LETTER — **Communicated by Peter Thomas**

Comment on "Characterization of Subthreshold Voltage Fluctuations in Neuronal Membranes," by M. Rudolph and A. Destexhe

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In two recent articles, Rudolph and Destexhe (2003, 2005) studied a leaky integrator model (an RC-circuit) driven by correlated ("colored") gaussian conductance noise and Gaussian current noise. In the first article, they derived an expression for the stationary probability density of the membrane voltage; in the second, they modified this expression to cover a larger parameter regime. Here we show by standard analysis of solvable limit cases (white noise limit of additive and multiplicative noise sources; only slow multiplicative noise; only additive noise) and by numerical simulations that their first result does not hold for the general colored-noise case and uncover the errors made in the derivation of a Fokker-Planck equation for the probability density. Furthermore, we demonstrate analytically (including an exact integral expression for the time-dependent mean value of the voltage) and by comparison to simulation results that the extended expression for the probability density works much better but still does not exactly solve the full colored-noise problem. We also show that at stronger synaptic input, the stationary mean value of the linear voltage model may diverge and give an exact condition relating the system parameters for which this takes place.

1 Introduction

The inherent randomness of neural spiking has stimulated the exploration of stochastic neuron models for several decades (Holden, 1976; Tuckwell, 1988, 1989). The subthreshold membrane voltage of cortical neurons shows strong fluctuations in vivo caused mainly by synaptic stimuli coming from as many as tens of thousands of presynaptic neurons. In the theoretical literature, these stimuli have been approximated in different ways. The most biophysically realistic description is to model an extended neuron with different sorts of synapses distributed over the dendrite and possibly the soma, with each synapse following its own kinetics when excited by random incoming pulses that change the local conductance. In a point-neuron model for the membrane potential in the spike generating zone, this amounts to an effective conductance noise for each sort of synapse. If the contribution of a single spike is small and the effective input rates are high, the incoming spike trains can be well approximated by gaussian white noise; this is known as the diffusion approximation of spike train input (see, e.g., Holden, 1976). Furthermore, these conductance fluctuations driving the membrane voltage dynamics will be correlated in time (the noise will be "colored") due to the synaptic filtering (Brunel & Sergi, 1998). Assuming the validity of the diffusion approximation, two further common approximations found in the theoretical literature are to (1) replace the conductance noise by a current noise and (2) neglect the correlation of the noise and use a white noise. Exploring the validity of these approximations has been the aim of a number of recent theory articles (Rudolph & Destexhe, 2003, 2005; Richardson, 2004; Richardson & Gerstner, 2005).

Rudolph and Destexhe (hereafter referred to as R&D) recently studied the subthreshold voltage dynamics driven by colored gaussian conductance and current noises, with the goal of deriving analytical expressions for the probability density of the voltage fluctuations in the absence of a spike-generating mechanism. Such expressions are desirable because they permit one to use experimentally measured voltage traces in vivo to determine (or at least to obtain constraints on) synaptic parameters. R&D gave a one-dimensional Fokker-Planck equation for the evolution of the probability density of the voltage variable and solved this equation in the stationary state. Comparing this solution to results of numerical simulations they found good agreement with simulations of the full model. In a recent article, however, they discovered a disagreement of their formula to simulations in extreme parameter regimes (Rudolph & Destexhe, 2005). R&D proposed an extended expression that is functionally equivalent to their original formula; it results from effective correlation times that were introduced into their original formula in a heuristic manner. According to R&D, this new expression fits simulation results well for various parameter sets.

In this comment we show that both proposed formulas are not exact solutions of the mathematical problem that R&D posed. We demonstrate this by the analysis of limit cases by means of an exact analytical result for the mean value of the voltage as well as by numerical simulation results. The failure of the first formula is pronounced; for example, it fails dramatically if the synaptic correlation times are varied by only one order of magnitude relative to R&D's standard parameters. The extended expression, although not an exact solution of the problem, seems to provide a reasonable approximation for the probability density of the membrane voltage if the conductance noise is not too strong. We also show that if the conductance noise is strong, the model itself and not only the solutions proposed by R&D becomes problematic: the moments of the voltage, such as its stationary mean value, diverge. For the mean value we will give an exact solution and identify by means of this solution the parameters for which a divergence is observed.

This letter is organized as follows. In the next section, we introduce the model that R&D studied. Then we study the limit cases of only white noise (section 3), of only additive colored noise (section 4), and of slow ("static") multiplicative noise (section 5). In section 6 we derive expressions for the time-dependent and the stationary mean value of the voltage at arbitrary values of the correlation times. Section 7 is devoted to a comparison of numerical simulations to the various theoretical formulas. We summarize and discuss our findings in section 8. In the appendix, we uncover the errors in the derivation of the Fokker-Planck equation that R&D made. We anticipate that our results will help future investigations of the neural colored noise problem.

2 Basic Model

The current balance equation for a patch of passive membrane is

$$C_m \frac{dV(t)}{dt} = -g_L(V(t) - E_L) - \frac{1}{a} I_{syn}(t), \tag{2.1}$$

where C_m is the specific membrane capacity, a is the membrane area, and g_L and E_L the leak conductance and reversal potential, respectively. The total synaptic current is given by

$$I_{syn} = g_e(t)(V(t) - E_e) + g_i(t)(V(t) - E_i) - I(t), \tag{2.2}$$

with $g_{e,i}$ being the noisy conductances for excitatory and inhibitory synapses and $E_{e,i}$ the respective reversal potentials; $I(t)$ is an additional noisy current. With respect to the conductances, R&D assume the diffusion approximation to be valid. This means approximating the superposition of incoming presynaptic spikes at the excitatory and inhibitory synapses by gaussian white noise. Including a first-order linear synaptic filter, the conductances are consequently described by Ornstein-Uhlenbeck processes (OUP); similarly, R&D also assume a OUP for the current $I(t)$

$$\frac{dg_e(t)}{dt} = -\frac{1}{\tau_e}(g_e(t) - g_{e0}) + \sqrt{\frac{2\sigma_e^2}{\tau_e}}\xi_e(t) \tag{2.3}$$

$$\frac{dg_i(t)}{dt} = -\frac{1}{\tau_i}(g_i(t) - g_{i0}) + \sqrt{\frac{2\sigma_i^2}{\tau_i}}\xi_i(t) \tag{2.4}$$

$$\frac{dI(t)}{dt} = -\frac{1}{\tau_I}(I(t) - I_0) + \sqrt{\frac{2\sigma_I^2}{\tau_I}}\xi_I(t). \tag{2.5}$$

Here the functions $\xi_{e,i,I}(t)$ are independent gaussian white noise sources with $\langle \xi_k(t)\xi_l(t')\rangle = \delta_{k,l}\delta(t-t')$ (here $k, l \in \{e, i, I\}$, and the brackets $\langle \cdots \rangle$ stand for a stationary ensemble average). The processes g_e, g_i, and I are gaussian distributed around the mean values g_{e0}, g_{i0}, and I_0 with variances σ_e^2, σ_i^2, and σ_I^2, respectively:

$$\rho_e(g_e) = \frac{1}{\sqrt{2\pi\sigma_e^2}} \exp\left[-(g_e - g_{e0})^2/(2\sigma_e^2)\right] \tag{2.6}$$

$$\rho_i(g_i) = \frac{1}{\sqrt{2\pi\sigma_i^2}} \exp\left[-(g_i - g_{i0})^2/(2\sigma_i^2)\right] \tag{2.7}$$

$$\rho_I(I) = \frac{1}{\sqrt{2\pi\sigma_I^2}} \exp\left[-(I - I_0)^2/(2\sigma_I^2)\right]. \tag{2.8}$$

As discussed by R&D, these solutions permit unphysical negative conductances, which become especially important if g_{e0}/σ_e and g_{i0}/σ_i are small.

Furthermore, the three processes are exponentially correlated with the correlation times given by τ_e, τ_i, and τ_I, respectively

$$\left\langle (g_e(t) - g_{e0})\,(g_e(t+\tau) - g_{e0})\right\rangle = \sigma_e^2 \exp[-|\tau|/\tau_e] \tag{2.9}$$

$$\left\langle (g_i(t) - g_{i0})\,(g_i(t+\tau) - g_{i0})\right\rangle = \sigma_i^2 \exp[-|\tau|/\tau_i] \tag{2.10}$$

$$\left\langle (I(t) - I_0)\,(I(t+\tau) - I_0)\right\rangle = \sigma_I^2 \exp[-|\tau|/\tau_I]. \tag{2.11}$$

Note that R&D used another parameter to quantify the strength of the noise processes: $D_{\{e,i,I\}} = 2\sigma_{e,i,I}^2/\tau_{e,i,I}$. Here we will not follow this unusual scaling[1] but consider variations of the correlation times at either fixed variance $\sigma_{e,i,I}^2$ of the OUPs or fixed noise intensities $\sigma_{e,i,I}^2\tau_{e,i,I}$.

Eq. (1) can be looked upon as a one-dimensional dynamics driven by multiplicative and additive colored noises. Equivalently, it can be, together

[1] In general, two different intensity scalings for an OUP $\eta(t)$ are used in the literature see, e.g., Hänggi & Jung, 1995). (1) Fixing the noise intensity $Q = \int_0^\infty dT\langle \eta(t)\eta(t+T)\rangle = \sigma^2\tau$, allowing for a proper white noise limit by letting τ approach zero. With fixed noise intensity and $\tau \to \infty$ (static limit), the effect of the OUP vanishes, since the variance of the process tends to zero. (2) Fixing the noise variance σ^2, which leads to a finite effect of the noise for $\tau \to \infty$ (static limit) but makes the noise effect vanish as $\tau \to 0$. R&D use functions $\alpha_{\{e,i,I\}}(t)$, the long-time limit of which is proportional to the noise intensity $\sigma_{e,i,I}^2\tau_{e,i,I}$.

with equations 2.3, 2.4, and 2.5, regarded as a four-dimensional nonlinear dynamical system driven by only additive white noise. For such a process it is in general quite difficult to calculate the statistics, such as the stationary probability density $P_0(V, g_e, g_i, I)$ or the stationary marginal density for the driven variable $\rho(V) = \int\int\int dg_e dg_i dI\, P_0(V, g_e, g_i, I)$ unless so-called potential conditions are met (see, e.g., Risken, 1984). It can be easily shown that the above problem does not fulfill these potential conditions, and no solution has yet been found.

