Approximating the response-stimulus correlation for the integrate-and-fire neuron

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Abstract

The reverse correlation and its analytical counterpart, the response-stimulus correlation, describe the expected stimulus just before a present response. With growing complexity of the neuron model, calculating the response-stimulus correlation becomes more and more difficult. We present an approximation of this measure for the integrate-and-fire neuron with reversal potentials and introduce some of the calculations involved. [1]

Key words: reverse correlation, response-stimulus correlation, Itô calculus, leaky integrate-and-fire neuron, reversal potentials

Introduction

The response-stimulus correlation (RSC) is a function describing the probability of a stimulus spike to occur before a response spike and hence is a measure for the significance of the response. In this paper an approximation of the RSC and an introduction to some of the involved calculations are presented. The paper is structured the following way: after this introduction a short comment on the significance of RSC and reverse correlation as well as a brief scetch of the taken approach are made. In the model section the calculations are shown in more detail and an expression for the approximated reverse correlation is obtained for the integrate-and-fire neuron with reversal potentials driven by white noise. In the results section the quality of the approximation is demonstrated and in the last section the main results are summed up and some implications and open questions are addressed.

A neuron has fired a response spike at a certain time $t_0 = 0$. What is the probability that the neuron has received a stimulus spike at $\Delta t - t_0$? This

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probability, expressed as a function of Δt, is the reverse correlation. It can be obtained experimentally by averaging the time cause of a measured stimulus before a response spike, and it is used to determine the kind of stimulus to which a neuron is sensitive. Because the term "reverse correlation" has a fixed connotation hinting at an experimental context we will use the term response-stimulus correlation (RSC) if we refer to a solely analytical background. Otherwise the terms are synonymous.

The RSC is an important factor in the inner workings of a neuron. As well as determining the weight change in spike-timing based learning mechanisms like STDP [Song et al., 2000] it is involved in shaping the frequency-dependent transfer function of a neural population [W. Gerstner, 2002]. It is a general measure for the significance of a response spike, and can be interpreted as a measure for the sensitivity of the responding neuron to variations of its stimulus in amplitude and time [P. Dayan, 2001]. To our knowledge there has been only one notable attempt to obtain the reverse correlation analytically [Gerstner, 2000], using a SRM model with a population approach.

The suggested approximation is derived the following way: the Itô stochastic differential equation (SDE) for the free membrane potential is solved and the expectation of the solution is given. Simulations show that the expected free membrane potential is time-symmetric. Using this symmetry the flow of the potential before a spike is followed backwards in time, and the mean conditional conductance is extracted. From this expected conductance, a measure for the number of stimulus spikes to be expected at $\pm\Delta t$ can be obtained, which is equivalent to the RSC.

Derivation of the RSC

An integrate-and-fire neuron with reversal potentials is used which is expressed as a differential equation [W. Gerstner, 2002]. If the synaptic conductance incorporates some form of noise, this differential equation becomes a stochastic differential equation (SDE). To be consistent with the usual notation for SDEs and to denote the noisyness of the increments, the stochastic variable G_t^i is introduced. Let g_i^{syn} be the sum of all single-synapse conductances with the same reversal potential v_i, then G_t^i describes the cummulative conductance of synapse type i over time, i.e. $G_t^i = \int_0^t g_t^i dt$. The membrane potential then satisfies the Itô SDE (which is interpreted as an integral equation on a filtered probability space $\{\Omega, \mathcal{F}, (\mathcal{F}_t)_{0\leq t\leq\infty}, \mathcal{P}\}$)

$$\tau dV_t = (v_m - V_t)dt + R\sum_i (v_i - V_t)dG_t^i \tag{1}$$

where τ is the time constant of the membrane, the membrane resistance R is set to $\frac{ms}{\tau}\Omega$, v_m is the membrane's resting potential, v_i the reversal potential of synapse type i and G_t^i the cummulative conductance of synapse type i. In case the potential V_t hits the threshold v_θ it is reset to a reset value V_0. Note that if G_t has independent increments, V_t becomes a diffusion-process, which includes Markov and renewal properties.

A typical cortical neuron fires at very low rates [Baddeley et al., 1997], therefore the possibility that the potential exceeds the threshold in the vicinity of t_0 is neglected. To find the path after a spike at $t_0 = 0$ it is then sufficient to solve (1) "as it is", without the threshold condition (free membrane potential). If G_t^i is a semimartingale, this can be done using Itô calculus. The obtained explicit solution is:

$$
\begin{aligned}
V_t &= \exp -\phi_t \left(V_0 + \int_0^t \exp \phi_t \, d\psi_t \right); \qquad (2) \\
&\phi_t = \frac{1}{\tau} t + \sum_i G_t^i + \frac{1}{2} \sum_i \left[G^i, G^i \right]_t \\
&\psi_t = \frac{1}{\tau} v_m t + \sum_i v_i G_t^i + \sum_i v_i \left[G^i, G^i \right]_t
\end{aligned}
$$

