
Know Thy Neighbour: A Normative Theory of Synaptic Depression Supplementary Information

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1 Inference with an OU process and a non-linear Poisson model

We write the Ornstein-Uhlenbeck (OU) process in discrete time as follows:

$$u_t = \alpha u_{t-1} + \theta u_r \Delta t + W_t \sqrt{\Delta t} \quad (1)$$

with $\alpha = 1 - \theta \Delta t$ where $W_t \stackrel{\text{iid}}{\sim} \mathcal{N}(W_t; 0, \sigma_W^2)$ is normally distributed. So the Markov dynamics can be written as

$$p(u_t | u_{t-1}) = \mathcal{N}(u_t; \alpha u_{t-1} + \theta u_r \Delta t, \sigma_W^2 \Delta t) \quad (2)$$

Now if we assume that at time $t - 1$, the distribution of the membrane potential given the spiking history is normally distributed,

$$p(u_{t-1} | s_{1..t-1}) = \mathcal{N}(u_{t-1}; \mu_{t-1}, \sigma_{t-1}^2) \quad (3)$$

then the distribution of the membrane potential at time t given the same spiking history will be also a Gaussian:

$$p(u_t | s_{1..t-1}) = \mathcal{N}(u_t; \underbrace{\alpha \mu_{t-1} + \theta u_r \Delta t}_{\tilde{\mu}}, \underbrace{\sigma_W^2 \Delta t + \alpha^2 \sigma_{t-1}^2}_{\tilde{\sigma}^2}) \quad (4)$$

Finally, we can write the probability density of the membrane potential given the whole past spiking history up to time t :

$$p(u_t|s_{1..t}) = \left(\frac{g(u_t)}{\gamma}\right)^{s_t} \left(\frac{1-g(u_t)\Delta t}{1-\gamma\Delta t}\right)^{1-s_t} \mathcal{N}(u_t; \tilde{\mu}, \tilde{\sigma}^2) \quad (5)$$

where the normalizing factor γ is given by

$$\gamma = \int g(u_t) \mathcal{N}(u_t; \tilde{\mu}, \tilde{\sigma}^2) du_t \quad (6)$$

2 Optimal membrane potential estimator for exponential gain function

Let us now consider an exponential transfer function g :

$$g(u) = g_0 \exp(\beta u) \quad (7)$$

Let us first note that the product of an exponential and a gaussian gives an unnormalized gaussian:

$$g(u_t) \mathcal{N}(u_t; \tilde{\mu}, \tilde{\sigma}^2) = \underbrace{g_0 \exp\left(\beta \tilde{\mu} + \frac{\beta^2 \tilde{\sigma}^2}{2}\right)}_{\gamma} \mathcal{N}(u_t; \tilde{\mu} + \beta \tilde{\sigma}^2, \tilde{\sigma}^2) \quad (8)$$

The expected membrane potential at time t becomes

$$\begin{aligned} \mu_t &= \frac{s_t}{\gamma} \langle u_t g(u_t) \rangle_{u_t; \tilde{\mu}, \tilde{\sigma}^2} + \frac{1-s_t}{1-\gamma\Delta t} \langle u_t (1-g(u_t)\Delta t) \rangle_{u_t; \tilde{\mu}, \tilde{\sigma}^2} \\ &= s_t (\tilde{\mu} + \beta \tilde{\sigma}^2) + (1-s_t) \left(\tilde{\mu} - \frac{\Delta t \gamma \beta \tilde{\sigma}^2}{1-\gamma\Delta t} \right) \\ &\simeq \tilde{\mu} + \beta \tilde{\sigma}^2 (s_t - \gamma \Delta t) \end{aligned} \quad (9)$$

where the last approximation becomes exact in the limit of small Δt . We can now rewrite the above expression in an exact way as a differential equation (since we take the limit of small Δt):

