Upcrossing-rate dynamics for a minimal neuron model receiving spatially distributed synaptic drive

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The spatiotemporal stochastic dynamics of the voltage as well as the upcrossing rate are derived for a model neuron comprising a long dendrite with uniformly distributed filtered excitatory and inhibitory synaptic drive. A cascade of ordinary and partial differential equations is obtained describing the evolution of first-order means and second-order spatial covariances of the voltage and its rate of change. These quantities provide an analytical form for the general, steady-state and linear response of the upcrossing rate to dynamic synaptic input. It is demonstrated that this minimal dendritic model has an unexpectedly sustained high-frequency response despite synaptic, membrane and spatial filtering.


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I. INTRODUCTION

Neurons are spatially extended cells receiving a high density of synapses on their dendrites [1] and can be modelled as threshold devices that integrate filtered stochastic input from presynaptic populations. Over the last decades there have been significant advances in the mathematical analysis of neuronal input-output functions, typically in an approximation in which the cell is treated as isopotential [2]. Simultaneously, there has been growing interest in how spatially induced voltage differences throughout the dendritic arbour might support computational capacities beyond the isopotential approximation. These latter studies have been overwhelmingly simulational [3] due to the difficulty in accounting for spatial structure and non-linear filtering.

There is a relative sparsity of results for stochastic synaptic integration in neurons with explicit spatial structure [4–9]. However, earlier studies of isopotential neurons demonstrate that analytical statements derived from reduced models provide a general and enduring framework that are an important guide for biophysically detailed but particular simulational studies. With this in mind, here a minimal model of spatiotemporal integration is considered and solved for both the stochastic voltage and firing-rate dynamics.

We first derive a set of partial differential equations that describe the spatiotemporal voltage fluctuations under dendritic integration of stochastic synaptic drive. We then adapt Rice’s level-crossing approximation [10], widely used for isopotential models [11–18], to demonstrate that the high-frequency response of the upcrossing rate exhibits a much weaker effect of the cascade of synaptic, membrane and spatial filtering than might naively be expected.

II. MODEL

The voltage \( V(x,t) \) of an infinite dendrite, with a threshold crossing \( V_{th} \) tested at \( x=0 \) only, obeys

\[
\partial_t V = \alpha_i (E_i - V) + H_e (E_e - V) + H_h (E_h - V) + D \partial^2_x V \quad (1)
\]

where the leak and synaptic conductances per unit area have been divided by capacitance per unit area to give rate-like quantities \( \alpha_i, H_e, H_h \) and where \( E_i, E_e, E_h \) are the associated reversal potentials. We will use the notation \( s = e, i \) throughout to denote excitation or inhibition, respectively. The diffusive term of constant strength \( D = \lambda^2 \alpha_i \), where \( \lambda \) is the electrotonic length, captures the effect of axial-current flow through the dendritic core. Structurally, the model can be interpreted as a neuron with two long dendrites stemming from a small soma that has no additional conductance load.

The response to an isolated excitatory synaptic input \( \tau_e H_e + H_e \propto \delta(x) \delta(t) \), where \( \tau_e \) is the excitatory synaptic time constant, is plotted in Fig. 1A and 1B. In the latter panel the temporal profiles at different distances are compared to that of an isopotential model where \( D = 0 \) and \( \tau_e H_e + H_e \propto \delta(t) \). The time to peak for nearby input is shorter than for the isopotential model and so the cross-over behaviour (see Fig. 1B inset) suggests that the minimal dendritic model might have a more rapid response to synaptic drive than the isopotential model, despite the additional spatial filtering.

To examine whether this is or is not the case, we developed a model of spatially distributed synaptic drive with...
but spatially independent and obey
\[
\partial_t V = \alpha_t (E_t - \langle V \rangle) + \langle h_c \rangle (E_c - \langle V \rangle) + \langle h_i \rangle (E_i - \langle V \rangle) \\
\tau_v \partial_t h_c = \alpha_c - \langle h_c \rangle \quad \text{and} \quad \tau_h \partial_t h_i = \alpha_i - \langle h_i \rangle.
\]

The fluctuating components \(v, h_c, h_i\) are functions of space and time and obey the partial-differential equations
\[
\partial_t v = h_e E_c + h_i E_i - \mathcal{H}v + D \partial_x^2 v \\
\tau_v \partial_t h_c = \sqrt{\alpha_c} \lambda_c \eta_c - h_c \\
\tau_i \partial_t h_i = \sqrt{\alpha_i} \lambda_i \eta_i - h_i
\]
where \(E_c = (E_v + h_e (x_0, t)) - \mathcal{H}v\) and \(H(t) = \alpha \tau_i + \langle h_i \rangle + \langle H_i \rangle\) are spatially independent, though generally time dependent. Note that in deriving Eqs. (3-4) we have dropped relatively less significant terms like \(\langle v \eta_i \rangle\) [5, 20] so the voltage has Gaussian statistics. Fig. 1C and 1D provide examples of the spatiotemporal dynamics and an upcrossing event.

The upcrossing rate [10] is a non-linear function of two first-order and three second-order voltage moments \(r_{uv}(V), \langle v^2 \rangle, \langle \dot{v} \rangle, \langle \dot{v}^2 \rangle\) with the full form provided in the Appendix. The first-order moments are given by Eq. set (3). To obtain the second-order moments we derive partial differential equations for the same-time space-separated covariances. Introducing the shorthand \(h^2_x = \langle h_i(x_1, t) h_i(x_2, t) \rangle\) where \(x = x_2 - x_1\) we first formally solve for the same-time synaptic autocovariance
\[
\langle h_i^2 \rangle_x = \delta(x) \frac{\lambda_i}{\tau_i^2} \int_{-\infty}^{t} dt' e^{-(t'-t)/\tau_i} \alpha_i(t').
\]
This integral is also the solution of a linear partial-differential equation for \(h_i^2_x\) (see Eq. 6). We can also derive partial-differential equations for other covariances by taking various moments of equations set (4) to give
\[
\frac{\tau_v}{2} \partial_t \langle h_i^2 \rangle_x = \delta(x) \frac{\alpha_i}{\tau_i^2} h_i^2_x - \langle h_i^2 \rangle_x
\]
\[
\partial_t \langle v h_i \rangle_x = \mathcal{E}_v \langle h_i^2 \rangle_x - \mathcal{H} \langle \dot{v} h_i \rangle_x + D \partial_x^2 \langle v h_i \rangle_x
\]
\[
\frac{1}{2} \partial_t \langle v^2 \rangle_x = \mathcal{E}_v \langle v h_i \rangle_x + \mathcal{E}_c \langle \delta_i^2 \rangle_x - \mathcal{H} \langle \dot{v}^2 \rangle_x + D \partial_x^2 \langle v^2 \rangle_x
\]
where additionally we have \(\langle \dot{v}^2 \rangle_x = \partial_t \langle v^2 \rangle_x / 2\). For the autocovariance of \(\dot{v}\) we will need the relation
\[
\langle \dot{v} h_i \rangle_x = \partial_t \langle v h_i \rangle_x + \langle v^2 \rangle_x / \tau_v
\]
derived by multiplying the synaptic conductance equation (4) by \(v\) and taking moments while noting that \(\langle v \eta_i \rangle = 0\) due to causality. The above relation is used for the autocovariance of the rate-change of voltage
\[
\langle \dot{v}^2 \rangle_x = \mathcal{E}_c \langle \dot{v} h_i \rangle_x + \mathcal{E}_i \langle \dot{v} h_i \rangle_x - \mathcal{H} \langle \dot{v}^2 \rangle_x + D \partial_x^2 \langle \dot{v}^2 \rangle_x
\]
The covariance equations (6-10), with \(s = c, i\) provide a feedforward cascade allowing all moment-like quantities
to be derived for the upcrossing dynamics by solving for the \( x \) and \( t \) dependence and then setting \( x = 0 \).

It should be noted that these equations are valid for arbitrary presynaptic rate dynamics and are not linear approximations. An example of the response to changes in the presynaptic rates comprising onset/offset and multiple frequency components is provided in Fig. 2. It can be seen that moments including \( \dot{V} \) or \( \ddot{v} \) have sustained responses at higher frequencies.

### III. STEADY-STATE PROPERTIES

Before calculating frequency-dependent properties, we first derive forms for the different spatial covariances and moments required for the steady-state upcrossing rate. The notation \( \bar{Q} \) is used for the steady-state value of a quantity \( Q(t) \).

