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# Analytical approaches to the study of integrate-and-fire neurons

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Integrate-and-fire (IF) models permit the study of spiking behavior for many types of neuron without the need to model the specific spiking mechanism (e.g. using the Hodgkin-Huxley equations). This simplification has the advantage, not only of being less computationally expensive for simulation, but also of allowing useful mathematical techniques to be employed, such as the Gaussian approximation, the renewal equation and the Fokker-Planck equation. These particular techniques are useful for the study of spiking behavior with noisy inputs, an occurrence that is common in the central nervous system. The strengths of pursuing an analytical approach over simulation include computational efficiency, the potential to provide novel insights into the effect and significance of model parameters, and a powerful means to study changes in model behavior when parameters are varied within biologically plausible ranges. An analytical approach has been successfully applied in a number of studies including autoassociative memory [1], cortical background activity [2], synfire chains [5] and gain modulation [3]. For the approach to have wider applicability it will be essential to extend existing techniques so that they may be applied to situations of increasing biological realism and interest. In this poster results are presented that extend analysis of IF neurons receiving Poisson input to the situation in which synapses are (1) conductance-based (i.e. incorporating reversal potentials) and (2) also have finite time constants.

Early work on the spiking statistics of IF neurons considered the case where synaptic input was modeled as an instantaneous (delta function) current injection. This led to the so-called Siegert formula, which relates the mean spiking-rate of the neuron to the mean and variance of the membrane potential, the threshold and the membrane time constant. In this poster, two spiking-rate formulae are presented that incorporate instantaneous conductance-based synapses; one derived from the renewal equation and a Gaussian approximation and the other derived from the Fokker-Planck equation. Although the Fokker-Planck approach is expected to provide a better approximation, the renewal approach most clearly shows the main effect of introducing conductance based synapses: namely to introduce an effective membrane time constant that is less than the passive time constant due to the activation of the synapses. Simulations show that both formulae provide good approximations when the synaptic time constant is small compared to threshold.

The main difficulty in incorporating synapses with finite time constants is that the noise in the membrane potential becomes colored (i.e. correlated in time), which violates the Markovian assumption underlying both the Fokker-Planck and renewal approaches. A Fokker-Planck equation may still be formulated in this case, but

with an extra dimension for each synapse-type to be modeled, which in turn leads to difficulties because detailed balance is violated, thus spoiling the symmetry on which the solution of the one dimensional equation is based. Recently methods were developed that allow approximate solutions of the higher dimensional equations by expanding in the square root,  $\kappa$ , of the ratio of synaptic to membrane time constant [4].  $\kappa$  measures how colored the noise is, so that  $\kappa = 0$  implies white noise, while larger values indicate that the correlations in time are of increasing range. The hierarchy of equations resulting from the expansion can be approximately solved to first order by finding solutions that exactly fulfill the boundary conditions associated with either the reset or the threshold potential and asymptotically matching them to a solution that applies when potential is far away from either reset or threshold. The solution near the reset potential is straight-forward, however the solution near threshold is given by a half-range expansion problem in which boundary conditions must be satisfied on half the boundary using only half the eigenvectors. Brunel has used this entire approach ( $\kappa$  expansion through to half range expansion) to obtain a formula for the mean firing rate when synapses are current-based [2]. Here the approach is adapted to the case in which separate excitatory and inhibitory synapses are conductance-based. Results from both cases show that, to first order, the effect of a finite synaptic time constant may be interpreted as giving an effective threshold and reset potential, which are both greater than their normal values:  $V_{eff}^T = V^T + \alpha\kappa\sigma$  and  $V_{eff}^R = V^R + \alpha\kappa\sigma$ , where  $V^T$  and  $V^R$  are the threshold and reset values of the membrane potential (respectively),  $\sigma$  is the standard deviation of the membrane potential and  $\alpha$  is a constant that depends on the ratio of the excitatory to inhibitory synaptic time constants. Simulations show that the formula provides a good approximation provided  $\kappa < 0.3$ . For larger values of  $\kappa$  the deviation between formula and simulation becomes significant and higher order corrections are required.

The results presented here incorporate biological details that can be significant to the firing statistics of IF neurons. They provide tools that improve the quantitative accuracy of neuronal models and allow phenomena to be investigated that were inaccessible with simpler models.

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