Information transmission by stochastic synapses with short-term depression: neural coding and optimization

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Abstract

The ability of dynamic synapses with short-term depression to transmit the information present in the presynaptic spike train to the postsynaptic neuron is discussed. Both by minimizing the estimation error and by maximizing the information transmitted to the postsynaptic neuron it is found that for Poisson inputs dynamic synapses are not able to estimate the rate better than static ones. However, short-term depression becomes relevant when more realistic temporally correlated spike trains are used as an input. For the simple model of vesicle depletion considered here the optimal vesicle recovery time is rather low, about a hundred milliseconds for realistic values of the input parameters. All these questions are addressed by computing analytically the distribution of intervals between consecutive synaptic responses for arbitrary renewal processes. © 2002 Published by Elsevier Science B.V.

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1. Introduction

The short-term synaptic dynamics of cortical neurons has received considerable attention [5,6] during the last few years. It has been suggested that this dynamics could be used to transmit the information in the presynaptic spike train to the postsynaptic neuron efficiently [3]. If the input train has positive correlations within a time scale τ_c, spikes will carry some redundancy that should not be transmitted if the synaptic resources are to be used optimally. Given the statistical properties of the input trains

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the synaptic parameters could be chosen in such a way that, e.g., the input redundancy is reduced, a condition that would fix their values.

In this work we explore the consequences that requirements of optimal transmission have on the synaptic response. This is done for a simple synaptic model with a single vesicle release site. At any time either zero or one vesicle is available for release. After the arrival of a presynaptic spike, if a vesicle is docked, neurotransmitter is released with probability U and transmission takes place. After depletion, a time period elapses before a new vesicle docks which leads to depression of the synapse. The time required for the docking of a new vesicle after release is governed by a Poisson process with mean time τ. This is one of the simplest models [2] which when averaged over trials or over synapses reduces to the phenomenological models of Refs. [5,6], which account for the experimental results.

Two different optimization criteria are implemented: maximization of the precision with which the input rate can be estimated from the observation of synaptic responses and maximization of the information that these responses have about the input rate.

2. Statistics of the synaptic response

The input trains to this synapse are taken as a general renewal process with ISI distribution $\rho_{\mathrm{ISI}}(t)$ and constant rate v. Since there is only one vesicle and the docking mechanism is renewal, the synaptic responses will also be a renewal process. Then the distribution $\rho_{\mathrm{e}}(\Delta)$ of the time interval Δ between consecutive EPSPs can be evaluated, obtaining

$$\tilde{\rho}_{\mathrm{e}}(s) = U \frac{[\tilde{\rho}_{\mathrm{ISI}}(s) - \tilde{\rho}_{\mathrm{ISI}}(s + 1/\tau)]}{[1 - \tilde{\rho}_{\mathrm{ISI}}(s)(1 - U)][1 - \tilde{\rho}_{\mathrm{ISI}}(s + 1/\tau)]}, \tag{1}$$

where the tilde denotes Laplace transforms. All the relevant quantities for this work can be obtained from this distribution.

We have considered exponentially correlated input trains characterized by the rate v, the coefficient of variation of the ISIs CV and the correlation time τ_{c}: $C(t, t') = v(CV^2 - 1)/(2\tau_{\mathrm{c}})\mathrm{e}^{-|t-t'|/\tau_{\mathrm{c}}}$.

The CV sets the amplitude and the sign of the correlation function. It is easily checked that the ISI distribution of the only renewal process with this correlation is $\rho_{\mathrm{ISI}}(t) = (1 - \varepsilon)\beta_1 \mathrm{e}^{-\beta_1 t} + \varepsilon\beta_2 \mathrm{e}^{-\beta_2 t}$. The parameters $[\beta_1, \beta_2, \varepsilon]$ are functions of the three physical input parameters $[v, CV, \tau_{\mathrm{c}}]$. Eq. (1) gives the distribution $\rho_{\mathrm{e}}(\Delta)$ as a sum of four exponentials which amplitudes and characteristic times are functions of the input parameters $[v, CV, \tau_{\mathrm{c}}]$ and of the synaptic parameters $[\tau, U]$.

