Active dendrites: adaptation to spike-based communication – supplementary information –

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A Appendix

In the first three sections of this appendix (Sec. A.1-A.3) we will compute differential equations for the time evolution of the posterior mean and variance of $\mathbf{u}$ after observing the presence or absence of spiking. We begin with the effect of the hidden OU-dynamics of the system and then we combine it with the observation of a particular spike pattern (either no spike, or a single spike from one of the cells). We assume (or, more precisely, pretend) that after each time step the posterior is multivariate Gaussian (hence we are performing assumed density filtering), so we only track the first two moments of the posterior. Note that, unlike in previous approaches we attempted, we are *not* computing the whole posterior in the limit, and then compute the mean and variance of this *approximate* posterior; rather, we compute the *exact* posterior and only take the limit for computing its mean and variance.

In section A.4 we describe our model extended correlated *up* and *down* states.

In the last section (Sec. A.5) we describe the dendritic estimator used in Sec. 3.3 of the main text.

A.1 Dynamics

We describe the distribution of the membrane potentials at time t (which is in fact the posterior computed from all previous observations) by a multivariate normal distribution:

$$\mathrm{P}(\mathbf{u}_t|\mathbf{s}_{0:t}) = \mathcal{N}(\mathbf{u}_t|\boldsymbol{\mu}_t, \boldsymbol{\Sigma}_t) \tag{13}$$

Equation 7 describes the changes of the membrane potentials in a time bin and defines the conditional probability

$$\mathrm{P}(\mathbf{u}_{t+\delta t}|\mathbf{u}_t) = \mathcal{N}(\mathbf{u}_{t+\delta t}|\alpha \boldsymbol{u}_t + c, \mathbf{Q}\delta t) \tag{14}$$

Combining the prior (Eq. 13) with the OU-dynamics of the membrane potential (Eq. 14) leads to the distribution of the membrane potential at the next time step

$$\mathrm{P}(\mathbf{u}_{t+\delta t}|\mathbf{s}_{0:t}) = \mathcal{N}(\mathbf{u}_{t+\delta t}|\overbrace{\alpha\boldsymbol{\mu}_t + c}^{\tilde{\boldsymbol{\mu}}_t}, \overbrace{\mathbf{Q}\delta t + \alpha^2\boldsymbol{\Sigma}_t}^{\tilde{\boldsymbol{\Sigma}}_t}). \tag{15}$$

Note, that $\mathrm{P}(\mathbf{u}_{t+\delta t}|\mathbf{s}_{0:t})$ does not incorporate the observation of $\mathbf{s}_{t+\delta t}$, and in the next section we will use it as a prior to combine it with the likelihood of generating the particular spiking pattern observed in time bin $t + \delta t$.

A.2 Observation

Our goal is to compute the posterior mean and variance of $\mathbf{u}$ after observing the presence or absence of spiking. As the probability of observing more than one spikes within a time window of δt approaches zero with δt^2 as $\delta t \to 0$, we do not elaborate on those cases. So in total, we have four

quantities to compute:

$$\boldsymbol{\mu}_0(\delta t) \triangleq \int \mathbf{u}\,\mathrm{P}(\mathbf{u}|\mathbf{s}=\mathbf{0})\;\mathrm{d}\mathbf{u} \tag{16}$$

$$\boldsymbol{\Sigma}_0(\delta t) \triangleq \int \mathbf{u}\mathbf{u}^{\mathrm{T}}, \mathrm{P}(\mathbf{u}|\mathbf{s}=\mathbf{0})\;\mathrm{d}\mathbf{u} - \boldsymbol{\mu}_0^2 \tag{17}$$

$$\boldsymbol{\mu}_i(\delta t) \triangleq \int \mathbf{u}\,\mathrm{P}\big(\mathbf{u}|\mathbf{s}=\boldsymbol{e}^i\big)\;\mathrm{d}\mathbf{u} \tag{18}$$

$$\boldsymbol{\Sigma}_i(\delta t) \triangleq \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\,\mathrm{P}\big(\mathbf{u}|\mathbf{s}=\boldsymbol{e}^i\big)\;\mathrm{d}\mathbf{u} - \boldsymbol{\mu}_i^2 \tag{19}$$

where $\boldsymbol{e}^i$ is a vector with elements $e^i_j = \delta(i,j)$. Ultimately, we are going to derive differential equations for these quantities by taking the $\delta t \to 0$ limit and dividing by δt. Derivatives denoted by $'$ are always taken with respect to δt. We only need to compute terms in these quantities up to first order in δt because the other terms will eventually vanish. In fact, for the case of $\boldsymbol{\mu}_i$ and $\boldsymbol{\Sigma}_i$, we only need to compute terms up to zeroth order in δt since the number of time bins with spikes does not scale with δt while the number of bins without spikes scales as $1/\delta t$.

