaneously reset to its resting level. Although this type of model has
been extensively used for representing large-scale neuronal networks, an
important drawback is that it neglects the variations of Na\(^+\) and K\(^+\) con-
ductances, which may have important effects in spike generation (Mainen,
1995). Moreover, central neurons have been shown to contain a large spec-
trum of other intrinsic currents which have a determinant effect on firing
Hodgkin-Huxley

$V$

$\alpha_m$

$\beta_m$

$\alpha_h$

$\beta_h$

$\alpha_n$

$\beta_n$

$m$

Pulse-based
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:

\[
\begin{align*}
\alpha_m &= 0, & \beta_m &= \beta_M \\
\alpha_h &= \alpha_H, & \beta_h &= 0 \\
\alpha_m &= 0, & \beta_h &= \beta_N
\end{align*}
\]

(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 \(+70\) mV and using Table...
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 ± 0.08 ms) and of the membrane threshold (−50.1 ± 0.3 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.
Figure 2: Comparison of repetitive firing with three different models. A single compartment cell (same parameters as in equation 1) was simulated with injection of three depolarizing current pulses of increasing amplitudes (1 nA, 2 nA, and 4 nA). Top trace: Simulation using the original Hodgkin-Huxley model. Middle trace: Simulation using pulse-based equations (identical parameters as in Figure 1, right). Bottom trace: Simple integrate-and-fire model (the spike consisted of a sudden rise to 50 mV, immediately followed by a reset to −90 mV and an absolute refractory period of 1.5 ms; same threshold as the pulse-based mechanism). All models had identical passive properties.

thalamic reticular (RE) neurons (Destexhe, Bal, McCormick, & Sejnowski, 1996). These neurons have a set of intrinsic sodium, potassium, calcium, and cationic currents, allowing the cell to produce different types of bursts of action potentials (see Steriade, McCormick, & Sejnowski, 1993). Although single TC and RE cells do not necessarily generate sustained oscillations, interconnected TC and RE cells with excitatory (AMPA-mediated) and inhibitory (GABAergic) synapses can display spindle oscillations, as seen from
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<sub>A</sub>-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<sub>A</sub>-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
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(^a)</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.
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 variable $n$. This is the main factor that affected the frequency of firing in Figure 3. However, we cannot exclude the possibility that more sophisticated
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 applied to other types of currents, such as synaptic currents (Destexhe et al., 1994a; Lytton, 1996), then this approach could provide a considerable acceleration of computation time.

How can PB models be improved? An obvious improvement would be to apply the PB approximation to a simplified model of action potentials, such as that of Hindmarsh and Rose (1982), leading to PB models with fewer variables. Another improvement would be to add a relative refractory period or a variable threshold, for example, by making the threshold depend on the value of the inactivation variable $h_i$. More optimal values of rate constants than equation 2.4 could also be obtained by fitting the model directly to HH equations using several templates, such as that of Figs. 2.


Rinzel, J. (1985). Excitation dynamics: Insights from simplified membrane mod-