Linear LIF model for gamma distributions of ISIs

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Abstract

We found that cortical neurons in a rat premotor area called the Frontal Orienting Fields (FOF) have ISI distributions well matched by Gamma(k, θ), where k averaged 3.07 ± 1.09 (mean $\pm$ sd). The gamma shape estimator which we use (**k**) is based on the statistics of ratios of pairs of consecutive intervals and can be easily fit nonparametrically as a function of either time in the trial or firing rate (**r**) or both. The **k** estimator is more robust to outliers than estimators obtained from probabilistic models fitted with GLMs. We found that **k**(**r**) was approximately constant for 329/504 neurons, increasing for 135/504 neurons and had a peak for 44/504 neurons. There were also significant interactions between behavior and regularity, not accounted for by firing rate modulations alone. For example, some neurons fired more regularly during the execution of movements. Others fired more regularly when a reward was delivered but not when it was absent. We then showed that a simple linear leaky integrate and fire (LLIF) model with a calcium activated K$^+$ current (I_{AHP}) and a relatively long membrane time constant accounts well for gamma distributions of ISIs of a wide range of shapes and means. By fitting a single parameter of the AHP-LLIF model we obtain a model with the properties: 1) **k**(**r**) is constant unless 2) τ_{AHP} is too short or too long, in which cases **k**(**r**) is increasing and peaked respectively; 3) the scale of the synaptic noise sets **k** but has little influence on **r**. Thus, one fitted parameter qualitatively accounts for the entire heterogeneous range of observed FOF firing statistics.

In a theoretical framework, assuming an arbitrary stochastic LLIF neuron defined by $\tau_m dV/dt = -(V - E_L) + f(t) + dW$ with known synaptic noise statistics dW, time constant τ_m and ISI distribution $p(t)dt$ but unknown input $f(t)$ and unknown threshold V_t, we show how to numerically determine $f(t)$ and V_t. For $p(t) \sim$ Gamma(k, θ) we obtained $f(t) \approx -A \exp(-t/B)$, $A, B > 0$ which prompted us to model $f(t)$ as a negative AHP current. Conversely, we produced gamma distributions of various shapes and means from the AHP-LLIF model defined by $\tau_m dV/dt = -(V - E_L) - A \exp(-t/\tau_{AHP}) + dW$ when $\tau_{AHP} \in [10, 40]$ ms and $\tau_m \in [40, 100]$ ms, but not for other settings of the time constants.

We determined the Fisher information and the Shannon channel capacity for AHP-LLIF neurons and found that in principle both measures of coding efficiency increase indefinitely with the amplitude and duration of I_{AHP}, even though we kept the mean firing rates fixed. We postulate that if the AHP-LLIF model is correct for real neurons, there must exist evolutionary disadvantages to having regularly firing neurons. One commonly held assumption is that regularly firing neurons respond sluggishly to quickly changing inputs. The AHP-LLIF neuron (a population of these) in fact responds quickly and accurately to rising transients (as a population), but inaccurately to falling transients and to fluctuating high inputs.

The AHP-LLIF model predicts that sustained firing should enhance the K$^+$ current by accumulation of residual calcium, thereby increasing **k**. We saw this trend clearly in 69% of the FOF neurons as an upwards shift of the fitted **k**(**r**) curves. The average size of the effect was a 24% increase of **k**.
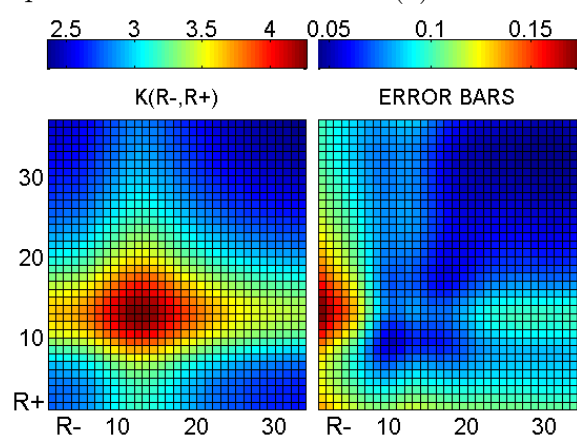
k fitted as a function of $\mathbf{r}_-$ and $\mathbf{r}_+$ for a single neuron in a cubic spline basis with no interaction terms. Error bars were computed by bootstrapping.

We also fit **k** as a function of $\mathbf{r}_-$ (**r** just before the time of the observation) and $\mathbf{r}_+$ (**r** just after the observation). These fits revealed peaks in $\mathbf{k}(\mathbf{r}_-, \mathbf{r}_+)$ for 40% of the neurons (see figure for one such example). The peaks were clustered around $(15.34, 15.60) \pm (4.38, 4.20)$ Hz (5 outliers excluded). We are unsure at the moment whether the AHP-LLIF model alone can capture the full amplitude of these peaks.

On top of firing rate modulations and modulations from sustained firing, we also found interactions between **k** and behavior. We believe the interactions are caused by different network states which result in different dW noise inputs. Scaling dW in the model results in scaling **k** with little effect on **r**. Therefore **k** provides to us (and to all downstream neurons) a measure of the variance of the input, just like **r** provides a measure of the mean input. This might or might not have a computational role for networks of neurons, but for us $(\mathbf{r}(t), \mathbf{k}(t))$ is a useful joint measure of single cell activity which can be correlated with behavior.