

Average firing rate of a neural network with dynamical disorder

This article has been downloaded from IOPscience. Please scroll down to see the full text article.

1995 J. Phys. A: Math. Gen. 28 2457

(<http://iopscience.iop.org/0305-4470/28/9/009>)

View [the table of contents for this issue](#), or go to the [journal homepage](#) for more

Download details:

IP Address: 171.66.16.68

The article was downloaded on 02/06/2010 at 03:03

Please note that [terms and conditions apply](#).

Average firing rate of a neural network with dynamical disorder

Paul C Bressloff

Department of Mathematical Sciences, Loughborough University of Technology, Loughborough, Leicester LE11 3TU, UK

Received 13 December 1994, in final form 14 February 1995

Abstract. We analyse the effects of time-varying synaptic background activity on the steady-state firing rate of a compartmental model neural network with shunting. The background is taken to be a multi-component dichotomous coloured noise process distributed randomly across the compartments of each neuron. We exploit the formal similarity between the neural network model and a model of excitons moving on a lattice with random modulations of the local energy at each site. In particular, we use a dynamical coherent potential approximation and the method of partial cumulants to evaluate the single-neuron Green's function averaged over the stochastic background. This is then used to determine the firing rate. It is found that the firing rate increases with the variance and correlation time of the coloured noise process.

1. Introduction

Recent neurobiological experiments [1, 2] have demonstrated that background synaptic activity can influence the behaviour of cortical neurons. The basic mechanism underlying such an effect is that of shunting; increases in the conductance of excitatory and/or inhibitory synapses leads to local reductions in the membrane time constant τ of a neuron. It has been found that variations in the level of background activity can lead to a ten-fold reduction in τ , so this is a significant effect with a number of important consequences. (i) In the presence of constant inputs, a reduction in τ due to background activity produces a corresponding reduction in the steady-state membrane potential and thus a lower firing rate [3]. (ii) Background activity can influence the mode of operation carried out by a neuron, since for small τ a neuron acts like a coincidence detector whereas for larger τ it performs the role of a temporal integrator. (iii) Spatially non-uniform patterns of background activity impinging on the extensive dendritic tree of a neuron results in a corresponding modulation of the spatial variation of τ across the tree [4]. This could, for example, influence how well distal dendrites contribute to events at the cell body or soma. (iv) Stochastic background activity is a source of multiplicative rather than additive noise.

In a previous paper, we studied the effects of background synaptic inputs on the steady-state firing rate of a compartmental model recurrent neural network [3]. The inputs were assumed to be time-independent and randomly distributed across the compartments of each neuron. Using mean-field theory, the firing rate was expressed in terms of the ensemble-averaged single-neuron Green's function. The latter was shown to satisfy a matrix equation identical in form to that found in the tight-binding-alloy (TBA) model of excitations on a one-dimensional disordered lattice [5, 6]. Standard techniques from statistical physics such as the coherent potential approximation were then used to perform the ensemble averaging

and thereby determine the firing rate. The main results obtained were (i) the steady-state firing rate of a compartmental model network decreases as the mean level of background activity (distributed across the neurons) increases and, more surprisingly, (ii) an increase in the (spatial) variance of the background activity distribution (for fixed mean) leads to an increase in the firing rate.

One of the simplifying assumptions of [3] was to take the background activity to be time-independent. However, an individual neuron's output activity is generally time-varying and has a strong stochastic component. (Often a neuron's output spike train is modelled as a stochastic renewal process [7]). One would expect from the law of large numbers that much of this stochasticity would be suppressed when the outputs of many neurons are combined to form the background field. On the other hand, one might expect variations in the level of background activity to occur on a longer time-scale, reflecting changes in the overall level of a network's attention to a particular task, perhaps, or a change in effective state. (One may even speculate on the role of neuromodulators in controlling levels of background activity). Another possible mechanism is the spontaneous emergence of states of synchronous activity, which is thought to play an important role in neuronal information processing [8, 9]. Hence, it is of interest to investigate the consequences of such temporal fluctuations in background activity, especially given the non-trivial behaviour already found for time-independent fluctuations in [3].

In this paper, therefore, we consider a compartmental model recurrent network with time-dependent stochastic background activity. We shall assume, for simplicity, that the background activity to each compartment randomly jumps between a finite number of discrete values (multi-component dichotomous noise). As in [3], spatial correlations between background inputs to different compartments of the same neuron and between different neurons are neglected. Given that one has to deal with multiplicative noise (point (iv)), the temptation is to consider the limiting case of a white noise process, which is the usual approach [7]. However, in this paper we shall show how it is possible to tackle the more general example of multiplicative coloured noise. Our basic method is to establish a formal similarity between the neural network model and a physical system in a heat bath [10]. This then allows us to use various techniques from non-equilibrium statistical physics. It also explains why we choose a dichotomous noise process since this is often used to model the effects of a heat bath and allows exact calculations to be made. However, it is possible to extend our analysis to other types of coloured noise process, which of these is most reasonable from the biological viewpoint is currently unknown to the author. (Note that viewing the effects of stochastic dendritic inputs in terms of a heat bath has also been considered by Bulsara *et al* [11]).

We use a dynamical version of the coherent potential approximation [12] to reduce the compartmental model with multi-site temporal fluctuations to an equivalent system with an effective site-independent constant background. This leads to a self-consistency condition for the background involving the averaged single-neuron Green's function for a compartmental model with temporal fluctuations at a single site or compartment. Following [13, 14], we calculate the latter using the time convolution generalized master equation (TC-GME) formalism [15] and the method of partial cumulants [16, 17]. Solving the resulting self-consistency condition then allows us to determine the average firing rate of the network.