where $[X, Y]_t$ denotes the covariation process of two stochastic variables X_t and Y_t [Protter, 1995], V_0 is the potential just after the spike is emitted at t_0, also called reset volage. The expected free membrane potential $\bar{V}_t := \mathrm{E}(V_t)$ is

$$
\begin{aligned}
\bar{V}_t &= \exp -\bar{\phi}_t \left(V_0 + \int_0^t \exp \bar{\phi}_s \, d\bar{\psi}_s \right); \qquad (3) \\
&\bar{\phi}_t = \frac{1}{\tau} t + \sum_i \bar{G}_t^i \\
&\bar{\psi}_t = \frac{1}{\tau} v_m t + \sum_i v_i \bar{G}_t^i
\end{aligned}
$$

where $\bar{G}_t^i := \mathrm{E}(G_t^i)$ is the expected cummulative conductance.

Making a prediction about the mean stimulus at a time lag $-\Delta t$ before the response spike involves looking into the past. Given a stable stimulus, V_t will converge to a static expectation $\bar{V}_\infty$. With no further constraints, $\bar{V}_t$ can be expected to rest at this static expectation - the longer the time lag $-\Delta t$ into the past, the higher the probability of finding the potential at $\bar{V}_\infty$. Moving backwards in time, the membrane potential is drawn to $\bar{V}_\infty$ just in the same way as it is when moving into the future. Therefore when starting at $V_{-0} = V_{+0} = v_\theta$, trajectories into past and future should look the same - V_t is even, a thought which is sustained by simulations (figure 1). Because the derivative of an even function is odd, the membrane voltage and its derivative satisfy

$$\bar{V}_{-t} = \bar{V}_t; \quad \bar{V}_{\pm 0} = v_\theta \tag{4}$$

$$d\bar{V}_{-t} = -d\bar{V}_t; \quad \bar{V}_{\pm 0} = v_\theta. \tag{5}$$

Relying on the time symmetry of V_t, it is easy to approximate the probability for a stimulus to have occured at time $-t$ before the response. The relations (4) and (5) and the condition $\bar{V}_0 = v_\theta$ are inserted into (1), which yields the time reversed free membrane potential. Rearranging to get an expression for the sum of all currents gives

$$\sum_i (v_i - V_t) d\mathcal{G}^i_{\pm\Delta t} \;=\; \pm d\bar{V}_{\Delta t} - \frac{1}{\tau}(v_m - \bar{V}_{\Delta t}), \tag{6}$$

where $\mathcal{G}^i_{\pm\Delta t}$ is the expected conditional cummulative conductance given a response at $t_0 = 0$ and Δt is the positive time difference between stimulus and response $\Delta t = |t_r - t_s|$. For the sake of simplicity, calculations will be continued with one synapse type only (excitatory synapses dG^{ex}_t and a reversal potential v_{ex}). Dividing (6) by $(v_{ex} - V_t)$ then results in an extremely simple formula for the spike-triggered conductance $d\mathcal{G}^{ex}_{\pm\Delta t}$:

$$d\mathcal{G}^{ex}_{\pm\Delta t} \;=\; \frac{\pm d\bar{V}_{\Delta t} - \frac{1}{\tau}(v_m - \bar{V}_{\Delta t})dt}{v_{ex} - \bar{V}_{\Delta t}} \tag{7}$$

This is the mean conditional conductance given a response spike has occured at $t_0 = 0$. Please note that due to the model-intrinsic jump at t_0, $\bar{V}_{+0} = v_\theta$ and $\bar{V}_{-0}$ equals the reset voltage.

To provide an explicit example for these rather general expressions, excitatory conductances are approximated using a static input plus some white noise, which is provided by the derivative of the Wiener process. The cumulative values for the SDE are thus:

$$\begin{aligned} G_t &= \mu t + \sigma W_t \\ [G, G]_t &= \sigma^2 t \\ \bar{G}_t &= \mu t \end{aligned}$$

Since the Wiener process is a martingale, G_t will be a semimartingale, therefore equation (1) becomes meaningful and the expectations can be calculated. Inserting the above model values into equations (7) and (3) yields:

$$\begin{aligned} \bar{V}_t &= e^{-\bar{\phi}t}(\bar{V}_0 - \bar{V}_\infty) + \bar{V}_\infty; \quad \bar{V}_\infty \;=\; \frac{\bar{\phi}}{\bar{\psi}} \\ \pm d\bar{V}_t &= \mp\bar{\phi}e^{-\bar{\phi}t}(\bar{V}_0 - \bar{V}_\infty)dt \end{aligned}$$