The steady-state means are calculated using \( \langle \dot{H}_s \rangle = \dot{\alpha}_s \) for the two synaptic conductances. These give the steady-state average voltage as the standard weighted average of reversal potentials \( \langle \bar{V} \rangle \equiv (\alpha_e E_e + \alpha_i E_i) / \tau_v \), where \( 1/\tau_v = \bar{H} = \alpha_e + \alpha_i + \dot{\alpha} \). For the steady-state fluctuating components, it proves convenient to introduce an effective space constant \( \lambda_v \) defined through \( \lambda_v^2 = D \tau_v \). We note that the steady-state synaptic conductance fluctuations in Eq. (6) are delta-correlated in space \( \langle \dot{H}_e \dot{H}_i \rangle = \delta(x) \alpha_e / 2 \tau_v \) and so when substituted into the steady-state version of Eq. (7) will provide a gradient condition on \( \langle \dot{H}_e \dot{H}_i \rangle \) at \( x = 0 \). Given \( \psi = \psi_0 e^{-|x|k} \) solves \( \ddot{\psi} = k^2 \psi - 2k \delta(x) \psi_0 \) we have

\[
\langle \dot{H}_e \rangle_x = \frac{\bar{\alpha}_e}{4 \bar{\alpha}_s} \alpha_s \bar{\tau}_v \tau_s \sqrt{\frac{\tau_s}{\tau_s + \tau_v}} e^{-|x|k_s}
\]  

(11)

where \( k_s^2 \lambda_v^2 = (\tau_v + \tau_i) / \tau_s \). An illustration for excitation and inhibition is provided in Fig. 3A, upper panel. The equation for the steady-state voltage autocovariance is separated into excitatory and inhibitory components \( \langle \ddot{v}^2 \rangle_x = \langle \ddot{v}_e^2 \rangle_x + \langle \ddot{v}_i^2 \rangle_x \) and solved similarly (see Appendix)

\[
\langle \ddot{v}^2 \rangle_x = \frac{\bar{\alpha}_e}{4 \bar{\alpha}_s} \alpha_s \bar{\tau}_v \tau_s \sqrt{\frac{\tau_s}{\tau_s + \tau_v}} e^{-|x|k_s}
\]  

(12)

where \( k_c = 1 / \lambda_v \). Unlike the covariance between voltage and a synaptic drive, the voltage autocovariance has zero gradient at the origin (see Fig. 3A, middle panel). The final quantity needed for the steady-state upcrossing rate is the autocovariance of \( \dot{v} \) that takes the form \( \langle \ddot{v}^2 \rangle_x = \mathcal{E}_e \langle \ddot{v}_e \dot{v}_e \rangle_x / \tau_{s} + \mathcal{E}_i \langle \ddot{v}_i \dot{v}_i \rangle_x / \tau_{i} \). Each synaptic component of this quantity is easily expressed using the second of the two results in Eq. (11) and so

\[
\langle \ddot{v}^2 \rangle_x = \frac{\bar{\alpha}_e}{4 \bar{\alpha}_s} \alpha_s \bar{\tau}_v \tau_s \sqrt{\frac{\tau_s}{\tau_s + \tau_v}} e^{-|x|k_s}
\]  

(13)

with an illustration provided in Fig. 3A, lower panel. The result for \( \langle \ddot{V} \rangle \) and Eqs (12-13) evaluated at \( x = 0 \) provide the quantities needed for the steady-state upcrossing rate (see Fig. 3C).

### IV. FIRING-RATE RESPONSE

We now derive the frequency-dependent response by considering weak sinusoidal modulations of the incoming excitatory synaptic rate \( \alpha_e(t) = \dot{\alpha}_e(t) e^{i\omega t} \) and expand all state variables to leading order in \( \dot{\alpha}_e \). We will use the notation for some quantity \( Q(t) = \bar{Q} + \dot{Q} e^{i\omega t} \) with \( \bar{Q} \) the steady-state value and \( \dot{Q} \) the linear response proportional to \( \dot{\alpha}_e \). At this level, the upcrossing rate response \( \dot{Q}_{\text{loc}} \) will be a linear function of the modulated moments (see Appendix).

The strategy is similar to that taken for the steady state but with Eqs. (6-10) solved in the frequency domain. The calculation is algebraically lengthy so here we provide the high-frequency asymptotics with the full forms given in the Appendix. At the mean level

\[
\langle \ddot{V} \rangle = \frac{\bar{\alpha}_e}{(i\omega)^2 \tau_e} \text{and} \langle \dot{\dot{V}} \rangle = \frac{\bar{\alpha}_e}{i\omega \tau_e}
\]  

(14)
so the rate-of-change of the average voltage is the dominant deterministic contribution to the upcrossing-rate response at higher frequencies.

For the fluctuating components, the driving excitatory synaptic modulation is again delta-correlated in space \( \langle \hat{h}_e^2 \rangle = \delta(x) \hat{\alpha}_e \lambda_e / 2 \tau_e (1 + i \omega \tau_e / 2) \) but with a frequency-dependent amplitude due to synaptic filtering. Using this result, solving for the response of the voltage and synaptic covariances, the high-frequency asymptote of the voltage variance is found:

\[
\langle \hat{v}^2 \rangle \sim \frac{2 \hat{\alpha}_e \tau_e}{i \omega \tau_v} \langle \hat{v}^2 \rangle
\]

and so decays as \( 1 / \omega^2 \). From \( \langle \hat{v} \hat{v} \rangle = (i \omega / 2) \langle \hat{v}^2 \rangle \) this also gives the weaker decay of \( \langle \hat{v} \hat{v} \rangle \sim 1 / i \omega \). Finally, the asymptote of the variance of the rate-of-change of voltage

\[
\langle \hat{v}^2 \rangle \sim \frac{\lambda_e}{2 \tau_e} \frac{1}{\lambda_v \sqrt{2 i \omega \tau_v}}
\]

can be seen to have the weakest decay and therefore is dominant at high frequencies.

This is the key and somewhat surprising result for the dynamics of the dendritic model: the high-frequency asymptotics decay as \( 1 / \sqrt{i \omega} \) and, through its linear dependence on \( \langle \hat{v}^2 \rangle \) as seen in Eq. (26) of the Appendix, so also must the high-frequency response of the firing rate in the upcrossing approximation

\[
\frac{\hat{r}_{uc}}{r_{uc}} \sim \frac{\lambda_e}{4 \tau_e \langle \hat{v}^2 \rangle} \frac{1}{\lambda_v \sqrt{2 i \omega \tau_v}}.
\]

This can be contrasted to the result for the isopotential point-neuron model that has an upcrossing response decaying as \( 1 / i \omega \) at higher frequencies (see reference [15] and the Appendix). In Figs. 3D and 3E an illustration of the amplitude and phase of the response is shown. These frequency-domain results are compatible with the earlier observation in Fig. 1B that EPSPs on a dendrite can be sharper in time than for an isopotential model.

V. DISCUSSION

The analyses presented here are predicated on a number of biophysical approximations and therefore should be considered as providing the basis for future refinement.

Firstly, the membrane model does not include voltage-gated currents such as Ih that can affect low frequency components of the firing-rate response. These could be included using a quasi-active membrane approximation [21, 22] with additional state variables coupled to the voltage dynamics.

The minimal model presented here also approximates spatial extent as infinite (valid for dendrites significantly longer than the effective electrotonic length \( \lambda_e \)), is homogeneous and has no increased conductance at the position \( x = 0 \) of the nominal soma. Recent analysis [9] showed significant effects of geometry on the functional forms of steady-state upcrossing rates. The derivation of Eqs. (6-10) rely on a long, homogeneous approximation and so adaptation of the method to more realistic geometries might be a technical challenge, though the spatial-mode expansion technique used by Tuckwell [6] is a potential

FIG. 3: Steady-state (A-C) and upcrossing-rate response (D-E) showing a weakly attenuated response at high frequencies. (A) Steady-state spatial covariances of synaptic and voltage variables. (B) Steady-state synaptic drive covaried to provide a particular mean voltage (x-axis) at fixed conductance levels. For an isopotential neuron with matched voltage mean, variance and conductance a difference in the rate of change of voltage is seen (lower panel, blue). (C) Steady-state upcrossing rate as a function of mean voltage for the dendritic (black) and isopotential model (blue). (D) Upcrossing-rate response by frequency normalised by \( \hat{\alpha}_e \). Note that the dendritic-model response shows qualitatively weaker attenuation at high-frequency \( \sim 1 / \sqrt{i \omega} \) than the reference isopotential model \( \sim 1 / i \omega \). Inset shows same curves normalised at zero frequency in which it is seen that the response of the dendritic and isopotential models are broadly similar even over moderate frequencies despite the additional spatial filtering. (E) Upcrossing phase as a function of frequency with a \(-45^\circ\) asymptote for the dendritic case and \(-90^\circ\) for the isopotential model. Parameters used are the same as Fig. 1.
strategy to account for closed-end effects.