The main result of this analysis is that a time-varying stochastic background leads to an increase in the steady-state firing rate of a network compared to a constant background of the same average intensity. Such an increase grows with the variance and the correlation time of the underlying coloured noise process. Although this is derived using dichotomous noise, we believe that the result is quite general.

2. Model

Consider a model neuron consisting of an infinite chain of identical dendritic compartments labelled $n = 0, \pm 1, \pm 2, \dots$. For simplicity, the soma is assumed to be a point processor that is isopotential with the central compartment $n = 0$. Let V_n denote the membrane potential of the n th compartment; the membrane potential at the soma then satisfies $V \equiv V_0$. An application of Kirchoff's law leads to the set of coupled equations

$$\frac{d}{dt} V_n(t) = -\frac{V_n}{\tau} + \frac{1}{\tau'}(V_{n+1} + V_{n-1} - 2V_n) + E_n[S^{(e)} - V_n] + I_n[S^{(i)} - V_n] \quad (1)$$

where τ and τ' are membrane time constants corresponding, respectively, to transverse and longitudinal currents in the dendritic chain, and the last two terms on the right-hand side describe excitatory and inhibitory synaptic inputs. The rates of excitatory and inhibitory input stimulation to the n th compartment are denoted by E_n and I_n , and $S^{(e)}$, $S^{(i)}$ are the associated membrane reversal potentials with $S^{(e)} > 0$ and $S^{(i)} \leq 0$. (For a detailed description of compartmental models see [18] and references therein). Comparing diagonal terms on the right-hand side of (1), we see that there is an input-dependent modulation of the membrane time constant τ given by $\tau^{-1} \rightarrow \tau^{-1} + E_n + I_n$. In other words, both excitatory and inhibitory synaptic inputs reduce the effective transverse membrane time constant of the neuron. One immediate consequence of such a reduction is that large increases in somatic membrane potential due to high rates of input excitation cannot be sustained for very long. In the case of constant inputs, one finds that the steady-state membrane potential increases linearly with inputs at low levels of excitation but decreases again to some finite fixed value as the level of excitation becomes large. This in turn means that networks of such neurons can support states of self-sustained firing well below the maximum possible firing rate [19–21].

A simple illustration of the above feature can be obtained by taking the spatial distribution of inputs across the chain to have the form of non-recurrent lateral inhibition [3]. That is, an input that excites the m th compartment also inhibits all other compartments of the chain (see figure 1). More specifically,

$$E_n = a_n E \quad \sum_n a_n = 1 \quad I_n = \sum_{m \neq n} E_m \quad (2)$$

where the a_n , which determine the relative distribution of excitation across the chain, are held fixed. Under such a choice of inputs, the modulation of the time constant becomes site-independent thus considerably simplifying the analysis. (Later on we shall consider site-dependent modulations of this pattern of inputs arising from background activity. However,

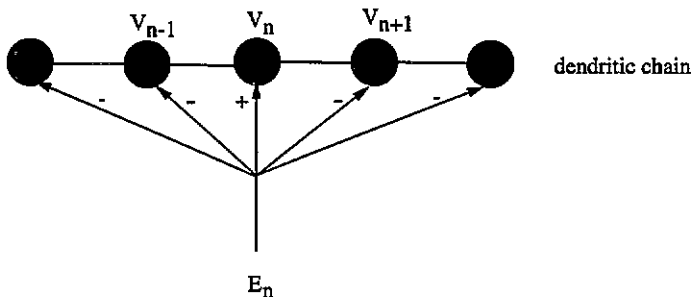


Figure 1. Pattern of excitatory and inhibitory inputs for non-recurrent lateral inhibition

the results then obtained concerning the effects of such background activity apply equally well to input distributions other than the one specified by equation (2). The latter is chosen for convenience). Assuming that the total excitation rate E is time-independent and $S^{(i)} = 0$ (shunting inhibition), one can integrate equation (1) to obtain the solution

$$V_m(t) = e^{-Et} \sum_n G_{mn}^{(0)}(t) V_n(0) + E \int_0^t \sum_n a_n e^{-E(t-t')} G_{mn}^{(0)}(t-t') dt' \tag{3}$$

where

$$G^{(0)}(t) = e^{tQ^{(0)}} \quad Q_{mn}^{(0)} = -\left(\frac{1}{\tau} + \frac{2}{\tau'}\right) \delta_{m,n} + \frac{1}{\tau'} (\delta_{m,n-1} + \delta_{m,n+1}). \tag{4}$$

