The Intrinsic Time Scale of Transient Neuronal Responses

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In a generic neuron model, we present the linear response theory for the firing rate in response to both time dependent input currents and noise amplitudes. In both cases the signal transmission is strongly attenuated for frequencies above the stationary firing rate. For high frequencies both the mean input and the noise transmission function decay as $\omega^{-2}$, independent of model details. Our results indicate that previously suggested mechanisms for near instantaneous transmission of information are not consistent with the spike generation mechanism of real neurons.

PACS numbers: 87.19.La, 87.10.+e, 05.40.-a, 05.45.-a

Neurons have been divided into several classes based on the kind of excitability they exhibit. In our study we focus on Type-I excitability which can be encountered in many neurons withing the cortex \cite{1}. In models of Type-I neurons, repetitive firing typically emerges via a saddle-node bifurcation. The normal form of this bifurcation is equivalent to a phase oscillator, the $\theta$-Neuron \cite{2}. It has been shown that it has the same mechanism of excitability and super-threshold behavior as cortical neurons \cite{3}. Its dynamics is:

$$\tau \dot{\theta} = (1 - \cos \theta) + I(t)(1 + \cos \theta),$$

where $\tau$ is the time constant and $I(t)$ represents the total synaptic input to the neuron. Each time the oscillator crosses the point $\theta = \pi$ a spike is said to be “fired”. For constant inputs this model exhibits a periodic firing regime for $I > I_c = 0$ with firing rate $\nu = \sqrt{T/\pi \tau}$, and an excitable regime for $I < 0$. We analyze the response of an ensemble of such neurons, which is given by the ensemble averaged firing rate $\nu(t)$. The input current $I(t)$ is decomposed,

$$I(t) = I_0 + \sigma \sqrt{\tau} \zeta(t),$$

into a mean current $I_0$ and a noise term which reflects the fluctuations induced by the synaptic inputs $\zeta(t)$. The noise is modeled by an Ornstein-Uhlenbeck process with a correlation time $\tau_c$:

$$\tau_c \frac{dz}{dt} = -z + \eta(t),$$

where $\eta(t)$ is Gaussian white noise. In the limit $\tau_c \to 0$, $z(t)$ becomes white noise. In the following, we have chosen the time constant $\tau = 0.25\text{ms}$ which results in a spike duration of about $1\text{ms}$ as found in real neurons. $I_0$ and $\sigma$ have been chosen to give realistic $\theta$-correlation times of approximately $10\text{ms}$ and firing rates in the range $1 - 20\text{Hz}$.

The state of an ensemble of such neurons is described by a probability density function $P(\theta, z, t)$. Its dynamics is determined by the Fokker-Planck equation:

$$\partial_t P = \hat{L}P,$$

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In the brain information is processed through a hierarchy of neural layers. Based on the observation that human subjects can successfully distinguish complex visual stimuli in only a few hundred milliseconds \cite{4}, it has been argued that the processing time of individual layers must be very small. Recently two different mechanisms have been proposed for the practically instantaneous relaying of information at the single neuron level. They utilize the fact that in vivo cortical neurons exhibit substantial subthreshold fluctuations of their membrane potentials, due to the large number of presynaptic neurons \cite{5}. The first mechanism assumes that information is transferred by a time dependent noise amplitude \cite{6,7}, the second assumes information transfer via a modulation of the mean input in the presence of temporally correlated background noise \cite{8,9}. These studies, which are based on a seminal work by Knight \cite{10}, have been conducted on integrate-and-fire models. These models, however, are highly idealized models of cortical neurons. Their main ingredient is a fixed voltage threshold. Each time the membrane potential reaches this threshold, a spike is said to be emitted. Real neurons, however, as well as biophysically realistic conductance based neuron models do not have a fixed voltage threshold and are rather comparable to excitable systems. This naturally raises the question whether the response properties found in simple threshold models are preserved if one considers models with a more realistic spike generating mechanisms. In this letter we address this question by a combination of analytical and numerical techniques considering a generic Type-I neuron model, the $\theta$-Neuron \cite{2}. We show that in a realistic regime the response to a transient stimulus, both in the mean input as well as in the noise amplitude is not instantaneous as predicted by the integrate-and-fire models. Moreover, we show that the maximum transmission frequency is approximately determined by the stationary firing rate. Thus our results suggest that the $\theta$-Neuron reproduces the dynamical behavior of cortical neurons faithfully, while still being tractable analytically.
with the operator,
\[ \hat{L} = -\tau^{-1} \partial_\theta \left( (1 - \cos \theta) + \left( I_0 + \sigma \tau^{1/2} z \right) (1 + \cos \theta) \right) + \tau^{-1} \partial_z z + \frac{1}{2} \tau^{-2} \partial_z^2, \]
periodic boundary conditions in the \( \theta \)-direction and natural boundary conditions in the \( z \)-direction. The firing rate \( \nu(t) \) is identical to the total probability current through the line \( \theta = \pi \):
\[ \nu(t) = 2\tau^{-1} \int_{-\infty}^{\infty} P(\pi, z, t) \, dz. \]