R&D have proposed a solution for the stationary marginal density of the membrane voltage $\rho(V)$ for colored noises of arbitrary correlation times driving their system. Their solution for the stationary probability of the membrane voltage reads

$$\rho_{RD}(V) = N \exp\left[\frac{a_1}{2b_2}\ln\left(b_2 V^2 + b_1 V + b_0\right) + \frac{2b_2 a_0 - a_1 b_1}{b_2\sqrt{4b_2 b_0 - b_1^2}} \arctan\left(\frac{2b_2 V + b_1}{\sqrt{4b_2 b_0 - b_1^2}}\right)\right], \tag{2.12}$$

with N being the normalization constant and with these abbreviations:

$$a_0 = \frac{1}{(C_m a)^2}\left(2C_m a(g_L E_L a + g_{e0} E_e + g_{i0} E_i) + I_0 C_m a + \sigma_e^2 \tau_e E_e + \sigma_i^2 \tau_i E_i\right)$$
$$a_1 = -\frac{1}{(C_m a)^2}\left(2C_m a(g_L a + g_{e0} + g_{i0}) + \sigma_e^2 \tau_e + \sigma_i^2 \tau_i\right)$$
$$b_0 = \frac{1}{(C_m a)^2}\left(\sigma_e^2 \tau_e E_e^2 + \sigma_i^2 \tau_i E_i^2 + \sigma_I^2 \tau_I\right)$$
$$b_1 = -\frac{2}{(C_m a)^2}\left(\sigma_e^2 \tau_e E_e + \sigma_i^2 \tau_i E_i\right)$$
$$b_2 = \frac{1}{(C_m a)^2}\left(\sigma_e^2 \tau_e + \sigma_i^2 \tau_i\right). \tag{2.13}$$

In a subsequent Note on their article, Rudolph and Destexhe (2005) considered the case of only multiplicative colored noise ($\sigma_I = 0$) and showed that the solution in equation 2.12 does not fit numerical simulations for certain parameter regimes. They claim that this disagreement is due to a filtering problem not properly taken into account in their previous work. They proposed a new solution for the case of only multiplicative noise that is functionally equivalent to equation 2.12 for $\sigma_I = 0$ but simply replaces correlation times by effective correlation times,

$$\tau'_{e,i} = \frac{2\tau_{e,i}\tau_0}{\tau_e + \tau_0}. \tag{2.14}$$

where $\tau_0 = aC_m/(ag_L + g_{e0} + g_{i0})$. Explicitly, this extended expression is given by

$$\rho_{RD,ext}(V) = N' \exp\left[A_1 \ln\left(\frac{\sigma_e^2 \tau'_e}{(C_m a)^2}(V - E_e)^2 + \frac{\sigma_i^2 \tau'_i}{(C_m a)^2}(V - E_i)^2 \right) + A_2 \arctan\left(\frac{\sigma_e^2 \tau'_e (V - E_e) + \sigma_i^2 \tau'_i (V - E_i)}{(E_e - E_i)\sqrt{\sigma_e^2 \tau'_e \sigma_i^2 \tau'_i}} \right) \right] \tag{2.15}$$

with the abbreviations

$$A_1 = -\frac{2C_m a(g_{e0} + g_{i0}) + 2C_m a^2 g_L + \sigma_e^2 \tau'_e + \sigma_i^2 \tau'_i}{2\left(\sigma_e^2 \tau'_e + \sigma_i^2 \tau'_i\right)} \tag{2.16}$$

$$A_2 = \frac{g_L a\left(\sigma_e^2 \tau'_e (E_L - E_e) + \sigma_i^2 \tau'_i (E_L - E_i)\right) + \left(g_{e0}\sigma_i^2 \tau'_i - g_{i0}\sigma_e^2 \tau'_e\right)(E_e - E_i)}{(E_e - E_i)\sqrt{\sigma_e^2 \tau'_e \sigma_i^2 \tau'_i}\left(\sigma_e^2 \tau'_e + \sigma_i^2 \tau'_i\right)/(2C_m a)}. \tag{2.17}$$

The introduction of the effective correlation times was justified by considering the effective-time constant (ETC) or gaussian approximation from Richardson (2004) (see below), which reduces the system to one with additive noise. The new formula, equation 2.15, fits well their simulation results for various combinations of parameters (Rudolph & Destexhe, 2005).

In this comment, we will show that neither of these formulas yields the exact solution of the mathematical problem. As we will show first, the original formula fails significantly outside the limited parameter range investigated in R&D (2003). Apparently the second formula provides a good fit for a number of parameter sets. It also reproduces two of the simple limit cases, in which the first formula fails. By means of the third limit case as well as of an exact solution for the stationary mean value (derived in section 6), we can show that the new formula is not an exact result either.

To demonstrate the invalidity of the first expression in the general case, we will show that equation 2.12 fails in three limits that are tractable by standard techniques: (1) the white noise limit of all three colored noise sources, that is, keeping the noise intensities $\sigma_{e,i,I}^2 \tau_{e,i,I}$ fixed and letting all noise correlation times tend to zero $\tau_{e,i} \to 0$; (2) the case of additive colored noise only; and (3) the limit of large $\tau_{e,i}$ in the case of multiplicative colored noises with fixed variances σ_e^2 and σ_i^2. In all cases, we also ask whether mean and variance can be expected to be finite as R&D tacitly assumed.

We will also compare both solutions proposed by R&D as well as our own analytical results for the limit cases to numerical simulation results. While the failure of the first formula, equation 2.12, is pronounced except for a small parameter regime, deviations of the extended expression, equation 2.15, are much smaller and for six different parameter sets inspected, the new formula can be regarded at least as a good approximation. Parameters can be found, however, where deviations of this new formula from numerical simulations become more serious.

To simplify the notation we will use the new variable $v = V - \Delta$ with

$$\Delta = \frac{g_L a E_L + g_{e0} E_e + g_{i0} E_i + I_0}{g_L a + g_{e0} + g_{i0}}. \tag{2.18}$$

Then the equations can be recast into

$$\dot{v} = -\beta v - y_e(v - V_e) - y_i(v - V_i) + y_I \tag{2.19}$$

$$\dot{y}_{e,i,I} = -\frac{y_{e,i,I}}{\tau_{e,i,I}} + \sqrt{\frac{2\tilde{\sigma}^2_{e,i,I}}{\tau_{e,i,I}}}\xi_{e,i,I}(t) \tag{2.20}$$

with the abbreviations

$$\beta = \frac{g_L a + g_{e0} + g_{i0}}{a C_m} \tag{2.21}$$

$$V_{e,i} = E_{e,i} - \Delta \tag{2.22}$$

$$\tilde{\sigma}_{e,i,I} = \sigma_{e,i,I}/(a C_m). \tag{2.23}$$

Once we have found an expression for the probability density of v, the density for the original variable V is given by the former density taken at $v = (V - \Delta)$. Finally, we briefly explain the effective-time constant (ETC) or gaussian approximation (cf. Richardson, 2004; Richardson & Gerstner, 2005, and references there), which we will refer to later. Assuming weak noise sources, the voltage will fluctuate around the deterministic equilibrium value $v = 0$ with an amplitude proportional to the square root of the sum of the noise variances; for example, for only excitatory conductance fluctuations we would have a proportionality to the standard deviation of y_e, that is, $\langle |v| \rangle \propto \sqrt{\langle y_e^2 \rangle}$. From this we can see that the multiplicative terms $y_e V$ and $y_I V$ make a contribution proportional to the squares of the standard deviations and can therefore be neglected for weak noise. The resulting dynamics contains only additive noise sources:

$$\dot{v} = -\beta v + y_e V_e + y_i V_i + y_I. \tag{2.24}$$

The stationary probability density is a gaussian,

$$\rho_{ETC}(v) = \frac{\exp\left[-v^2/\left(2\langle v^2\rangle_{ETC}\right)\right]}{\sqrt{2\pi\langle v^2\rangle_{ETC}}} \tag{2.25}$$

with zero mean and a variance given by Richardson (2004):

$$\langle v^2\rangle_{ETC} = V_e^2\frac{\sigma_e^2\tau_e/\beta}{1+\beta\tau_e} + V_i^2\frac{\sigma_i^2\tau_i/\beta}{1+\beta\tau_i} + \frac{\sigma_I^2\tau_I/\beta}{1+\beta\tau_I}. \tag{2.26}$$

The solution takes into account the effect of the mean conductances on the effective membrane time constant $1/\beta$ through equation 2.21.

3 The White Noise Limit

If we fix the noise intensities

$$Q_{e,i,I} = \tilde{\sigma}_{e,i,I}^2\tau_{e,i,I}, \tag{3.1}$$

we may consider the limit of white noise by letting $\tau_{e,i,I} \to 0$. A special case of this has been recently considered by Richardson (2004) with $\sigma_I = 0$ (only multiplicative noise is present).

In the white noise limit, the three OUPs approach mutually independent white noise sources,

$$y_e \to \sqrt{2Q_e}\xi_e(t), \quad y_i \to \sqrt{2Q_i}\xi_i(t), \quad y_I \to \sqrt{2Q_I}\xi_I(t), \tag{3.2}$$

and thus the current balance equation, equation 2.19, becomes

$$\dot{v} = -\beta v - \sqrt{2Q_e}(v-V_e)\xi_e(t) - \sqrt{2Q_i}(v-V_i)\xi_i(t) + \sqrt{2Q_I}\xi_I(t), \tag{3.3}$$

which is equivalent[2] to a driving by a single gaussian noise $\xi(t)$,

$$\dot{v} = -\beta v + \sqrt{2Q_e(v-V_e)^2 + 2Q_i(v-V_i)^2 + 2Q_I}\,\xi(t), \tag{3.4}$$

with $\langle\xi(t)\xi(t')\rangle = \delta(t-t')$. Since we approach the white noise limit having in mind colored noises with negligible correlation times, equation 3.4 has to be interpreted in the sense of Stratonovich (Risken, 1984; Gardiner, 1985).

[2] The sum of three independent gaussian noise sources gives one gaussian noise, the variance of which equals the sum of the variances of the single noise sources.

The drift and diffusion coefficients then read (Risken, 1984)

$$D^{(1)} = -\beta v + Q_e(v - V_e) + Q_i(v - V_i) = -\beta v + \frac{1}{2}\frac{dD^{(2)}}{dv} \tag{3.5}$$

$$D^{(2)} = Q_I + Q_e(v - V_e)^2 + Q_i(v - V_i)^2, \tag{3.6}$$

and the stationary solution of the probability density is given by Risken (1984),

$$\rho_{wn}(v) = N \exp\left[-\ln\left(D^{(2)}\right) + \int^{v} dx \frac{D^{(1)(x)}}{D^{(2)(x)}}\right], \tag{3.7}$$

where the subscript *wn* refers to white noise.

After carrying out the integral, the solution can be written as follows,

$$\rho_{wn}(v) = N \exp\left[-\frac{\beta + \tilde{b}_2}{2\tilde{b}_2} \ln\left(\tilde{b}_2 v^2 + \tilde{b}_1 v + \tilde{b}_0\right) + \frac{\beta \tilde{b}_1}{\tilde{b}_2\sqrt{4\tilde{b}_0\tilde{b}_2 - \tilde{b}_1^2}} \arctan\left(\frac{2\tilde{b}_2 v + \tilde{b}_1}{\sqrt{4\tilde{b}_0\tilde{b}_2 - \tilde{b}_1^2}}\right)\right] \tag{3.8}$$

with these abbreviations:

$$\tilde{b}_0 = Q_I + Q_e V_e^2 + Q_i V_i^2 \tag{3.9}$$

$$\tilde{b}_1 = -2(Q_e V_e + Q_i V_i) \tag{3.10}$$

$$\tilde{b}_2 = Q_e + Q_i. \tag{3.11}$$

Different versions of the white noise case have been discussed and also analytically studied in the literature (see, e.g., Hanson & Tuckwell, 1983; Lánský & Lánská, 1987; Lánská, Lánský, & Smith, 1994; Richardson, 2004). In particular, equation 3.8 is consistent with the expression for the voltage density in a leaky integrate-and-fire neuron driven by white noise[3] given by Richardson, (2004).

