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Stationary transmission distribution of random spike trains by dynamical synapses

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Many nonlinearities in neural media are strongly dependent on spike timing jitter and intrinsic dynamics of synaptic transmission. Here we are interested in the stationary density of evoked postsynaptic potentials transmitted by depressing synapses for Poisson spike trains of fixed mean rates. We present a nonperturbative iterative method for computing the stationary density over increasing intervals. We conclude by showing how this method generalizes to other types of synapses, such as facilitating and hybrid synapses.

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Differential equations with random impulse stimulation are useful tools for modeling diverse phenomena such as earthquakes and traffic behavior. More recently, phenomenological stochastic differential equations were introduced that describe synaptic interactions in neural media. It has previously been shown that noise and dynamical synaptic transmission can give rise to a broad variety of dynamical behaviors in networks of pulse-coupled neurons, e.g., oscillations, phase-locking, synchronization, and stabilization/destabilization of the asynchronous firing state [1–5]. As a first step toward understanding the detailed interplay between noise and dynamical synaptic transmission, we here study how the irregularity of spike timing translates into irregularity of synaptic amplitudes. We investigate whether as for other systems [6], exact solutions to the stationary synaptic amplitude density can be computed.

During their normal operation, cortical neurons fire very irregularly [7]. A phenomenologically accurate description of this irregularity is that of a Poisson spike train $\rho(t)=\Sigma_i\delta(t-t_i)$, according to which interspike intervals (ISI's) occur randomly according to an exponential distribution [8]. That is, the probability $p(T_i)$ of observing the interspike interval $T_i=t_{i+1}-t_i$ is given by

$$p(T_i)=\frac{1}{\lambda}e^{-T_i/\lambda}, \tag{1}$$

where the parameter λ corresponds to the mean ISI and λ^2 to the variance.

Many cortical neurons have dynamic (facilitating and/or depressing) synapses that elicit variable excitatory postsynaptic potentials (EPSP's), depending on the history of presynaptic activity [9–11]. If a presynaptic spike train is regular (periodic), then the amplitudes of evoked postsynaptic potentials of a dynamical synapse approach a steady value; if it is not regular, then EPSP amplitudes vary. We will first consider depressing synapses, for which EPSP amplitudes become smaller, the higher the presynaptic firing frequency. A simple phenomenological model in which EPSP amplitudes are multiplicatively reduced after each presynaptic spike and recover exponentially between spikes gives an excellent fit to experimental data [12]. Accordingly, the amplitude $a_i=a(t_i)$ of an EPSP generated by a presynaptic spike at time t_i obeys the following kinetic model [15]:

$$\frac{d}{dt}a(t)=\frac{a_0-a(t)}{\tau}+\ln(\gamma)a(t)\rho(t), \tag{2}$$

where a_0 is the resting amplitude, γ the depressing factor $(0<\gamma<1)$, and τ the recovery time constant. γ corresponds to the factor by which EPSP amplitudes are reduced after each spike. The shape and duration of EPSP's are neglected in this description. For simplicity, in the following, we set the resting amplitude to $a_0=1$ mV.

Under stationarity assumptions, the mean EPSP amplitude $\overline{a}=\langle a_i\rangle_i$ of Poisson spike trains has a particularly simple expression [13]

$$\overline{a}=\frac{1}{1+(1-\gamma)\tau\lambda^{-1}}. \tag{3}$$

Equation (3) can be derived simply by noting that $\overline{a}$ corresponds to the amplitude at which the rate of amplitude decrease equals the rate of amplitude increase in Eq. (2), $(1-\gamma)\overline{a}/\lambda=(1-\overline{a})/\tau$. It is currently unknown how to calculate the stationary probability density $q(a)$ of EPSP amplitudes. Here we present a nonapproximative iterative method.