We may identify $G^{(0)}(t-t')$ as the membrane potential response function or Green's function of the dendritic chain. That is, $G_{mn}^{(0)}(t-t')$ determines the membrane potential of compartment m at time t in response to a unit impulse stimulation of compartment n at time t' . Note that the Green's function only depends on the time difference $t-t'$. Using standard results from the theory of diffusion on lattices, the Green's function has the explicit form

$$G_{mn}^{(0)}(t) = e^{-t/\tau} I_{|n-m|}(2t/\tau') = \int_{-\pi}^{\pi} \frac{dk}{2\pi} e^{ik(m-n)} e^{-t\epsilon(k)} \tag{5}$$

where I_p is a modified Bessel function of integer order and

$$\epsilon(k) = \frac{1}{\tau} + \frac{2}{\tau'} (1 - \cos k). \tag{6}$$

In the limit $t \rightarrow \infty$, equation (3) shows that the steady-state potential at the soma in response to constant non-recurrent lateral inhibition is [3]

$$V^\infty(E) = S^{(e)} E \sum_n a_n G_{0n}^{(0)}(E) \tag{7}$$

where $G^{(0)}(E)$ is the Laplace transform of $G^{(0)}(t)$,

$$G_{mn}^{(0)}(E) = \int_0^\infty e^{-t'E} G_{mn}^{(0)}(t') dt'. \tag{8}$$

Note that the first term on the right-hand side of (3) is a transient term that vanishes in the limit $t \rightarrow \infty$, reflecting the fact that the matrix $Q^{(0)}$ has negative definite eigenvalues. An explicit expression for $G^{(0)}(E)$ may be obtained by substituting (5) into (8) and performing a contour integral. The result is [3]

$$G_{mn}^{(0)}(E) = \tau' \frac{(\lambda_-(E))^{|m-n|}}{\lambda_+(E) - \lambda_-(E)} \tag{9}$$

where

$$\lambda_{\pm}(E) = 1 + \frac{\tau'(E + \tau^{-1})}{2} \pm \sqrt{\left(1 + \frac{\tau'(E + \tau^{-1})}{2}\right)^2 - 1}. \tag{10}$$

It follows from (7) and (9) that for low levels of excitation E , the steady-state somatic potential is approximately a linear function of E . However, as E increases, the reduction in the membrane time constant becomes more and more significant so that V_∞ begins to decrease. For large E ,

$$V^\infty(E) \approx S^{(e)} \sum_n a_n (\lambda_-(E))^n \tag{11}$$

with $\lambda_-(E) \rightarrow 0$ as $E \rightarrow \infty$. Hence, $\lim_{E \rightarrow \infty} V_\infty(E) = S^{(e)} a_0$.

Now consider a population of such excitatory neurons with all-to-all coupling such that the net rate of excitation E impinging on an individual neuron is determined by the average firing rate of the population. Within a mean-field approximation, the steady-state behaviour is then given by the self-consistency condition [19]

$$\beta E = f(V^\infty(E)) \quad f(V) = \frac{f_{max}}{1 + e^{-\gamma(V-\kappa)}} \quad (12)$$

where β , γ and κ are constants, and the sigmoid function $f(V)$ represents the instantaneous firing rate of a neuron. The maximum firing rate f_{max} is determined by the absolute refractory period. Using graphical methods [19,20], it can be shown that there are two stable solutions to (12), one corresponding to the quiescent state $E = 0$ and the other to a state with firing rate well below f_{max} . Note that if the voltage-dependent modulation of the membrane time constant were neglected, then $V^\infty(E)$ would be linear in E and the second stable state would have a firing rate close to f_{max} .

Another consequence of the input-dependent modulation of membrane time constants is the influence of background synaptic activity. Indeed, recent experiments have found that variations in background activity can lead to the membrane time constant taking a range of values between 5–80 ms [1,2]. In our previous paper [3], we included background activity into the above neural network model by assuming that there is an additional time-independent random background contribution to the inhibitory rate I_n such that $I_n = \sum_{m \neq n} E_m + \xi_n$. The ξ_n were distributed randomly across the population of neurons according to a site-independent probability density $\rho(\xi)$. Mean-field arguments now result in the self-consistency condition $\beta E = \langle f(V^\infty(E)) \rangle_\xi$. Using the fact that the network settles into a state of low firing rate, the function f can be linearized so that the evaluation of the steady-state firing rate reduces to the problem of calculating the Laplace transform of the ensemble-averaged Green's function $\langle G_{0n}(t) \rangle_\xi$ where $G(t) = e^{t(Q^{(0)} + \text{diag}(\xi))}$. Exploiting the formal similarity between our compartmental model and the tight-binding alloy model describing excitations on a disordered lattice [5,6], a coherent potential approximation scheme can be used to perform the ensemble averaging. This involves taking each dendritic compartment to have an effective site-independent background activity $\Lambda(E)$ for which the associated Green's function is $G(E) = G^{(0)}(E + \Lambda(E))$. The self-energy term $\Lambda(E)$ is assumed to take into account any statistical fluctuations (at least at the single-site level), and this leads to a self-consistency condition for $\Lambda(E)$. Solving this self-consistency condition, we can then determine the average firing rate [3].

In this paper, we extend the above analysis to the case of time-dependent stochastic background activity. For concreteness, suppose that each neuron of the network has the pattern of stimulation given by (2) together with (i) a constant site-independent background contribution I and (ii) a stochastic contribution $\xi_n(t)$ at compartment or site n ,

$$I_n(t) = \sum_{m \neq n} E_m + \xi_n(t) + I. \quad (13)$$

We shall assume that the stochastic process $\xi_n(t)$ is generated independently for each neuron (cross-correlations between neurons are zero) according to a multi-component dichotomous coloured noise process [13,14]. That is, $\xi_n(t) = \sum_{i=1}^M \xi_n^{(i)}(t)$ where each $\xi_n^{(i)}(t)$ is a stationary dichotomous coloured noise process and the composed process is determined completely in terms of the first and second moments

$$\langle \xi_n^{(i)}(t) \rangle = 0 \quad \langle \xi_n^{(i)}(t) \xi_m^{(j)}(t') \rangle = \delta_{ij} \delta_{nm} \gamma^2 \exp(-\lambda|t - t'|). \quad (14)$$

Here $\langle \dots \rangle$ denotes averaging over the stochastic process, γ is the strength of the background fluctuations, and λ^{-1} is the correlation time. Note that the composed process $\xi_n(t)$ jumps

between the values $\pm\gamma\pm, \gamma\pm\dots\pm\gamma$ (M terms). On physical grounds, we require that $I + \xi(t) \geq 0$ for all n (since this quantity represents a rate of inhibition). This leads to the condition $M\gamma \leq I$.