A number of approximations of the synaptic drive have been made including the Gaussian approximation of finite-amplitude shot noise. This typically has validity when statistically independent, high-rate, low-amplitude inputs are summed. Given the distinct response seen in isopotential neurons when shot noise is included [23, 24], a worthwhile extension would be to examine finite-amplitude effects on the dynamics. This is particularly important for spatiotemporal integration as the relative number of summed inputs within an effective electrotonic length will be less than the global input into an isopotential model.

Finally, though widely used in neuroscience, the upcrossing approximation should be critically evaluated in this spatial context and compared to biophysical models of spike generation. Rapid responses have already been identified in these models due to spiking non-linearities or somatic-dendritic coupling [25–30]. Extensions of the current study could examine the high-frequency response seen in isopotential neurons when shot noise is amplitude inputs are summed. Given the distinct reliability when statistically independent, high-rate, low-amplitude inputs are summed, a worthwhile extension would be to expand the approach to account for closed-end effects.

\[ r_{uc}(t) = \phi(v_{th}) \int_{-\infty}^{\infty} d\dot{v} \dot{V} \psi(\dot{v}) \psi(v|v_{th}) \]  

where \( v_{th}(t) = V_{th} - (V) \). For the Gaussian-distributed voltages considered in this paper, the distributions can be written

\[ \phi(v) = \frac{1}{\sqrt{2\pi\langle v^2 \rangle}} \exp \left( -\frac{v^2}{2\langle v^2 \rangle} \right) \]  

and

\[ \psi(\dot{v}|v) = \frac{1}{\sqrt{2\pi s^2}} \exp \left( -\frac{(\dot{v} - \kappa v)^2}{2s^2} \right) \]

where the variances \( \langle v^2 \rangle \), \( \langle \dot{v}^2 \rangle \), covariance \( \langle \dot{v}v \rangle \) and other parameters \( \kappa = \langle \dot{v}v \rangle / \langle v^2 \rangle \) and \( s^2 = \langle \dot{v}^2 \rangle - \kappa^2 \langle v^2 \rangle \) are all potentially time dependent. Using these results we get for the upcrossing rate

\[ r_{uc}(t) = \frac{1}{2\pi} \sqrt{\frac{s^2}{\langle v^2 \rangle}} e^{-v_{th}^2/2\langle v^2 \rangle} \int_{-\beta}^{\infty} du (2u + 2\beta)e^{-u^2} \]

where \( \beta = \sqrt{\langle \dot{V} \rangle + \kappa^2 v_{th}^2 / \sqrt{2s^2}} \). The integral can be rewritten in terms of Gaussians and the error function

\[ r_{uc}(t) = \frac{1}{2\pi} \sqrt{\frac{s^2}{\langle v^2 \rangle}} e^{-v_{th}^2/2\langle v^2 \rangle} \left( e^{-\beta^2 + \sqrt{\pi} \beta [1 + \text{erf}(\beta)]} \right) \]

which is identical to the result arrived at by Badel [15]. An example of the upcrossing rate in a regime that is non-linear in the synaptic driving terms is illustrated in Fig. 2C (lower panel).

APPENDIX A. Upcrossing-rate dynamics

The time-dependent rate \( r_{uc}(t) \) that a fluctuating membrane voltage \( V \) crosses a threshold \( V_{th} \) from below is considered. Following Rice [10], this can be written as

\[ r_{uc}(t) = \int_{0}^{\infty} d\dot{V} \dot{V} \Psi(V_{th}, \dot{V}) \]  

where \( \dot{V} \) is the rate-of-change of voltage and \( \Psi(V, \dot{V}) \) is the joint probability density. The derivations that will be used for the dynamics, steady state and linear response were given by Badel [15] in the context of a related isopotential neuronal model. We repeat that derivation and provide intermediate steps for transparency.

It is first convenient to expand the voltage and its rate of change around their time-dependent mean values \( \langle V \rangle \) and \( \langle \dot{V} \rangle \) so the fluctuating excesses \( v \) and \( \dot{v} \) have zero mean: for example, \( \dot{V}(t) = (V(t)) + \dot{v} \). Writing the joint distribution for \( v \) and \( \dot{v} \) as the conditional distribution \( \psi(\dot{v}|v) \) multiplied by the marginal voltage density \( \phi(v) \) we have

\[ r_{uc}(t) = \phi(v_{th}) \int_{-\infty}^{\infty} d\dot{v} (\dot{V} + \dot{v}) \psi(\dot{v}|v_{th}) \]  

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Steady-state upcrossing rate

For a quantity \( Q(t) \) evaluated in the steady state we use the notation \( \langle Q \rangle \). The steady-state upcrossing rate simplifies because \( \langle \dot{V} \rangle = 0 \) and \( \langle \dot{v}v \rangle = \partial_t \langle v^2 \rangle / 2 = 0 \) so that \( \beta = 0 \) and \( s^2 = \langle \dot{v}^2 \rangle \) giving

\[ r_{uc} = \frac{1}{2\pi} \sqrt{\frac{\langle \dot{v}^2 \rangle}{\langle v^2 \rangle}} \exp \left( -\frac{\dot{v}_{th}^2}{2\langle v^2 \rangle} \right) \]

where \( \dot{v}_{th} = V_{th} - \langle V \rangle \). Figure 3C provides an illustration of the steady-state upcrossing rate.

Linear response of the upcrossing rate

We now consider a weak harmonic modulation of the incoming presynaptic rates. This will induce weak modulations, with some amplitude and phase shift, in any dependent quantity \( Q(t) \) that we can conveniently write in complex form \( Q(t) = \bar{Q} + \bar{Q}e^{i\omega t} \). Before expanding the
upcrossing form, let us examine some of the component quantities. For \( \beta \) and \( s^2 \) we have

\[
\hat{\beta} = \frac{1}{\sqrt{2\langle \dot{v}^2 \rangle}} \left( \langle \dot{V} \rangle + \tau_{th} \langle \dot{v}^2 \rangle \right) \quad \text{and} \quad \hat{s}^2 = \langle \dot{v}^2 \rangle. \tag{25}
\]

Then, for the upcrossing rate itself, we get that the ratio of the modulation to the steady-state rate is [15]

\[
\hat{r}_{uc} = \hat{v}_{th} = \frac{\hat{v}_{th} \langle \dot{v} \rangle}{\langle \dot{v} \rangle} = 1 + \frac{1}{2} \hat{v}_{th} \langle \dot{v}^2 \rangle \frac{\langle \dot{v} \rangle^2 \langle \dot{v}^2 \rangle - 1}{\langle \dot{v}^2 \rangle} + \sqrt{\frac{\pi}{2\langle \dot{v}^2 \rangle}} \hat{v}_{th} \langle \dot{v} \rangle + \frac{1}{2} \langle \dot{v}^2 \rangle \hat{v}_{th} + \frac{1}{\langle \dot{v}^2 \rangle} \langle \dot{v}^2 \rangle. \tag{26}
\]

In the above equation, the first two terms provide the deterministic contribution and the last three terms are contributions from modulated fluctuating quantities. The amplitude and phase of the upcrossing linear response is shown in Figs. 3D and 3E, respectively.

**APPENDIX B. Dendritic model**

The differential equations for the deterministic (mean) components in Eqs. (3) and the partial differential equations for the fluctuating components (covariances) in Eqs. (6-10) completely determine the moment dynamics in the Gaussian approximation of the model. These equations are driven by the rate-like terms \( \alpha_c(t) \), \( \alpha_i(t) \) that are proportional to the presynaptic excitatory and inhibitory rates. Also appearing in the equations are the total conductance \( H(t) = \alpha t + \langle H_e \rangle + \langle H_i \rangle \) and electromotive forcing terms \( E_c(t) = E_n - \langle V \rangle \). Together, these equations represent a feedforward cascade that provide all the required quantities needed for the upcrossing rate.

There are a number of approaches that can be taken to find the solution of these equations in the steady state or at the linear-response level. For example direct solution in space using substitution for the inhomogeneous components or using spatial Fourier transforms. Here we will use the former real-space approach and therefore the following result will often be useful

\[
\partial_x^2 \psi = k^2 \psi - 2k\delta(x)\psi_0 \quad \text{with soln.} \quad \psi = \psi_0 e^{-|x|k}. \tag{27}
\]

**Steady state: dendritic model**

We first derive the various same-time space-separated covariances in the steady state as these will be used to calculate the time dependence. 