We start by assuming that we know the amplitude a_i of the ith EPSP. We then calculate the conditional probability density of a_{i+1} (the dependence on i will drop in our final result by assuming stationarity). By integrating Eq. (2) between two spikes at times t_i and t_{i+1}, we can calculate the dependence of a_{i+1} on both a_i and T_i:

$$a_{i+1}=\gamma a_i e^{-T_i/\tau}+1-e^{-T_i/\tau}. \tag{4}$$

The conditional density $p(a_{i+1}|a_i)$ is defined as the probability of observing the amplitude a_{i+1}, given that the previous amplitude was a_i. We can relate the conditional density to the ISI density in Eq. (1), by noting that the probability that the $(i+1)$th amplitude is confined in an infinitesimal interval around a_{i+1} is equal to the probability that the interspike interval is confined in an infinitesimal interval around T_i, or

$$p(a_{i+1}|a_i)da_{i+1}=p(T_i)dT_i. \tag{5}$$

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In order to obtain an expression for $p(a_{i+1}|a_i)$, we have to eliminate T_i in Eq. (5). We do this by solving Eq. (4) for T_i and replacing the result into Eq. (5). By defining $s=\tau/\lambda$, we find

$$p(a_{i+1}|a_i)=s(1-\gamma a_i)^{-s}(1-a_{i+1})^{s-1} \tag{6}$$

for $a_{i+1}\geqslant\gamma a_i$ and

$$p(a_{i+1}|a_i)=0 \tag{7}$$

for $a_{i+1}<\gamma a_i$. The reason why $p(a_{i+1}|a_i)$ vanishes for $a_{i+1}<\gamma a_i$ is that an EPSP amplitude cannot be smaller than γ times the previous amplitude. It is easy to verify that $p(a_{i+1}|a_i)$ in Eqs. (6) and (7) is properly normalized, i.e., $\int_0^1 p(a_{i+1}|a_i)da_{i+1}=1$.

By knowing $p(a_{i+1}|a_i)$, we can infer how the ith probability density $p_i(a_i)$ for the ith amplitude is mapped onto the density $p_{i+1}(a_{i+1})$ for the $(i+1)$th amplitude

$$p_{i+1}(a_{i+1})=\int_0^1 p(a_{i+1}|a_i)p_i(a_i)da_i. \tag{8}$$

We are interested in the stationary density $q(a)$ in Eq. (8) by setting $p_{i+1}(a)=p_i(a)\coloneqq q(a)$. This leads to the following integral equation:

$$q(a)=s(1-a)^{s-1}\int_0^{\min(1,a/\gamma)}(1-\gamma a')^{-s}q(a')da'. \tag{9}$$

The difficulty of Eq. (9) arises from the fact that the upper limit of the integral depends on a.

It is possible to solve Eq. (9) by numerical iteration. First, choose an arbitrary starting density, for example the uniform density. Then, insert this density on the right hand side of Eq. (9) and derive a new density on the left, to be reinserted on the right and so forth. This iteration procedure is expected to converge to a solution $q(a)$, because this sequence forms a Markov chain which is known to approach a stationary density [14] [note that in principle $q(a)$ does not have to be unique]. This numerical scheme represents a clear computational advantage over a Monte Carlo simulation of Eq. (2).

In the following we show how $q(a)$ can also be computed analytically. By taking the derivative of Eq. (9) with respect to a, we can express the integral Eq. (9) as two differential equations for $q(a)$, valid in nonoverlaping regions

$$\frac{dq(a)}{da}=\frac{(s-1)q(a)}{a-1} \quad (\gamma\leqslant a), \tag{10}$$

$$\frac{dq(a)}{da}=\frac{(s-1)q(a)}{a-1}+\frac{sq(a/\gamma)}{\gamma(1-a)} \quad (a<\gamma). \tag{11}$$

We can solve Eq. (10) to find that for large a, $q(a)$ has the form of a power function

$$q(a)=c(a-1)^{s-1} \quad (\gamma\leqslant a), \tag{12}$$

where c is an unknown integration constant that ultimately can be determined by normalization $\int_0^1 q(a)da=1$. Interestingly, near the resting amplitude, $q(a)$ does not explicitly depend on γ (though it may implicitly depend on γ via the normalization factor c).

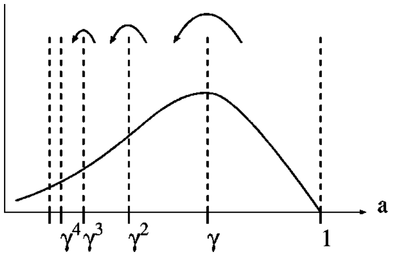

FIG. 1. Iterative scheme for computing the stationary density. The solution in the interval $[\gamma,1]$ defines the inhomogeneous term for the differential equation in the interval $[\gamma^2,\gamma]$. The solution there constitutes the inhomogeneous term for the subsequent interval and so forth.

