Numerical Evaluation of the Siegert Formula

We want to determine the firing rate of an LIF neuron with exponentially decaying postsynaptic currents driven by a mean input μ and fluctuations of strength σ . For small synaptic time constant τ_s compared to the membrane time constant τ_m , it is given by the "Siegert" [1]

$$\phi(\mu,\sigma) = \left(\tau_{\rm ref} + \tau_{\rm m}\sqrt{\pi}I(\tilde{V}_{\rm th},\tilde{V}_{\rm r})\right)^{-1}$$
(1)

$$I(\tilde{V}_{\rm th}, \tilde{V}_{\rm r}) = \int_{\tilde{V}_{\rm r}}^{V_{\rm th}} e^{s^2} (1 + \operatorname{erf}(s)) ds$$
⁽²⁾

with the refractory period $\tau_{\rm ref}$, the shifted and scaled threshold voltage $\tilde{V}_{\rm th} = \frac{V_{\rm th}-\mu}{\sigma} + \frac{\alpha}{2}\sqrt{\frac{\tau_{\rm s}}{\tau_{\rm m}}}$, the shifted and scaled reset voltage $\tilde{V}_{\rm r} = \frac{V_{\rm r}-\mu}{\sigma} + \frac{\alpha}{2}\sqrt{\frac{\tau_{\rm s}}{\tau_{\rm m}}}$, and the constant $\alpha = \sqrt{2}|\zeta(1/2)|$ where $\zeta(x)$ denotes the Riemann zeta function.

Numerically, the integral in Eq. (2) is problematic due to the interplay of e^{s^2} and erf(s) in the integrand. The main trick here is to use the scaled complementary error function

$$\operatorname{erf}(s) = 1 - e^{-s^2} \operatorname{erfcx}(s) \tag{3}$$

to extract the leading exponential contribution. For positive s, we have $0 \leq \operatorname{erfcx}(s) \leq 1$, i.e. the exponential contribution is in the prefactor e^{-s^2} which nicely cancels with the e^{s^2} in the integrand.

Strong Inhibition

We have to consider different cases; let us start with strong inhibitory input such that $0 < \tilde{V}_{\rm r} < \tilde{V}_{\rm th}$ or equivalently $\mu < V_{\rm r} + \frac{\alpha}{2}\sigma\sqrt{\frac{\tau_{\rm s}}{\tau_{\rm m}}}$. In this regime, the error function in the integrand is positive. Expressing it in terms of $\operatorname{erfcx}(s)$, we get

$$I(\tilde{V}_{\rm th}, \tilde{V}_{\rm r}) = 2 \int_{\tilde{V}_{\rm r}}^{\tilde{V}_{\rm th}} e^{s^2} - \int_{\tilde{V}_{\rm r}}^{\tilde{V}_{\rm th}} \operatorname{erfcx}(s) ds.$$

The first integral can be solved in terms of the Dawson function D(s), which is bound between ± 1 and conveniently implemented in scipy; the second integral gives a small correction which can be evaluated using Gauss-Legendre quadrature [2]. We get

$$I(\tilde{V}_{\rm th}, \tilde{V}_{\rm r}) = 2e^{\tilde{V}_{\rm th}^2} D(\tilde{V}_{\rm th}) - 2e^{\tilde{V}_{\rm r}^2} D(\tilde{V}_{\rm r}) - \int_{\tilde{V}_{\rm r}}^{\tilde{V}_{\rm th}} \operatorname{erfcx}(s) ds$$

We extract the leading contribution $e^{ ilde{V}_{
m th}^2}$ from the denominator and arrive at

$$\phi(\mu,\sigma) = \frac{e^{-\tilde{V}_{\rm th}^2}}{e^{-\tilde{V}_{\rm th}^2}\tau_{\rm ref} + \tau_{\rm m}\sqrt{\pi}\left(2D(\tilde{V}_{\rm th}) - 2e^{-\tilde{V}_{\rm th}^2 + \tilde{V}_{\rm r}^2}D(\tilde{V}_{\rm r}) - e^{-\tilde{V}_{\rm th}^2}\int_{\tilde{V}_{\rm r}}^{\tilde{V}_{\rm th}}\operatorname{erfcx}(s)ds\right)}$$
(4)

as a numerically safe expression for $0 < \tilde{V}_{\rm r} < \tilde{V}_{\rm th}$

Strong Excitation

Now let us consider the case of strong excitatory input such that $\tilde{V}_{\rm r} < \tilde{V}_{\rm th} < 0$ or $\mu > V_{\rm th} + \frac{\alpha}{2}\sigma\sqrt{\frac{\tau_{\rm s}}{\tau_{\rm m}}}$. In this regime, we can change variables $s \to -s$ to make the domain of integration positive again. Using $\operatorname{erf}(-s) = -\operatorname{erf}(s)$ as well as $\operatorname{erfcx}(s)$, we get

$$I(\tilde{V}_{\rm th}, \tilde{V}_{\rm r}) = \int_{|\tilde{V}_{\rm th}|}^{|\tilde{V}_{\rm r}|} \operatorname{erfcx}(s) ds.$$

