Firing-Rate Response of a Neuron Receiving Excitatory and Inhibitory Synaptic Shot Noise

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The synaptic coupling between neurons in neocortical networks is sufficiently strong so that relatively few synchronous synaptic pulses are required to bring a neuron from rest to the spiking threshold. However, such finite-amplitude effects of fluctuating synaptic drive are missed in the standard diffusion approximation. Here exact solutions for the firing-rate response to modulated presynaptic rates are derived for a neuron receiving additive excitatory and inhibitory synaptic shot noise with exponential amplitude distributions. The shot-noise description of the neuronal response to synaptic dynamics is shown to be richer and qualitatively distinct from that predicted by the diffusion approximation. It is also demonstrated how the framework developed here can be generalized to multiplicative shot noise so as to better capture effects of the inhibitory reversal potential.

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Shot-noise processes, in which a state variable irregularly jumps by positive or negative amounts, are seen in diverse systems from electronics to meteorology. A biophysical application can be found in neuronal integration in which the charging of the leaky membrane capacitance by positive and negative synaptic currents constitutes a two-sided shot-noise process with decay, with the additional feature of a threshold for action-potential initiation. Early models [1,2] treated fluctuating synaptic input as being composed of pulses with finite amplitudes. Though recent studies of synaptic shot noise have been made [3–7] the majority of theoretical, simulational, and experimental work has employed the diffusion approximation in which presynaptic rates are considered high and amplitudes low. However, the pyramidal neurons that form the dense neocortical networks have synaptic connections with amplitudes in the range 0.2–6 mV with a mean of 1.3 mV [8] and when presynaptic correlations [9] are accounted for the effective amplitudes will be even higher. Given that the voltage difference between rest and threshold is around 10 mV for these cells [10] it is likely that finite-amplitude effects missed by the diffusion approximation will play an important role in shaping the response properties of neurons *in vivo*. Here a convenient framework for treating shot-noise processes in threshold systems is developed in which first-order operators relate excitatory or inhibitory fluxes to the probability density. The framework will be used to derive the firing-rate response to modulated presynaptic rates—a key quantity that characterizes the dynamics and phase transitions of spiking neural networks [11–14].

The model.—A neuron of voltage v and time constant $\tau = 20$ ms, receives additive excitatory synaptic pulses at Poisson-distributed arrival times t_{ek} at rate $R_e(t)$ with amplitudes $a_{ek} > 0$ drawn from a distribution $A_e(a)$, and similarly for inhibition ($a_{ik} < 0$)

$$\frac{dv}{dt} = -\frac{v}{\tau} + \sum_{\{t_e\}} a_{ek}\delta(t - t_{ek}) + \sum_{\{t_i\}} a_{ik}\delta(t - t_{ik}). \quad (1)$$

An action potential is registered when the voltage reaches a threshold $v_{\rm th} = 10$ mV following which it is immediately reset to $v_{\rm re} = 5$ mV. Of interest will be the steady-state and response properties of a population of neurons and so it proves convenient to move to a population-based formalism in which we consider the probability density $P(v)$ and flux $J(v)$ of neuronal voltages. The continuity equation linking these two quantities can be written as

$$\frac{\partial P}{\partial t} + \frac{\partial J}{\partial v} = r(t)(\delta(v - v_{\rm re}) - \delta(v - v_{\rm th})), \quad (2)$$

where $r(t)$ is the instantaneous firing rate of the population. The flux is resolved into three components corresponding to the drift, synaptic excitation, and inhibition

$$J = -vP/\tau + J_e + J_i. \quad (3)$$

The fluxes arising from the Poissonian synaptic drives may be written as integrals over the postsynaptic voltage density and synaptic-amplitude distributions A_e and A_i

$$J_e(v, t) = R_e(t) \int_{-\infty}^{v} dw P(w, t) \int_{v-w}^{\infty} da A_e(a), \quad (4)$$

and similarly for inhibition. The excitatory flux at threshold is equal to the firing rate whereas the inhibitory flux at threshold is zero. Hence, $J_e(v_{\rm th}) = J(v_{\rm th}) = r(t)$ and $J_i(v_{\rm th}) = 0$ so that from Eq. (3) the threshold density is zero $P(v_{\rm th}) = 0$. For a biophysically reasonable case [8] of exponentially distributed amplitudes $A_e(a) = \theta(a)e^{-a/a_e}/a_e$ and $A_i(a) = -\theta(-a)e^{-a/a_i}/a_i$ for inhibition (where $a_e > 0$ and $a_i < 0$ are mean postsynaptic potentials) the synaptic-flux integral equations (4) may be replaced by linear differential equations