Substituting equations (2) and (13) into (1) leads to the stochastic differential equation

$$\frac{d}{dt}V(t) = Q(t)V(t) - EV(t) + ES^{(e)}\alpha \quad (15)$$

with $S^{(i)} = 0$,

$$Q(t) = (Q^{(0)} - I)V(t) + Q^{(1)}(t)V(t) \quad Q_{mn}^{(1)}(t) = -\xi_n(t)\delta_{n,m} \quad (16)$$

and α is a vector whose components α_n determine the distribution of excitation across the dendritic chain. Equation (15) describes a system perturbed by multiplicative coloured noise. In general, it is not possible to analyse such systems without some further simplifying approximations, for example, taking a white noise limit so that Fokker-Planck techniques can be used [11]. However, for our particular model such simplifications will not be necessary since we can treat the effects of the noise exactly. It is clear from equations (16) and (4) that the constant background I reduces the time constant τ according to $\tau^{-1} \rightarrow \tau^{-1} + I$.

Integrating equation (15) and neglecting transients we obtain

$$V_m(t) = E \int_0^t \sum_n \alpha_n e^{-E(t-t')} G_{mn}(t, t') dt' \quad (17)$$

where

$$G(t, t') = T \left[\exp \left(\int_{t'}^t Q(t'') dt'' \right) \right] \quad (18)$$

and T denotes the time-ordering operator. That is, $T[Q(t)Q(t')] = Q(t)Q(t')\theta(t-t') + Q(t')Q(t)\theta(t'-t)$ where $\theta(x) = 1$ if $x \geq 0$ and $\theta(x) = 0$ if $x < 0$. Note that time-translation invariance no longer holds as shown by the fact that $G(t, t')$ does not simply depend on the time difference $t-t'$. However, this invariance is recovered when the Green's function is averaged over the stochastic process since the latter is a stationary process. Thus we can define an averaged Green's function H such that

$$H(t-t') = \langle G(t, t') \rangle. \quad (19)$$

It follows that the averaged somatic membrane potential has a unique steady-state given by

$$\langle V^\infty(E) \rangle = S^{(e)} E \sum_n \alpha_n H_{0n}(E) \quad (20)$$

where $H(E)$ is the Laplace transform of the averaged Green's function $H(t)$. Using mean-field arguments and a linear output function f , (which is reasonable since we are interested in the state of low firing rate), the level of excitation E in the network is determined by the self-consistency condition (cf [3])

$$\beta E = \langle V^\infty(E) \rangle + \alpha \quad (21)$$

for constants α and β .

In section 3 we calculate the average Green's function $H(t)$ using techniques from non-equilibrium statistical physics. However, those not interested in the technical details can go straight to section 4 where the results of our analysis are presented.

3. Calculation of average Green's function

In this section, we calculate the Laplace transform of the averaged single-neuron Green's function, $H(E)$, by exploiting the formal similarity between the stochastic compartmental model equation (15) and the dynamical equation describing excitons moving on a one-dimensional lattice with random modulations of the local energy at each site [12–14]. The latter is a well known example of a physical system in a heat bath. We can then solve the mean-field equation (21) to determine the average firing rate of the compartmental model network.

3.1. Dynamical coherent potential approximation

The bare Green's function $G(t, t_0)$ of (18) satisfies the differential equation

$$\frac{d}{dt}G(t, t_0) = Q(t)G(t, t_0) \quad G(t_0, t_0) = 1. \quad (22)$$

Following Sumi [12], we use a *dynamical coherent potential approximation* to replace the random fluctuations $\xi_n(t)$ appearing in the matrix $Q(t)$ of (16) by an effective site-independent constant synaptic background Λ . The associated Green's function is

$$\hat{G}(t) = \exp(t\hat{Q}) \quad \hat{Q} = Q^{(0)} - (\Lambda + I)1. \quad (23)$$

It follows that the Laplace transform $\hat{G}(E) = G^{(0)}(E + \Lambda + I)$. The self-energy term Λ is determined by a self-consistency condition, which ensures that any statistical fluctuations at the single-site level are taken into account. Within this coherent potential approximation, the averaged Green's function $H(E)$ appearing in the mean-field equation (20) is simply $\hat{G}(E)$.