In particular, there is no exponential contribution involved in this regime. Thus, we get

$$\phi(\mu,\sigma) = \frac{1}{\tau_{\rm ref} + \tau_{\rm m}\sqrt{\pi} \int_{|\tilde{V}_{\rm th}|}^{|\tilde{V}_{\rm r}|} \operatorname{erfcx}(s)ds}$$
(5)

as a numerically safe expression for $\tilde{V}_{\rm r} < \tilde{V}_{\rm th} < 0.$

Intermediate Regime

In the intermediate regime, we have $\tilde{V}_r \leq 0 \leq \tilde{V}_{th}$ or $V_r + \frac{\alpha}{2}\sigma\sqrt{\frac{\tau_s}{\tau_m}} \leq \mu \leq V_{th} + \frac{\alpha}{2}\sigma\sqrt{\frac{\tau_s}{\tau_m}}$. Thus, we split the integral at zero and use the previous steps for the respective parts to get

$$I(\tilde{V}_{\rm th}, \tilde{V}_{\rm r}) = 2e^{\tilde{V}_{\rm th}^2} D(\tilde{V}_{\rm th}) + \int_{\tilde{V}_{\rm th}}^{|\tilde{V}_{\rm r}|} \operatorname{erfcx}(s) ds.$$

Note that the sign of the second integral depends whether $|\tilde{V}_r| > \tilde{V}_{th}$ (+) or not (-). Again, we extract the leading contribution $e^{\tilde{V}_{th}^2}$ from the denominator and arrive at

$$\phi(\mu,\sigma) = \frac{e^{-\tilde{V}_{\rm th}^2}}{e^{-\tilde{V}_{\rm th}^2}\tau_{\rm ref} + \tau_{\rm m}\sqrt{\pi}\left(2D(\tilde{V}_{\rm th}) + e^{-\tilde{V}_{\rm th}^2}\int_{\tilde{V}_{\rm th}}^{|\tilde{V}_{\rm r}|}\operatorname{erfcx}(s)ds\right)}$$
(6)

as a numerically safe expressions for $\tilde{V}_{\rm r} \leq 0 \leq \tilde{V}_{\rm th}$

Gauss-Legendre Quadrature

To solve the remaining integral of $\operatorname{erfcx}(s)$ numerically, we use Gauss-Legendre quadrature [2]. By construction, Gauss-Legendre quadrature of order k solves integrals over polynomials of order k on the interval [-1, 1] exactly. Thus, it gives very good results if the integrand is well approximated by a polynomial. To apply it, one simply transforms the domain of integration

$$\int_{b}^{b} f(s)ds = \frac{b-a}{2} \int_{-1}^{1} f\left(\frac{b-a}{2}u + \frac{b+a}{2}\right) du \approx \frac{b-a}{2} \sum_{i=1}^{k} w_{i} f\left(\frac{b-a}{2}u_{i} + \frac{b+a}{2}\right)$$

where the u_i are the roots of the Legendre polynomial of order k and the w_i appropriate weights such that a polynomial integrand is integrated exactly.

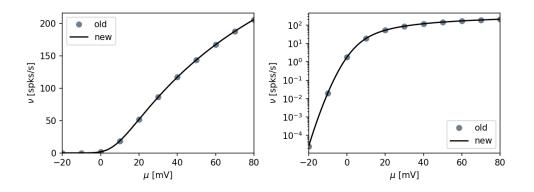


Figure 1: Comparison of the new implementation based on Eq. (4)—Eq. (6) against the implementation used for the tn_corr lecture for $\sigma = 10$ mV. Order of Gauss-Legendre quadrature: 100. Further parameters: $\tau_{\rm m} = 10$ ms, $\tau_{\rm s} = 0$ ms, $\tau_{\rm ref} = 2$ ms, $V_{\rm th} = 20$ mV, $V_{\rm r} = 0$ mV.

Results

This procedure, i.e. Eq. (4)—Eq. (6), seems to work quite nicely, see Fig. 1. Also beyond the case shown, there were no differences visible in the numerical results. Even the case $\sigma \ll 1$, where the old implementation eventaully breaks, works flawlessly. Conveniently, the new implementation is more than two orders of magnitude faster because it is fully vectorised.

References

- [1] N. Fourcaud and N. Brunel, Neural Comput. 14, 2057 (2002).
- [2] W. H. Press, S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery, Numerical Recipes: The Art of Scientific Computing (Cambridge University Press, 2007), 3rd ed., ISBN 0-521-88068-8.