**Synaptic autocovariances \( \langle \tilde{h}_e^2 \rangle_x \).** From Eq. (6), these are simply delta-correlated in space

\[
\langle \tilde{h}_e^2 \rangle_x = \delta(x) \frac{\lambda_e}{2\tau_e}. \tag{28}
\]

**Voltage and synaptic covariances \( \langle \tilde{h}_e \tilde{h}_i \rangle_x \).** In the steady-state, Eq. (7) reduces to

\[
D \frac{\partial^2}{\partial x^2} \langle \tilde{h}_e \tilde{h}_i \rangle_x = \left( \frac{1}{\tau_e} + \frac{1}{\tau_i} \right) \langle \tilde{h}_e \tilde{h}_i \rangle_x - \bar{E}_s \langle h_i^2 \rangle_x. \tag{29}
\]

Remembering that \( D = \lambda^2_e/\tau_e \) and looking at the form of Eq. (27) identifies \( \lambda^2_e k_i^2 = (\tau_e + \tau_i)/\tau_e \). From the prefactor of the delta-correlated inhomogeneous term, the solution must therefore be

\[
\langle \tilde{h}_e \tilde{h}_i \rangle_x = \frac{1}{2\lambda_e \lambda_i} \left[ \frac{\bar{E}_s}{2\tau_e} \lambda_e \lambda_i \right] e^{-|x|k_e}. \tag{30}
\]

**Voltage autocovariance \( \langle \tilde{v}^2 \rangle_x \).** There are two inhomogeneous terms in its equation

\[
D \frac{\partial^2}{\partial x^2} \langle \tilde{v}^2 \rangle_x = \frac{1}{\tau_v} \langle \tilde{v}^2 \rangle_x - \bar{E}_s \langle \tilde{v} \tilde{h}_i \rangle_x - \bar{E}_s \langle \tilde{v}_i \tilde{h}_i \rangle_x \tag{31}
\]

so it can be resolved into \( \langle \tilde{v}^2 \rangle_x = \langle \tilde{v}^2 \rangle_x^e + \langle \tilde{v}^2 \rangle_x^i \). Trying \( \langle \tilde{v}^2 \rangle_x^e = \psi_s + c_s \langle \bar{v} \tilde{h}_i \rangle_x \) and using Eq. (29) to remove the double derivative requires setting \( c_s = -\tau_e \bar{E}_s \) to cancel the inhomogeneous term. This leaves

\[
D \frac{\partial^2}{\partial x^2} \psi_s = \frac{1}{\tau_v} \psi_s - \bar{E}_s \langle \tilde{v} \tilde{h}_i \rangle_x. \tag{32}
\]

Introducing \( k^2_v = 1/\lambda^2_v \) the solution for \( \psi_s \) is

\[
\psi_s = \frac{\bar{E}_s^2}{4} \frac{\alpha_v}{\lambda_v} \frac{\lambda_e}{\lambda_i} e^{-|x|k_e}. \tag{33}
\]

Putting these forms in \( \langle \tilde{v}^2 \rangle_x^s = \psi_s + c_s \langle \bar{v} \tilde{h}_i \rangle_x \) gives

\[
\langle \tilde{v}^2 \rangle_x^s = \frac{\bar{E}_s^2}{4} \frac{\alpha_v}{\lambda_v} \frac{\lambda_e}{\lambda_i} \left( e^{-|x|k_e} - \sqrt{\frac{\tau_e}{\tau_i + \tau_v}} e^{-|x|k_v} \right). \tag{34}
\]

It can be noted that this gives the voltage autocovariance a zero gradient at \( x = 0 \).

**Rate-of-change-of-voltage autocovariance \( \langle \tilde{v}^2 \rangle_x \).** In the steady-state this is simply

\[
\langle \tilde{v}^2 \rangle_x = \frac{\bar{E}_s^2}{\tau_v} \langle \tilde{v} \tilde{h}_i \rangle_x + \frac{\bar{E}_s^2}{\tau_i} \langle \tilde{v} \tilde{h}_i \rangle_x \tag{35}
\]

where the forms for \( \langle \bar{v} \tilde{h}_i \rangle_x \) have already been given above.

**Deterministic weak oscillations: dendritic model**

Modulation of the excitatory presynaptic drive \( \tilde{h}_e \) only is considered, so the modulated inhibitory drive is zero \( \tilde{h}_i = 0 \). With this in mind, expanding the deterministic equations (Eq. set 3) at the level of the linear response
to excitatory oscillations gives the following quantities of interest
\[ \langle \hat{H}_e \rangle = \hat{H} = \frac{\hat{\alpha}_e}{1 + i \omega \tau_e}, \quad \langle \hat{H}_i \rangle = 0 \] (36)
so
\[ \langle \hat{V} \rangle = \frac{\varepsilon_s \langle \hat{H}_e \rangle}{1 / \tau_v + i \omega} = \frac{\hat{\alpha}_s \tau_v \varepsilon_s}{(1 + i \omega \tau_v)(1 + i \omega \tau_v)} \] (37)
and the modulated rate-of-change of the voltage is given by \( \langle \hat{V} \rangle = i \omega \langle \hat{V} \rangle \). Note also that \( \hat{\xi}_s = -\langle \hat{V} \rangle \) for \( s = e, i \).

**Weak oscillations and fluctuations: dendritic model**

We now replace the double spatial derivatives in the order of the cascade of equations, remembering again that for modulated excitatory drive only we have \( \hat{\alpha}_i = 0 \) throughout.

**Synaptic autocovariances \( \langle \hat{h}_e^2 \rangle_x \).** These are delta-correlated
\[ \langle \hat{h}_e^2 \rangle_x = \delta(x) \frac{\hat{\alpha}_e \lambda_e}{2 \tau_e} \frac{1}{1 + i \omega \tau_e / 2} \] and \( \langle \hat{h}_i^2 \rangle_x = 0 \). (38)

**Voltage and synaptic covariances \( \langle \hat{v} \hat{h}_e \rangle_x \).** This obeys
\[ D \theta^2_x \langle \hat{v} \hat{h}_e \rangle_x = \left( i \omega + \frac{1}{\tau_v} + \frac{1}{\tau_e} \right) \langle \hat{v} \hat{h}_e \rangle_x \]
\[ + \hat{H} \langle \hat{v} \hat{h}_e \rangle_x - \xi_s \langle \hat{h}_e \rangle_x^2 - \hat{\xi}_e \langle \hat{h}_e \rangle_x^2 \] (39)

We then use a substitution of the form \( \langle \hat{v} \hat{h}_e \rangle_x = \psi_s + a_s \langle \hat{h}_e \rangle_x \) and use the result of Eq. (29) to remove the double spatial derivatives on \( \langle \hat{v} \hat{h}_e \rangle_x \). Setting \( a_s = -\hat{\xi}_e / i \omega \) then removes the remaining inhomogeneous term in \( \langle \hat{v} \hat{h}_e \rangle_x \)
\[ \theta^2_x \psi_s = \left( \frac{i \omega}{2} + \frac{1}{\tau_v} \right) \langle \hat{v} \hat{h}_e \rangle_x + \hat{H} \langle \hat{v} \hat{h}_e \rangle_x - \xi_s \langle \hat{h}_e \rangle_x^2 - \hat{\xi}_e \langle \hat{h}_e \rangle_x^2 \] (40)

Note that we would have \( \hat{\alpha}_i = 0 \) in the first term for the inhibitory form \( \langle \hat{v} \hat{h}_i \rangle_x \).