A.2.1 No spike ($\mathbf{s}=\mathbf{0}$)

We will denote the likelihood in this case as

$$f_0(\mathbf{u},\delta t) \triangleq \mathrm{P}(\mathbf{s}=\mathbf{0}|\mathbf{u}) = \prod_i e^{-\delta t\, g\, e^{\beta u_i}} \tag{20}$$

Its derivative with respect to δt will also be needed later, which can be expressed as:

$$f_0'(\mathbf{u},\delta t) = \sum_i -g\, e^{\beta u_i} \prod_j e^{-\delta t\, g\, e^{\beta u_j}} \tag{21}$$

In particular, we note that at $\delta t = 0$ these yield the following values:

$$f_0(\mathbf{u},0) = 1 \tag{22}$$

$$f_0'(\mathbf{u},0) = \sum_i -g\, e^{\beta u_i} \tag{23}$$

Computing the posterior mean, $\boldsymbol{\mu}_0$ By its definition, Eq. 16, and in the $\delta t \to 0$ limit

$$\boldsymbol{\mu}_0(\delta t) = \frac{\overbrace{\int \mathbf{u}\,\mathrm{P}(\mathbf{u})\, f_0(\mathbf{u},\delta t)\;\mathrm{d}\mathbf{u}}^{\mathbf{m}_0(\delta t)}}{\underbrace{\int \mathrm{P}(\mathbf{u})\, f_0(\mathbf{u},\delta t)\;\mathrm{d}\mathbf{u}}_{a_0(\delta t)}} \simeq \boldsymbol{\mu}_0(0) + \delta t\, \boldsymbol{\mu}_0'(0) \tag{24}$$

We will need derivatives of the numerator, $\mathbf{m}_0(\delta t)$, and denominator, $a_0(\delta t)$, of the above expression:

$$\mathbf{m}_0'(\delta t) = \int \mathbf{u}\,\mathrm{P}(\mathbf{u})\, f_0'(\mathbf{u},\delta t)\;\mathrm{d}\mathbf{u} \tag{25}$$

$$a_0'(\delta t) = \int \mathrm{P}(\mathbf{u})\, f_0'(\mathbf{u},\delta t)\;\mathrm{d}\mathbf{u} \tag{26}$$

and in particular the values the numerator and denonimator and their derivatives take at $\delta t = 0$:[1]

$$\mathbf{m}_0(0) = \int \mathbf{u}\,\mathrm{P}(\mathbf{u})\,f_0(\mathbf{u},0)\;\mathrm{d}\mathbf{u} = \tilde{\boldsymbol{\mu}}_t \tag{27}$$

$$a_0(0) = \int \mathrm{P}(\mathbf{u})\,f_0(\mathbf{u},0)\;\mathrm{d}\mathbf{u} = 1 \tag{28}$$

$$\mathbf{m}_0'(0) = \int \mathbf{u}\,\mathrm{P}(\mathbf{u})\,f_0'(\mathbf{u},0)\;\mathrm{d}\mathbf{u} = -\sum_i \int \mathbf{u}\,\mathrm{P}(\mathbf{u})\,g\,e^{\beta u_i}\,\mathrm{d}\mathbf{u} = -\bar{\gamma}\tilde{\boldsymbol{\mu}}_t - \beta\tilde{\boldsymbol{\Sigma}}_t\boldsymbol{\gamma} \tag{29}$$

$$a_0'(0) = \int \mathrm{P}(\mathbf{u})\,f_0'(\mathbf{u},0)\;\mathrm{d}\mathbf{u} = -\sum_i \int \mathrm{P}(\mathbf{u})\,g\,e^{\beta u_i}\,\mathrm{d}\mathbf{u} = -\bar{\gamma} \tag{30}$$

where $\boldsymbol{\gamma}$ is a vector whose elements $\gamma_i = g\,e^{\beta\mu_i + \frac{\beta^2\Sigma_{ii}}{2}}$ are the firing rate of the neurons[2], and $\bar{\gamma} = \sum_i \gamma_i$ is the population firing rate.