$$\frac{\partial J_e}{\partial v} + \frac{J_e}{a_e} = R_e P - r(t)\delta(v - v_{\rm th}) \quad \text{and} \quad \frac{\partial J_i}{\partial v} + \frac{J_i}{a_i} = R_i P \tag{5}$$

rendering the shot-noise master equation solvable: Eqs. (2), (3), and (5) are linear in fluxes and probability density and so can be solved analytically for firing-rate quantities using Laplace transforms or integrated numerically using the threshold integration method [15] for voltage-dependent quantities.

Generalized amplitude distributions.—The amplitude distributions considered here are single exponentials, but the framework extends to more general distributions expressible as a sum of exponentials $A(a) = \sum_m \alpha^{(m)} e^{-a/a^{(m)}}/a^{(m)}$, with $\alpha^{(m)}$ positive or negative and $\sum_m \alpha^{(m)} = 1$. Each exponential component has a flux obeying an equation of the form (5) with, if the component is excitatory ($a^{(m)} > 0$), a corresponding contribution $r^{(m)}$ to the firing rate where $\sum_m r^{(m)} = r$. A full analytical treatment of this generalization is beyond the scope of this Letter, but examples of two-component excitatory processes are provided [16].

Subthreshold-voltage moments.—For later comparison to the diffusion approximation, the subthreshold ($v_{\rm th} \to \infty$ so $r = J = 0$) voltage mean and variance are first derived. This is achieved using bilateral Laplace transforms $\tilde{f}(s) = \int_{-\infty}^{\infty} dv e^{sv} f(v)$ where the transform of the subthreshold probability density is the generating function $Z_0(s)$ for the subthreshold-voltage moments. Transforming the synaptic-flux equations (5) and substituting the fluxes into the transform of Eq. (3) gives

$$\frac{dZ_0}{ds} = \left(\frac{a_e \tau R_{e0}}{1 - a_e s} + \frac{a_i \tau R_{i0}}{1 - a_i s}\right) Z_0, \tag{6}$$

where R_{e0}, R_{i0} are steady-state excitatory and inhibitory presynaptic rates (a zero subscript will denote a steady-state quantity). Integrating, and noting that $Z_0(0) = 1$ because probability densities integrate to unity, gives $Z_0(s) = 1/(1 - a_e s)^{\tau R_{e0}}(1 - a_i s)^{\tau R_{i0}}$. The generating function for the subthreshold cumulants is $W_0 = \log(Z_0)$ so the nth cumulant is $\frac{d^n}{ds^n} W_0(s)|_{s=0}$. For the subthreshold mean μ_0 and variance σ_0^2 this yields

$$\mu_0 = a_e \tau R_{e0} + a_i \tau R_{i0}, \qquad \sigma_0^2 = a_e^2 \tau R_{e0} + a_i^2 \tau R_{i0}, \tag{7}$$

which are the two parameters typically used to characterize synaptic drive in the diffusion approximation.

Steady-state rate.—The threshold $v_{\rm th}$ is now reinstated to obtain the steady-state quantities required later for the firing-rate response (the first-passage-time density has recently been derived elsewhere [17], although see [16] for the spike-train spectrum). Laplace-transforming equations (2), (3), and (5), and substituting for the fluxes yields the following equation for the transformed steady-state density $\tilde{P}_0(s)$:

$$\frac{d\tilde{P}_0}{ds} = \left(\frac{a_e \tau R_{e0}}{1 - a_e s} + \frac{a_i \tau R_{i0}}{1 - a_i s}\right)\tilde{P}_0 - \frac{\tau r_0}{s}\left(\frac{e^{s v_{\rm th}}}{1 - a_e s} - e^{s v_{\rm re}}\right), \tag{8}$$

where r_0 is the *a priori* unknown steady-state rate. Note that the term in brackets comprising the presynaptic rates can [using Eq. (6)] be rewritten as $Z_0^{-1} dZ_0/ds$. Making this substitution, combining the derivatives and integrating between s and $1/a_e$ gives

$$\tilde{P}_0(s) = \tau r_0 \int_s^{1/a_e} \frac{dc}{c} \frac{Z_0(s)}{Z_0(c)}\left(\frac{e^{c v_{\rm th}}}{1 - a_e c} - e^{c v_{\rm re}}\right). \tag{9}$$