**Voltage autocovariance \( \langle \hat{v}^2 \rangle_x \).** This obeys
\[ D \theta^2_x \langle \hat{v}^2 \rangle_x = \left( \frac{i \omega}{2} + \frac{1}{\tau_v} \right) \langle \hat{v}^2 \rangle_x + \hat{H} \langle \hat{v}^2 \rangle_x \]
\[ - \xi_s \langle \hat{v} \hat{h}_e \rangle_x - \hat{\xi}_e \langle \hat{v} \hat{h}_e \rangle_x - \xi_i \langle \hat{v} \hat{h}_i \rangle_x - \hat{\xi}_i \langle \hat{v} \hat{h}_i \rangle_x \] (41)

We can separate this into components for excitation and inhibition, each of which satisfies
\[ D \theta^2_x \langle \hat{v}^2 \rangle_x^s = \left( \frac{i \omega}{2} + \frac{1}{\tau_v} \right) \langle \hat{v}^2 \rangle_x^s + \hat{H} \langle \hat{v}^2 \rangle_x^s \]
\[ - \xi_s \langle \hat{v} \hat{h}_e \rangle_x - \hat{\xi}_e \langle \hat{v} \hat{h}_e \rangle_x. \] (42)

These can be solved by substituting \( \langle \hat{v}^2 \rangle_x^s = a \langle \hat{v}^2 \rangle_x^s + b_s \langle \hat{v} \hat{h}_e \rangle_x + c_s \langle \hat{h}_e \rangle_x^2 + \psi_s, \) giving
\[ a \theta^2_x \langle \hat{v}^2 \rangle_x^s + b_s \theta^2_x \langle \hat{v} \hat{h}_e \rangle_x + c_s \theta^2_x \langle \hat{h}_e \rangle_x^2 + \theta^2_x \psi_s = \]
\[ \left( \frac{i \omega}{2} + \frac{1}{\tau_v} \right) \left( a \langle \hat{v}^2 \rangle_x^s + b_s \langle \hat{v} \hat{h}_e \rangle_x + c_s \langle \hat{h}_e \rangle_x^2 + \psi_s + \hat{H} \langle \hat{v}^2 \rangle_x^s - \xi_s \langle \hat{h}_e \rangle_x^2 - \hat{\xi}_e \langle \hat{h}_e \rangle_x^2 \right). \] (43)

We then set \( a, b_s, \text{ and } c_s \) to remove the inhomogeneous terms in \( \langle \hat{v}^2 \rangle_x^s, \langle \hat{v} \hat{h}_e \rangle_x \), and \( \langle \hat{h}_e \rangle_x \) respectively:
\[ a = \frac{2 \hat{H}}{i \omega}, \quad b_s = \frac{-\xi_s}{1 + i \omega \tau_e / 2}, \quad \text{and } c_s = \frac{\tau_v (a_s \hat{\xi}_e - b_s \hat{H})}{1 - i \omega \tau_e / 2} \] (45)

and leave an equation for \( \psi_s \) of the form
\[ D \theta^2_x \psi_s = \left( \frac{i \omega}{2} + \frac{1}{\tau_v} \right) \psi_s \]
\[ + b_s \xi_s \langle \hat{h}_e \rangle_x + b_s \hat{\xi}_e \langle \hat{h}_e \rangle_x + c_s \xi_s \langle \hat{h}_e \rangle_x^2. \] (46)

This equation has solution
\[ \psi_s = -\frac{1}{4 \tau_e} \left( \frac{\xi_s}{1 + i \omega \tau_e / 2} + c_s \hat{\xi}_e \hat{\alpha}_s \tau_v \right) \]
\[ \times e^{-\frac{t}{\lambda_e}} \] (47)
which together with the other inhomogeneous forms in \( \langle \hat{v}^2 \rangle_x^s = a \langle \hat{v}^2 \rangle_x^s + b_s \langle \hat{v} \hat{h}_e \rangle_x + c_s \langle \hat{h}_e \rangle_x^2 + \psi_s \) completes the
solution for one synaptic component of the modulated variance.

Rate-of-change of voltage autocovariance \( \langle \dot{\hat{v}}^2 \rangle_x \). This has form

\[
\langle \dot{\hat{v}}^2 \rangle_x = \frac{\tau_s}{\tau_v} \langle \hat{v} \hat{h} \rangle_x + \frac{\tau_s}{\tau_v} \langle \hat{v} \hat{h} \rangle_x + \frac{\tau_s}{\tau_v} \langle \hat{v} \hat{h} \rangle_x + \frac{\tau_s}{\tau_v} \langle \hat{v} \hat{h} \rangle_x - \frac{1}{\tau_v} \langle \dot{\hat{v}} \rangle_x + D \hat{D}^2 \langle \dot{\hat{v}} \rangle_x.
\]

(48)

We again separate out the solution in terms of the components involving excitation and inhibition

\[
\langle \dot{\hat{v}}^2 \rangle_x = \frac{\tau_s}{\tau_v} (1 + i \omega \tau_v) \langle \hat{v} \hat{v} \rangle_x + \frac{\tau_s}{\tau_v} \langle \hat{v} \hat{h} \rangle_x
\]

\[
- \frac{i \omega}{2 \tau_v} \langle \dot{\hat{v}}^2 \rangle_x + \frac{i \omega}{2} D \hat{D}^2 \langle \dot{\hat{v}}^2 \rangle_x
\]

(49)

where we have also made use of the simplifying relations for \( \langle \dot{\hat{v}} \hat{h} \rangle_x \) and \( \langle \dot{\hat{v}} \hat{v} \rangle_x \) in the steady-state and linear-response levels. We now substitute for the following term

\[
D \hat{D}^2 \langle \dot{\hat{v}}^2 \rangle_x = \left( \frac{i \omega}{2} + \frac{1}{\tau_s} \right) \langle \dot{\hat{v}}^2 \rangle_x
\]

\[
+ \hat{H} \langle \dot{\hat{v}}^2 \rangle_x - \hat{E}_x \langle \hat{v} \hat{h} \rangle_x - \hat{E}_x \langle \hat{v} \hat{h} \rangle_x
\]

(50)

and tidy things up to get

\[
\langle \dot{\hat{v}}^2 \rangle_x = \frac{\tau_s}{\tau_v} \left( 1 + i \omega \tau_v \right) \langle \hat{v} \hat{v} \rangle_x + \frac{\tau_s}{\tau_v} \left( 1 - i \omega \tau_v \right) \langle \hat{v} \hat{h} \rangle_x
\]

\[
+ \left( \frac{i \omega}{2} \right)^2 \langle \dot{\hat{v}}^2 \rangle_x + \frac{i \omega}{2} \hat{H} \langle \dot{\hat{v}}^2 \rangle_x
\]

(51)

which is expressed in terms of quantities already derived.

Low-frequency limit: dendritic model

In the limit \( \omega \to 0 \), the various frequency-dependent quantities \( \hat{Q} \) obtained by taking derivatives of corresponding steady-state quantities with respect to \( \dot{\alpha} \)

\[
\lim_{\omega \to 0} \hat{Q} = \dot{\alpha} e^{-\frac{\omega}{\tau_v}} \frac{d}{d \dot{\alpha}} \hat{Q}
\]

(52)

where it should be remembered that \( \tau_v, \lambda_v, \tau_e, \tau_i \) all depend on \( \dot{\alpha} \). The following results are useful

\[
\frac{d}{d \dot{\alpha}} \frac{1}{\tau_v} = 1, \quad \frac{d}{d \dot{\alpha}} \tau_v = -\tau_v^2
\]

\[
\frac{d}{d \dot{\alpha}} \tau_e = -\frac{d}{d \dot{\alpha}} (\hat{V}) = -\tau_v \hat{E}_e \text{ and } \frac{d}{d \dot{\alpha}} \frac{1}{\lambda_v} = 1 \frac{\tau_v}{2 \lambda_v}.
\]

(53)

It is also useful to introduce the following definition and its derivatives

\[
x_s = \frac{\tau_e}{\tau_v + \tau_e} \text{ so } \frac{d}{d \dot{\alpha}} x_s = \tau_v x_s (1 - x_s) = \frac{x_s^2}{\tau_v^2} x_s^2.
\]

(54)

Finally, note that because \( \hat{V} \) or \( \langle \hat{v} \rangle \) are both complete temporal derivates, their temporal Fourier transforms vanish in the \( \omega = 0 \). We now provide the forms of the remaining moments.

Voltage and synaptic covariance \( \langle \hat{v} \hat{h} \rangle_x \). In terms of \( x_c \) and \( x_i \) these can be written

\[
\lim_{\omega \to 0} \langle \hat{v} \hat{h} \rangle_x = \frac{\dot{\alpha} \tau_v}{4 \tau_e} \frac{\lambda_v}{\lambda_v} \sqrt{x_e} \left( 1 - \frac{x_e}{2} \right)
\]

\[
\lim_{\omega \to 0} \langle \hat{v} \hat{i} \rangle = -\frac{\dot{\alpha} \tau_v}{4 \tau_i} \frac{\lambda_i}{\lambda_v} \sqrt{x_i} \alpha \tau_v \left( \hat{E}_e + \hat{E}_i \frac{x_i}{2} \right).
\]

(55)

Voltage variance \( \langle \hat{v}^2 \rangle_x \). We can split this term into excitatory and inhibitory components and use the same definitions for \( x_c \) and \( x_i \) as above

\[
\lim_{\omega \to 0} \langle \hat{v}^2 \rangle_x = \frac{\dot{\alpha} \tau_v}{4 \tau_e} \frac{\lambda_v}{\lambda_v} \times
\]

\[
\left( (1 - 2 \alpha \tau_v) (1 - \sqrt{x_e}) - \frac{\dot{\alpha} \tau_v}{2} (1 - \sqrt{x_e}) \right)
\]

\[
\lim_{\omega \to 0} \langle \hat{v}^2 \rangle_i = -\frac{\dot{\alpha} \tau_v}{4 \tau_i} \frac{\lambda_i}{\lambda_v} \times
\]

\[
\left( 2 \hat{E}_e \hat{E}_i (1 - \sqrt{x_i}) + \hat{E}_i^2 \left( 1 - \sqrt{x_i} \right) \right).
\]