Equipped with these quantities, we first compute the zeroth-order term of Eq. 24:

$$\boldsymbol{\mu}_0(0) = \frac{\mathbf{m}_0(0)}{a_0(0)} = \tilde{\boldsymbol{\mu}}_t \tag{31}$$

and then the coefficient in the first-order term of Eq. 24:

$$\boldsymbol{\mu}_0'(0) = \frac{\mathbf{m}_0'(0)\,a_0(0) - \mathbf{m}_0(0)\,a_0'(0)}{\left[a_0(0)\right]^2} \tag{32}$$

$$= -\bar{\gamma}\tilde{\boldsymbol{\mu}}_t - \beta\tilde{\boldsymbol{\Sigma}}_t\boldsymbol{\gamma} + \bar{\gamma}\tilde{\boldsymbol{\mu}}_t \tag{33}$$

$$= -\beta\tilde{\boldsymbol{\Sigma}}_t\boldsymbol{\gamma} \tag{34}$$

Substituting Eqs. 31 and 34 into Eq. 24 we obtain:

$$\boldsymbol{\mu}_0 \simeq \tilde{\boldsymbol{\mu}}_t - \delta t\beta\tilde{\boldsymbol{\Sigma}}_t\boldsymbol{\gamma} \tag{35}$$

Computing the posterior covariance, $\boldsymbol{\Sigma}_0$ The logic is essentially the same as the one we followed to compute $\boldsymbol{\mu}_0$ in the previous section.

By its definition, Eq. 17, and in the $\delta t \to 0$ limit

$$\boldsymbol{\Sigma}_0(\delta t) + \boldsymbol{\mu}_0(\delta t)\,\boldsymbol{\mu}_0(\delta t)^{\mathrm{T}} = \frac{\overbrace{\int \mathbf{u}\mathbf{u}^{\mathrm{T}}\,\mathrm{P}(\mathbf{u})\,f_0(\mathbf{u},\delta t)\;\mathrm{d}\mathbf{u}}^{\mathbf{c}_0(\delta t)}}{\underbrace{\int \mathrm{P}(\mathbf{u})\,f_0(\mathbf{u},\delta t)\;\mathrm{d}\mathbf{u}}_{a_0(\delta t)}} \simeq \boldsymbol{\Sigma}_0(0) + \delta t\,{\boldsymbol{\Sigma}_0}'(0) \tag{36}$$

The denominator (and thus its derivative) is the same as in the previous section, and the derivative of the numerator is:

$$\mathbf{c}_0'(\delta t) = \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\,\mathrm{P}(\mathbf{u})\,f_0'(\mathbf{u},\delta t)\;\mathrm{d}\mathbf{u} \tag{37}$$

and in particular the values of the numerator and its derivative at $\delta t = 0$ are:

$$\mathbf{c}_0(0) = \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\,\mathrm{P}(\mathbf{u})\,f_0(\mathbf{u},0)\;\mathrm{d}\mathbf{u} = \tilde{\boldsymbol{\Sigma}}_t + \tilde{\boldsymbol{\mu}}_t\tilde{\boldsymbol{\mu}}_t^{\mathrm{T}} \tag{38}$$

$$\mathbf{c}_0'(0) = \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\,\mathrm{P}(\mathbf{u})\,f_0'(\mathbf{u},0)\;\mathrm{d}\mathbf{u} = -\sum_i \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\,\mathrm{P}(\mathbf{u})\,g\,e^{\beta u_i}\,\mathrm{d}\mathbf{u}$$

$$= -\bar{\gamma}(\tilde{\boldsymbol{\Sigma}}_t + \tilde{\boldsymbol{\mu}}_t\tilde{\boldsymbol{\mu}}_t^{\mathrm{T}}) - 2\beta\tilde{\boldsymbol{\mu}}_t\boldsymbol{\gamma}^{\mathrm{T}}\tilde{\boldsymbol{\Sigma}}_t - \beta^2\tilde{\boldsymbol{\Sigma}}_t\boldsymbol{\Gamma}\tilde{\boldsymbol{\Sigma}}_t \tag{39}$$

[1] For the last two equations we used the following simple identity:

$$g\,e^{\beta u_i}\,\mathcal{N}(\mathbf{u};\boldsymbol{\mu},\boldsymbol{\Sigma}) = g\,e^{\beta\mu_i + \frac{\beta^2\Sigma_{ii}}{2}}\,\mathcal{N}\Big(\mathbf{u};\boldsymbol{\mu} + \beta\boldsymbol{\Sigma}\boldsymbol{e}^i,\boldsymbol{\Sigma}\Big)$$

.

