Computing A(f) and $Q_{ii}(f)$

In this section, we present the theoretical techniques that we use to compute the spike train cellular response function A(f) and power spectrum $Q_{ii}(f)$ for the ELL model; these techniques are fully presented elsewhere [1] and we refer the reader there for further details.

Consider a leaky integrate and fire neuron model driven by a combination of a weak signal s(t) and a white noise forcing $\xi(t)$:

$$\frac{dV}{dt} = \frac{\mu - V}{\tau} + \epsilon s(t) + \sigma \xi(t), \tag{1}$$

where μ is a drift term, σ is the intensity of a stochastic process, and $\epsilon \ll \sigma$. The voltage distribution p(V,t) associated with the Eq. 1 obeys the Fokker-Planck equation [2]:

$$\frac{\partial p}{\partial t} = -\frac{\partial j}{\partial V} = \frac{\partial}{\partial V} \left[\left(\frac{V - \mu}{\tau} - \epsilon s(t) \right) p \right] + \frac{\sigma^2}{2} \frac{\partial^2 p}{\partial V^2},\tag{2}$$

where j(V,t) is the probability flux. The boundary conditions for the probability distribution and flux at threshold are $p(V_{th}) = 0$ and $j(V_{th}, t) = r(t)$, where r(t) is the firing rate. Furthermore, the flux obeys j(V,t) = r(t) for $V \in [V_{re}, V_{th}]$ and 0 otherwise, when the system is stationary.

For $\epsilon = 0$ we obtain the steady state distribution $p_0(V)$ and flux $j_0(V)$ via:

$$\frac{\partial p_0}{\partial V} = -\frac{2}{\sigma^2} \left[j_0 + \frac{1}{\tau} (V - \mu) p_0 \right],$$

$$\frac{\partial j_0}{\partial V} = r_0 \delta(V - V_{re}) - r_0 \delta(V - V_{th}).$$
(3)

Numerically solving the above equations and using the normalization condition $\int_{-\infty}^{Vth} p_0(V) dV = 1$, we can solve for the steady state firing rate r_0 .

To compute the second-order spike train statistics, we consider the time-dependent Fokker-Planck equation in the Fourier domain:

$$\frac{\partial P}{\partial V} = -\frac{2}{\sigma^2} \left[J + \frac{1}{\tau} (V - \mu) P \right],$$

$$\frac{\partial J}{\partial V} = -2\pi i f P - R(f) \delta(V - V_{th}) + R(f) \delta(V - V_{re}),$$
(4)

where P(V, f), J(V, f), and R(f) denote the Fourier transform of p(V, t), j(V, t), and r(t), respectively. Further, R(f) is computed with initial condition $V = V_{re}$. Solving this equation yields the Fourier transform of the first passage time density D(f) [1]. For the stationary case, we compute the power spectrum using a well known relation from renewal theory relating passage time statistics to autocovariance [3]:

$$Q_{ii}(f) = r_0 \left(1 + 2\Re \left[\frac{D(f)}{1 - D(f)} \right] \right), \tag{5}$$

where $\Re[\cdot]$ denotes the real component.

Finally, we compute the cellular response A(f). We let $s(t) = e^{2\pi i f t}$ to provide a weak, periodic input to the neuron. Decomposing the probability density, flux, and firing rate into steady state and modulated components:

$$p = p_0 + p_1 e^{2\pi i f t}, \ j = j_0 + j_1 e^{2\pi i f t}, \ r = r_0 + r_1 e^{2\pi i f t},$$
(6)

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and then solving the Fokker-Planck equation in the Fourier domain for the time-dependent terms, we obtain a new set of equations:

$$\frac{\partial P_1}{\partial V} = -\frac{2}{\sigma^2} \left[J_1 + \frac{1}{\tau} (V - \mu) + \epsilon P_0 \right],$$

$$\frac{\partial J_1}{\partial V} = -2\pi i f P_1 - R_1 \delta (V - V_{re}),$$
(7)

with boundary conditions $P_1(V_{th}, f) = 0$, and importantly the flux perturbation at spike threshold:

$$J_1(V_{th}, f) = A(f).$$
 (8)

These equations were solved numerically [1] obtaining a solution for the cellular response A(f).

The above theory provided the components $Q_{ii}(f)$ and A(f) required to compute the spike count correlation coefficient between the pair of superficial ELL neuron outputs.

References

- Richardson M (2008) Spike-train spectra and network response functions for non-linear integrateand-fire neurons. Biol Cybern 99: 381–392.
- 2. Risken H (1996) The Fokker-Planck equation: Methods of solution and applications. New York: Springer, 488 pp.
- 3. Cox DR, Isham V (1980) Point processes. London: Chapman and Hall, 206 pp.