In the limit of temporally uncorrelated input, \( \tau_e \to 0 \), the rate can be calculated analytically \[12\] \[13\] which gives:
\[ \nu_{\text{WN}} = \frac{4\tau \sqrt{\pi}}{\sigma} \int_0^\infty dy \exp \left\{ -\frac{4}{\sigma^2} \left( \frac{y^6}{3} + I_0 y^2 \right) \right\} \]

To investigate how the neuron responds to time dependent synaptic inputs it is important to consider both the response to a time dependent mean input current \( I = I_0 + e e^{i\omega t} + \sqrt{\sigma} \zeta(t) \) and a time dependent noise amplitude \( I = I_0 + \sqrt{\sigma} (\sigma + e e^{i\omega t}) \). Inserting the modulated input current into Eq. \[1\] and expanding \( P_0(\theta, z, t) = \hat{L} P_0(\theta, z) + \epsilon \hat{P}_\omega (\theta, z) e r + \cdots \) gives in linear order in \( \epsilon \) \[13\]:
\[ i\omega \hat{P}_\omega (\theta, z) = \hat{L} \hat{P}_\omega - f(\theta, z), \]
with \( f(\theta, z) = -\tau^{-1} \partial_\theta (1 + \cos \theta) P_0(\theta, z) \) for modulated input currents and \( f(\theta, z) = -\tau^{-1/2} \partial_\theta (1 + \cos \theta) z P_0(\theta, z) \) for modulated noise amplitudes. The formal solution of eq. \[4\] is:
\[ \hat{P}_\omega (\theta, z) = e^{i\omega t} \int_{-\infty}^t e^{(t-t') \hat{L}} f(\theta, z) e^{i\omega t'} \, dt'. \]
This integral can be solved in terms of eigenfunctions \( P_k(\theta, z) \) of the operator \( \hat{L} \):
\[ \lambda_k P_k(\theta, z) = \hat{L} P_k(\theta, z), \]
with the associated eigenvalues \( \lambda_k \). Because of the applied boundary conditions the spectrum \( \{\lambda_k\} \) is discrete and, since detailed balance is not fulfilled, eigenvalues \( \lambda_k \) and the corresponding eigenfunctions \( P_k(\theta, z) \) are either real or form complex conjugate pairs. Moreover, the eigenfunctions are typically not orthogonal. However, an orthonormal set of basis functions \( \{\phi_k\} \) can be constructed from them by Gram-Schmidt orthogonalization (in Dirac notation) with expansion coefficients \( a_k^\dagger \):
\[ |\phi_k\rangle (\theta, z) = \sum_{i=1}^k a_k^\dagger P_i(\theta, z). \]
Inserting \( \sum_k |\phi_k\rangle \langle \phi_k| = 1 \) into Eq. \[4\] yields,
\[ \hat{P}_\omega (\theta, z) = e^{-i\omega t} \sum_{k, l \leq k} b_k a_l^\dagger \int_{-\infty}^t e^{-i(\omega t' + (t-t') \lambda_l)} P_l(\theta, z) \]
\[ = \sum_{k, l \leq k} a_k^\dagger b_k \frac{1}{\omega - \lambda_l} P_l(\theta, z), \]
with \( b_k = \langle \phi_k | f \rangle \). The rate response is then given by:
\[ \nu(t) = 2\tau^{-1} \int_{-\infty}^\infty \left( P_m(\pi, z) + \hat{P}_\omega (\pi, z) e^{i\omega t} \right) \, dz = \nu_0 + \nu_1(\omega) e^{i(\omega t + \phi(\omega))}. \]
The limit \( \omega \to \infty \) can be treated analytically. Since \( f(\pi, z) \) vanishes at \( \theta = \pi \), the modulus of \( \hat{P} \) at this point has to be proportional to \( \omega^{-2} \):
\[ \left( i\omega - \hat{L} \right) \hat{P}_\omega (\pi, z) e^{-i\omega t} = -f(\pi, z) = 0. \]
An expansion in \( \omega^{-1} \) reveals that the relative phase of \( \nu_1(\omega) \) is \( -\pi \) in this limit. We would like to stress that this decay is universal and does not depend on model details. It is only due to the insensitivity to external inputs at the point where a spike is emitted, i.e. \( f(\pi, z) = 0 \).