Having derived $q(a)$ for $\gamma\leqslant a$, we can solve Eq. (10) in the region $\gamma^2\leqslant a<\gamma$. In that region, Eq. (10) is a inhomogeneous differential equation, where the second term on the right constitutes the inhomogeneous term. From Eq. (12), we substitute $q(a/\gamma)=c(a/\gamma-1)^{s-1}$ into the inhomogeneous term. For $q(a)$ in Eq. (10) we make the ansatz $q(a)=\kappa(a)(a-1)^{s-1}$, from which we find the following expression for the derivative of the unknown function $\kappa(a)$:

$$\frac{d\kappa(a)}{da}=-\frac{\tau c}{\lambda\gamma^s(a-1)}\left(1-\frac{\gamma-1}{a-1}\right)^{s-1}. \tag{13}$$

Assuming s takes an integer value, the solution of Eq. (13) can be written as

$$\kappa(a)=\frac{\tau c}{\lambda\gamma^s}\left[\sum_{n=1}^{s-1}\binom{s-1}{n}\frac{(1-\gamma)^n}{n(a-1)^n}-\ln(1-a)+c_2\right], \tag{14}$$

where the large brackets indicate the binomial coefficient and c_2 is an integration constant that can be determined by continuity of $q(a)$ at γ, i.e.,

$$c_2=\sum_{n=1}^{s-1}\binom{s-1}{n}\frac{(-1)^n}{n}-\ln(1-\gamma)-\frac{\lambda\gamma^s}{\tau}. \tag{15}$$

Figure 1 shows a schematic depiction of our iterative scheme for computing $q(a)$ in the remaining region $a<\gamma^2$. The procedure is as follows: we use the solution $q(a)$ in the region $\gamma^2\leqslant a<\gamma$ as an inhomogeneous term (the last term) in Eq. (10), determing $q(a)$ in the region $\gamma^3\leqslant a<\gamma^2$. This equation is again solved by simple integration (the integral involving the logarithm is laborious for large s and but be simplified for example by Taylor expansion); the integration constant can be inferred from continuity in γ^2. In this way we can work our way back to the origin, deriving $q(a)$ over a iteratively increasing interval. In practice we can stop the procedure after a few iterations, knowing that the density has to vanish near zero amplitudes.

The intuition behind why our derivation of the stationary density is of a fractal nature is that amplitudes in the interval

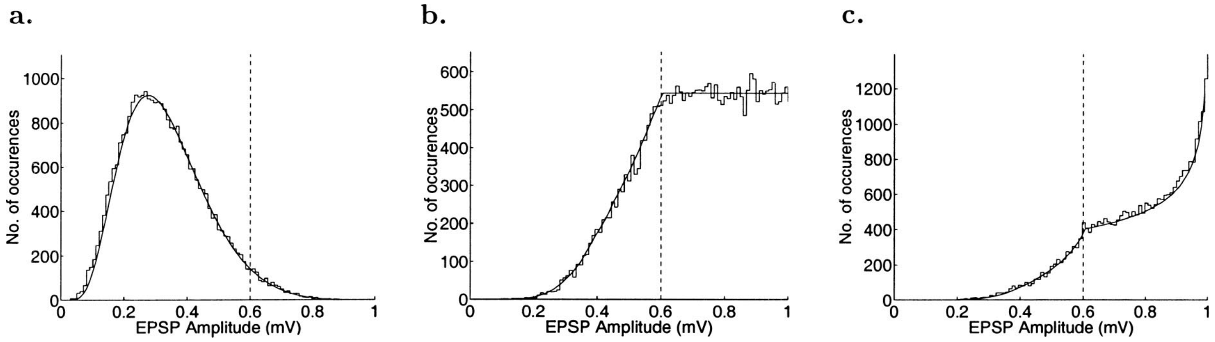

FIG. 2. EPSP amplitude histograms for a depressing synapse and three different mean interspike intervals. The full line shows the analytically derived stationary density—identical to the overlayed density computed by 20 numerical iterations of Eq. (8) with an integration stepsize of 0.01 mV. The vertical dashed line at 0.6 mV indicates the amount by which a fully recovered synapse is depressed after a spike, i.e., $\gamma=0.6$. $a_0=1$ mV, $\tau=500$ ms. (a) Small mean ISIs ($\lambda=100$ ms). (b) Marginal mean ISIs ($\lambda=500$ ms). (c) Large mean ISIs ($\lambda=670$ ms).