(56)

Rate-of-change of voltage variance \( \langle \dot{\hat{v}}^2 \rangle_x \). The excitatory and inhibitory components are proportional to \( \langle \hat{v} \hat{c} \rangle_x \) and \( \langle \hat{v} \hat{i} \rangle_x \) so that

\[
\lim_{\omega \to 0} \langle \dot{\hat{v}}^2 \rangle_x = \frac{\dot{\alpha} \tau_v}{4 \tau_e} \frac{\lambda_v}{\lambda_v} \sqrt{x_e} \left( 1 - \dot{\alpha} \tau_v \left( 2 + \frac{x_e}{2} \right) \right)
\]

\[
\lim_{\omega \to 0} \langle \dot{\hat{v}}^2 \rangle_i = -\frac{\dot{\alpha} \tau_v}{4 \tau_i} \frac{\lambda_i}{\lambda_v} \sqrt{x_i} \alpha \tau_v \left( 2 \hat{E}_e \hat{E}_i + \hat{E}_i^2 \frac{x_i}{2} \right).
\]

(57)

High-frequency asymptotics: dendritic model

For a modulation of the excitatory component, to leading order, the deterministic components needed are

\[
\langle \hat{V} \rangle \sim \frac{\dot{\alpha} \tau_v}{(i \omega)^2 \tau_v}, \quad \langle \hat{V} \rangle \sim \frac{\dot{\alpha} \tau_v}{i \omega \tau_v}
\]

\[
\langle \hat{E}_e \rangle = \hat{H} \sim \frac{\dot{\alpha} \tau_v}{i \omega \tau_v}, \quad \text{and } \hat{E}_e = \hat{E}_i = -\langle \hat{V} \rangle.
\]

(58)

Note that \( \langle \hat{H} \rangle = 0 \) because \( \dot{\alpha} = 0 \). The dominant contribution to the deterministic component to the upcrossing rate is therefore \( 1/i \omega \) and comes from the rate-of-change of voltage term. We now take the covariances in turn.

Voltage and synaptic covariance \( \langle \hat{v} \hat{h} \rangle_x \). For the covariances between voltage and synaptic drive we have

\[
\langle \hat{v} \hat{h} \rangle \sim \frac{\dot{\alpha} \tau_v}{i \omega \tau_v} \frac{\lambda_v}{i \omega \tau_v} \frac{1}{\sqrt{i \omega \tau_v}} \text{ and }
\]

\[
\langle \hat{v} \hat{i} \rangle \sim \frac{\dot{\alpha} \tau_v}{i \omega \tau_v} \frac{\lambda_i}{i \omega \tau_v} \frac{1}{\sqrt{i \omega \tau_v}}.
\]

(59)
Voltage variance \( \langle \hat{v}^2 \rangle \) and \( \langle \hat{w} \hat{v} \rangle \). Examining the forms of the various terms in Eq. set (45) we see that \( a \sim 1/\omega^2 \), \( b_e \sim 1/\omega \) and \( c_e \sim 1/\omega^3 \). The term multiplying the exponential therefore decays as \( 1/\omega^{5/2} \) and is less significant that the \( a \langle \hat{v}^2 \rangle \) term, which dominates the inhomogeneous parts of the solution. Using the asymptotics for \( a \) then gives

\[
\langle \hat{v}^2 \rangle \sim -\frac{\alpha_e \tau_v}{\nu \tau_e} \frac{2}{\nu \tau_e} \langle \hat{v}^2 \rangle \quad \text{and} \quad \langle \hat{w} \hat{v} \rangle \sim -\frac{\alpha_e}{\nu \tau_e} \langle \hat{v}^2 \rangle
\]  

(60)

where the latter result follows from \( \langle \hat{w} \hat{v} \rangle = (i\omega/2) \langle \hat{v}^2 \rangle \).

Rate-of-change of voltage variance \( \langle \dot{v}^2 \rangle \). It is useful to re-arrange the form of this equation so that

\[
\langle \dot{v}^2 \rangle_x = \left( \frac{i\omega}{2} \right)^2 \frac{(\langle v^2 \rangle_x + \frac{2}{i\omega} \langle \psi \hat{v} \rangle_x + \frac{2\xi}{i\omega} \langle \psi h \rangle_x \right)},
\]

To leading order, the part in the square brackets is equivalent to \( \psi \), in the solution for \( \langle \hat{v}^2 \rangle \) (see Eq. 47 and above). The leading order component of \( \psi \) \((x = 0)\) is

\[
\psi \sim -\frac{\xi^2}{4\tau_x^2} \frac{k_v}{\nu} \frac{1}{\alpha_e \tau_v} \frac{1}{\nu \tau_e} \sqrt{2i/\omega\tau_v}.
\]

(62)

so that we have

\[
\langle \dot{v}^2 \rangle \sim \alpha_e \tau_v \frac{\xi^2}{4\tau_x^2} \frac{k_v}{\nu} \frac{1}{\alpha_e \tau_v} \frac{1}{\nu \tau_e} \sqrt{2i/\omega\tau_v}.
\]

(63)

APPENDIX C. Isopotential model

As a reference model to compare the additional effect of spatiotemporal filtering we consider an isopotential neuron receiving temporally filtered synaptic drive. This type of model has been analysed previously [20] including using the upcrossing approximation [15]. The model comprises two synaptic conductances filtered at excitatory and inhibitory time scales \( \tau_e \) and \( \tau_i \). These conductances drive a voltage equation that also includes a leak conductance. As before, it proves convenient to introduce rate-like quantities that are conductances divided by the membrane capacitance.

\[
\frac{dV}{dt} = \alpha_e (E_e - V) + H_e (E_e - V) + H_i (E_i - V)
\]

\[
\tau_e \frac{dH_e}{dt} = \alpha_e - H_e + \sqrt{\alpha_e k_e} \xi_e (t)
\]

\[
\tau_i \frac{dH_i}{dt} = \alpha_i - H_i + \sqrt{\alpha_i k_i} \xi_i (t).
\]

(64)

The time-dependent quantities \( \alpha_e(t) \) where \( s = e \) or \( i \) are proportional to the presynaptic rate whereas the \( k \) parameters are constant. We use a Gaussian approximation for the synaptic drive so that \( \xi_e(t) \) is a white-noise process with zero mean, autocovariance \( \langle \xi_e(t) \xi_e(t') \rangle = \delta(t - t') \) and it is assumed that excitatory and inhibitory synaptic drives are uncorrelated.

Similarly to the approach used for the long-dendrite model, we separate voltages and conductances into deterministic and zero-mean fluctuating components \( V = V + \hat{V} \) and \( H_e = H_e + \hat{H}_e \). At the level of the stochastic differential equation for voltage, we drop less significant terms that are second order in the fluctuating components like \( \hat{v} h_s \) with the result that \( v \) also has Gaussian statistics. In terms of the quantities \( \alpha_s \), the deterministic equations for the isopotential neuron are identical to the dendritic case given in Eq. set 3. The fluctuating components, however, obey

\[
\dot{\hat{v}} = h_e \xi_e + h_i \xi_i - \hat{H} v
\]

\[
\tau_e \hat{h}_e = \sqrt{\alpha_e k_e} \xi_e - h_e
\]

\[
\tau_i \hat{h}_i = \sqrt{\alpha_i k_i} \xi_i - h_i
\]

(65)

where we have again the notation \( \xi_e(t) = E_e - \langle V \rangle \) and \( \hat{H}(t) = \alpha_e \langle H_e \rangle + \langle H_i \rangle \). Note that the difference between this isopotential reference model and the dendritic case (Eq. set 4) is the absence of a second spatial derivative in the equation for the voltage and that the synaptic quantities are instead driven by temporal Gaussian white noise not spatiotemporal Gaussian white noise.