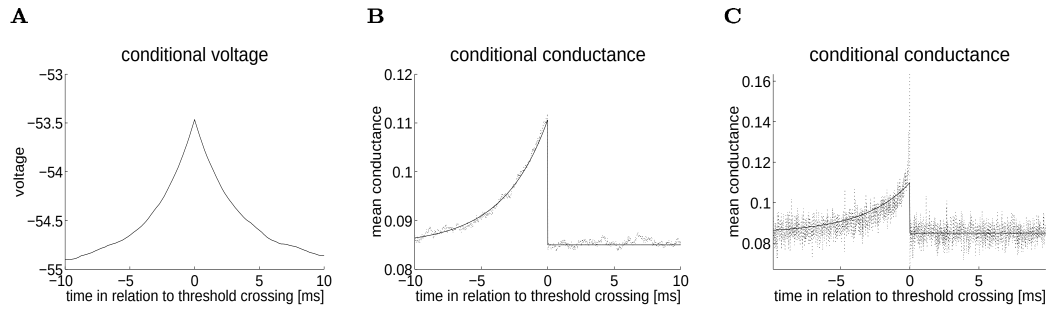

Fig. 1. **Numeric simulation vs. predicted expectation**
A. Voltage trace for simulated free membrane potential. The time symmetry is clearly visible. **B.** Simulated (dots) and predicted mean (line) RSC for free membrane potential. **C.** Simulated (dots) and predicted mean (line) RSC for thresholded membrane potential. All figures where generated using an integrate-and-fire neuron with a time constant of $5ms$, one (excitatory) reversal potential at $-20mV$, and a noisy conductance $dGt = 0.085\frac{pS}{t}\cdot dt + 0.01\frac{pS}{t}\cdot dW_t$. The threshold v_θ was set so that the neuron would fire with a rate of $3Hz$. Simulation results where obtained by averaging equation (2) over 500 sample paths, predictions where made by equation (8) with $V_{-0} = V_{+0} = v_\theta$ for the free membrane potential, $V_{-0} = v_\theta$, $V_{+0} = -60mV$ for the thresholded membrane potential.

with $\bar{\phi} = \frac{1}{\tau} + \mu$ and $\bar{\psi} = \frac{1}{\tau} v_m + \mu v_{ex}$. Finally, the value for the conditional conductance which we get by dividing $d\mathcal{G}^{ex}_{\pm\Delta t}$ by dt will be

$$\bar{g}^{ex}_{\pm\Delta t} = \frac{d}{dt}\mathcal{G}^{ex}_{\pm\Delta t} = \frac{e^{-\bar{\phi}\Delta t}\left(V_{\pm 0} - \bar{V}_\infty\right)\left(1 \mp \bar{\phi}\right) - \frac{1}{\tau}\left(v_m - \bar{V}_\infty\right)}{-e^{-\bar{\phi}\Delta t}\left(V_{\pm 0} - \bar{V}_\infty\right) + v_{ex} - \bar{V}_\infty} \tag{8}$$

As the conductance model doesn't incorporate a decay, (8) states the expected value of the driving noise, which is proportional to the number of stimulus spikes given a response at $t_0 = 0$.

Results

Simulations show the time-symmetry of the conditional membrane potential (figure 1A). The main difference of the hresholded voltage and the free voltage is generated near the threshold. The threshold acts a probability drain which distorts the flow of the conditional voltage in its vicinity. Therefore at the moment just before the response the error of the approximation is at maximum (compare figures 1B and 1C). Obviously the general shape of the RSC is created by the mean flow of the spike triggered voltage, while the spiky part just before the response is shaped by the hard threshold (see figure 1C).

For any $\pm\Delta t \to \pm\infty$ the above expression will result in $d\mathcal{G}^i_{\pm\Delta t} = d\bar{G}_{\Delta t}$, indicating that stimulus spikes are indepentant of the response spike. If V_t is Markov, then the same goes for any $+\Delta t > 0$. This can be seen quite nicely in figure 1C.

Summary

An Itô calculus approach was used to derive an explicit solution of the membrane equation (equation 2) and its expectation (equation 3). The conditional conductance can be stated independantly from the noise model provided G_t is a semimartingale (equation 7), and the RSC can be given explicitly for the case where synaptic conductances are modelled by white noise (equation 8). An example was simulated numerically to demonstrate the quality of the approximation (figure 1).

The advantage of the Itô approach is the possibility to insert any noise model into (1) and calculate the expected solution. Incorporating synaptic conductances driven by an Ornstein-Uhlenbeck process into the neuron model is subject of current work. It is emphasized that the key in obtaining the RSC is the correct approximation of the voltage. Possibly a threshold-aware voltage can be estimated using a corrected voltage distribution as proposed by [W. Gerstner, 2002, p.212]. Other currently investigated questions are the formulation of the RSC for multiple channel types, as well as using correlations in the stimulus.

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