Since equation 2.12 was proposed by R&D as the solution for the probability density at arbitrary correlation times of the colored noise sources, it should be also valid in the white noise limit and agree with equation 3.8. On closer inspection, it becomes apparent that both equations 2.12 and 2.15

[3] The density equation 3.8 results from equation 2.18, in Richardson (2004) when firing and reset in the integrate-and-fire neuron become negligible. This can be formally achieved by letting threshold and reset voltage go to positive infinity.

have the structure of the white noise solution, equation 3.8. Comparing the factors of the terms in the exponential, we find that the first solution (in terms of the shifted voltage variable and using the noise intensities, equation 3.1) can be written as

$$\rho_{RD}(v, Q_e, Q_i, Q_I) = \rho_{wn}(v, Q_e/2, Q_i/2, Q_I/2), \tag{3.12}$$

where the additional arguments of the functions indicate the parametric dependence of the densities on the noise intensities. According to equation 3.12, if formulated in terms of the noise intensities (and not the noise variances), the first formula proposed by R&D does not depend on the correlation times $\tau_{e,i,I}$ at all. Furthermore, it is evident from equation 3.12 that the expression is incorrect in the white noise limit. If all correlation times $\tau_{e,i,I}$ simultaneously go to zero, the density approaches the white noise solution with only half of the true values of the noise intensities. The density will certainly depend on the noise intensities and will change if one uses only half of their values.

We may also rewrite R&D’s extended expression, equation 2.15, in terms of the white noise density:

$$\rho_{RD,ext}(v, Q_e, Q_i) = \rho_{wn}(v, Q_e/(1+\beta\tau_e), Q_i/(1+\beta\tau_i), Q_I = 0). \tag{3.13}$$

This expression agrees with the original solution by R&D only for the specific parameter set,

$$\tau_e = \tau_i = 1/\beta. \tag{3.14}$$

We note that since the extended expression can be expressed by means of the white noise density, it makes sense to describe the extended expression by means of effective noise intensities,

$$Q'_{e,i} = \frac{Q_{e,i}}{1+\beta\tau_{e,i}} \tag{3.15}$$

rather than in terms of the effective correlation times $\tau'_{e,i}$ (cf. equation 2.14) used by R&D. The assertion behind equation 3.13 is the following: the probability density of the membrane voltage is always equivalent to the white noise density; correlations in the synaptic input (i.e., finite values of $\tau_{e,i,I}$) lead to rescaled (smaller) noise intensities $Q'_{e,i}$ given in equation 3.15.

If we consider the white noise limit of the right-hand side of equation 3.13, we find that the extended expression equation 2.15 reproduces this limit:

$$\lim_{\tau_e, \tau_i \to 0} \rho_{RD,ext}(V, Q_e, Q_i) = \rho_{wn}(V, Q_e, Q_i, Q_I = 0). \tag{3.16}$$

So there is no problem with the extended expression in the white noise limit.

3.1 Divergence of Moments in the White Noise Limit and in R&D's Expressions for the Probability Density. We consider the density equation 3.8 in the limits $v \to \pm\infty$ and conclude whether the moments and, in particular, the mean value of the white noise density are finite; similar arguments will be applied to the solutions proposed by R&D.

At large v and to leading order in $1/v$, we obtain

$$\rho_{wn}(v) \sim |v|^{-\frac{\beta+\tilde{b}_2}{\tilde{b}_2}} N\tilde{b}_2^{-\frac{\beta+\tilde{b}_2}{2\tilde{b}_2}} \exp\left[\pm\frac{\beta\tilde{b}_1}{\tilde{b}_2\sqrt{4\tilde{b}_0\tilde{b}_2-\tilde{b}_1^2}}\frac{\pi}{2}\right] \quad \text{as} \quad v \to \pm\infty. \tag{3.17}$$

When calculating the nth moment, we have to multiply with v^n and obtain a nondiverging integral only if $v^n\rho_{wn}(v)$ decays faster than v^{-1}. This is the case only if $n - (\beta + \tilde{b}_2)/\tilde{b}_2 < -1$ or using equation 3.11,

$$\left|\langle v^n\rangle_{wn}\right| < \infty \ \text{ iff } \ \beta > n(Q_e + Q_i), \tag{3.18}$$

where "iff" stands for "if and only if" and the index wn indicates that we consider the white noise case. Note that no symmetry argument applies for odd n since the asymptotic limits differ for ∞ and $-\infty$ according to equation 3.17. For the mean, this implies that

$$|\langle v\rangle_{wn}| < \infty \ \text{ iff } \ \beta > Q_e + Q_i; \tag{3.19}$$

otherwise, the integral diverges.

In general, the power law tail in the density is a hint that (for white noise at least) we face the problem of rare strong deviations in the voltage that are due to the specific properties of the model (multiplicative gaussian noise). Because of equation 3.12, similar conditions (differing by a prefactor of $1/2$ on the respective right-hand sides) also apply for the finiteness of the mean and variance of the original solution, equation 2.12, proposed by R&D. For the mean value of this solution one, obtains the condition

$$|\langle v\rangle_{RD}| < \infty \ \text{ iff } \ \beta > \frac{Q_e + Q_i}{2}, \tag{3.20}$$

which should hold true in the general colored noise case but does not agree with the condition in equation 3.19 even in the white noise case.

From the extended expression we obtain

$$|\langle v\rangle_{RD,ext}| < \infty \ \text{ iff } \ \beta > \frac{Q_e}{1+\beta\tau_e} + \frac{Q_i}{1+\beta\tau_i}. \tag{3.21}$$

Note that equation 3.21 agrees with equation 3.19 only in the white-noise case (i.e. for $\tau_e, \tau_i \to 0$). Below we will show that equation 3.19 gives the correct condition for a finite mean value in the general case of arbitrary correlation times, too. Since for finite τ_e, τ_i, the two conditions equation 3.19 and equation 3.21 differ, we can already conclude that the equation 2.15 that led to condition equation 3.21 cannot be the exact solution of the original problem.

4 Additive Colored Noise

Setting the multiplicative colored noise sources to zero, R&D obtain an expression for the marginal density in case of additive colored noise only (cf. equations 3.7–3.9 in R&D)

$$\rho_{add,RD}(V) = N\exp\left[-\frac{a^2 g_L C_m (V - E_L - I_0/(g_L a))^2}{\sigma_I^2 \tau_I}\right], \tag{4.1}$$

which corresponds in our notation and in terms of the shifted variable v to

$$\tilde{\rho}_{add,RD}(v) = N\exp\left[-\frac{\beta v^2}{Q_I}\right]. \tag{4.2}$$

Evidently, once more a factor 2 is missing in the white noise case (where the process $v(t)$ itself becomes an OUP), since for an OUP, we should have $\rho \sim \exp[-\beta v^2/(2Q_I)]$. However, there is also a missing additional dependence on the correlation time.

For additive noise only, the original problem given in equation 2.1 reduces to

$$\dot{v} = -\beta v + y_I, \tag{4.3}$$

$$\dot{y}_I = -\frac{1}{\tau_I} y_I + \frac{\sqrt{2Q_I}}{\tau_I}\xi_I(t). \tag{4.4}$$

This system is mathematically similar to the gaussian approximation or effective-time constant approximation, equation 2.25, in which no multiplicative noise is present as well. The density function for the voltage is well known; for clarity, we show here how to calculate it.

The system, equations 4.3 and 4.4, obeys the two-dimensional Fokker-Planck equation,

$$\partial_t P(v, y_I, t) = \left[\partial_v(\beta v - y_I) + \partial_{y_I}\left(\frac{y_I}{\tau_I} + \frac{Q_I}{\tau_I^2}\partial_{y_I}\right)\right]P(v, y_I, t) \tag{4.5}$$

The stationary problem ($\partial_t P_0(v, y_I) = 0$) is solved by an ansatz $P_0(v, y) \sim \exp[Av^2 + Bvy + Cy^2]$, yielding the solution for the full probability density:

$$P_0(v, y_I) = N \exp\left[\frac{c}{2}\left(y_I^2 - 2\beta v y_I - \frac{Q_I \beta}{\tau_I^2} c v^2\right)\right], \quad c = -\frac{\tau_I(1 + \beta\tau_I)}{Q_I}. \tag{4.6}$$

Integrating over y_I yields the correct marginal density,

$$\rho_{add}(v) = \sqrt{\frac{\beta(1 + \beta\tau_I)}{2\pi Q_I}} \exp\left[-\frac{\beta v^2}{2Q_I}(1 + \beta\tau_I)\right], \tag{4.7}$$

which is in disagreement with equation 4.2 and hence also with equation 4.1. From the correct solution given in equation 4.7, we also see what happens in the limit of infinite τ for fixed noise intensity Q_I: the exponent tends to minus infinity except at $v = 0$, or, put differently, the variance of the distribution tends to zero, and we end up with a δ function at $v = 0$. This limit makes sense (cf. note 1) but is not reflected at all in the original solution, equation 2.15, given by R&D.

We can also rewrite the solution in terms of the white noise solution in the case of vanishing multiplicative noise:

$$\rho_{add}(v) = \rho_{wn}(v, Q_e = 0, Q_i = 0, Q_I/[1 + \beta\tau_I]). \tag{4.8}$$

Thus, for the additive noise is true, what has been assumed by R&D in the case of multiplicative noise: the density in the general colored noise case is given by the white noise density with a rescaled noise intensity $Q_I' = Q_I/[1 + \beta\tau_I]$ (or equivalently, rescaled correlation time $\tau_I' = 2\tau_I/[1 + \beta\tau_I]$ in equation 4.2 with $Q_I = \sigma^2\tau_I'$).

We cannot perform the limit of only additive noise in the extended expression, equation 2.15, proposed by R&D because this solution was meant for the case of only multiplicative noise. If, however, we generalize that expression to the case of additive and multiplicative colored noises, we can consider the limit of only additive noise in this expression. This is done by taking the original solution by R&D, equation 2.12, and replacing not only the correlation times of the multiplicative noises $\tau_{e,i}$ by the effective ones $\tau'_{e,i}$ but also that of the additive noise τ_I by an effective correlation time,

$$\tau'_I = \frac{2\tau_I}{1 + \tau_I \beta}. \tag{4.9}$$

If we now take the limit $Q_e = Q_i = 0$, we obtain the correct density,

$$\rho_{rud,ext,add}(v) = \rho_{wn}(v, Q_e = 0, Q_i = 0, Q_I/[1 + \beta\tau_I]), \tag{4.10}$$

as becomes evident on comparing the right-hand sides of equation 4.10 and equation 4.8. Finally, we note that the case of additive noise is the only limit that does not pose any condition on the finiteness of the moments.

5 Static Multiplicative Noises Only (Limit of Large $\tau_{e,i}$)

Here we assume for simplicity $\tilde{\sigma}_I = 0$ and consider multiplicative noise with fixed variances $\tilde{\sigma}^2_{e,i}$ only. If the noise sources are much slower than the internal timescale of the system, that is, if $1/(\beta\tau_e)$ and $1/(\beta\tau_i)$ are practically zero, we can neglect the time derivative in equation 2.19. This means that the voltage adapts instantaneously to the multiplicative ("static") noise sources which is strictly justified only for $\beta\tau_e, \beta\tau_i \to \infty$. If τ_e, τ_i attain large but finite values ($\beta\tau_i, \beta\tau_i \gg 1$), the formula derived below will be an approximation that works the better the larger these values are. Because of the slowness of the noise sources compared to the internal timescale, we call the resulting expression the "static-noise" theory for simplicity. This *does not* imply that the total system (membrane voltage plus noise sources) is not in the stationary state: we assume that any initial condition of the variables has decayed on a timescale t much larger than $\tau_{e,i}$.[4] For a simulation of the density, this has the practical implication that we should choose a simulation time much larger than any of the involved correlation times.