[2] More precisely, this is the firing rate if we use Bernoulli approximation for the Poisson spiking, which is valid only if δt is sufficiently small.

where $\boldsymbol{\Gamma}$ is a diagonal matrix with elements $\Gamma_i = g\, e^{\beta\mu_i + \frac{\beta^2 \Sigma_{ii}}{2}}$, i.e., the firing rate of the neurons.

Equipped with these quantities, we first compute the zeroth-order term of Eq. 36:

$$\boldsymbol{\Sigma}_0(0) = \frac{\mathbf{c}_0(0)}{a_0(0)} = \tilde{\boldsymbol{\Sigma}}_t + \tilde{\boldsymbol{\mu}}_t^2 \tag{40}$$

and then the coefficient in the first-order term of Eq. 36:

$$\begin{aligned}
{\boldsymbol{\Sigma}_0}'(0) &= \frac{\mathbf{c}_0'(0)\, a_0(0) - \mathbf{c}_0(0)\, a_0'(0)}{[a_0(0)]^2} && (41)\\
&= -\bar{\gamma}(\tilde{\boldsymbol{\Sigma}}_t + \tilde{\boldsymbol{\mu}}_t \tilde{\boldsymbol{\mu}}_t^{\mathrm{T}}) - 2\beta \tilde{\boldsymbol{\mu}}_t \boldsymbol{\gamma}^{\mathrm{T}} \tilde{\boldsymbol{\Sigma}}_t - \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t + \bar{\gamma}\left[\tilde{\boldsymbol{\Sigma}}_t + \tilde{\boldsymbol{\mu}}_t \tilde{\boldsymbol{\mu}}_t^{\mathrm{T}}\right] && (42)\\
&= -2\beta \tilde{\boldsymbol{\mu}}_t \boldsymbol{\gamma}^{\mathrm{T}} \tilde{\boldsymbol{\Sigma}}_t - \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t && (43)
\end{aligned}$$

Substituting Eqs. 40 and 43 into Eq. 36 we obtain:

$$\boldsymbol{\Sigma}_0 + \boldsymbol{\mu}_0 \boldsymbol{\mu}_0^{\mathrm{T}} \simeq \tilde{\boldsymbol{\Sigma}}_t + \tilde{\boldsymbol{\mu}}_t \tilde{\boldsymbol{\mu}}_t^{\mathrm{T}} - 2\delta t \beta \tilde{\boldsymbol{\mu}}_t \boldsymbol{\gamma}^{\mathrm{T}} \tilde{\boldsymbol{\Sigma}}_t - \delta t \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t \tag{44}$$

and by substituting Eq. 35 into this, and again ignoring terms that are higher than first order in δt, we can express $\boldsymbol{\Sigma}_0$ as:

$$\begin{aligned}
\boldsymbol{\Sigma}_0 &\simeq \tilde{\boldsymbol{\Sigma}}_t + \tilde{\boldsymbol{\mu}}_t \tilde{\boldsymbol{\mu}}_t^{\mathrm{T}} - 2\delta t \beta \tilde{\boldsymbol{\mu}}_t \boldsymbol{\gamma}^{\mathrm{T}} \tilde{\boldsymbol{\Sigma}}_t - \delta t \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t + \\
&\quad - \left[\tilde{\boldsymbol{\mu}}_t - \delta t \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\gamma}\right] \left[\tilde{\boldsymbol{\mu}}_t - \delta t \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\gamma}\right]^{\mathrm{T}} && (45)\\
&\simeq \tilde{\boldsymbol{\Sigma}}_t - \delta t \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t - \delta t^2 \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\gamma} \boldsymbol{\gamma}^{\mathrm{T}} \tilde{\boldsymbol{\Sigma}}_t^{\mathrm{T}} && (46)
\end{aligned}$$

Thus:

$$\boldsymbol{\Sigma}_0 \simeq \tilde{\boldsymbol{\Sigma}}_t - \delta t \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t \tag{47}$$

A.2.2 Spike ($\mathbf{s} = \boldsymbol{e}^i$)

We consider the case when one of the cells emitted one or more spikes in a time bin, $s_i = 1$, while $s_{j \neq i} = 0$. The logic here is the same as that followed in the "no spike" case, except that we only keep terms that are constant with respect to δt (see argument above).