The derivation of the self-consistency condition for Λ proceeds along analogous lines to [12]. First, write the matrix $Q(t)$ as

$$Q_{mn}(t) = [\hat{Q}]_{mn} + (\Lambda - \xi_m(t))\delta_{mn}. \quad (24)$$

The background Λ is determined by the condition that statistical fluctuations arising from the second term on the right-hand side vanish at each single site. (Under the coherent potential approximation one neglects multi-site correlations). It then suffices to consider a compartmental model in which temporal fluctuations occur at only one site $n = 0$, say. The corresponding matrix \hat{Q} is

$$\begin{aligned} \tilde{Q}_{mn}(t) &= \hat{Q}_{mn} + (\Lambda - \xi_0(t))\delta_{m0}\delta_{n0} \\ &= \tilde{Q}_{mn}^{(0)} + \tilde{Q}_{mn}^{(1)}(t) \end{aligned} \quad (25)$$

with

$$\tilde{Q}_{mn}^{(0)} = \hat{Q}_{mn} + \Lambda\delta_{m0}\delta_{n0} \quad \tilde{Q}_{mn}^{(1)}(t) = -\xi_0(t)\delta_{m0}\delta_{n0}. \quad (26)$$

Define a new pair of Green's functions

$$\tilde{G}^{(0)}(t) = \exp(t\tilde{Q}^{(0)}) \quad (27)$$

$$\tilde{H}(t) = \left\langle T \left[\exp \left(\int_0^t \tilde{Q}(t') dt' \right) \right] \right\rangle. \quad (28)$$

Under the coherent potential approximation, the Green's function $\hat{G}(E)$ calculated using \hat{Q} should equal the averaged Green's function $\hat{H}(E)$ obtained using $\tilde{Q}(t)$. In order to determine Λ it is sufficient to consider the particular component $m = n = 0$ [12]. Setting

$\hat{g}(E) = \hat{G}_{00}(E)$, $g(E) = \bar{G}_{00}^{(0)}(E)$ and $h(E) = \bar{H}_{00}(E)$ we have the self-consistency condition

$$h(E) = \hat{g}(E) \equiv G_{00}^{(0)}(E + \Lambda + I). \quad (29)$$

Below we shall show that $h(E)$ depends on Λ through its dependence on $g(E)$, where the latter is approximated by

$$g(E) = [\hat{g}(E)^{-1} - \Lambda]^{-1}. \quad (30)$$

3.2. Single-site dynamical disorder and the method of partial cumulants

Dynamical CPA has reduced the problem to one of calculating the averaged Green's function $h(E)$ of a compartmental model with *single-site* dynamical disorder. The latter can be achieved using the *time-convolution generalized master equation* (TC-GME) approach [15] and the method of *partial cumulants* [16, 17]. Consider the Green's function equation

$$\frac{d}{dt} G(t, t_0) = \bar{Q}(t) G(t, t_0) \quad G(t_0, t_0) = \mathbf{1}. \quad (31)$$

In the generalized master equation approach, one averages (31) without first solving it; this naturally leads to the partial cumulants, which can be calculated explicitly. To achieve the averaging procedure, it is convenient to introduce the projection operator \mathcal{P} , which *averages everything to the right of it* and to let $\mathcal{L} = 1 - \mathcal{P}$. By definition, $\bar{H} = \mathcal{P}G$. The operator \mathcal{P} commutes with any deterministic matrix such as $\bar{Q}^{(0)}$, that is, $\mathcal{P}\bar{Q}^{(0)} = \bar{Q}^{(0)}\mathcal{P}$. The vanishing of the first moment in (14) implies that $\mathcal{P}\bar{Q}^{(1)}(t)\mathcal{P} = 0$. Acting from the right on both sides of equation (31) with the operator \mathcal{P} or \mathcal{L} , we obtain the two equations

$$\frac{d}{dt} \mathcal{P}G(t, t_0) = \bar{Q}^{(0)}\mathcal{P}G(t, t_0) + \mathcal{P}\bar{Q}^{(1)}(t)\mathcal{L}G(t, t_0) \quad (32)$$

and

$$\frac{d}{dt} \mathcal{L}G(t, t_0) = \{\bar{Q}^{(0)} + \mathcal{L}\bar{Q}^{(1)}(t)\}\mathcal{L}G(t, t_0) + \bar{Q}^{(1)}(t)\mathcal{P}G(t, t_0). \quad (33)$$

Solving for the quantity $\mathcal{L}G(t, t_0)$ by integrating equation (33) and using the identity $G(t_0, t_0) = \mathbf{1}$, we obtain an integro-differential equation for the averaged Green's function,

$$\frac{d}{dt} \bar{H}(t) = \bar{Q}^{(0)}\bar{H}(t) + \int_0^t K(t-t')\bar{H}(t') dt' \quad (34)$$

where K is the so-called memory operator of this time-convolution generalized master equation

$$K(t-t') = \mathcal{P}\bar{Q}^{(1)}(t)T \left[\exp \left(\int_0^{t'} [\bar{Q}^{(0)} + \mathcal{L}\bar{Q}^{(1)}(t')] dt' \right) \right] \bar{Q}^{(1)}(t'). \quad (35)$$

In equation (34), we have exploited the time translation invariance of the averaged Green's function to set $t_0 = 0$.