$[\gamma^{k+1},\gamma^k]$ are conditional on the rapid succession of k presynaptic spikes; the occurrence of which is dependent on the occurence of a rapid succession of $k-1$ presynaptic spikes, etc.

The results of our calculation are compared to a Monte Carlo simulation of the original Eqs. (1) and (2) and to a numerical evaluation of Eq. (9), see Figs. 2(a), 2(b), and 2(c). The original equations were simulated by generating a spike train of 30 000 spikes with different mean ISIs λ. We find a good fit of our calculation to both the Monte Carlo simulation and the numerical computation. Qualitatively, we find that if the mean ISI is small compared to the recovery time constant of the depressing synapse, then the stationary distribution of EPSP amplitudes looks approximately similar to a Gaussian with a small mean amplitude [Fig. 2(a)]. If the mean ISI is equal to the recovery time constant, then the stationary distribution is marginal and all amplitudes larger than γ are equal in probability [Fig. 2(b)]. In the last case where the mean ISI is smaller than the recovery time constant, the stationary distribution rises sharply for amplitudes larger than γ, meaning that most EPSP's have amplitudes close to the resting amplitude. Thus the shape of $q(a)$ depends very sensitively on the ratio τ/λ, with a marginal behavior at $\lambda=\tau$.

An interesting question is whether the mean EPSP amplitude elicited by a Poisson spike train of a given mean rate is smaller or larger than the steady amplitude elicited by a regular spike train of the same rate. For the regular spike train, we calculate the steady EPSP amplitude by setting $a_s := a_i = a_{i+1}$ in Eq. (4), leading to

$$a_s=\frac{1-e^{-\lambda/\tau}}{1-\gamma e^{-\lambda/\tau}}. \tag{16}$$

In this equation, λ corresponds to the fixed ISI of the presynaptic spike train. It is easy to show that the λ dependence of a_s is similar to that of $\overline{a}$ in Eq. (3). However, for all λ we have that $a_s<\overline{a}$, i.e., the mean amplitude elicited by a Poisson spike train is smaller than the steady amplitude of a regular spike train of the same firing rate. Intuitively, this can be understood by the fact that the Poisson spike train contains some very short interspike intervals, among which the second spike always elicits EPSP's of particularly small amplitudes, hence the shift to lower mean amplitudes.

We have found that a regular spike train is the most efficient input that can be transmitted by a depressing synapse. This can be seen as follows. Given N spikes in a large time interval T, we ask how to choose the individual interspike intervals $T_i (i=1,\dots,n)$, such that the sum of EPSP amplitudes is maximized. The constrained optimization of

$$E=\sum_{i=1}^{N} a_i+\alpha\left(T-\sum_{i=1}^{N} T_i\right), \tag{17}$$

where α is a Lagrange multiplier can be done by replacing the T_i's by the a_i's using Eq. (4) and setting

$$\frac{\partial E}{\partial a_i}=0. \tag{18}$$

Doing this, we find that $a_i=a_j=a$ and that E is maximized for a regular spike train with $T_i=T/N$.

Our results for depressing synapses can be extended to facilitating and hybrid synapses. According to Ref. [12], a simple model for EPSP amplitudes b elicited by a facilitating synapse is

$$\frac{d}{dt}b=\frac{b_0-b}{\tau_b}+\zeta\rho(t). \tag{19}$$

Unlike depression, facilitation is best described in an additive manner, by the constant $\zeta>0$ (multiplicative facilitation can lead to unbounded behavior). We can again use an iterative scheme for computing the stationary density $r(b)$ for a facilitating synapse, given a presynaptic Poisson spike train. Setting $b_0=1$ mV we find the analytical solution near the resting amplitude

$$r(b)=c(b-1)^{\tau_b/\lambda-1}, \quad 1<b<1+\zeta. \tag{20}$$

Maximizing E in Eq. (17) for a facilitating synapse does not result in a regular spike train. On the contrary, the sum of

EPSP amplitudes is largest when the interspike intervals are as small as possible, e.g., when the presynaptic neuron is bursting.