We will denote the likelihood in this case as

$$\begin{aligned}
f_i(\mathbf{u}, \delta t) \triangleq \mathrm{P}\big(\mathbf{s} = \boldsymbol{e}^i | \mathbf{u}\big) &= \delta t\, g\, e^{\beta u_i} e^{-\delta t\, g\, e^{\beta u_i}} \prod_{j \neq i} e^{-\delta t\, g\, e^{\beta u_j}} && (48)\\
&= \delta t\, g\, e^{\beta u_i} \prod_{j} e^{-\delta t\, g\, e^{\beta u_j}} && (49)
\end{aligned}$$

Its derivative will also be needed later, which can be expressed as:

$$f_i'(\mathbf{u}, \delta t) = g\, e^{\beta u_i} \prod_j e^{-\delta t\, g\, e^{\beta u_j}} - \delta t\, g\, e^{\beta u_i} \sum_j g\, e^{\beta u_j} \prod_k e^{-\delta t\, g\, e^{\beta u_k}} \tag{50}$$

In particular, we note that at $\delta t = 0$ these yield the following values:

$$\begin{aligned}
f_i(\mathbf{u}, 0) &= 0 && (51)\\
f_i'(\mathbf{u}, 0) &= g\, e^{\beta u_i} && (52)
\end{aligned}$$

Computing the posterior mean, $\boldsymbol{\mu}_i$ By its definition, Eq. 18, and in the $\delta t \to 0$ limit (only retaining the zeroth-order term)

$$\boldsymbol{\mu}_i(\delta t) = \frac{\overbrace{\int \mathbf{u}\, \mathrm{P}(\mathbf{u})\, f_i(\mathbf{u}, \delta t)\, \mathrm{d}\mathbf{u}}^{\mathbf{m}_i(\delta t)}}{\underbrace{\int \mathrm{P}(\mathbf{u})\, f_i(\mathbf{u}, \delta t)\, \mathrm{d}\mathbf{u}}_{a_i(\delta t)}} \simeq \boldsymbol{\mu}_i(0) \tag{53}$$

Since both $\mathbf{m}_i(\delta t) \to 0$ and $a_i(\delta t) \to 0$ as $\delta t \to 0$, we need to use l'Hôpital's rule to compute $\boldsymbol{\mu}_i(0)$:

$$\lim_{\delta t \to 0} \boldsymbol{\mu}_i(\delta t) = \frac{\mathbf{m}_i'(0)}{a_i'(0)} \tag{54}$$

and for this we will need the following two derivatives:

$$\mathbf{m}_i'(\delta t) = \int \mathbf{u}\, \mathrm{P}(\mathbf{u})\, f_i'(\mathbf{u}, \delta t)\, \mathrm{d}\mathbf{u} \tag{55}$$

$$a_i'(\delta t) = \int \mathrm{P}(\mathbf{u})\, f_i'(\mathbf{u}, \delta t)\, \mathrm{d}\mathbf{u} \tag{56}$$

and in particular the values that these derivatives take at $\delta t = 0$:

$$\mathbf{m}_i'(0) = \int \mathbf{u}\, \mathrm{P}(\mathbf{u})\, f_i'(\mathbf{u}, 0)\, \mathrm{d}\mathbf{u} = \int \mathbf{u}\, \mathrm{P}(\mathbf{u})\, g\, e^{\beta u_i}\, \mathrm{d}\mathbf{u} = g\, e^{\beta \mu_i + \frac{\beta^2 \Sigma_{ii}}{2}} (\tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i) \tag{57}$$

$$a_i'(0) = \int \mathrm{P}(\mathbf{u})\, f_i'(\mathbf{u}, 0)\, \mathrm{d}\mathbf{u} = \int \mathrm{P}(\mathbf{u})\, g\, e^{\beta u_i}\, \mathrm{d}\mathbf{u} = g\, e^{\beta \mu_i + \frac{\beta^2 \Sigma_{ii}}{2}} \tag{58}$$