In order to calculate the memory operator, we perform an expansion of the time-ordered exponential in (35), which effectively corresponds to a power series expansion in the background strength γ (equations (14) and (26) imply that $\bar{Q}^{(1)}(t) \approx \gamma$). Since the random background is now assumed to impinge on a single compartment alone (single-site modulation), one finds that the memory operator matrix $K(t)$ has a single non-zero matrix element, that is, $K_{mn}(t) = k(t)\delta_{m,0}\delta_{n,0}$ with

$$k(t) = \sum_{n=1}^{\infty} \int_0^t dt_{2n-2} \dots \int_0^{t_2} dt_1 c^{(2n)}(0, t_1, \dots, t_{2n-2}, t) \prod_{i=1}^{2n-1} \bar{G}_{00}^{(0)}(\tau_i). \quad (36)$$

Here $\tau_i = t_i - t_{i-1}$, $i = 1, \dots, 2n-1$ (with $t_0 = 0$, $t_{2n-1} = t$), $\tilde{G}^{(0)}(t)$ is the Green's function in zero time-varying background (equation (27)), and $c^{(2n)}(0, t_1, \dots, t)$, $n = 1, 2$ are the partial cumulants for the stochastic process $\xi(t)$,

$$c^{(2n)}(0, t_1, \dots, t_{2n-2}, t) = \mathcal{P}\xi(t)\mathcal{L}\xi(t_{2n-2})\mathcal{L}\dots\mathcal{L}\xi(t_1)\mathcal{L}\xi(0). \quad (37)$$

Note that all partial cumulants of odd order are zero due to the fact that the stochastic process has zero mean.

The partial cumulants for dichotomous coloured noise are calculated in [17] using diagrammatic techniques. It turns out that $c^{(2n)}$ depends on the same set of time differences τ_i as appears in the product on the right-hand side of (36) such that the individual terms of the expansion (36) display a multi-convolution form. Therefore, as shown in [17, 13], we can Laplace transform equation (36) and after some rearrangement express $k(E)$ as a continued fraction

$$k(E) = \frac{\gamma^2 \theta_1^M}{g(E + \lambda)^{-1} - \frac{\gamma^2 \theta_2^M}{g(E + 2\lambda)^{-1} - \frac{\gamma^2 \theta_3^M}{\dots - \frac{\gamma^2 \theta_M^M}{g(E + M\lambda)^{-1}}}} \quad (38)$$

where λ^{-1} is the correlation time, $\theta_k^M = k(M+1-k)$ and $g(E)$ is given by equation (30). Note that the continued fraction can be rewritten in the standard form

$$\frac{1}{a_1 + \frac{1}{a_2 + \frac{1}{\dots + \frac{1}{a_M}}}} \quad (39)$$

where

$$a_k = b_k/g(E + k\lambda) \quad b_k = -\frac{1}{\theta_k^M \gamma^2 b_{k-1}} \quad b_1 = \frac{1}{\gamma^2 \theta_1^M}. \quad (40)$$

It is clear that $\{b_1, b_2, \dots, b_M\}$ forms an alternating sequence. This differs from the analogous quantum mechanical expression [13] where the b_k 's are all positive. The source of this difference is that in the quantum mechanical setting the various matrix operators are multiplied by a factor $-i/\hbar$, which leads to the insertion of a term $(-1)^{n+1}$ into the sum over n in (36). The presence of an alternating sequence means that $k(z)$ can have singularities for real z . However, these singularities will be absent in our model since the matrix $\tilde{Q}^{(0)} + \tilde{Q}^{(1)}(t)$ has negative definite eigenvalues, which reflects the passive nature of the system.

Having obtained the Laplace transform of the memory operator, we can now proceed to solve (34). Laplace transforming both sides of (34) gives

$$H(E) = [EI - \tilde{Q}^{(0)} - K(E)]^{-1}. \quad (41)$$

A series expansion and an application of Dyson's equation then yields

$$\tilde{H}_{mn}(E) = \tilde{G}_{mn}^{(0)}(E) + \frac{\tilde{G}_{m0}^{(0)}(E)k(E)\tilde{G}_{0n}^{(0)}(E)}{1 - k(E)g(E)}. \quad (42)$$

3.3. Self-consistency condition for effective synaptic background

We conclude that using dynamical CPA, the averaged Green's function is approximated by

$$H(E) \approx G^{(0)}(E + \Lambda(E) + I) \tag{43}$$

where $\Lambda(E)$ satisfies the self-consistency condition (29). The latter involves the averaged Green's function $h(E)$ of a compartmental model with single-site disorder, which can be obtained using the method of partial cumulants. In particular, setting $m = n = 0$ in (42),

$$h(E) = \frac{g(E)}{1 - k(E)g(E)}. \tag{44}$$

Combining equations (29) and (30) into (44) one finds that the self-consistency condition for Λ reduces to

$$\Lambda = -k(E, \Lambda). \tag{45}$$

The dependence of $k(E)$ on the background field through the presence of $g(E)$ in equation (38) has been made explicit. As we shall now demonstrate, equation (45) yields a unique non-zero solution for the effective background satisfying $\Lambda(E) < 0$. First, consider the case $M = 1$. Equations (38), (45) and (30) yield the self-consistency condition

$$\Lambda = -\gamma^2 g(E + \lambda) = -\frac{\gamma^2}{\hat{g}(E + \lambda)^{-1} - \Lambda}. \tag{46}$$

This is a quadratic in Λ which has the solution

$$\Lambda = \frac{1}{2}[\hat{g}(E + \lambda)^{-1} - \sqrt{\hat{g}(E + \lambda)^{-2} + 4\gamma^2}] \tag{47}$$

(only the negative square root is valid since we require $\Lambda(E) \rightarrow 0$ as $\gamma \rightarrow 0$). Although $\hat{g}(E)$ itself depends on Λ (equation (29)), it is clear from (47) that $\Lambda(E) < 0$. Equation (46) is the extension of our previous result for static disorder (equation (4.18) of [3]) to the case of dynamical disorder. The dynamical nature of the process is reflected by the presence of the correlation time λ^{-1} ; the static result is recovered in the limit $\lambda \rightarrow 0$.