Probability densities integrate to unity, $\tilde{P}_0(0) = 1$, so

$$\frac{1}{\tau r_0} = \int_0^{1/a_e} \frac{dc}{c} \frac{1}{Z_0(c)}\left(\frac{e^{c v_{\rm th}}}{1 - a_e c} - e^{c v_{\rm re}}\right) \tag{10}$$

gives the steady-state rate as a function of four independent synaptic variables R_{e0}, R_{i0}, a_e, a_i. To take the diffusion limit of this integral it is convenient to note that $Z_0 = e^{W_0}$ where $W_0(c) = c\mu_0 + c^2\sigma_0^2/2! + \cdots$ is the subthreshold cumulant-generating function. In the diffusion limit of small synaptic amplitudes and high synaptic rates the integral (10) can be approximated as

$$\frac{1}{\tau r_0} \simeq \int_0^{\infty} \frac{dy}{y} e^{-y^2/2}(e^{y y_{\rm th}} - e^{y y_{\rm re}}) + O\left(\frac{a_{e,i}}{\sigma_0}\right), \tag{11}$$

where $y_{\rm th} = (v_{\rm th} - \mu_0)/\sigma_0$ and analogously for $y_{\rm re}$. This is the simplified form [12] of the Ricciardi diffusion approximation [18] and projects the underlying finite-amplitude synaptic drive onto a two-variable subspace spanned by the subthreshold-voltage mean μ_0 and variance σ_0^2 [Eq. (7)] only. In Fig. 1 the shot-noise [Eq. (10)] and diffusion approximation [Eq. (11)] rates are compared. Even for relatively modest amplitudes of 2 mV (see introduction) the rate prediction of the diffusion approximation deviates from the full shot-noise result [panel 1(a)] and misses the shot-noise skew [5,6] of the underlying voltage distribution [panel 1(b)] calculated using the threshold integration method [16]. The time course in panel 1(b)(i), featuring significant ($a_e/v_{\rm th} = 0.2$) excitatory postsynaptic potentials, is reminiscent of *in vivo* recordings [19].

Rate response to modulated presynaptic rates.—A modulation of either excitatory or inhibitory ($\kappa = e, i$) firing rates $R_\kappa(t) = R_{\kappa 0} + R_{\kappa 1} e^{i\omega t}$ is now considered. At first order this will induce a modulation in the probability density $P(t) = P_0 + P_1 e^{i\omega t}$ where P_1 is of order $R_{\kappa 1}$, with similar forms for all fluxes and the firing rate. At first order, the transformed fluxes from the continuity and synaptic-flux equations (2) and (5) can be substituted into the net flux [Eq. (3)] to give an equation for the modulated density

$$\frac{d\tilde{P}_1}{ds} = \left(\frac{a_e \tau R_{e0}}{1 - a_e s} + \frac{a_i \tau R_{i0}}{1 - a_i s} - \frac{i\omega\tau}{s}\right)\tilde{P}_1 + \frac{a_\kappa \tau R_{\kappa 1}}{1 - a_\kappa s}\tilde{P}_0 - \frac{\tau r_\kappa}{s}\left(\frac{e^{s v_{\rm th}}}{1 - a_e s} - e^{s v_{\rm re}}\right), \tag{12}$$