We plot in Fig. 1(right) the dependence of the CV_{e} (the coefficient of variation of Δ) on τ. An increase in τ initially causes a decrease in the CV_{e} making the output train more regular. The value of τ for which the minimum is reached increases with the input CV. The EPSP's rate takes the form $v_{\mathrm{e}} = vU[1 + \tau vU + \tau U(CV^2 - 1)/2(\tau + \tau_{\mathrm{c}})]^{-1}$. As Fig. 1(left) shows, it saturates to $1/\tau$ as the input rate v increases. This occurs above a
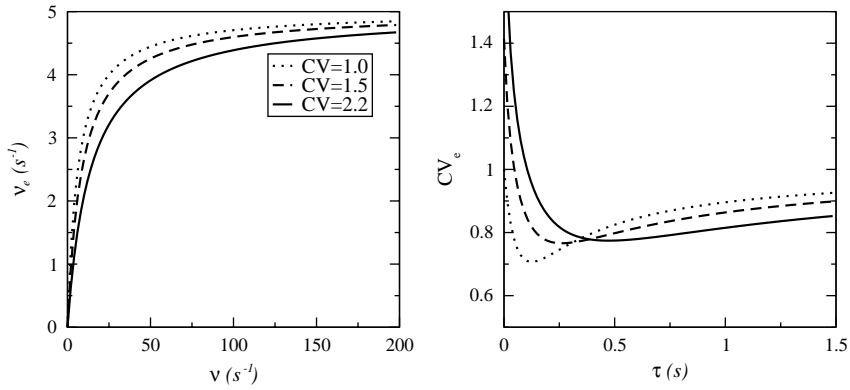
Fig. 1. Left: the EPSPs rate vs. the input rate v. $\tau = 0.2$ s. Right: CV_e vs. τ for several values of CV and $v = 10$ s^{-1}. Legend applies to both plots. Other parameters are $U = 0.8$ and $\tau_c = 0.05$ s.

frequency v_{sat} such that $U v_{sat} \tau = 1 + \tau U (CV^2 - 1)/2(\tau + \tau_c)$ indicating that correlations shift the saturation frequency towards larger values.

3. Information analysis

Now we have arrived at one of the main issues of this work which is to determine whether depressing synapses are optimal to transmit information about the input rate. This is done with two different criteria: the first is to optimize the accuracy with which the input rate is estimated; this requires the evaluation of the Fisher information for a given output (synaptic response) code. The second is to get at the postsynaptic terminal as much information (again about the input rate) as possible; this is carried out by optimizing the mutual information. Although related to the latter, another criterion considered here is the minimization of EPSP's autocorrelations [3].

3.1. Estimation of the input rate v

The inverse of the Fisher information provides a lower bound on the mean squared error in the estimation of the input rate. We have computed it for the EPSP count code given by the number of EPSPs in a large time window T (denoted by $n_e(T)$), and for the EPSP time code provided by the observation of the time intervals $\varDelta$. The first $J(v|n_e)$, can be evaluated for large T as

$$J(v|n_e) = \frac{T}{CV_e^2 v_e} \left(\frac{\partial v_e}{\partial v} \right)^2 . \tag{2}$$

The second, $J(v|\varDelta)$, was obtained from: $J(v|\varDelta)) = - \int_0^\infty \rho_e(\varDelta)(\partial^2/\partial v^2) \log(\rho_e(\varDelta)) \, d\varDelta$.

We define τ_{opt} as the value of τ for which J is maximal. The Fisher information as a function of τ is exhibited in Fig. 2(left) for the two codes. $J(v|n_e)$ is represented per EPSP by dividing it by the mean number of synaptic responses in T, $v_e T$. Likewise
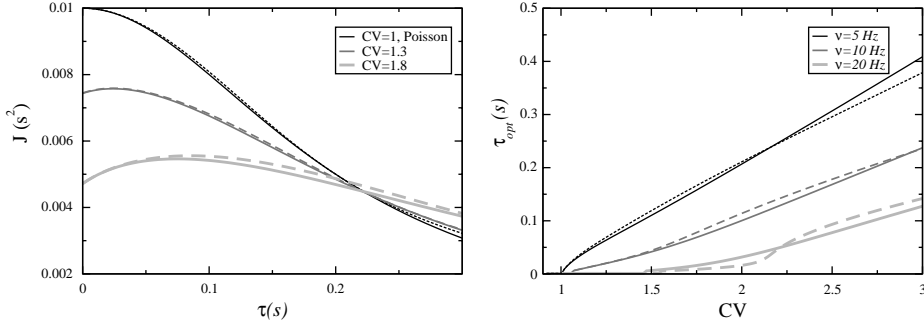
Fig. 2. Left: Fisher information about the input rate v conveyed in one interval between EPSPs, $J(v|\Delta)$ (dashed lines), and in the EPSP count per EPSP, $J(v|n_e)/\langle n_e(T)\rangle$ (solid lines), vs. the recovery mean time τ for several values of *CVs*, with $v = 10$ Hz. Right: the optimal recovery time τ_{opt} which maximizes J vs. the input *CV*, for several values of the input rate v. In both plots $U = 0.5$ and $\tau_c = 0.1$ s.