Voltage-moment equations: isopotential model

The deterministic equation set (3) provides a complete description of dynamics of the first moments \( \langle V \rangle \) and \( \langle \hat{V} \rangle \). We now derive a set of differential equations for the second moments of the voltage and its derivative. First we can solve for the variance of one of the synaptic drives. This can be written as filter integral over the quantity \( \alpha_e(t) \)

\[
\langle h_e^2 \rangle = \frac{k_e}{\tau_e^2} \int_{-\infty}^{t} dt' \alpha_e(t') e^{-2(t-t')/\tau_e}
\]

(66)

and because the filter is exponential, it can be rewritten in the differential form

\[
\tau_e \frac{d\langle h_e^2 \rangle}{dt} = \frac{\alpha_e k_e}{2\tau_e} \langle h_e^2 \rangle - \langle \hat{h}_e^2 \rangle.
\]

(67)

We next cross-multiply the stochastic differential equations for \( v \) and \( h_s \) by \( h_s \) and \( v \) and average to get

\[
\langle \hat{v} h_s \rangle = \xi_e \langle h_e^2 \rangle - \hat{H} \langle v h_s \rangle \quad \text{and} \quad \langle v h_s \rangle = -\langle \hat{v} h_s \rangle/\tau_v.
\]

(68)

where the causality \( \langle \xi_e v \rangle = 0 \) has been used in the latter equation. Adding these gives the complete derivative \( \langle \hat{v} h_s \rangle + \langle v h_s \rangle = \partial_t \langle v h_s \rangle \) and so

\[
\frac{d\langle v h_s \rangle}{dt} = \xi_e \langle h_e^2 \rangle - \left( \hat{H} + \frac{1}{\tau_e} \right) \langle v h_s \rangle.
\]

(69)
We can also multiply the stochastic differential equation for $v$ by $v$ and average to get
\[ \frac{1}{2} \frac{d \langle v^2 \rangle}{dt} = \mathcal{E}_v (v h_e) + \mathcal{E}_i (v h_i) - \mathcal{H} (v^2) = \langle v \dot{v} \rangle \] (70)
which provides equations for both $\langle v^2 \rangle$ and $\langle v \dot{v} \rangle$. For the autocovariance of the rate-of-change of voltage we multiply the differential equation for $v$ by $\dot{v}$ and average
\[ \langle \dot{v}^2 \rangle = \mathcal{E}_v (\dot{v} h_e) + \mathcal{E}_i (\dot{v} h_i) - \mathcal{H} (\dot{v} v) \] (71)
All together, these differential equations and subsidiary relations for the synaptic drive and voltage provide all that is required to apply the upcrossing method to the isopotential model.

**Steady state: isopotential model**

The steady state $\langle \bar{V} \rangle$ for the mean voltage is identical to that given for the dendritic model; however, the variance and variance of the rate-of-change of voltage are different. First we note that $\langle \dot{\bar{V}}^2 \rangle = \bar{\alpha}_e \bar{\kappa}_e / \bar{\tau}_e$ and that it is useful to use the steady-state relation $\tau_e \langle \bar{\dot{h}}_e \rangle = \langle \bar{h}_e \rangle$. Then comparing the relevant equations above we have
\[ \langle \dot{v}^2 \rangle = \frac{\mathcal{E}_v^2}{2} \kappa_e \bar{\alpha}_e \tau_e \left( \frac{\tau_e}{\tau_v} \right) + \frac{\mathcal{E}_i^2}{2} \kappa_i \bar{\alpha}_i \tau_e \left( \frac{\tau_v}{\tau_v + \tau_i} \right) \] (72)
which can be seen in Fig. 3B (middle panel) for a case matched to the dendritic model. For the variance of the rate-of-change of voltage we have
\[ \langle \dot{v}^2 \rangle = \frac{\mathcal{E}_v^2}{2 \tau_e^2} \kappa_e \bar{\alpha}_e \tau_v \left( \frac{\tau_e}{\tau_v} \right) + \frac{\mathcal{E}_i^2}{2 \tau_i^2} \kappa_i \bar{\alpha}_i \tau_v \left( \frac{\tau_v}{\tau_v + \tau_i} \right) \] (73)
which is also illustrated in Fig. 3B (lower panel). Other useful quantities are
\[ \langle v h_e \rangle = \frac{\mathcal{E}_e \langle \bar{h}_e \rangle}{\mathcal{H}} \quad \text{and} \quad \langle \dot{v} h_e \rangle = \frac{\mathcal{E}_e \langle \bar{h}_e \rangle}{1 + \tau_e \mathcal{H}} \] (74)
and similarly for inhibition.

**Response to weak oscillations: isopotential model**

We again consider a weak oscillation of the excitatory drive such that $\alpha_e(t) = \bar{\alpha}_e + \hat{\alpha}_e \exp \omega t$ and keep terms in all calculations up to first order in $\hat{\alpha}_e$. The deterministic, first-order moments of the various quantities are identical to the case of the long-dendrite considered previously. The second-order moments are different, and for the conductances we have
\[ \langle \bar{h}_e^2 \rangle = \frac{\hat{\alpha}_e \bar{\kappa}_e}{2 \bar{\tau}_e} \frac{1}{1 + i \omega \bar{\tau}_e / 2} \quad \text{and} \quad \langle \dot{\bar{h}}^2 \rangle = 0. \] (75)
The next quantities of interest are the covariances between the conductance and voltage.
\[ \langle v \dot{h}_e \rangle = \frac{\mathcal{E}_e \langle \bar{h}_e \rangle}{\omega + \mathcal{H} + 1/\tau_e} \] and
\[ \langle \dot{v} h_i \rangle = -\frac{\langle \bar{v} \rangle \langle \bar{h}_e \rangle + \mathcal{H} (v h_i)}{\omega + \mathcal{H} + 1/\tau_i} \] (76)
where $\langle \bar{h}_e \rangle = 0$ has been used. The oscillatory voltage variance can be expressed in terms of these quantities
\[ \langle \dot{v}^2 \rangle = \frac{\mathcal{E}_v}{\mathcal{H} (v h_e) + \mathcal{E}_i (v h_i) - \mathcal{H} (v h_i) - \mathcal{H} (v^2)} \] (77)
and the covariance has the relation $\langle \dot{v} \rangle = \omega \langle \dot{v} \rangle$ and is therefore obtained directly from the above. Finally, to calculate the variance of $\dot{v}$ we need
\[ \langle \dot{v}^2 \rangle = \frac{\mathcal{E}_e \langle \bar{h}_e \rangle - \langle \bar{h}_e \rangle \langle \bar{h}_e \rangle - \mathcal{H} (v h_e)}{\omega + \mathcal{H} + 1/\tau_e} \] (78)
and the same for inhibition, again noting that $\langle \bar{h}_e \rangle = 0$. We can then write that
\[ \langle \dot{v}^2 \rangle = \mathcal{E}_e \langle \dot{v} \rangle + \mathcal{E}_i \langle \dot{v} \rangle - \mathcal{H} (v h_e) + \mathcal{H} (v h_i) \] (79)
where the steady-state result $\langle \dot{v} \rangle = 0$ has been used.

**Low-frequency limit: isopotential model**

When $\omega = 0$ the $\langle \bar{V} \rangle$ and $\langle \dot{v} \rangle$ terms vanish as they are time derivatives of other quantities and therefore proportional to $\omega$. It remains to calculate $\langle \dot{\bar{V}} \rangle$, $\langle \dot{\bar{v}}^2 \rangle$ and $\langle \dot{\bar{v}} \dot{\bar{v}} \rangle$, and when $\omega = 0$ these can be calculated by taking the derivatives of the steady-state values with respect to $\alpha_e$. Again, it is useful to use the shorthand $x_e = \tau_e / (\tau_v + \tau_i)$ and similarly for inhibition.
\[ \lim_{\omega \to 0} \langle v h_e \rangle = \hat{\alpha}_e \tau_e \frac{\mathcal{E}_e \kappa_e}{2 \tau_e} x_e \left( 1 - \alpha_e \tau_v - \alpha_e \tau_x \right) \] (80)
\[ \lim_{\omega \to 0} \langle \dot{v} h_i \rangle = -\hat{\alpha}_e \tau_v \frac{\kappa_i}{2 \tau_i} \tau_e \bar{\alpha}_e \bar{x}_i \left( \mathcal{E}_e + \mathcal{E}_i \bar{x}_i \right). \]
For the low frequency limit of the variance modulation we break the response into excitatory and inhibitory components which take the form
\[ \lim_{\omega \to 0} \langle \dot{v}^2 \rangle = \hat{\alpha}_e \tau_e \frac{\mathcal{E}_e \kappa_e}{2 \tau_e} x_e \left( 1 - 3 \alpha_e \tau_v - \alpha_e \tau_x \right) \] (81)
\[ \lim_{\omega \to 0} \langle \dot{v}^2 \rangle = -\hat{\alpha}_e \tau_v \frac{\kappa_i}{2 \tau_i} \tau_e \bar{\alpha}_e \bar{x}_i \left( \mathcal{E}_e + \mathcal{E}_i \bar{x}_i \right). \]
Taking a similar approach with the variance of the rate-of-change of voltage gives
\[ \lim_{\omega \to 0} \langle \dot{\bar{v}}^2 \rangle = \hat{\alpha}_e \tau_e \frac{\mathcal{E}_e \kappa_e}{2 \tau_e} x_e \left( 1 - 2 \alpha_e \tau_v - \alpha_e \tau_x \right) \] (82)
\[ \lim_{\omega \to 0} \langle \dot{\bar{v}}^2 \rangle = -\hat{\alpha}_e \tau_v \frac{\kappa_i}{2 \tau_i} \tau_e \bar{\alpha}_e \bar{x}_i \left( \mathcal{E}_e + \mathcal{E}_i \bar{x}_i \right). \]
High-frequency asymptotics: isopotential model