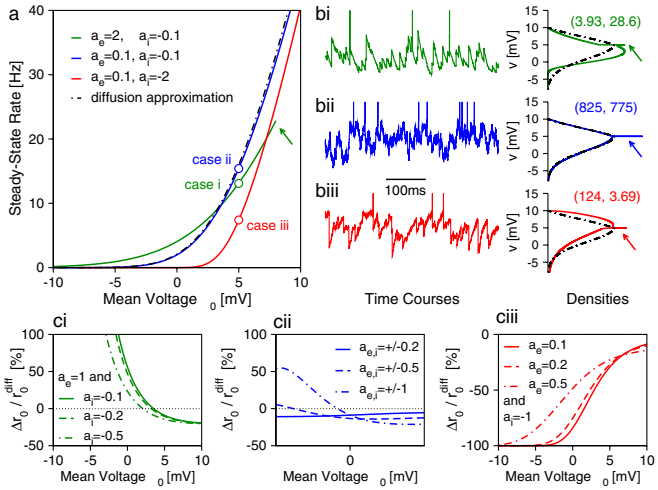

FIG. 1 (color online). Steady state for three example shot-noise cases that are predicted to have identical behavior under the diffusion approximation: (i) large excitatory jumps (green), (ii) small excitatory and inhibitory jumps (blue) and (iii) large inhibitory jumps (red), each for fixed $\sigma_0 = 4$ mV as a function of μ_0 [equation set (7) determines R_{e0} and R_{i0}]. (a) Steady-state rates [Eq. (10)] show a clear departure from the diffusion approximation [black, Eq. (11)] except for the small amplitude case (blue). Note that not all μ_0, σ_0 are accessible with positive presynaptic rates (green curve, $\mu_0 > 8$ mV). The pairs of mean amplitudes (in mV) are marked in the panel. (b) Example time courses and steady-state densities (from threshold integration [16]) for the three cases [$\mu_0 = 5$ mV on panel (a), symbols; presynaptic rates $R_{e0}\tau$, $R_{i0}\tau$ in panel (b)] compared with the diffusion approximation (black). The density discontinuity at reset (arrows) has amplitude $\tau r_0/v_{\rm th}$ [Eqs. (2) and (3)] and so persists even in the diffusion limit [case (ii)]. (c) Additional examples of the disparity between shot-noise and diffusion-approximation rates $(r_0^{\rm shot} - r_0^{\rm diff})/r_0^{\rm diff}$ [see Eqs. (10) and (11) all for cases where $\sigma_0 = 4$ mV, so that $r_0^{\rm diff}$ is that given in panel (a)].

where r_κ is the modulated firing rate. Introducing $Z_1(s) = Z_0(s)/s^{i\omega\tau}$ and combining derivatives gives

$$Z_1 \frac{d}{ds}\frac{\tilde{P}_1}{Z_1} + \frac{\tau r_\kappa}{s}\left(\frac{e^{sv_{\rm th}}}{1-a_e s} - e^{sv_{\rm re}}\right) = \frac{a_\kappa \tau R_{\kappa 1}}{1-a_\kappa s}\tilde{P}_0. \quad (13)$$

From the normalization of probability $\tilde{P}_1(0) = 0$. Both sides of Eq. (13) are now divided by Z_1 and s integrated over the range $0 \to 1/a_e$ on the limits of which the terms containing $\tilde{P}_1$ vanish. This gives the rate response

$$r_\kappa = R_{\kappa 1}\frac{\int_0^{1/a_e}\frac{ds a_\kappa}{1-a_\kappa s}\frac{1}{Z_1(s)}\tilde{P}_0(s)}{\int_0^{1/a_e}\frac{ds}{s}\frac{1}{Z_1(s)}\left(\frac{e^{sv_{\rm th}}}{1-a_e s} - e^{sv_{\rm re}}\right)} \quad (14)$$

which, on substitution for $\tilde{P}_0(s)$ in Eq. (9), gives

$$r_\kappa = R_{\kappa 1}\tau r_0\frac{\int_0^{1/a_e}\frac{ds}{s}\frac{1}{Z_0(s)}\left(\frac{e^{sv_{\rm th}}}{1-a_e s} - e^{sv_{\rm re}}\right)\int_0^s \frac{dc a_\kappa c^{i\omega\tau}}{1-a_\kappa c}}{\int_0^{1/a_e}\frac{ds}{s}\frac{1}{Z_0(s)}\left(\frac{e^{sv_{\rm th}}}{1-a_e s} - e^{sv_{\rm re}}\right)s^{i\omega\tau}}. \quad (15)$$

The low-frequency limit is identical to the gradient of the steady-state rate so $r_\kappa \to R_{\kappa 1} dr_0/dR_{\kappa 0}$ when $\omega\tau \to 0$, as expected. The leading-order high-frequency form for either excitation or inhibition is straightforward to derive: integrating the first of equation set (5) gives the firing rate in terms of the rate of jumps across threshold

$$r(t) = R_e(t)\int_{-\infty}^{v_{\rm th}} e^{-(v_{\rm th}-v)/a_e}P(v,t)dv. \quad (16)$$