The eigenvalues and eigenfunctions of the time-independent operator \( \hat{L} \) determine \( \nu_1(\omega) \) completely. We computed them using a matrix representation of Eq. \[4\] obtained by expanding \( P_k(\theta, z) \) into a complete set of orthonormal functions:
\[ P_k(\theta, z) = \sum_{n,m=0}^{\infty} \sum_{n',m'=0}^{\infty} a_{n,m} \left( 2^{n+1} \sqrt{\pi/2} \tau c \right)^{-1/2} e^{i n \theta} H_m(\sqrt{2\tau c} z) e^{-z^2 \tau c}. \]
where \( H_m(z) \) are the Hermite polynomials \[14\]. Inserting this into Eq. \[4\], multiplying from left with \( \left( 2^{n' + 1} \sqrt{\pi/2} \tau c \right)^{-1/2} e^{i n' \theta} H_{m'}(\sqrt{2\tau c} z) e^{-z^2 \tau c} \) and integrating over the entire domain leads to the following eigenvalue problem:
\[ \lambda a_{n,m} = \sum_{n',m'} L_{n,m,n',m'} a_{n',m'}. \]
Because the Fokker-Planck operator has only two Fourier components in the \( \theta \)-direction and is polynomial in the \( z \)-direction, \( \hat{L} \) is sparse with:
\[ L_{nm,n',m'} = \begin{cases} -i\tau^{-1} (1 + i0) n - \tau_c^{-1} m & \text{for } |m| < 1 \text{ and } \text{for } n < m \text{ and } n' \geq m' + 1 \text{ and } n' \geq m + 1 \text{ and } n' + 1 = m' \text{ and } n' + 1 = m + 1. \end{cases} \]
We solve \[5\] numerically using the Arnoldi-method \[15\], a high performance iterative algorithm. Figure \[1\] shows the spectrum and the stationary density for two different correlation times \( \tau_c \), together with the spectrum in the white noise limit. The eigenvalues are arranged in a series of wedges. The tip of each wedge is located at integer multiples of \( \tau_c^{-1} \). The different wedges account for the decay of excitations in the
z-direction, whereas the eigenvalues within a wedge account for the decay (real part) and oscillation (imaginary part) of excitations in the \( \theta \) -direction. In the limit \( \tau_c \to 0 \) the spectrum exhibits only one wedge (open circles). For \( \tau_c = 10 \text{ms} \) (upper plot), the interaction between eigenvalues leads to deviations from the white noise limit only for strongly damped modes. The deviations become more pronounced only for large values of \( \tau_c = 50 \text{ms} \) (lower plot). In both regimes the stationary density strongly deviates from a separable density.

![Figure 1: Spectrum of operator \( \hat{L} \) (a,c) and stationary density (b,d) for \( \tau_c = 10 \text{ms}, \nu_0 = 10 \text{Hz} \) (a,b) and \( \tau_c = 50 \text{ms}, \nu_0 = 8 \text{Hz} \) (c,d) [13]. The open circles denote the result in the limit \( \tau_c \to 0 \). In all cases \( \sigma = 10^{-3}, I_0 = 0 \). For increasing \( \tau_c \) the tips of the wedges move closer to the imaginary axis.

Examples of the response amplitude \( \nu_1(\omega) \) and the phase \( \phi(\omega) \) are depicted for different values of \( \nu_0 \) in Fig. 2 for both mean input and noise stimulation. In the case of mean input modulation, the linear response amplitude exhibits a resonance maximum at approximately the frequency of its stationary firing rate and then decays rapidly to zero. The response phase starts at zero and then drops to \(-\pi\). For a modulation in the noise amplitude the behavior is similar, except for additional resonances at higher frequencies, which are, however, strongly damped.