Setting the time derivative in equation 2.19 to zero, we can determine at which position the voltage variable will be for a given quasi-static pair of (y_e, y_i) values, yielding

$$v = \frac{y_e V_E + y_i V_i}{\beta + y_e + y_i}. \tag{5.1}$$

[4] In the strict limit of $\beta\tau_e, \beta\tau_i \to \infty$, this would imply that t goes stronger to infinity than the correlation times $\tau_{e,i}$ do.

This sharp position will correspond to a δ peak of the probability density

$$\delta\left(v - \frac{y_e V_E + y_i V_i}{\beta + y_e + y_i}\right) = \frac{|y_i(V_i - V_e) - \beta V_e|}{(v - V_e)^2}\delta\left(y_e + \frac{\beta v + y_i(v - V_i)}{(v - V_e)}\right) \tag{5.2}$$

(here we have used $\delta(ax) = \delta(x)/|a|$). This peak has to be averaged over all possible values of the noise, that is, integrated over the two gaussian distributions in order to obtain the marginal density:

$$\begin{aligned}\rho_{static}(v) &= \langle \delta(v - v(t)) \rangle \\ &= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \frac{dy_e dy_i}{2\pi\tilde{\sigma}_i\tilde{\sigma}_e}\frac{|y_i(V_i - V_e) - \beta V_e|}{(v - V_e)^2}\delta\left(y_e + \frac{\beta v + y_i(v - V_i)}{(v - V_e)}\right) \\ &\quad \times \exp\left[-\frac{y_e^2}{2\tilde{\sigma}_e^2} - \frac{y_i^2}{2\tilde{\sigma}_i^2}\right] \end{aligned} \tag{5.3}$$

Carrying out these integrals yields

$$\rho_{static}(v) = \frac{\tilde{\sigma}_e\tilde{\sigma}_i|V_e - V_i|}{\pi\beta^2\mu(v)}e^{-\frac{v^2}{2\mu(v)}}\left[e^{-\frac{\nu(v)}{\mu(v)}} + \sqrt{\frac{\pi\,\nu(v)}{\mu(v)}}\mathrm{erf}\left(\sqrt{\frac{\nu(v)}{\mu(v)}}\right)\right], \tag{5.4}$$

where erf(z) is the error function (Abramowitz & Stegun, 1970) and the functions $\mu(v)$ and $\nu(v)$ are given by

$$\mu(v) = \frac{\tilde{\sigma}_e^2(v - V_e)^2 + \tilde{\sigma}_i^2(v - V_i)^2}{\beta^2} \tag{5.5}$$

$$\nu(v) = \frac{\left[\tilde{\sigma}_e^2 V_e(v - V_e) + \tilde{\sigma}_i^2 V_i(v - V_i)\right]^2}{2\tilde{\sigma}_e^2\tilde{\sigma}_i^2(V_e - V_i)^2}. \tag{5.6}$$

If one of the expressions by R&D, equation 2.12 or 2.15, would be the correct solution, it should converge for $\sigma_I = 0$ and $\tau_{e,i} \to \infty$ to the formula for the static case, equation 5.4. In general, this is not the case since the functional structures of the white-noise solution and of the static-noise approximation are quite different. There is, however, one limit case in which the extended expression yields the same (although trivial) function. If we fix the noise intensities $Q_{e,i}$ and let the correlation times go to infinity, the variances will go to zero and the static noise density, equation 5.4, approaches a δ peak at $v = 0$. Although the extended expression, equation 2.15, has a different functional dependence on system parameters and voltage, the same thing happens in the extended expression for $\tau_{e,i} \to \infty$ because the effective noise intensities $Q'_{e,i} = Q_{e,i}/(1 + \beta\tau_{e,i})$ approach zero in this limit. The white noise solution at vanishing noise intensities is, however, also a δ peak at $v = 0$. Hence, in the limit of large correlation time at fixed noise intensities, both the static noise theory, equation 5.4, and the extended expression yield the probability density of a noise-free system and therefore agree. For fixed variance where a nontrivial large-τ limit of the probability density exists, the static noise theory and the extended expression by R&D differ as we will also numerically verify.

A final remark concerns the asymptotic behavior of the static noise solution, equation 5.4. The asymptotic expansions for $v \to \pm\infty$ show that the density goes like $|v|^{-2}$ in both limits. Hence, in this case, we cannot obtain a finite variance of the membrane voltage at all (the integral $\int dv\ v^2 \rho_{static}(v)$ will diverge). The mean may be finite since the coefficients of the v^{-2} term are symmetric in v. The estimation in the following section, however, will demonstrate that this is valid only strictly in the limit $\tau_{e,i} \to \infty$ but not at any large but finite value of $\tau_{e,i}$. So the mean may diverge for large but finite $\tau_{e,i}$.

6 Mean Value of the Voltage for Arbitrary Values of the Correlation Times

By inspection of the limit cases, we have already seen that the moments do not have to be finite for an apparently sensible choice of parameters. For the white noise case, it was shown that the mean of the voltage is finite only if $\beta > Q_e + Q_i$.

Next, we show by direct analytical solution of the stochastic differential equation, equation 2.19, involving the colored noise sources, equation 2.20, that this condition (i.e., equation 3.19), holds in general, and thus a divergence of the mean is obtained for $\beta < Q_e + Q_i$.

For only one realization of the process, equation 2.19, the driving functions $y_e(t)$, $y_i(t)$, and $y_I(t)$ can be regarded as just time-dependent parameters in a linear differential equation. The solution is then straightforward (see also Richardson, 2004, for the special case of only multiplicative noise):

$$v(t) = v_0 \exp\left[-\beta t - \int_0^t du(y_e(u) + y_i(u))\right] + \int_0^t ds(V_e y_e(s) + V_i y_i(s) + y_I(s))e^{-\beta(t-s)} \exp\left[-\int_s^t du(y_e(u) + y_i(u))\right]. \tag{6.1}$$

The integrated noise processes $w_{e,i}(s,t) = \int_s^t du y_{e,i}(u)$ in the exponents are independent gaussian processes with variance

$$\langle w_{e,i}^2(s,t)\rangle = 2Q_{e,i}(t - s - \tau_{e,i} + \tau_{e,i} e^{-(t-s)/\tau_{e,i}}). \tag{6.2}$$

For a gaussian variable, we know that $\langle e^{w}\rangle = e^{\langle w^2\rangle/2}$ (Gardiner, 1985). Using this relation for the integrated noise processes together with equation 6.2 and expressing the average $\langle y_{e,i}(s)\exp[-\int_s^t du y_{e,i}(u)]\rangle$ by a derivative of the exponential with respect to s, we find an integral expression for the mean value

$$\langle v(t)\rangle = v_0 e^{(Q_e+Q_i-\beta)t}\exp\left[-\tau_e f_e(t) - \tau_i f_i(t)\right] - \int_0^t ds\{V_e f_e(s) + V_i f_i(s)\} e^{(Q_e+Q_i-\beta)s-\tau_e f_e(s)-\tau_i f_i(s)}, \tag{6.3}$$

where $f_{e,i}(s) = Q_{e,i}(1-\exp[-s/\tau_{e,i}])$. The stationary mean value corresponding to the stationary density is obtained from this expression in the asymptotic limit $t \to \infty$. We want to draw attention to the fact that this mean value is finite exactly for the same condition as for the white noise case—for

$$|\langle v\rangle| < \infty \;\text{ iff }\; \beta > Q_e + Q_i \tag{6.4}$$

First, this is so because otherwise the exponent $(Q_e + Q_i - \beta)t$ in the first line is positive and the exponential diverges for $t \to \infty$. Furthermore, if $\beta < Q_e + Q_i$, the exponential in the integrand diverges at large s.

In terms of the original parameters of R&D, the condition for a finite stationary mean value of the voltage reads

$$|\langle v\rangle| < \infty \;\text{ iff }\; g_L a + g_{e0} + g_{i0} > \frac{\sigma_e^2\tau_e + \sigma_i^2\tau_i}{aC_m} \tag{6.5}$$

Note that this depends also on a and C_m, and not only on the synaptic parameters. R&D use as standard parameter values (Rudolph & Destexhe, 2003, p. 2589) $g_{e0} = 0.0121$ μS, $g_{i0} = 0.0573$ μS, $\sigma_e = 0.012$ μS, $\sigma_i = 0.0264$ μS, $\tau_e = 2.728$ ms, $\tau_i = 10.49$ ms, $a = 34636$ μm^2, and $C_m = 1$ $\mu\text{F/cm}^2$. They state that the parameters have been varied in numerical simulations from 0% to 260% relative to these standard values covering more than "the physiological range observed in vivo" (Rudolph & Destexhe, 2003). Inserting the standard values into the relation, equation 6.5, yields

$$0.0851\mu\text{S} > 0.0221\,\mu\text{S}. \tag{6.6}$$

So in this case, the mean will be finite. However, using twice the standard value for the inhibitory noise standard deviation—$\sigma_i = 0.0528$ μS (corresponding to 200% of the standard value) and all other parameters as before, leads to a diverging mean because we obtain 0.0852 μS on the right-hand side of equation 6.5, while the left-hand side is unchanged. This means, even in the parameter regime that R&D studied, that the model predicts an infinite mean value of the voltage. A stronger violation of equation 6.5 will be observed by either increasing the standard deviations $\sigma_{e,i}$ and/or correlation times $\tau_{e,i}$ or decreasing the mean conductances $g_{e,i}$. We also note that for higher moments, and especially for the variance, the condition for finiteness will be even more restrictive, as can be concluded from the limit cases investigated before.

The stationary mean value at arbitrary correlation times can be inferred from equation 6.3 by taking the limit $t \to \infty$. Assuming the relation, equation 6.4, holds true, we can neglect the first term involving the initial condition v_0 and obtain

$$\langle v \rangle = -\int_0^\infty ds \{V_e f_e(s) + V_i f_i(s)\} \exp[(Q_e + Q_i - \beta)s - \tau_e f_e(s) - \tau_i f_i(s)]. \tag{6.7}$$

We can also use equation 6.7 to recover the white noise result for the mean as, for instance, found in Richardson (2004) by taking $\tau_{e,i} \to 0$. In this case, we can integrate equation 6.7 and obtain

$$\begin{aligned}\langle v \rangle_{wn} &= -\{V_e Q_e + V_i Q_i\} \int_0^\infty ds \exp[(Q_e + Q_i - \beta)s] \\ &= -\frac{V_e Q_e + V_i Q_i}{\beta - Q_e - Q_i}.\end{aligned} \tag{6.8}$$

Because of the similarity of the R&D solution to the white noise solution (cf. equation 3.12), we can also infer that the mean value of the former density is

$$\langle v \rangle_{RD} = -\frac{V_e Q_e + V_i Q_i}{2\beta - Q_e - Q_i}. \tag{6.9}$$

Note the different prefactor of β in the denominator, which is due to the factor 1/2 in noise intensities of the solution, equation 2.12, by R&D.