For large $\omega$, the leading-order contributions can be shown to decay as $1/\omega$ and comprise contributions from $\langle \hat{V} \rangle$, $\langle \hat{v} \rangle$ and $\langle \hat{v}^2 \rangle$. The forms for the first two are fairly straightforward to derive

$$\langle \hat{V} \rangle \sim \frac{\dot{\alpha}_e \bar{F}_e}{i\omega \tau_e} \quad \text{and} \quad \langle \hat{v} \rangle = -\frac{\dot{\alpha}_e}{i\omega \tau_e} \langle \bar{v}^2 \rangle.$$  \hspace{1cm} (81)

The third term is more complicated. We use

$$\langle \hat{v} \rangle_e = \bar{F}_e \langle \hat{h}_e \rangle - \bar{H} \langle \bar{v} \rangle_e + O \left( \frac{1}{\omega^2} \right)$$  \hspace{1cm} (82)

and similarly for $\langle \hat{h} \rangle$ though note that $\langle \hat{h}_e \rangle = 0$. Then

$$\langle \hat{v}^2 \rangle = \bar{F}_e \langle \hat{v} \rangle_e + \bar{F}_i \langle \hat{v} \rangle_i - \bar{H} \langle \hat{v} \rangle + O \left( \frac{1}{\omega^2} \right)$$  \hspace{1cm} (83)

where for large $\omega$ we have

$$\langle \hat{h}_e^2 \rangle \sim \frac{\dot{\alpha}_e \kappa_e}{i\omega \tau_e^2} \quad \text{and} \quad \bar{H} \sim \frac{\dot{\alpha}_e}{i\omega \tau_e}.$$  \hspace{1cm} (84)

The quantities above can then be substituted into the linear response form of the upcrossing rate, which will therefore also have a $1/\omega$ behaviour at high frequencies.

APPENDIX D. Simulations and figures

Simulational code was written using the Julia programming language [19] and all code used for figures is provided in the Supplemental Material. The simulations were implemented using a forward Euler scheme typically with $\Delta_t = 0.02\text{ms}$ and $\Delta_e = 20\mu\text{m}$ so that

$$H_e(x_m, t_{n+1}) = H_e(x_m, t_n) + \Delta_t \left( \alpha(t_n) \frac{E - V(x_m, t_n)}{\tau_v} + \phi^h_{nn} \frac{\phi^\theta_{nn}}{\Delta_e \Delta_t} \right)$$  \hspace{1cm} (85)

and for the voltage

$$V(x_m, t_{n+1}) = V(x_m, t_n) + \Delta_t \left( \alpha(t_n) (E_e - V(x_m, t_n)) + \Delta_t \left( H_e(x_m, t_n) (E_e - V(x_m, t_n)) + \Delta_t \left( H_i(x_m, t_n) (E_i - V(x_m, t_n)) \right) \right) \right) \right)$$  \hspace{1cm} (86)

where $\phi^\theta_{nn}$ are independent Gaussian random numbers with zero mean and unit variance. The system was implemented using periodic boundary conditions with size $L = 2000\mu\text{m}$ being sufficiently larger than spatial correlation lengths. Given the homogeneity of the system, statistical quantities such as the upcrossing could be evaluated at all positions simultaneously and averaged, thereby increasing the efficiency of the simulations.

For the isopotential neuron the discretisation is across time only so the equations are

$$H_e(t_{n+1}) = H_e(t_n) + \frac{\Delta_t}{\tau_v} \left( \alpha(t_n) H_e(t_n) + \sqrt{\alpha(t_n) \kappa_e} \phi^h_{nn} \frac{\phi^\theta_{nn}}{\Delta_t} \right)$$  \hspace{1cm} (87)

and for the voltage

$$V(t_{n+1}) = V(t_n) + \Delta_t \left( \alpha(t_n) (E_e - V(t_n)) + \Delta_t \left( H_e(t_n) (E_e - V(t_n)) + H_i(t_n) (E_i - V(t_n)) \right) \right)$$  \hspace{1cm} (88)

where $\phi^h_{nn}$ are independent Gaussian random numbers with zero mean and unit variance.

Note that for both the dendritic and isopotential models, the schemes above can be straightforwardly modified to simulate the systems in the Gaussian approximation of the voltage in which terms that are second-order in zero-mean fluctuating quantities like $vh_e$ are dropped from the voltage dynamics.

The patterned input used in Figure 2

The time-dependent input used in Fig. 2 comprised functions $\alpha_e(t)$ and $\alpha_i(t)$ lasting one second. Outside the range 250 to 750ms these rates were zero. Within this range both had constant value with $\alpha_e = 0.00566kHz$ and $\alpha_i = 0.01100kHz$ (which would give a constant upcrossing rate of 5Hz, anticipating Fig. 3C) with the excitatory rate $\alpha_e(t)$ having four functions additionally superimposed. These functions $A(t)$ were parameterised as

$$A_k(t; a, t_k, \sigma, f_k) = a \exp \left( -\frac{(t - t_k)^2}{2\sigma^2} \right) \cos(2\pi f_k t)$$  \hspace{1cm} (89)

where $a = 0.03kHz$, $t_k = 350, 450, 550, 650\text{ms}$, $\sigma = 20\text{ms}$ and $f = 0.02, 0.05, 0.100, 0.200kHz$.

Illustration of steady-state properties

Given the many components of the model, there is a broad choice of parameter combinations that might be used to illustrate behaviour. In the context of examining the steady-state behaviour (Fig. 3B, 3C) the choice was made to vary $\alpha_e$ and $\alpha_i$ at fixed ratio between $\tau_v$ and $\tau_c = 1/\alpha$ to give a particular $\langle \bar{V} \rangle$. Given the forms

$$\frac{1}{\tau_v} = \alpha_c + \alpha_e + \alpha_i \quad \text{and} \quad \langle \bar{V} \rangle = \tau_v (E_c \alpha_c + E_e \alpha_e + E_i \alpha_i)$$  \hspace{1cm} (90)

we therefore have the conditions

$$\dot{\alpha}_c = \frac{(\langle \bar{V} \rangle - E_c) - (E_e - E_c) \alpha_c \tau_v}{(E_e - E_c) \tau_v}$$  \hspace{1cm} \text{and}

$$\dot{\alpha}_i = \frac{(E_e - \langle \bar{V} \rangle) - (E_e - E_c) \alpha_i \tau_v}{(E_e - E_i) \tau_v}.$$  \hspace{1cm} (91)
Such that the steady-state mean voltage $\langle V \rangle$, conductance state $\tau_v$ and voltage variance $\langle \dot{V}^2 \rangle$ were all matched. The mean properties of the model are identical by design and set by $\bar{\alpha}_e$ and $\bar{\alpha}_i$. To match the variance, we choose $\kappa_e$ and $\kappa_i$ by comparing Eqs. (34) and (72) so that

$$\kappa_e = \frac{1}{2} \frac{\lambda_e}{\lambda_v} \left( \frac{\tau_v + \tau_i}{\tau_v} \right) \left( 1 - \sqrt{\frac{\tau_i}{\tau_v + \tau_i}} \right). \quad (92)$$

Matching the isopotential and dendritic models

To provide as fair a comparison as possible between the models, we set the parameters of the isopotential model such that the steady-state mean voltage $\langle V \rangle$, conductance state $\tau_v$ and voltage variance $\langle \dot{V}^2 \rangle$ were all matched. Though the voltage mean and variance (Fig. 3B middle panel) as well as the conductance state parameterised by $\tau_v$ are matched, it is not possible [9] to simultaneously match the variance of the rate-of-change of voltage (see Fig. 3B, lower panel) and so the upcrossing rates will not be the same; this can seen in Fig. 3C.

[28] G. Eyal et al, Dendrites impact the encoding capabilities