Whereas in general all eigenfunctions and eigenvalues contribute to the rate response, the relatively simple Lorentz-like shape of the response functions suggests that one frequency effectively dominates the neurons’ behavior. We observed that this cut-off frequency is given by the imaginary part of the first excited eigenvalue of the first wedge for the current response, and by the corresponding eigenvalue of the second wedge for the noise response. This is demonstrated by the green dashed lines in Fig. 2. These are the sum of two Lorentzians with their maxima at the positive and negative frequency given by the imaginary part of the second eigenvalue in the corresponding wedge. The reason for this is apparent from for the decomposition of \( f(\theta, z) \) into eigenfunctions of the Fokker-Planck operator \( \hat{L} \):

\[
f(\theta, z) = \sum_l \alpha_l P_l(\theta, z).
\]

It has no contribution from the stationary density, since \( \int f(\theta, z) d\theta = 0 \), and for mean input modulations has a maximum contribution for the eigenfunctions corresponding to second eigenvalue in the first wedge. For noise modulations it has a maximum contribution for the eigenfunction corresponding to the second eigenvalue in the second wedge. The imaginary parts of the second eigenvalues in the first two wedges are, however, almost identical for the parameters used.

The cut-off frequency for subthreshold mean inputs \( I_0 < 0 \) is depicted in Fig. 3 together with the dependence on the noise correlation time \( \tau_c \). The cut-off frequency increases for increasing values of \( I_0 \) but always stays below the stationary rate \( \nu_0 \). Increasing the noise correlation time at \( I_0 = 0 \) shifts the cut-off frequency to slightly larger values compared to \( \nu_0 \).

Thus our analysis demonstrates that in a realistic regime responses much faster than \( \nu_0^{-1} \) are strongly damped, since the transmission function decays as \( \omega^{-2} \). We would like to conclude this letter with a comparison of the dynamic behavior of the \( \theta \)-neuron with a biophysical realistic conductance based neuron [16] as well as with the classical leaky integrate-and-fire (LIF) model. Figure 4 shows the step response of the three models for an identical current correlation, identical initial and final firing rates and similar membrane potential correlation times. The dynamics of the \( \theta \)-neuron and the con-
ductance based model agree well, their response time is about 10ms. The dashed line shows the linear response result, which predicts a slower response but is of the same order of magnitude. The LIF model on the other hand responds practically instantaneously. This is due to the fact that in the LIF model high input frequencies are not substantially damped, i.e. the response amplitude does not decay for large frequencies. This is impossible in the \( \theta \)-neuron in which the response amplitude always decays as \( \omega^{-2} \). We would like to stress that this decay is a universal property due to the insensitivity to input currents at the point where a spike is fired and is independent of model details. Thus, although one observes that the response times of both, the \( \theta \)-neuron and the LIF model decrease with increasing \( \tau_c \), the mathematical origin and nature of this dependence is very different. Whereas in the \( \theta \)-neuron it is a consequence of the dependence of the eigenvalues on \( \tau_c \), in integrate-and-fire models they result from the voltage threshold.

In conclusion, we presented the linear response theory for the firing rate of the \( \theta \)-neuron in response to both time dependent input currents and time dependent noise amplitudes. For an effective numerical treatment we derived a sparse matrix representation of the Fokker-Planck operator. Using the eigenvalues and eigenfunctions of this operator, we showed that the transmission amplitude is in both cases strongly damped for frequencies above a cut-off frequency. In a wide range of parameters this cut-off frequency is always below the mean firing rate. We showed that the response behavior agrees well with the dynamics of a conductance based model neuron and is different from the behavior of the LIF model. Our results indicate that the \( \theta \)-neuron, although simple, captures well the dynamical properties of real neurons. They also reveal that previously proposed mechanisms of practically instantaneous transmission of information are incompatible with the spike generating mechanism of real neurons. Our findings suggest that the \( \theta \)-neuron reproduces the dynamical behavior of cortical neurons with Type-I excitability faithfully, while still being tractable analytically.

We acknowledge useful discussion with M. Bethge, P. Latham, A. Morrison, K. Pawelzik, M. Timme and C. v. Vreeswijk. This research was supported in part by the National Science Foundation under Grant No. PHY99-07949.

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[17] The basis for the numerical diagonalization has been truncated to \( n = -N \ldots N \) in the \( \theta \)- and \( k = 0 \ldots K \) in the \( z \)-direction with \( N = 6000 \) and \( K = 40 \). This results in a matrix of size \((4.8 \cdot 10^5)^2\) for which we computed up to the first 200 eigenvalues and eigenfunctions.