Consider now a modulation of the excitatory presynaptic rates. At first order in the modulated quantities there will be one term proportional to $R_{e1}P_0(v)$ and a second to $R_{e0}P_1(v,t)$. With the expectation that $P_1(v,t) \to 0$ for high-frequency modulation and comparing the first term to the steady-state rate [proportional to $R_{e0}P_0(v)$], a constant high-frequency limit $r_e \to r_0 R_{e1}/R_{e0}$ is found, whereas a similar argument for inhibition gives $r_i \to 0$. Corrections to these limiting results can be extracted from Eq. (15) by making the substitution $s = e^{-x}/a_e$, rotating in the complex plane $x \to q/i\omega\tau$, and expanding in powers of inverse frequency. For example, the integral in the denominator of Eq. (15) becomes a series of gamma functions

$$c_0\int_0^\infty dq e^{-q}q^{R_{e0}\tau-1}\left(1 + c_1\frac{q}{i\omega\tau} + \cdots\right), \quad (17)$$

where $c_0 = e^{v_{\rm th}/a_e}(1-a_i/a_e)^{R_{i0}\tau}/a_e^{i\omega\tau}(i\omega\tau)^{R_{e0}\tau}$ and

$$c_1 = \frac{1}{2} - \frac{v_{\rm th}}{a_e} - e^{-(v_{\rm th}-v_{\rm re})/a_e} - \frac{R_{e0}\tau}{2} + \frac{a_i R_{i0}\tau}{a_e - a_i}. \quad (18)$$

The numerator [Eq. (15)] can be similarly expanded yielding double integrals also expressible as a series of gamma functions. Common gamma functions in the numerator and denominator may be factored out to yield the rate-response for excitation in the high-frequency limit

$$r_e \simeq r_0\frac{R_{e1}}{R_{e0}}\left(1 - \frac{R_{e0}\tau}{i\omega\tau}\left(\frac{c_1}{R_{e0}\tau+1} + \frac{1}{2}\right)\right) \quad (19)$$

giving the amplitude $|r_e|$ of the response as a constant plus corrections of $O(1/\omega^2)$. For inhibition

$$r_i \simeq r_0\frac{R_{i1}\tau}{i\omega\tau}\frac{a_i}{a_e - a_i}\left(1 - \frac{(R_{e0}\tau+1)}{i\omega\tau}\frac{a_e}{a_e - a_i}\right) \quad (20)$$

is the asymptotic form, so the amplitude decays as $1/w\tau$ with a phase lag approaching $-3\pi/2$ (because $a_i < 0$). These analytical and asymptotic results are plotted in Fig. 2 for the cases (i), (ii), and (iii) treated in the previous section. The results can again be compared to the diffusion approximation for which modulation of a presynaptic firing rate R_κ induces a simultaneous modulation of both the mean $\mu_1 = R_{\kappa 1}\tau a_\kappa$ and variance $\sigma_1^2 = R_{\kappa 1}\tau a_\kappa^2$. The sum of mean r_μ and variance r_{σ^2} modulations [12,13,16], $r_\kappa = r_\mu + r_{\sigma^2}$, is also plotted in the panels of Fig. 2. As expected, cases (i) and (iii) deviate significantly from the diffusion approximation at all frequencies. Note that synaptic channels with large amplitudes show correspondingly greater susceptibilities to presynaptic rate modulation. The low synaptic-amplitude case (ii) agrees well for biophysically reasonable frequencies f, though there are deviations for $f > 10$ kHz. The asymptotics for the diffusion approximation have been derived elsewhere [12,13]