Substituting Eqs. 57-58 into Eq. 54 and in turn into Eq. 53, we obtain:

$$\boldsymbol{\mu}_i \simeq \tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i \tag{59}$$

Computing the posterior covariance, $\boldsymbol{\Sigma}_i$ By its definition, Eq. 19, and in the $\delta t \to 0$ limit (once again only retaining the zeroth-order term)

$$\boldsymbol{\Sigma}_i(\delta t) + \boldsymbol{\mu}_i(\delta t)\, \boldsymbol{\mu}_i(\delta t)^{\mathrm{T}} = \frac{\overbrace{\int \mathbf{u}\mathbf{u}^{\mathrm{T}}\, \mathrm{P}(\mathbf{u})\, f_i(\mathbf{u}, \delta t)\, \mathrm{d}\mathbf{u}}^{\mathbf{c}_i(\delta t)}}{\underbrace{\int \mathrm{P}(\mathbf{u})\, f_i(\mathbf{u}, \delta t)\, \mathrm{d}\mathbf{u}}_{a_i(\delta t)}} \simeq \boldsymbol{\Sigma}_i(0) \tag{60}$$

Once again, since both $\mathbf{c}_i(\delta t) \to 0$ and $a_i(\delta t) \to 0$ as $\delta t \to 0$, we need to use l'Hôpital's rule to compute $\boldsymbol{\Sigma}_i(0)$:

$$\lim_{\delta t \to 0} \boldsymbol{\Sigma}_i(\delta t) = \frac{\mathbf{c}_i'(0)}{a_i'(0)} - \boldsymbol{\mu}_i(0)\, \boldsymbol{\mu}_i(0)^{\mathrm{T}} \tag{61}$$

and for this we will need the derivative:

$$\mathbf{c}_i'(\delta t) = \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\, \mathrm{P}(\mathbf{u})\, f_i'(\mathbf{u}, \delta t)\, \mathrm{d}\mathbf{u} \tag{62}$$

and in particular the value that this derivative takes at $\delta t = 0$:

$$\mathbf{c}_i'(0) = \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\, \mathrm{P}(\mathbf{u})\, f_i'(\mathbf{u}, 0)\, \mathrm{d}\mathbf{u} = \int \mathbf{u}\mathbf{u}^{\mathrm{T}}\, \mathrm{P}(\mathbf{u})\, g\, e^{\beta u_i}\, \mathrm{d}\mathbf{u} \tag{63}$$

$$= g\, e^{\beta \mu_i + \frac{\beta^2 \Sigma_{ii}}{2}} \left(\left[\tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i \right] \left[\tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i \right]^{\mathrm{T}} + \tilde{\boldsymbol{\Sigma}}_t \right) \tag{64}$$

($a_i(\delta t)$ and hence $a_i'(\delta t)$ are the same as in the previous section.)

Substituting Eqs. 58, 59, and 64 into Eq. 61, we obtain:

$$\boldsymbol{\Sigma}_i \simeq \frac{g\, e^{\beta \mu_i + \frac{\beta^2 \Sigma_{ii}}{2}} \left(\left[\tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i \right] \left[\tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i \right]^{\mathrm{T}} + \tilde{\boldsymbol{\Sigma}}_t \right)}{g\, e^{\beta \mu_i + \frac{\beta^2 \Sigma_{ii}}{2}}} - \left[\tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i \right] \left[\tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{e}^i \right]^{\mathrm{T}} \tag{65}$$

Thus:

$$\boldsymbol{\Sigma}_i \simeq \tilde{\boldsymbol{\Sigma}}_t \tag{66}$$

In summary, we can write that:

$$\boldsymbol{\mu}_{0,t+1} = \tilde{\boldsymbol{\mu}}_t - \delta t \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\gamma} \tag{67}$$

$$\boldsymbol{\mu}_{i,t+1} = \tilde{\boldsymbol{\mu}}_t + \beta \tilde{\boldsymbol{\Sigma}}_t \mathbf{s}_{t+\delta t} \tag{68}$$

$$\boldsymbol{\Sigma}_{0,t+1} = \tilde{\boldsymbol{\Sigma}}_t - \delta t \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t \tag{69}$$