To explore the dependence of the effective background on λ , we shall consider the limits of weak and strong disorder. The degree of disorder is measured by $\delta = \gamma\tau'/2$. For small δ (weak disorder),

$$\Lambda(E) \approx -\gamma^2 G_{00}^{(0)}(E + \lambda) = -\frac{\gamma^2 \tau'}{2\sqrt{\left(1 + \frac{\tau'(E + I + \lambda + \tau^{-1})}{2}\right)^2 - 1}} \tag{48}$$

where we have used equations (9) and (29). On the other hand, in the case of strong disorder, $\hat{g}(E) \approx (E + I + \Lambda + \tau^{-1})^{-1}$ so that

$$\Lambda(E) \approx -\frac{\gamma^2}{E + I + \lambda + \tau^{-1}}. \tag{49}$$

In both cases, we see that the size of the effective background $|\Lambda(E)|$ is a monotonically decreasing function of λ with $\Lambda(E) \rightarrow 0$ as $\lambda \rightarrow \infty$.

Next consider the case $M = 2$. The self-consistency condition now becomes

$$\Lambda = -\frac{2\gamma^2}{g(E + \lambda)^{-1} - 2\gamma^2 g(E + 2\lambda)}. \tag{50}$$

Equation (30) and some algebra leads to the equation

$$\Lambda[1 - \Lambda\hat{g}(E + \lambda)][1 - \Lambda\hat{g}(E + 2\lambda)] = 2\gamma^2\hat{g}(E + \lambda)[2\hat{g}(E + 2\lambda)\Lambda - 1]. \tag{51}$$

By continuity from the solution $\Lambda(E) = 0$ at $\gamma^2 = 0$, we see that the only physical solution to equation (49) satisfies $\Lambda(E) < 0$. That is, when $\gamma^2 \ll 1$ we find that $|\Lambda| \ll 1$ and hence $\hat{g}(E + \lambda)\Lambda < 1$, $2\hat{g}(E + 2\lambda)\Lambda < 1$. Thus for small γ^2 the term in square brackets on the left-hand side of (51) is positive whilst the right-hand side is negative, which means that $\Lambda < 0$. This solution remains negative for all γ^2 . Similarly, one can show that the effective synaptic background is negative for any M . However, it should be noted that the physical restriction $M\gamma < I$ implies that $\gamma^2 \rightarrow 0$ as $M \rightarrow \infty$. Thus within the constraints of the model only low order dichotomous noise process will give a significant effect. In all cases $|\Lambda(E)|$ is a decreasing function of λ .

4. Results for average firing rate

The main results of the analysis of section 3 are as follows:

(i) The average Green's function $H(E)$ can be approximated by

$$H(E) \approx G^{(0)}(E + \Lambda(E) + I) \quad (52)$$

where $G^{(0)}$ is the Green's function for a uniform dendritic chain of compartments, equation (9), I is the constant component of the background and $\Lambda(E)$ is an effective background arising from the random fluctuating part $\xi_n(t)$ (see equation (13)). The effective background can be obtained by solving the self-consistency condition (45).

(ii) The effective background is negative, $\Lambda(E) < 0$, for all E .

(iii) $|\Lambda(E)|$ is a monotonically increasing function of the variance γ^2 and the correlation time λ^{-1} of the dichotomous coloured noise process $\xi_n(t)$.

Inspection of (5), (8) and (52) then shows that for a given excitatory input E the synaptic background given by (13) leads to a modification in the membrane time constant τ of the form

$$\tau^{-1} \rightarrow \tau^{-1} + I - |\Lambda(E)|. \quad (53)$$

As discussed in section 2, a reduction of the membrane time constant due to a constant (in space and time) synaptic background I results in a lowering of the steady-state firing rate of a recurrent compartmental model network. The analysis of this paper shows that the opposite effect occurs in the presence of a fluctuating background, as represented by the dichotomous noise process $\xi_n(t)$. Averaging over this process leads to a negative contribution to the effective background activity, which increases τ and hence the firing rate. The size of this negative contribution grows as one increases either the variance γ^2 or the correlation time λ^{-1} .

To give a simple illustration of the above, consider single-component dichotomous noise, and assume for simplicity that excitatory inputs only impinge on compartment $n = 1$, that is, $a_n = \delta_{n,1}$. Combining equations (20), (21) and (43), the steady-state firing rate of the network (in the linear approximation) is then $f = \beta E^*$ where E^* is the solution to the mean-field equation

$$\beta E = S^{(e)} E G_{01}^{(0)}(E + I + \Lambda(E)) + \alpha \quad (54)$$

and $\Lambda(E)$ is the solution to (46). The variation of the firing rate f with the variance γ^2 and λ is shown in figures 2 and 3, respectively. We have taken parameter values $\alpha = 0$, $\beta = 0.02$, $\tau = 1$ (which fixes the time-scale), $\tau' = 5$ and $S^{(e)} = 1$ (which fixes the units of the membrane potential). The constant component has the value $I = 1$, which corresponds to a reduction in τ by a factor of 2; the maximum allowed value of γ is then

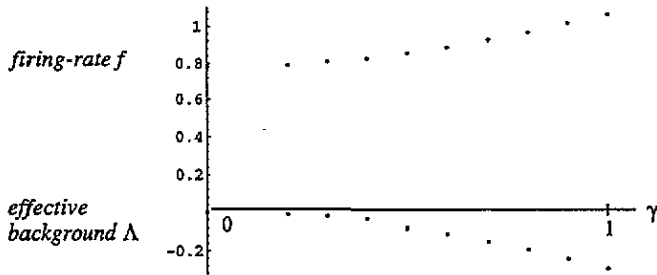


Figure 2. Firing rate f and effective background Λ as a function of standard deviation γ of single component dichotomous coloured noise process. Time is measured in units of τ^{-1} .