$$\dot{\mu} = -\theta(\mu - u_r) + \beta \sigma^2 (S(t) - \gamma) \quad (10)$$

where $S(t)$ is a delta spike train such that

$$s_k = \int_{k\Delta t}^{(k+1)\Delta t} S(t) dt \quad (11)$$

In a similar way, we can write the evolution of the membrane potential variance estimator when $s_t = 0$

$$\begin{aligned} \sigma_t^2 &= \frac{1}{1-\gamma\Delta t} \langle u_t^2 (1-g(u_t)\Delta t) \rangle_{u_t; \tilde{\mu}, \tilde{\sigma}^2} - \frac{1}{(1-\gamma\Delta t)^2} \langle u_t (1-g(u_t)\Delta t) \rangle_{u_t; \tilde{\mu}, \tilde{\sigma}^2}^2 \\ &= \frac{1}{1-\gamma\Delta t} \{ \tilde{\sigma}^2 + \tilde{\mu}^2 - \gamma\Delta t (\tilde{\sigma}^2 + (\tilde{\mu} + \beta \tilde{\sigma}^2)^2) \} - \left(\tilde{\mu} - \frac{\Delta t \gamma \beta \tilde{\sigma}^2}{1-\gamma\Delta t} \right)^2 \\ &= \tilde{\sigma}^2 - \gamma\Delta t \beta^2 \tilde{\sigma}^4 \left(1 + \frac{\gamma\Delta t}{(1-\gamma\Delta t)^2} \right) \\ &\simeq \tilde{\sigma}^2 - \gamma\Delta t \beta^2 \tilde{\sigma}^4 \end{aligned} \quad (12)$$

and when $s_t = 1$

$$\begin{aligned}
\sigma_t^2 &= \frac{1}{\gamma} \langle u_t^2 g(u_t) \rangle_{u_t; \tilde{\mu}, \tilde{\sigma}^2} - \frac{1}{\gamma^2} \langle u_t g(u_t) \rangle_{u_t; \tilde{\mu}, \tilde{\sigma}^2}^2 \\
&= \langle u_t^2 \rangle_{u_t; \tilde{\mu} + \beta \tilde{\sigma}^2, \tilde{\sigma}^2} - (\tilde{\mu} + \beta \tilde{\sigma}^2)^2 \\
&= \tilde{\sigma}^2
\end{aligned} \tag{13}$$

all together, this gives

$$\sigma_t^2 = \tilde{\sigma}^2 - \gamma \Delta t \beta^2 \tilde{\sigma}^4 (1 - s_t) \tag{14}$$

In a differential equation form, this gives

$$\dot{\sigma}^2 = \sigma_W^2 - 2\theta \sigma^2 - \gamma \beta^2 \sigma^4 \tag{15}$$

Note that in the limit of $\beta = 0$, the spiking information is irrelevant for the estimation of the distribution of u_t and therefore Eqs. 10 and 15 describe the evolution of the mean and variance for an OU process. In summary our dynamical system can be written as

$$\dot{\mu} = -\theta(\mu - u_r) + \beta \sigma^2 (S(t) - \gamma) \tag{16}$$

$$\dot{\sigma}^2 = -2\theta(\sigma^2 - \sigma_{\text{OU}}^2) - \gamma \beta^2 \sigma^4 \tag{17}$$

with the normalisation factor given by

$$\gamma = g_0 \exp\left(\beta \mu + \frac{\beta^2 \sigma^2}{2}\right) \tag{18}$$

3 Link to Short-Term Plasticity

The dynamics of the membrane potential estimator in Eqs 16 and 17 is closely related to the dynamics of short-term depression (see Eq. 12) in the main text). In order to highlight this link, let us denote by μ_∞ and σ_∞^2 respectively the stationary value of the mean and the variance estimator in the absence of spike i.e. they satisfy $\dot{\mu} = 0$ and $\dot{\sigma}^2 = 0$ when $S(t) = 0$.