$$\boldsymbol{\Sigma}_{i,t+1} = \tilde{\boldsymbol{\Sigma}}_t \tag{70}$$

where

$$\tilde{\boldsymbol{\mu}}_t = \alpha \boldsymbol{\mu}_t + c \tag{71}$$

$$\tilde{\boldsymbol{\Sigma}}_t = \mathbf{Q}\delta t + \alpha^2 \boldsymbol{\Sigma}_t \tag{72}$$

as defined in Eq. 15, and $\alpha = 1 - \frac{\delta t}{\tau}$ and $c = \frac{\delta t}{\tau} u_0$.

A.3 The optimal estimator

First, we write the time evolution of the mean:

$$\boldsymbol{\mu}_{t+1} = \tilde{\boldsymbol{\mu}}_t - \delta t \beta \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\gamma} + \beta \tilde{\boldsymbol{\Sigma}}_t \mathbf{s}_{t+\delta t} \tag{73}$$

$$\boldsymbol{\mu}_{t+1} - \boldsymbol{\mu}_t \simeq \frac{u_0 - \boldsymbol{\mu}_t}{\tau} \delta t - \delta t \beta \boldsymbol{\Sigma}_t \boldsymbol{\gamma} + \beta \boldsymbol{\Sigma}_t \mathbf{s}_{t+\delta t} + \mathcal{O}(\delta t^2) \tag{74}$$

$$\dot{\boldsymbol{\mu}} = \frac{u_0 - \boldsymbol{\mu}}{\tau} + \beta \boldsymbol{\Sigma} \left(\mathbf{s}(t) - \boldsymbol{\gamma} \right) \tag{75}$$

where we used that $\lim_{\delta t \to 0} \tilde{\boldsymbol{\Sigma}}_t = \boldsymbol{\Sigma}_t$ and $\mathbf{s}(t)$ is vector composed of the sequences of delta spike trains such that

$$\mathbf{s}_k = \int_{k\delta t}^{(k+1)\delta t} \mathbf{s}(t) \mathrm{d}t \tag{76}$$

The first term of Eq. 75 indicates that in the absence of observations the mean returns to the resting potential, u_0. The second term introduces a continuous decrease which is proportional to the firing rate, $\boldsymbol{\gamma}$, while the observation of a spike leads to an instantaneous step-like increase in the mean.

In a similar way we write the time evolution of the covariance matrix:

$$\boldsymbol{\Sigma}_{t+1} = \tilde{\boldsymbol{\Sigma}}_t - \delta t \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t \tag{77}$$

$$= \mathbf{Q}\delta t + \alpha^2 \boldsymbol{\Sigma}_t - \delta t \beta^2 \tilde{\boldsymbol{\Sigma}}_t \boldsymbol{\Gamma} \tilde{\boldsymbol{\Sigma}}_t \tag{78}$$

$$\boldsymbol{\Sigma}_{t+1} - \boldsymbol{\Sigma}_t \simeq \mathbf{Q}\delta t - \frac{2\delta t}{\tau} \boldsymbol{\Sigma}_t - \delta t \beta^2 \boldsymbol{\Sigma}_t \boldsymbol{\Gamma} \boldsymbol{\Sigma}_t + \mathcal{O}(\delta t^2) \tag{79}$$

$$\dot{\boldsymbol{\Sigma}} = \mathbf{Q} - \frac{2}{\tau} \boldsymbol{\Sigma} - \beta^2 \boldsymbol{\Sigma} \boldsymbol{\Gamma} \boldsymbol{\Sigma} \tag{80}$$

$$= \frac{2}{\tau} (\boldsymbol{\Sigma}_{OU} - \boldsymbol{\Sigma}) - \beta^2 \boldsymbol{\Sigma} \boldsymbol{\Gamma} \boldsymbol{\Sigma} \tag{81}$$

where $\boldsymbol{\Sigma}_{OU} = \frac{\mathbf{W}\tau}{2}$ is the prior covariance matrix of the presynaptic membrane potential, i.e., in the absence of any observation. As $\boldsymbol{\Sigma} < \boldsymbol{\Sigma}_{OU}$ the first term increases the covariance towards $\boldsymbol{\Sigma}_{OU}$, while the second term, which is always negative, introduces a decrease that is proportional to the estimated firing rate. As the absence of spikes is more informative when the rate is high, the decrease is steeper in this case. If the two opposite forces are equal $\boldsymbol{\Sigma}$ does not change any more. Note that $\boldsymbol{\gamma}$ and $\boldsymbol{\Gamma}$ are functions of both $\boldsymbol{\mu}$ and $\boldsymbol{\Sigma}$!