Finally, we can also determine easily the mean value for the extended expression by R&D (Rudolph & Destexhe, 2005) since this solution is also equivalent to the white noise solution with rescaled noise intensities. Using the noise intensities $Q'_{e,i}$ from equation 3.15, we obtain

$$\begin{aligned}\langle v \rangle_{RD,ext} &= -\frac{V_e Q'_e(\tau_e) + V_i Q'_i(\tau_i)}{\beta - Q'_e(\tau_e) - Q'_i(\tau_i)} \\ &= -\frac{V_e Q_e(1+\beta\tau_i) + V_i Q_i(1+\beta\tau_e)}{\beta(1+\beta\tau_i)(1+\beta\tau_e) - Q_e(1+\beta\tau_i) - Q_i(1+\beta\tau_e)}.\end{aligned} \tag{6.10}$$

We will verify numerically that this expression is not equal to the exact solution, equation 6.7. One can, however, show that for small to medium values of the correlation times $\tau_{e,i}$ and weak noise intensities, these differences are not drastic. If we expand both equation 6.3 and equation 6.10 for small noise intensities Q_e, Q_i (assuming for the former that the products $Q_e\tau_e$, $Q_i\tau_i$ are small, too), the resulting expressions agree to first order and also agree with a recently derived weak noise result for filtered Poissonian shot noise given by Richardson & Gerstner (2005, cf. eq. D.3):

$$\langle v\rangle_{RD,ext} \approx \langle v\rangle \approx -\frac{V_e Q_e(1+\beta\tau_i) + V_i Q_i(1+\beta\tau_e)}{\beta(1+\beta\tau_i)(1+\beta\tau_e)} + \mathcal{O}\left(Q_e^2, Q_i^2\right). \tag{6.11}$$

The higher-order terms differ, and that is why a discrepancy between both expressions can be seen at nonweak noise.

The results for the mean value achieved in this section are useful in two respects. First, we can check whether trajectories indeed diverge for parameters where the relation, equation 6.4, is violated. Second, the exact solution for the stationary mean value and the simple expressions resulting for the different solutions proposed by R&D can be compared in order to reveal their range of validity. This is done in the next section.

7 Comparison to Simulations

Here we compare the different formulas for the probability density of the membrane voltage and its mean value to numerical simulations for different values of the correlation times, restricting ourselves to the case of multiplicative noise only. For the simulations, we followed a single realization $v(t)$ using a simple Euler procedure. The probability density at a certain voltage is then proportional to the time spent by the realization in a small region around this voltage. Decreasing Δt or increasing the simulation time did not change our results.

We will first discuss the original expression, equation 2.12, proposed by R&D and the analytical solutions for the limit cases of white and static multiplicative noise, equations 3.8 and 5.4, respectively; later we examine the validity of the new extended expression. Finally, we also check the stationary and time-dependent mean value of the membrane voltage and discuss how well these simple statistical characteristics are reproduced by the different theories, including our exact result, equation 6.3.

To check the validity of the different expressions, we use first a dimensionless parameter set where $\beta = 1$ but also the original parameter set used by R&D (2003). In both cases, we consider variations of the correlation times between three orders of magnitude (standard values are varied between 10% and 1000%). Note that the latter choice goes beyond the range originally considered by R&D (2003), where parameter variations were limited to the range 0% to 260%.

7.1 Probability Density of the Membrane Voltage—Original Expression by R&D. In a first set of simulations, we ignore the physical dimensions of all the parameters and pick rather arbitrary but simple values ($\beta = 1$, $Q_i = 0.75$, $Q_e = 0.075$). Keeping the ratio of the correlation times ($\tau_I = 5\tau_e$) and the values of the noise intensities Q_e, Q_i fixed, we vary the correlation times. In Figure 1, simulation results are shown for $\tau_e = 10^{-2}$, 10^{-1}, 1, and 10. We recall that with a fixed noise intensity according to the result by R&D given in equation 2.12, the probability should not depend on τ_e at all.

It is obvious, however, in Figure 1a that the simulation data depend strongly on the correlation times in contrast to what is predicted by equation 2.12. The difference between the original theory by R&D and the simulations is smallest for an intermediate correlation time ($\tau_e = 1$). In contrast to the general discrepancy between simulations and equation 2.12, the white noise formula, equation 3.8, and the formula from the static noise theory (cf. the solid and dotted lines in Figure 1b), agree well with the simulations at $\tau_e = 0.01$ (circles) and $\tau_e = 10$ (diamonds), respectively. The small differences between simulations and theory decrease as we go to smaller or larger correlation times, respectively, as expected. R&D also present results of numerical simulations (Rudolph & Destexhe, 2003), which seem to agree fairly well with their formula. In order to give a sense of the reliability of these data, we have repeated the simulations for one parameter set in Rudolph and Destexhe (2003, Fig. 2b). These data are shown in Figure 2 and compared to R&D's original solution, equation 2.12.

For this specific parameter set, the agreement is indeed relatively good, although there are differences between the formula and the simulation results in the location of the maximum as well as at the flanks of the density. These differences do not vanish by extending the simulation time or decreasing the time step; hence, the curve according to equation 2.12 does not seem to be an exact solution but at best a good approximation.

The disagreement becomes significant if the correlation times are changed by one order of magnitude (see Figure 3) (in this case, we keep the variances of the noises constant, as R&D have done, rather than the noise intensities as in Figure 1). The asymptotic formulas for either vanishing (see Figure 3a) or infinite (see 3b) correlation times derived in this article do a much better job in these limits. Note that the large correlation time used in Figure 3b is outside the range considered by R&D (2003). Regardless of the fact that the correlation times we have used in Figures 3a and 3b are possibly outside the physiological range, an analytical solution should also cover these cases. Regarding the question of whether the correlation time is short (close to the white noise limit), long (close to the static limit), or intermediate (as seems to be the case in the original parameter set of Figure 2b in Rudolph & Destexhe, 2003), it is not the absolute value of $\tau_{e,i,I}$ that matters

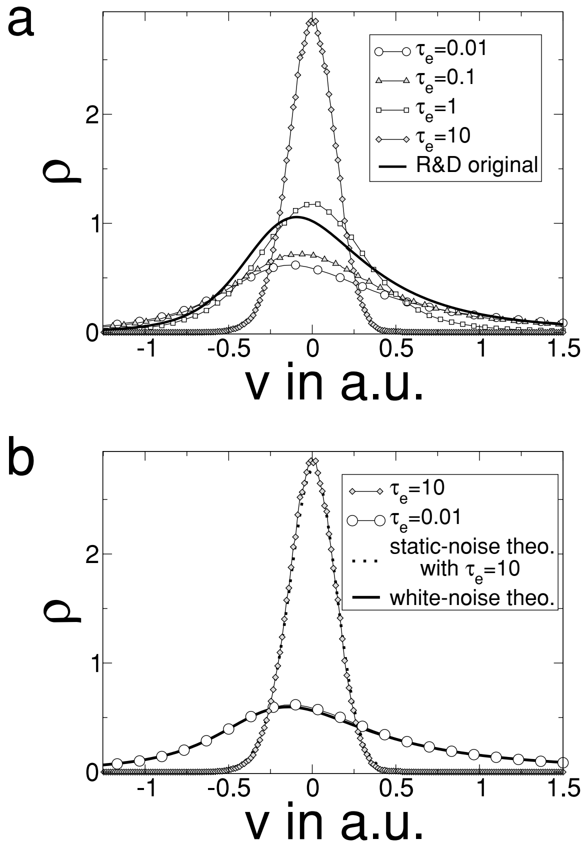

Figure 1: Probability density of the shifted voltage compared to results of numerical simulations. (a) Density according to equation 2.12 (theory by R&D) is compared to simulations at different correlation times as indicated ($\tau_i = 5\tau_e$). Since the noise intensities are fixed, the simulated densities at different τ_e should all fall onto the solid line according to equation 2.12, which is not the case. (b) The simulations at small ($\tau_e = 0.01$) and large ($\tau_e = 10$) correlation times are compared to our expressions found in the limit case of white and static noise: equations 3.8 and 5.4, respectively. Note that in the constant-intensity scaling, equation 5.4 depends implicitly on $\tau_{e,i}$ since the variances change as $\sigma_{e,i} = Q_{e,i}/\tau_{e,i}$. Parameters: $\beta = 1$, $Q_e = 0.075$, $Q_i = 0.75$, $Q_I = 0$, $\Delta t = 0.001$, and simulation time $T = 10^5$.

but the product $\beta\tau_{e,i,I}$. Varying one or more of the parameters g_L, g_{e0}, g_{i0}, a, or C_m can push the dynamics in one of the limit cases without the necessity of changing $\tau_{e,i,I}$.

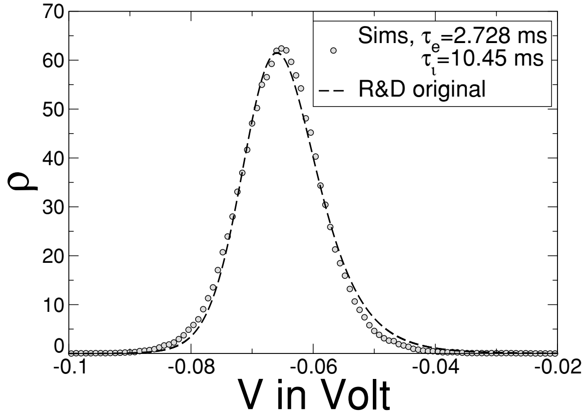

Figure 2: Probability density of membrane voltage corresponding to the parameters in Figure 2b of Rudolph and Destexhe (2003): $g_L = 0.0452$ mS/cm^2, $a = 34636$ μm^2, $C_m = 1$ μF/cm^2, $E_L = -80$ mV, $E_e = 0$ mV, $E_i = -75$ mV, $\sigma_e = 0.012$ μS, $\sigma_i = 0.0264$ μS, $g_{e0} = 0.0121$ μS, $g_{i0} = 0.0573$ μS; additive-noise parameters (σ_I, I_0) are all zero; we used a time step of $\Delta t = 0.1$ ms and a simulation time of 100 s.

7.2 Probability Density of the Membrane Voltage—Extended Expression by R&D. So far we have not considered the extended expression (R&D, 2005) with the effective correlation times. Plotting the simulation data shown in Figures 1a and 3 against this new formula gives a very good, although not perfect, agreement (cf. Figures 4a and 5a). Note, for instance, in Figure 4a that the height of the peak for $\tau_e = 1$ and the location of the maximum for $\tau_e = 0.1$ are slightly underestimated by the new theory. Since most of the data look similar to gaussians, we may also check whether they are described by the ETC theory (cf. equation 2.25). This is shown in Figures 4b and 5b and reveals that for the two parameter sets studied so far, the noise intensities are reasonably small such that the ETC formula gives an approximation almost as good as the extended expression by R&D. One exception to this is shown in Figure 4b: at small correlation times where the noise is effectively white ($\tau_e = 0.1$), the ETC formula fails since the noise variances become large. For $\tau_e = 0.01$, the disagreement is even worse (not shown). In this range, the extended expression captures the density better, in particular its nongaussian features (e.g., the asymmetry in the density).

Since the agreement of the extended expression to numerical simulations was so far very good, one could argue that it represents the exact solution to the problem and the small differences are merely due to numerical inaccuracy. We will check whether the extended expression is the exact solution in two ways. First, we know how the density behaves if both multiplicative noises are very slow ($\beta\tau_e, \beta\tau_i \gg 1$), namely, according to equation 5.4.