In the most general case, a synapse may have both facilitating and depressing components. A quantitatively good model is a multiplicative combination of the previous descriptions [12]. Accordingly, the amplitude h_i of the ith EPSP of a hybrid synapse is given by

$$h_i = a_i b_i , \tag{21}$$

where a_i is given by Eq. (4) and b_i can be derived similarly from Eq. (19). Finding the stationary distribution $t(a,b)$ of a hybrid synapse is more difficult. By assuming independence, $t(a,b) = q(a)r(b)$, it is possible to derive a good approximation for the mean amplitude $\overline{t} = \langle t_i \rangle_i$.

Maximizing E in Eq. (17) for a hybrid synapse is hard and so we make the simplifying assumptions $\tau_b = \tau$ and that the presynaptic spike train is regular with interspike interval T to be optimized. In other words, we maximize

$$h_s = a_s b_s \tag{22}$$

with respect to T, where $a_s = (1-x)/(1-\gamma x)$ is the steady amplitude of the depressing component, Eq. (16), $b_s = (1-x+\zeta x)/(1-x)$ is the steady amplitude of the facilitating component, and $x = e^{-T/\tau}$. We find that

$$\frac{dh_s}{dT} \geqslant 0 \quad \Leftrightarrow \quad \zeta \leqslant 1-\gamma. \tag{23}$$

Thus, for $\zeta \leqslant 1-\gamma$ the synapse behaves as a depressing synapse, otherwise it behaves as a facilitating synapse. There are no values for the synaptic parameters, for which the synapse has a bandpass characteristic, e.g., for which h_s is maximized at finite, nonzero time T.

We have presented a method for computing stationary transmission properties of dynamical synapses. We believe our method for computing stationary distributions of evoked membrane potentials to be relevant in general for problems involving stochastic descriptions of neural systems.

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[1] M. Tsodyks, K. Pawlzik, and H. Markram, Neural Comput. **10**, 821 (1998).
[2] W. Senn, I. Segev, and M. Tsodyks, Neural Comput. **10**, 815 (1998).
[3] J. Pham, K. Pakdaman, and J.-F. Vibert, Phys. Rev. E **58**, 3610 (1998).
[4] P. Bressloff, Phys. Rev. E **60**, 2160 (1999).
[5] M. Tsodyks, A. Uziel, and H. Markram, J. Neurosci. **20**, 1 (2000).
[6] C. Proppe, Int. J. Eng. Sci. **40**, 1165 (2002).
[7] H. Noda and R. Adey, Behav. Brain Sci. **18**, 513 (1970).
[8] W. Softky and C. Koch, J. Neurosci. **13**, 334 (1993).
[9] C. Sevens and Y. Wang, Neuron **21**, 415 (1995).
[10] L. Abbott, J. Varela, K. Sen, and S. Nelson, Science **275**, 220 (1997).
[11] M. V. Tsodyks and H. Markram, Proc. Natl. Acad. Sci. U.S.A. **94**, 719 (1997).
[12] J. Varela, K. Sen, J. Gibson, J. Fost, L. Abbott, and S. Nelson, J. Neurosci. **17**, 7926 (1997).
[13] F. Chance, S. Nelson, and L. Abbott, J. Neurosci. **15**, 4785 (1998).
[14] T. Cover and A. Thomas, *Information Theory* (Wiley, New York, 1991).
[15] Equation (2) is also sometimes written infinitesimally as $da(t) = (dt/\tau)[a_0 - a(t)] + (\gamma-1)a(t)\hat{\rho}(t)$, where $\hat{\rho}(t) = \Sigma_i \hat{\delta}(t-t_i)$ represents the sum of Kronecker delta functions $\hat{\delta}(0) = 1$. This latter equation illustrates how Eq. (2) can be numerically integrated on a computer. Note that the factor $\ln(\gamma)$ in Eq. (2) is transformed into $(\gamma-1)$ in this new equation, because the Kronecker delta function $\hat{\delta}(t)$ assumes values 0 and 1, whereas the Dirac delta function $\delta(t)$ is unbounded.