In summary the time evolution of the mean and the covariance of the presynaptic membrane potentials can be written as

$$\dot{\boldsymbol{\mu}} = \frac{1}{\tau} (u_0 - \boldsymbol{\mu}) + \beta \boldsymbol{\Sigma} \left(\mathbf{s}(t) - \boldsymbol{\gamma} \right) \tag{82}$$

$$\dot{\boldsymbol{\Sigma}} = \frac{2}{\tau} (\boldsymbol{\Sigma}_{OU} - \boldsymbol{\Sigma}) - \beta^2 \boldsymbol{\Sigma} \boldsymbol{\Gamma} \boldsymbol{\Sigma} \tag{83}$$

A.4 Modelling correlated up and down states

The global, binary states variable x has a first order Markovian dynamics described by the transition matrix $\boldsymbol{\rho}$ with state transition rates $\rho^x_{12} = \rho^x_{21} = \rho^x$ ($\rho^x_{11} = 1 - \rho^x_{21}\delta t$).

Similarly, the 'resting' potential of each presynaptic neuron, u_0, can switch between two different values, u_{up} and u_{down}. The dynamics of the resting potential is described by the transition probabilities, $\mathrm{P}(u_{0,t+\delta t} = u_{\text{up}}|u_{0,t} = u_{\text{down}}) = \rho_u \delta t$ and $\mathrm{P}(u_{0,t+\delta t} = u_{\text{down}}|u_{0,t} = u_{\text{up}}) = \rho_d \delta t$. The global state variable influences indirectly the state of the individual neurons by modulating their state transition matrices.

Specifically, when x is in the *up* state then $\rho_u = \rho_1$ and $\rho_d = \rho_2$, while in the global *down* state $\rho_u = \rho_2$ and $\rho_d = \rho_1$ where $\rho_1 \geq \rho_2$. In this case it is easy to show that the correlation between the resting potential of the neurons is $\frac{(\rho_1-\rho_2)^2}{(\rho_1+\rho_2)^2}$, and it can be parametrically changed by varying the ratio ρ_1/ρ_2.

A.5 The dendritic estimator

We model the spatially extended dendritic tree of neurons with a two layer feed-forward network of simple units (Fig. 3A). Synaptic inputs impinge on units in the first layer, corresponding to dendritic branches, and nonlinear integration of inputs arriving to a dendritic branch is modelled by a sigmoidal input-output function:

$$v^{\mathrm{d}}_j(t) = h\left(\sum_i w_{ji} v^{\mathrm{syn}}_i(t)\right) \tag{84}$$

where $h(x) = \frac{1}{1+e^{-x}}$ is the standard sigmoidal function, and the synaptic potentials are given by the following differential equation:

$$\frac{\mathrm{d}v^{\mathrm{syn}}_i}{\mathrm{d}t} = \frac{v^{\mathrm{syn}}_i - v_0}{\tau_{syn}} + J s_i(t) \tag{85}$$

where $s_i(t)$ is the spike train of the ith presynaptic neuron represented as a sum of Dirac-delta functions, τ_{syn} is the time constant of the synapse, v_0 is its resting potential and J is the coupling. The parameters of the static synapses, v_0, τ_{syn}, J, are set to minimise $(u_i - v^{\mathrm{syn}}_i)^2$. As each presynaptic neuron has the same dynamics and spiking process, the same set of parameters are used for each synapse. Finally the output of the neuron, that is the estimate of the dendritic estimator, $\tilde{v}_{\text{den}}(t)$, is the linear sum of the dendritic activations:

$$\tilde{v}_{\text{den}}(t) = \sum_{j=1}^{5} \tilde{c}_j v^{\mathrm{d}}_j(t) \tag{86}$$

We trained the model to estimate the sum of the presynaptic membrane potentials, $\sum_i u_i$, by changing its parameters, $\mathbf{w}$ and $\tilde{\mathbf{c}}$ using error backpropagation and gradient ascent.