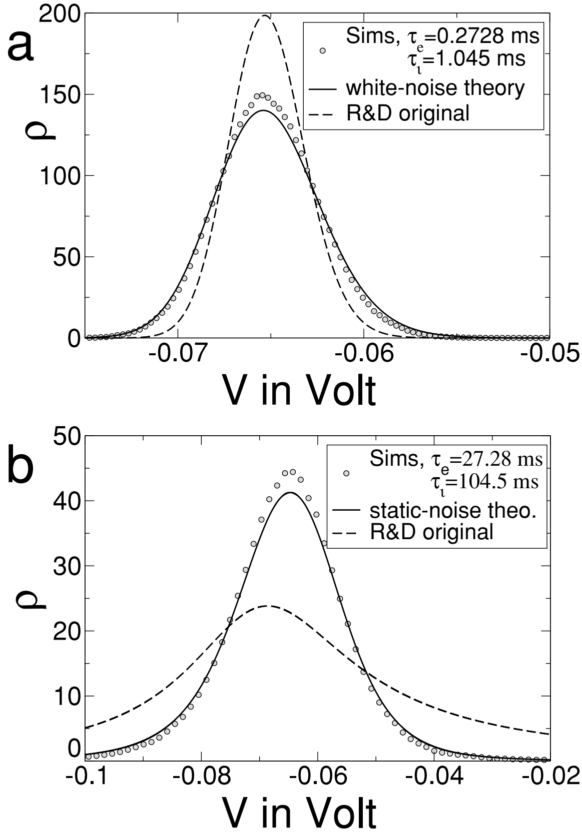

Figure 3: Probability density of membrane voltage for different orders of magnitude of the correlation times τ_e, τ_i. Parameters as in Figure 2 except for the correlation times, which were chosen one order of magnitude smaller (a) or larger (b).

We thus possess an additional control of whether the extended expression, equation 2.15, is exact by comparing it not only to numerical simulation results but also to the static noise theory. Second, we have derived an exact integral expression, equation 6.7, for the stationary mean value, so we can compare the stationary mean value according to the extended expression by R&D (given in equation 6.10) to the exact expression and to numerical simulations.

To check the extended expression against the static noise theory, we have to choose parameter values for which $\beta\tau_e$ and $\beta\tau_i$ are much larger than one; at the same time, the noise variances should be sufficiently large.

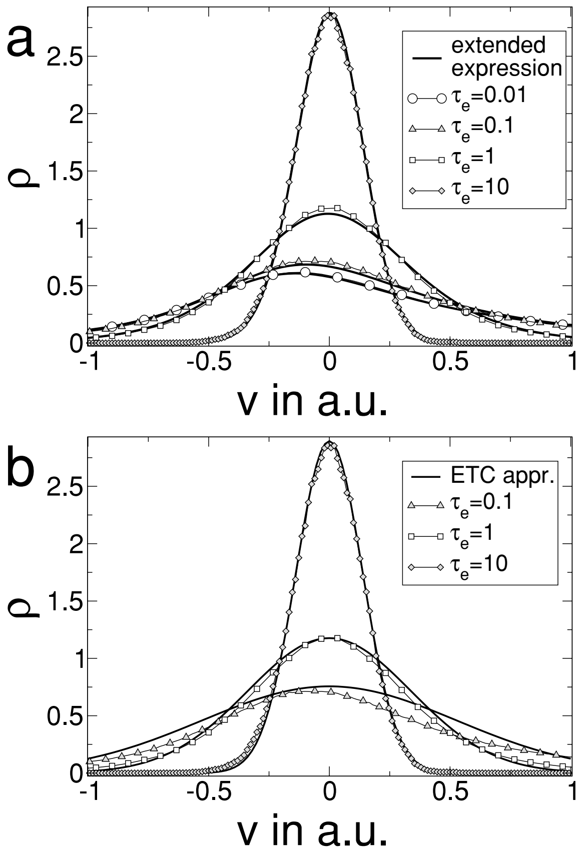

Figure 4: Probability density of membrane voltage for simulation data and parameters as in Figure 1a. The extended expression equation 2.15 (a) and the effective time constant approximation, equation 2.25 (b), are compared to results of numerical simulations.

We compare both theories, equation 2.15 and equation 5.4, once for the system equation 2.19, equation 2.20, with simplified parameters at strong noise ($Q_e = Q_i = 1$) and large correlation times ($\beta\tau_{e,i} = 20$) (see Figure 6a) and once for the original system (see Figure 6b). For the latter, increases in $\beta\tau_{e,i}$ can be achieved by increasing either g_L, g_{e0}, g_{i0} or the synaptic correlation times $\tau_{e,i}$. We do both and increase g_{e0} to the ten-fold of the standard value by R&D (i.e., $g_{e0} = 0.0121\,\mu S \rightarrow g_{e0} = 0.121\ \mu$S) and also multiply the standard values of the correlation times by roughly three (i.e., $\tau_e = 2.728$ ms, $\tau_i = 10.45$ ms $\rightarrow$ $\tau_e = 7.5$ ms, $\tau_i = 30$ ms); additionally, we choose a larger standard deviation for the inhibitory conductance than

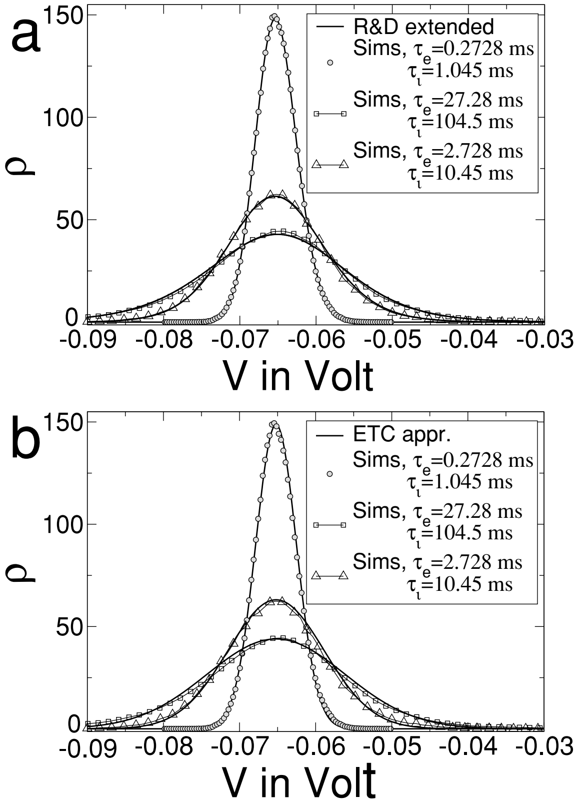

Figure 5: Probability density of membrane voltage for simulation data and parameters as in Figures 2 and 3. The extended expression, equation 2.15 (a), and the effective time constant approximation, equation 2.25 (b), are compared to results of numerical simulations.

in R&D's standard parameter set ($\sigma_i = 0.0264\ \mu$S $\rightarrow$ $\sigma_i = 0.045\ \mu$S). For these parameters, we have $\beta\tau_e \approx 4.2$ and $\beta\tau_i \approx 16.8$, so we may expect a reasonable agreement between static noise theory and the true probability density of the voltage obtained by simulation.

Indeed, for both parameter sets, the static noise theory works reasonably well. For the simulation of the original system (see Figure 6b), we also checked that the agreement is significantly enhanced (agreement within line width) by using larger correlation times (e.g., $\tau_e = 20$ ms, $\tau_i = 100$ ms) as can be expected. Compared to the static noise theory, the extended expression by R&D shows stronger although not large deviations. There are differences in the location and height of the maximum of the densities for

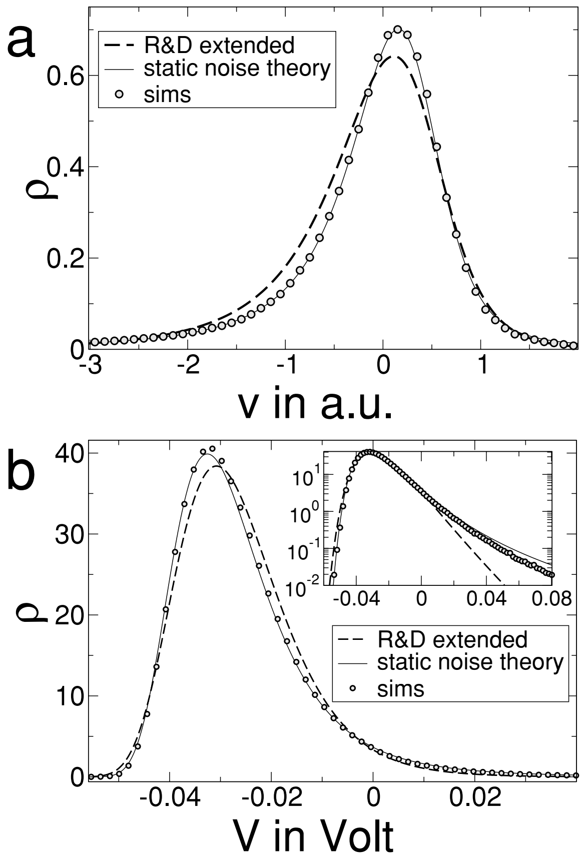

Figure 6: Probability density of membrane voltage for long correlation times; static noise theory, (equation 5.4, solid lines) and extended expression by R&D (equation 2.15, dashed lines) against numerical simulations (symbols). (a) Density of the shifted variable v with $Q_e = Q_i = 3$, $\beta = 1$, $\tau_e = \tau_i = 20$, $V_e = 1.5$, $V_i = -0.5$. Here, the mean value is infinite. In the simulation, we implemented reflecting boundaries affecting the density only in its tails (not shown in the figure). (b) Density for the original voltage variable with $g_L = 0.0452$ mS/cm^2, $a = 34,\ 636\ \mu$m^2, $C_m = 1\ \mu$F/cm^2, $E_L = -80$ mV, $E_e = 0$ mV, $E_i = -75$ mV, $\sigma_e = 0.012\ \mu$S, $\sigma_i = 0.045\ \mu$S, $g_{e0} = 0.121\ \mu$S, $g_{i0} = 0.0574\ \mu$S, $\tau_e = 7.5$ ms, $\tau_i = 30$ ms. Here the mean value is finite. Inset: Same data on a logarithmic scale.

both parameter sets; prominent also is the difference between the tails of the densities (see the Figure 6b inset). Hence, there are parameters that are not completely outside the physiological range, for which the extended expression yields only an approximate description and for which the static noise theory works better than the extended expression by R&D. This is in particular the case for strong and long-correlated noise.