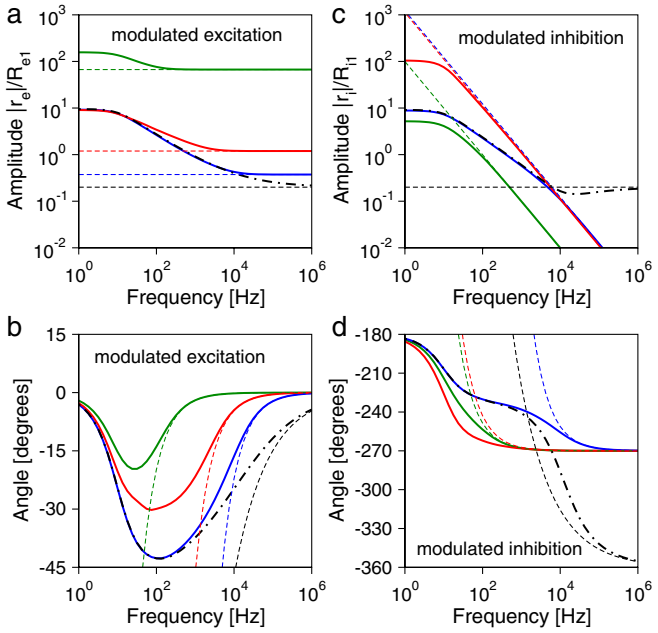

FIG. 2 (color online). Amplitude and phase of the normalized firing-rate response $r_\kappa/R_{\kappa 1}$ [Eq. (15)] for modulated excitatory R_{e1} [(a) and (b)] and inhibitory R_{i1} [(c) and (d)] presynaptic rates for the cases (i), (ii), and (iii) of Fig. 1(b) (same colors). Shot-noise results are compared to the diffusion approximation [12,13] with asymptotics [Eqs. (19)–(21)] also plotted (dashed lines).

$$r_\kappa \simeq r_0\left(\frac{\sigma_1^2}{\sigma_0^2}+\frac{1}{\sqrt{i\omega\tau}}\left(\frac{\mu_1}{\sigma_0}+\frac{\sigma_1^2}{\sigma_0^2}\frac{(v_{\rm th}-\mu_0)}{\sigma_0}\right)\right) \quad (21)$$

and show distinct scaling to shot noise ($1/\sqrt{i\omega\tau}$ versus $1/i\omega\tau$). It can be noted that the diffusion approximation does not distinguish between modulated excitation or inhibition at high frequencies: its prediction of a constant response to modulated inhibitory rates is qualitatively different to the shot-noise result [Eq. (20) and Fig. 2(c)].

Discussion.—The results derived above, for the leaky integrate-and-fire model receiving additive shot noise, demonstrate a rich dynamics that is not always well captured by the diffusion approximation. Though not solvable by Laplace transforms, the framework developed here can be generalized to include synaptic reversal potentials ϵ_e, ϵ_i. The additive synaptic terms in Eq. (1) are now replaced by $(\epsilon_e - v)\sum c_{ek}\delta(t-t_{ek})$ and similarly for inhibition. Interpreting multiplicative noise in the Stratonovich sense gives excitatory voltage jumps from w to v of size $(\epsilon_e - w)b$ where $b = (1-e^{-c})$ so that $0 \le b \le 1$. An amplitude distribution $B_e(b)$ is sought to reduce the synaptic flux

$$J_e(v) = R_e\int_{-\infty}^{v} dwP(w)\int_{(v-w)/(\epsilon_e-w)}^{1} dbB_e(b) \quad (22)$$

to a first-order differential equation. On differentiating Eq. (22) with respect to voltage and comparing the integral term containing $B_e(b)$ with that originally in Eq. (22) it is seen that if $(1-b)B_e(b) \propto \int_b^1 db' B_e(b')$ then the excitatory flux satisfies

$$\frac{\partial J_e}{\partial v}+\frac{\beta_e J_e}{\epsilon_e - v} = R_e P - r(t)\delta(v - v_{\rm th}). \quad (23)$$

The amplitude distribution is $B_e = \beta_e(1-b)^{\beta_e - 1}$ with the parameter β_e related to the typical synaptic amplitude at rest $a_e = \epsilon_e b_e$ via $\beta_e = 1/b_e - 1$. It can be noted that because $a_e/\epsilon_e \ll 1$ the distribution B_e is close to exponential (and similarly for inhibition). Hence, the amplitude distribution for which the multiplicative shot-noise integro-differential system reduces to a system of differential equations is experimentally justifiable. Together with inhibition, the resulting equations can be solved numerically by threshold integration [15,16]. However, the argument used for Eq. (16) is general and so the high-frequency limits for additive and multiplicative shot noise are the same. The combination of a more realistic exponential integrate-and-fire spike mechanism [20] that captures spike initiation in neocortical neurons [10] with synaptic shot noise is likely to have a more significant effect on the high-frequency response than synaptic conductance.

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