Let $\hat{x} = \sigma^2 / \sigma_\infty^2$ denote the scaled variance estimator such that \hat{x} takes values between 0 and 1. Indeed, the variance estimator reaches its maximal value after an infinite amount of time in the absence of spikes. From Eq. 17, we can write:

$$\dot{\hat{x}} = \frac{\sigma_W^2}{\sigma_\infty^2} - 2\theta \hat{x} - \gamma \beta^2 \sigma_\infty^2 \hat{x}^2 \tag{19}$$

In order to show the link between the STP resource variable x and the scaled variance \hat{x} , let us consider the low stimulation frequency limit. This means that the estimator variables μ and σ^2 will be close to their asymptotic value μ_∞ and σ_∞^2 . Therefore the normalisation factor $\gamma(t)$ can be approximated by

$$\begin{aligned}
\gamma(t) &\simeq \gamma_\infty \exp(\beta^2 \sigma_\infty^2 H(t)) \\
&\simeq \gamma_\infty (1 + \beta^2 \sigma_\infty^2 \theta^{-1} S(t))
\end{aligned} \tag{20}$$

where $H(t)$ is a unit square function of duration θ^{-1} , i.e.

$$H(t) = \begin{cases} 1 & \text{if } t^{\text{spike}} \leq t < t^{\text{spike}} + \theta^{-1} \\ 0 & \text{else} \end{cases} \tag{21}$$

and $\gamma_\infty = g_0 \exp\left(\beta\mu_\infty + \frac{\beta^2\sigma_\infty^2}{2}\right)$. Because we are in the low frequency limit, the scaled variance \hat{x} is very close to 1 and therefore we have $\hat{x}^2 \simeq \hat{x} \simeq 1$. With this approximation, we can rewrite Eq. 19 as

$$\begin{aligned}\dot{\hat{x}} &\simeq \frac{\sigma_W^2}{\sigma_\infty^2} - (\beta^2\sigma_\infty^2\gamma_\infty + 2\theta)\hat{x} - \beta^4\sigma_\infty^4\gamma_\infty\theta^{-1}\hat{x}S(t) \\ &\simeq \frac{1 - \hat{x}}{\hat{\tau}_D} - \hat{Y}\hat{x}S(t)\end{aligned}\quad (22)$$

with $\hat{\tau}_D = (\beta^2\sigma_\infty^2\gamma_\infty + 2\theta)^{-1}$ and $\hat{Y} = \beta^4\sigma_\infty^4\gamma_\infty\theta^{-1}$. The link between the estimator of the membrane potential μ and the membrane potential v in the STP description is straightforward. Let \hat{v} be the approximation of μ under the same assumptions as above. Its dynamics is given by

$$\dot{\hat{v}} = -\frac{\hat{v} - \hat{v}_0}{\hat{\tau}} + \hat{J}\hat{Y}S(t)\quad (23)$$

with $\hat{\tau} = \theta^{-1}$, $\hat{v}_0 = \mu_\infty$ and $\hat{J} = \beta\sigma_\infty^2/\hat{Y} = \theta(\gamma_\infty\beta^3\sigma_\infty^2)^{-1}$. For a numerical application, let us consider the OU parameters and the NP parameters given in Fig. 1 of the main text (i.e. $u_r = 0$ mV, $\theta^{-1} = 100$ ms, $\sigma_{OU}^2 = 1$ mV, $\beta^{-1} = 1$ mV, $g_0 = 10$ Hz). In this case, the approximated short-term dynamics parameters yield $\hat{J} = 1.6$, $\hat{\tau} = 100$ ms, $\hat{v}_0 = -0.61$ mV, $\hat{\tau}_D = 38$ ms, $\hat{Y} = 0.47$ and the fitted parameters of the short-term dynamics give $J = 4.6 \pm 1$, $\tau = 61 \pm 5$ ms, $v_0 = -0.57 \pm 0.02$ mV, $\tau_D = 74 \pm 19$ ms, $Y = 0.22 \pm 0.08$ (mean \pm s.e.m results of 5 independent fitting of 120 s long spike trains). Although the match between the two sets of parameters is not perfect they still fall in the right ball-park.