7.3 Mean Value of the Membrane Voltage. The second way to check the expressions by R&D was to compare their mean values to the exact expression for the stationary mean, equation 6.7. We do this for the transformed system, equation 2.19, equation 2.20, with dimensionless parameters. In Figure 7, the stationary mean value is shown as a function of the correlation time τ_e of the excitatory conductance. In the two panels, we keep the noise intensities Q_e and Q_i fixed; the correlation time of inhibition is small (in Figure 7a) or medium (in Figure 7b) compared to the intrinsic timescale ($1/\beta = 1$). We choose noise intensities $Q_i = 0.3$ and $Q_e = 0.2$ so that the mean value is finite because equation 6.4 is satisfied. In Figure 7a the disagreement between the extended expression by R&D (dash-dotted line) and the exact solution (thick solid line) is apparent for medium values of the correlation time. To verify this additionally, we also compare to numerical simulation results. The latter agree with our exact theory for the mean value within the numerical error of the simulation. We also plot two limits that may help to explain why the new theory by R&D works in this special case at very small and very large values of τ_E. At small values, both noises are effectively white, and we have already discussed that in this case, the extended expression for the probability density, equation 2.15, approaches the correct white noise limit. Hence, also the first moment should be correctly reproduced in this limit. On the other hand, going to large correlation time τ_e at fixed noise intensity Q_e means that the effect of the colored noise $y_e(t)$ on the dynamics vanishes. Hence, in this limit, we obtain the mean value of a system that is driven only by one white noise (i.e., $y_i(t)$). Also this limit is correctly described by R&D's new theory, since the effective noise intensity $Q_e' = 2Q_e/[1 + \beta\tau_e]$ vanishes for $\tau_e \to \infty$ if Q_e is fixed. However, for medium values of τ_e, the new theory predicts a larger mean value than the true value. The mean value, equation 6.9, of the original solution, equation 2.12 (dotted lines in Figure 7), leads to a mean value of the voltage that does not depend on the correlation time τ_e at all.

If the second correlation time τ_I is of the order of the effective membrane time constant $1/\beta$ (see Figure 7b), the deviations between the mean value of the extended expression and the exact solution are smaller but extend over all values of τ_e. In this case, the new solution does not approach the correct one in either of the limit cases, $\tau_e \to 0$ or $\tau_e \to \infty$. The overall deviations between the mean according to the extended expression are small. Also for both panels, the differences in the mean are small compared to the standard deviations of the voltage. Thus, the expression equation 6.10, corresponding to the extended expression, can be regarded as a good approximation for the mean value.

Finally, we illustrate the convergence or divergence of the mean if the condition equation 6.4 is obeyed or violated, respectively. First, we choose

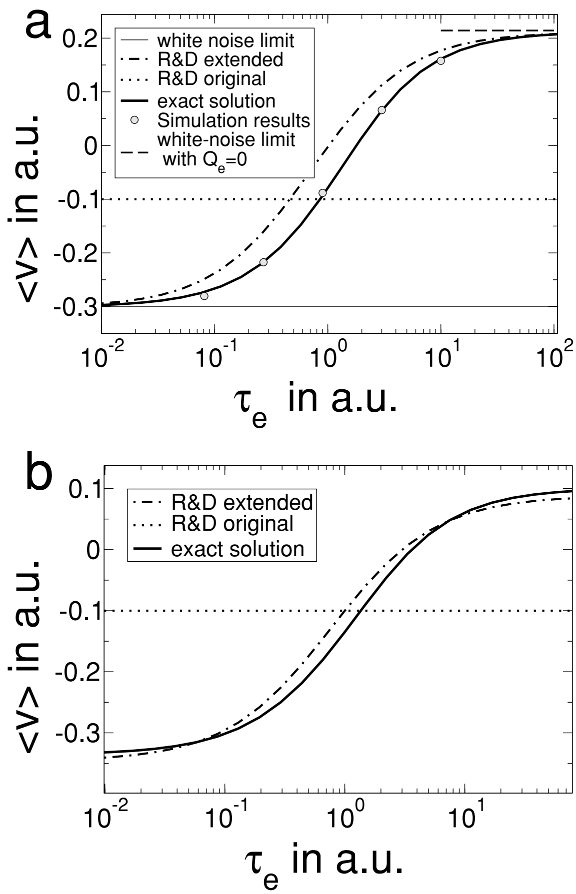

Figure 7: Stationary mean value of the shifted voltage (in arbitrary units) versus correlation time (in arbitrary units) of the excitatory conductance. Noise intensities $Q_e = 0.2$, $Q_i = 0.3$, $Q_I = 0$, and $\beta = 1$ are fixed in all panels. Correlation time of the inhibitory conductance: $\tau_i = 10^{-2}$ (a) and $\tau_i = 1$ (b). Shown are the exact analytical result, equation 6.7 (solid line); the mean value according to the original solution, equation 6.9 (dotted line); and the mean value according to the extended expression, equation 6.10 (dash-dotted line). In panel a, we also compare to the mean value of the white noise solution for $Q_e = 0.2$, $Q_i = 0.3$ (thin solid line) and for $Q_e = 0$, $Q_i = 0.3$ (dashed line), as well as to numerical simulation results (symbols).

the original system and the standard set of parameters by Rudolph and Destexhe (2003) and simulate a large number of trajectories in parallel. All of these are started at the same value ($V = 0$) and each with independent noise sources, the initial values of which are drawn from the stationary

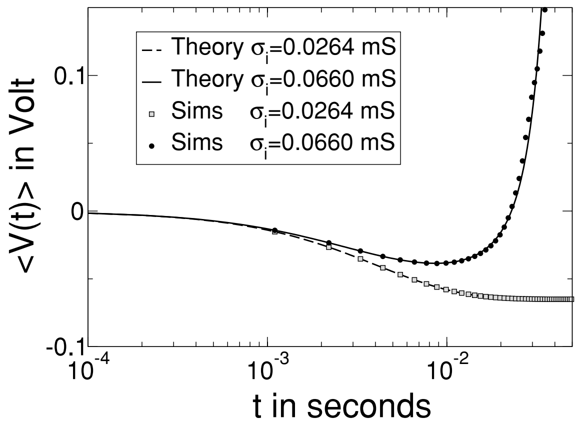

Figure 8: Time-dependent mean value of the original voltage variable (in volts) as a function of time (in seconds) for the initial value $V(t = 0) = 0$ V and different values of the inhibitory conductance standard deviation σ_i; numerical simulations of equations 2.19 and 2.20 (circles) and theory according to equation 6.3 (solid lines). For all curves, $g_{e0} = 0.0121$ μS, $g_{i0} = 0.0573$ μS, $\sigma_e = 0.012$ μS, $\tau_e = 2.728$ ms, $\tau_i = 10.49$ ms, $a = 34{,}636$ μm^2, and $C_m = 1$ μF/cm^2. For the dashed line (theory) and the gray squares (simulations), we choose $\sigma_i = 0.0264$ μS; hence, in this case, parameters correspond to the standard parameter set by Rudolph and Destexhe (2003). For the solid line (theory) and the black circles, we used $\sigma_i = 0.066$ μS corresponding to the 250% of the standard value by R&D. At the standard parameter set, the mean value saturates at a finite level, in the second case, the mean diverges and goes beyond 100 mV within 31 ms. Simulations were carried out for 10^6 voltage trajectories using an adaptive time step (always smaller than 0.01 ms) that properly took into account the trajectories that diverge the strongest. The large number of trajectories was required in order to get a reliable estimate of the time-dependent mean value in the case of strong noise ($\sigma_i = 0.066$ μS) where voltage fluctuations are quite large.

gaussian densities. In an experiment, this corresponds exactly to fixing the voltage of the neuron via voltage clamp and then to let the voltage freely evolve under the influence of synaptic input (that has not been affected by the voltage clamp). In Figure 8 we compare the time-dependent average of all trajectories to our theory, equation 6.3 (in terms of the original variable and parameters). For R&D's standard parameters, the mean value reaches after a relaxation of roughly 20 ms a finite value (V≈ -65 mV). The time course of the mean value is well reproduced by our theory, as it should be. Increasing one of the noise standard deviations to 2.5-fold of its standard value ($\sigma_i = 0.0264$ μS $\rightarrow$ 0.066 μS), which is still in the range inspected by

R&D, results in a diverging mean.[5] Again the theory (solid line) is confirmed by the simulation results (black circles). Starting from zero voltage, the voltage goes beyond 100 mV within 31 ms. In contrast to this, the mean value of the extended expression is finite (the condition equation 3.21 is obeyed) and the mean value formula for this density, equation 6.10, yields a stationary mean voltage of −66 mV. Thus, in the general colored noise case, the extended expression cannot be used to decide whether the moments of the membrane voltage will be finite.

We note that the divergence of the mean is due to a small number of strongly deviating voltage trajectories in the ensemble over which we average. This implies that the divergence will not be seen in a typical trajectory and that a large ensemble of realizations and a careful simulation of the rare strong deviations (adaptive time step) are required to confirm the diverging mean predicted by the theory. Thus, although the linear model with multiplicative gaussian noise is thought to be a simple system compared to nonlinear spike generators with Poissonian input noise, its careful numerical simulation may be much harder than that of the latter type of model.

8 Conclusions

We have investigated the formula for the probability density of the membrane voltage driven by multiplicative and/or additive (conductance and/or current noise) proposed by R&D in their original article. Their solution deviates from the numerical simulations in all three limits we have studied (white noise driving, colored additive noise, and static multiplicative noise). The deviation is significant over extensive parameter ranges. The extended expression by R&D (2005), however, seems to provide a good approximation to the probability density of the system for a large range of parameters.

In the appendix we show where errors have been made in the derivation of the Fokker-Planck equation on which both the original and extended expressions are based. Although there are serious flaws in the derivation, we have seen that the new formula (obtained by an ad hoc introduction of effective correlation times in the original solution) gives a very good reasonable approximation to the probability density for weak noise. What could be the reason for this good agreement?

The best, though still phenomenological, reasoning for the solution, equation 2.15, is as follows. First, an approximation to the probability

[5] These parameter values were not considered by R&D to be in the physiological range. We cannot, however, exclude that other parameter variations (e.g., decreasing the leak conductance or increasing the synaptic correlation times) will not lead to a diverging mean for parameters in the physiological range.

density should work in the solvable white noise limit:

$$\lim_{\tau_e,\tau_i\to 0} \rho_{appr}(v, Q_e, Q_i, \tau_e, \tau_i) = \rho_{wn}(v, Q_e, Q_i). \tag{8.1}$$

Second, we know that at weak multiplicative noise of arbitrary correlation time, the effective time constant approximation will be approached:

$$\rho_{appr}(v, Q_e, Q_i, \tau_e, \tau_i) = \rho_{ETC}(v, Q_e, Q_i, \tau_e, \tau_i), \quad (Q_e, Q_i \text{ small}). \tag{8.2}$$

The latter density given in equation 2.25 can be expressed by the white noise density with rescaled noise intensities (note that the variance in the ETC approximation given in equation 2.26 has this property); furthermore, it is close to the density for white multiplicative noise if the noise is weak:

$$\begin{aligned} \rho_{ETC}(v, Q_e, Q_i, \tau_e, \tau_i) &= \rho_{ETC}(v, Q_e/(1+\beta\tau_e), Q_i/(1+\beta\tau_i), 0, 0), \\ &\overset{(Q_e, Q_i \text{ small})}{\approx} \rho(v, Q_e/(1+\beta\tau_e), Q_i/(1+\beta\tau_i), 0, 0) \\ &= \rho_{wn}(v, Q_e/(1+\beta\tau_e), Q_i/(1+\beta\tau_i)). \end{aligned} \tag{8.3}$$

Hence, using this equation together with equation 8.1, one arrives at

$$\rho_{appr}(v, Q_e, Q_i, \tau_e, \tau_i) \approx \rho_{wn}(v, Q_e/(1+\beta\tau_e), Q_i/(1+\beta\tau_i)). \tag{8.4}$$

This approximation, which also obeys equation 8.1, is the extended expression by R&D. It is expected to function in the white noise and the weak noise limits and can be regarded as an interpolation formula between these limits. We have seen that for stronger noise and large correlation times (i.e., in a parameter regime where neither of the above assumptions of weak or uncorrelated noise holds true), this density and its mean value disagree with numerical simulation results as well as with our static noise theory. Regarding the parameter sets for which we checked the extended expression for the probability density, it is remarkable that the differences to numerical simulations were not stronger.