$J(v|\Delta)$ is the Fisher information given an interval between EPSPs. τ_{opt} is exhibited in Fig. 2(right) as a function of the *CV* for different values of *vs*. For Poisson inputs the Fisher information is maximal for $\tau=0$, that is, when there is no depression. For $CV < 1$ τ_{opt} is also 0 (data not shown). As the *CV* increases τ_{opt} also increases, showing that for positively correlated inputs depressing synapses are effective in improving the input rate estimation. The fact that $\tau_{opt} > 0$ for $CV > 1$ for $J(v|n_e)$ can be traced back to the dependence of CV_e and $\partial v_e/\partial v$ on τ (Eq. (2)). CV_e decreases as τ increases from 0 (Fig. 1(right)). This factor contributes to increase τ_{opt}. On the other hand, increasing τ also causes a decrease in the factor $\partial v_e/\partial v$ in Eq. (2). For large enough values of τ, $v > v_{sat}$, and both $J(v|n_e)$ and $J(v|\Delta)$ decrease (Fig. 2(left)). The smaller the input v is, the bigger τ has to be to made $v > v_{sat}$, and therefore a larger τ_{opt} can be obtained (Fig. 2(right)). Notice that $J(v|n_e)$ and $J(v|\Delta)$ are very similar.

3.2. Mutual information and autocorrelations

We now consider the information that a population of depressing synapses has about the input rate. This is done for the time code defined by the set of the EPSP intervals of those synapses. These variables are conditionally independent because they are generated from different realizations of the process.

$$I = \int d\vec{\Delta}\, dv \rho_e(\vec{\Delta}|v) f(v) \log_2 \frac{\rho_e(\vec{\Delta}|v)}{\rho_e(\vec{\Delta})}. \tag{3}$$

The input rate distribution $f(v)$ is chosen to be a Gaussian with mean $\bar{v}$ and variance $\bar{\sigma}$. The vector $\vec{\Delta}$ is the set of the EPSPs intervals defining the time code. For a large number of (conditionally) independent output variables I can be obtained from the Fisher information [1]:

$$I = -\int dv\, \rho(v) \log_2 \left(\sqrt{\frac{2\pi e}{N J(v|\Delta)}}\rho(v) \right), \tag{4}$$
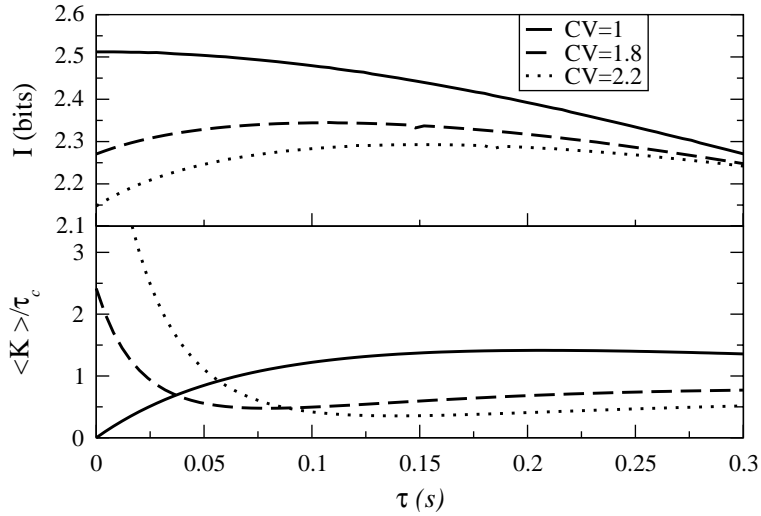
Fig. 3. Top: mutual information I vs. τ for several values of the input CV (time code with $N = 100$). Bottom: autocorrelations measured in terms of the average of K (Eq. (5)) over input frequencies vs. τ. In both figures $U = 0.2$, $\tau_c = 0.1$ s, $\bar{v} = 10$ s^{-1} and $\bar{\sigma} = 5$ s^{-1}.

where N is the number of output variables and $J(v|\Delta)$ the Fisher information given one Δ. I is given in Fig. 3(top) as a function of τ for several values of the input CV. Again for Poisson input trains the mutual information is maximal for $\tau = 0$, that is, in the absence of depression. The same holds for $CV < 1$. However, for input CV's larger than one τ_{opt} becomes non-zero and depressing synapses become advantageous to transmit information. An identical conclusion is reached from the analysis of autocorrelations. Defining

$$K = \int_0^\infty dt \left(\frac{v_e(t|t^{\text{sp}} = 0) - v_e}{v_e} \right)^2, \tag{5}$$

where $v_e(t|t^{\text{sp}})$ is the rate of the EPSPs at time t given that there was a spike at time 0. As can be seen in Fig. 3(bottom), $\langle K \rangle$, where the average is over the distribution of input v, is minimum for approximately the same values of τ that optimize the mutual information. Although this issue deserves further analysis, this is an example of the fact that redundancy can be minimized by maximizing the mutual information [4].

To conclude, depressing synapses are better than static ones to transmit information when the CV of the input train is larger than 1, for the two different optimization approaches used in this work. Below saturation the best estimation of the input rate is almost equally good for the two codes considered here. Optimization of the mutual information agrees with the minimization of the two-point correlation. While for the estimation of the rate the optimal solution is related to the minimum of the EPSP coefficient of variation (at least for the count code) for information transmission and decorrelation the optimum occurs for $CV_e \sim 1$. The optimal recovery time can reach

values around 100 ms for realistic values of the input parameters, but to achieve higher values it may require to consider models with a larger number of vesicles.

Acknowledgements

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