4 Derivation of the estimator performance in the slow dynamics limit

We derive here an analytical expression of the asymptotic error performed by the estimator μ (see Eq. 16). Let this performance error be defined as

$$E^2(t) = \langle (\mu(t) - u(t))^2 \rangle_{S,u}\quad (24)$$

where $\langle \cdot \rangle_{S,u}$ denotes the average over a double stochastic process. It first averages over the spiking statistics given a membrane potential trajectory u and then it averages over the distribution of membrane potential trajectories. In order to be tractable analytically, we have to make several assumptions.

First, we will assume that we are in the slow dynamics limit ($\epsilon \rightarrow 0$, see section 2.2 of the main text). So we consider the dynamics of μ given by Eq. 11 of the main text that we will recall here for convenience:

$$\frac{\sqrt{\gamma}}{\sigma_W}\dot{\mu} \simeq S(t) - \gamma\quad (25)$$

Now let $\bar{\mu} = \langle \mu \rangle_{S,u}$ denote the expected value of the estimator μ . Since, we consider the $\epsilon \rightarrow 0$ limit, the variance of the estimator σ^2 (see Eq. 17) scales with $\sqrt{\epsilon}$ and therefore we have $\langle g(\mu) \rangle \simeq g(\bar{\mu})$. We can use this property to calculate the expectation of Eq. 25:

$$\frac{\sqrt{g(\bar{\mu})}}{\sigma_W}\dot{\mu} \simeq r - g(\bar{\mu})\quad (26)$$

with $r = g(u_r + \beta\sigma_{OU}^2/2)$. Similarly, let $\bar{\sigma}^2 = \langle (\mu - \bar{\mu})^2 \rangle_{S,u}$ denote the variance of the estimator μ around its expected value $\bar{\mu}$. The time derivative of this variance $\bar{\sigma}^2$ yields

$$\begin{aligned}
\dot{\bar{\sigma}}^2 &= 2 \langle \mu \dot{\mu} \rangle - 2 \langle \mu \rangle \langle \dot{\mu} \rangle \\
&= 2\sigma_W \left\langle \mu \frac{S - \gamma}{\sqrt{\gamma}} \right\rangle - 2\sigma_W \langle \mu \rangle \left\langle \frac{S - \gamma}{\sqrt{\gamma}} \right\rangle
\end{aligned} \tag{27}$$

Since, we consider the $\epsilon \rightarrow 0$ limit, the variance of the estimator σ^2 (see Eq. 17) scales with $\sqrt{\epsilon}$ and therefore we have $\langle \gamma(\mu) \rangle \simeq \gamma(\bar{\mu})$. Hence, we have

$$\begin{aligned}
\frac{\sqrt{g(\bar{\mu})}}{2\sigma_W} \dot{\bar{\sigma}}^2 &\simeq \langle \mu(S - \gamma) \rangle - \bar{\mu}(r - \gamma) \\
&\simeq -g'(\bar{\mu})\bar{\sigma}^2 + \frac{r\sigma_W}{2\sqrt{g(\bar{\mu})}}
\end{aligned} \tag{28}$$

where $g'(u) = dg(u)/du$ is the derivative of the gain function. In order to get the last equation, we used

$$\langle \mu S \rangle - \bar{\mu}r = \frac{r\sigma_W}{2\sqrt{\gamma}} \tag{29}$$

and linearised the gain function around the expected value u_r of the OU process:

$$\langle \mu \gamma \rangle - \bar{\mu}\gamma \simeq g'(u_r)\bar{\sigma}^2 \tag{30}$$

Asymptotically, the estimation error can be written as

$$E = \bar{\sigma} \simeq \sqrt{\frac{\bar{r}\sigma_W}{2g'(u_r)\sqrt{g(u_r)}}} \tag{31}$$