Two issues remain. First, we have shown that the linear model with gaussian conductance fluctuations can show a diverging mean value. Certainly, for higher moments, as, for instance, the variance, the restrictions on parameters will be even more severe than that for the mean value (this can be concluded from the tractable limit cases we have considered). As demonstrated in the case of the stationary mean value, the parameter regime for such a divergence cannot be determined using the different solutions proposed by R&D.

Of course, a real neuron can be driven by a strong synaptic input without showing a diverging mean voltage—the divergence of moments found above is just due to the limitations of the model. One such limitation is the diffusion approximation on which the model is based. Applying this approximation, the synaptically filtered spike train inputs have been replaced by OUPs. In the original model with spike train input, it is well known that the voltage cannot go below the lowest reversal potential E_i or above the excitatory reversal potential E_e if no current (additive) noise is present (see, e.g., Lánský & Lánská, 1987, for the case of unfiltered Poissonian input). In this case, we do not expect a power law behavior of the probability density at large values of the voltage. Another limitation of the model considered by R&D is that no nonlinear spike-generating mechanism has been included. In particular, the mechanism responsible for the voltage reset after an action potential would prevent any power law at strong, positive voltage. Thus, we see that at strong, synaptic input, the shot-noise character of the input and nonlinearities in the dynamics cannot be neglected and even determine whether the mean of the voltage is finite.

The second issue concerns the consequences of the diffusion approximation for the validity of the achieved results. Even if we assume a weak noise such that all the lower moments like mean and variance will be finite, is there any effect of the shot-noise character of the synaptic input that is not taken into account properly by the diffusion approximation? Richardson and Gerstner (2005) have recently addressed this issue and shown that the shot-noise character will affect the statistics of the voltage and that its contribution is comparable to that resulting from the multiplicativity of the noise. Thus, for a consistent treatment, one should either include both features (as done by Richardson and Gerstner, 2005, in the limit of weak synaptic noise) or none (corresponding to the effective timescale approximation; cf. Richardson & Gerstner, 2005).

Summarizing, we believe that the use of the extended expression by R&D is restricted to parameters obeying

$$\beta \gg Q_e + Q_i. \tag{8.5}$$

This restriction is consistent with (1) the diffusion approximation on which the model is based, (2) a qualitative justification of the extended expression by R&D as given above, and (3) the finiteness of the stationary mean and variance. For parameters that do not obey the condition equation 8.5, one should take into account the shot-noise statistics of the synaptic drive. Recent perturbation results were given by Richardson and Gerstner (2005) assuming weak noise; we note that the small parameter in this theory is $(Q_e + Q_i)/\beta$ and therefore exactly equal to the small parameter in equation 8.5.

The most promising result in our letter seems to be the exact solution for the time-dependent mean value, a statistical measure that can be easily determined in an experiment and might tell us a lot about the synaptic dynamics and its parameters. The only weakness of this formula is that it is still based on the diffusion approximation, that is, on the assumption of gaussian conductance noise. One may, however, overcome this limitation by repeating the calculation for synaptically filtered shot noise.

Appendix: Analysis of the Derivation of the Fokker-Planck Equation

Here we show where in the derivation of the Fokker-Planck equation by R&D errors have been made.

Let us first note that although R&D use a so-called Ito rule, there is no difference between the Ito and Stratonovich interpretations of the colored noise–driven membrane dynamics. Since the noise processes possess a finite correlation time, the Ito-Stratonovich dilemma occurring in systems driven by white multiplicative noise is not an issue here.

To comprehend the errors in the analytical derivation of the Fokker-Planck equation in R&D, it suffices to consider the case of only additive OU noise. For clarity we will use our own notation: the OUP is denoted by $y_I(t)$, and we set $h_I = 1$ (the latter function is used in R&D for generality). R&D give a formula for the differential of an arbitrary function $F(v(t))$ in equation B.9.

$$dF(v(t)) = \partial_v F(v(t))dv + \frac{1}{2}\partial_v^2 F(v(t))(dv)^2. \tag{A.1}$$

R&D use the membrane equation in its differential form, which for vanishing multiplicative noises reads

$$dv = f(v)dt + dw_I, \tag{A.2}$$

where the drift term is $f(v) = -\beta v$ and w_I is the integrated OU process y_I:

$$w_I = \int_0^t ds\ y_I(s). \tag{A.3}$$

Inserting equation A.2 into equation A.1, we obtain

$$dF(v(t)) = \partial_v F(v(t)) f(v(t))dt + \partial_v F(v(t))dw_I + \frac{1}{2}\partial_v^2 F(v(t))(dw_I)^2. \tag{A.4}$$

This should correspond to equation B.10 in R&D for the case of zero multiplicative noise. However, our formula differs from equation B.10 in one important respect: R&D have replaced $(dw_I)^2$ by $2\alpha_I(t)dt$ using their Ito rule,[6] equation A.13a. Dividing by dt, averaging, and using the fact that for finite τ_I $dw_I(t)/dt = y_I(t)$, we arrive at

$$\frac{d\langle F(v(t))\rangle}{dt} = \langle \partial_v F(v(t)) f(v(t))\rangle + \langle \partial_v F(v(t)) y_I(t)\rangle + \frac{1}{2}\left\langle \partial_v^2 F(v(t)) \frac{(dw_I)^2}{dt}\right\rangle. \tag{A.5}$$

This should correspond to equation B.12 in R&D (again for the case of vanishing multiplicative noise) but is not equivalent to the latter equation for two reasons. First, R&D set the second term on the right-hand side to zero, reasoning that the mean value $\langle y_I(t)\rangle$ is zero (they also use an argument about $h_{\{e,i,I\}}$, which is irrelevant in the additive noise case considered here). Evidently if $y_I(t)$ is a colored noise, it will be correlated to its values in the past $y(t')$ with $t' < t$. The voltage $v(t)$ and any nontrivial function $F(v(t))$ is a functional of and therefore correlated to $y_I(t')$ with $t' < t$. Consequently, there is also a correlation between $y_I(t)$ and $F(v(t))$, and thus

$$\langle \partial_v F(v(t)) y_I(t)\rangle \neq \langle \partial_v F(v(t))\rangle \langle y_I(t)\rangle = 0. \tag{A.6}$$

Hence, setting the second term (which actually describes the effect of the noise on the system) to zero is wrong.[7] This also applies to the respective terms due to the multiplicative noise.

Second, the last term on the right-hand side of equation A.5 was treated as a finite term in the limit $t \to \infty$. According to R&D's equation A.13a (for $i = j$), equation 3.2, and equation 3.3, $\lim_{t\to\infty}\langle (dw_I)^2\rangle = \lim_{t\to\infty} 2\alpha_I(t)dt = \tilde{\sigma}_I^2 \tau_I dt$ and, thus $\langle (dw_I^2)\rangle/dt \to \tilde{\sigma}_I^2 \tau_I$ as $t \to \infty$. However, the averaged variance of $dw_I = y_I(t)dt$ is $\langle (dw_I)^2\rangle = \langle y_I(t)^2\rangle (dt)^2 = \tilde{\sigma}_I^2 (dt)^2$ and therefore the last term in equation A.5 is of first order in dt (since $(dw_I)^2/dt = y_I(t)^2 dt \sim dt$) and vanishes. This is the second error in the derivation.

We note that the limit in equation 3.3 is not correctly carried out. Even if we follow R&D in using their relations, equation A.13a, together with the correct relation, equation A.10a (instead of the white noise formula, equation A.12a), we obtain that for finite τ_I, the mean squared increment

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[6] Note that R&D use $\alpha_I(t)$ for two different expressions: according to equation B.8 for $\tilde{\sigma}_I^2[\tau_I(1 - \exp(-t/\tau_I)) - t] + w_I^2(t)/(2\tau_I)$ but also according to equation 3.2 for the average of this stochastic quantity.

[7] For readers still unconvinced of equation A.6, a simple example will be useful. Let $F(v(t)) = v^2(t)/2$. Then $\langle \partial_v F(v(t)) y_I(t)\rangle = \langle v(t) y_I(t)\rangle$. In the stationary state, this average can be calculated as $\int\int dv dy_I \; v y_I P_0(v, y_I)$ using the density equation 4.6. This yields $\langle v(t) y_I(t)\rangle = Q_I/[1 + \beta\tau_I]$, which is finite for all finite values of the noise intensity Q_I and correlation time τ_I. Note that this line of reasoning is valid only for truly colored noise ($\tau_I > 0$); the white noise case has to be treated separately.

$\langle (dw_I)^2 \rangle$ is zero in linear order in dt for all times t, which is in contradiction to equation 3.3 in R&D. This incorrect limit stems from using the white noise formula, equation (A.12a) which R&D assume to go from equation 3.2 to equation 3.3 in R&D (2003). The use of equation A.12a is justified by R&D by the steady-state limit $t \to \infty$ with $t/\tau_I \gg 1$. However, $t \to \infty$ with $t/\tau_I \gg 1$ does not imply that $\tau_I \to 0$ and that one can use equation A.12a, which holds true only for $\tau_I \to 0$. In other words, a steady-state limit does not imply a white noise limit.

We now show that keeping the proper terms in equation A.5 does not lead to a useful equation for the solution of the original problem. After applying what was explained above, equation A.5 reads correctly,

$$\frac{d\langle F(v(t))\rangle}{dt} = \left\langle \partial_v F(v(t)) f(v(t)) \right\rangle + \left\langle \partial_v F(v(t)) y_I(t) \right\rangle. \tag{A.7}$$

Because of the correlation between $v(t)$ and $y_I(t)$, we have to use the full two-dimensional probability density to express the averages:

$$\begin{aligned} \left\langle \partial_v F(v(t)) f(v(t)) \right\rangle &= \int dv \int dy_I (\partial_v F(v)) f(v) P(v, y_I, t) \\ &= \int dv (\partial_v F(v)) f(v) \rho(v, t) \\ \left\langle \partial_v F(v(t)) y_I(t) \right\rangle &= \int dv \int dy_I (\partial_v F(v)) y_I P(v, y_I, t). \end{aligned} \tag{A.8}$$

Inserting these relations into equation A.7, performing an integration by part, and setting $F(v) = 1$ leads us to

$$\partial_t \rho(v, t) = -\partial_v (f(v)\rho(v, t)) - \partial_v \left(\int dy_I \, y_I \, P(v, y, t) \right), \tag{A.9}$$

which is not a closed equation for $\rho(v, t)$ or a Fokker-Planck equation. The above equation with $f(v) = -\beta v$ can be also obtained by integrating the two-dimensional Fokker-Planck equation, equation 4.5, over y_I.

In conclusion, by neglecting a finite term and assuming a vanishing term to be finite, R&D have effectively replaced one term by the other; the colored noise drift term is replaced by a white noise diffusion term, the latter with a prefactor that corresponds to only half of the noise intensity. This amounts to a white noise approximation of the colored conductance noise, although with a noise intensity that is not correct in the white noise limit of the problem.

Acknowledgments

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