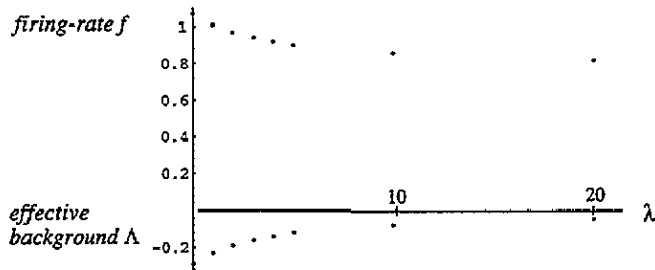


Figure 3. Firing rate f and effective background Λ as a function of inverse correlation time λ .

1. It is clear from figures 2 and 3 that f increases with γ (for $\lambda = 0$) but decreases with λ (for $\gamma = 1$). It can be seen that the maximum size of the effective reduction in background activity is approximately 0.3, which is almost a third of the constant level I ; hence, the effect of fluctuations is not negligible for this choice of parameters. It should be noted, however, that the results are sensitive to the particular value of τ' . For example if $\tau' \ll \tau$, then the effect of fluctuations is much smaller. The appropriate value of τ' is very much model-dependent, since it is determined by the particular geometry of the neurons. The time constant τ , on the other-hand, is more of a universal quantity being approximately independent of the geometry. Very similar results to the above are obtained when $M = 2$ and equation (50) is used to determine $\Lambda(E)$.

5. Discussion

Recent experiments indicate that due to shunting, variations in background synaptic activity can produce a range of values for the membrane time constant of a neuron between 5–80 ms. We have explored one consequence of such a feature, namely the effect of a fluctuating background on the steady-state firing rate of a recurrent network. In particular, we have shown that a fluctuating background leads to an increase in the firing rate compared to a constant background of the same average intensity. Such an increase grows with the variance and the correlation time of the underlying coloured noise process. We expect such a result to be quite general, that is, it does not require the stochastic background to be a dichotomous coloured noise process nor the distribution of external inputs to have the special form of non-recurrent lateral inhibition. For example, following [14] one could easily extend our analysis to incorporate a more general stochastic process that interpolates between dichotomous, Gaussian and compound Poisson processes. Other choices for the

distribution of inputs E_n across each neuron's compartments could be handled using some form of perturbation expansion about the uniform case considered here. A more interesting and difficult question concerns how spatial correlations in the distribution of stochastic background activity across the network affects the average firing rate.

Another possible extension of our analysis is studying the effects of a fluctuating background on the linear response of a lateral inhibitory network [22]. (Such a system can be described in terms of coupled differential equations almost identical in form to those of a compartmental model neuron). Here one is concerned with Fourier rather than Laplace transforms of the averaged Green's function so that E is replaced by $i\omega$ where ω is the frequency of response. Consequently, the self-energy contribution Λ becomes complex leading to a non-trivial modification in both the phase and amplitude of response.

Finally, given that background activity can influence the behaviour of a biological neural network, it is of interest to determine whether or not there is some mechanism for controlling such background activity (by the release of neuromodulators?), and if so, how this mechanism could be exploited by the system? We hope to explore this and other issues elsewhere.

References

- [1] Bernander O, Douglas R J, Martin A C and Koch C 1991 *Proc. Natl Acad. Sci. USA* **88** 11 569
- [2] Rapp M, Yarom Y and Segev I 1992 *Neural Comput.* **4** 518
- [3] Bressloff P C 1994 *J. Phys. A: Math. Gen.* **27** 4097
- [4] Holmes W R and Woody C D 1989 *Brain Res.* **505** 12
- [5] Ziman J M 1979 *Models of Disorder* (Cambridge: Cambridge University Press)
- [6] Elliott R J, Krumhansl J A and Leath P L 1974 *Rev. Mod. Phys.* **46** 465
- [7] Tuckwell H C 1988 *Introduction to Theoretical Neurobiology*. (Cambridge: Cambridge University Press)
- [8] Engel A K, Konig P, Krieter A K, Schillen T B and Singer W 1992 *Trends Neurosci.* **15** 218
- [9] Deppisch J, Pawelzik K, Geisel T 1994 *Biol. Cybern.* **71** 387
- [10] Kubo R 1963 *J. Math. Phys.* **4**, 174
- [11] Bulsara A R, Maren A J and Schnera G 1993 *Biol. Cybern.* **70** 145
- [12] Sumi H 1977 *J. Chem. Phys.* **67**, 2943
- [13] Chvosta P 1992 *Z. Phys. B* **86** 419
- [14] Neu P and Speicher R 1994 *Z. Phys. B* **95** 101
- [15] Nakajima S 1958 *Prog. Theor. Phys.* **20** 948
Zwanzig R 1960 *J. Chem. Phys.* **33** 1338
Mori H 1965 *Prog. Theor. Phys.* **33** 127
- [16] Terwiel R H 1974 *Physica* **74** 248
- [17] Mayurama K and Shibata F 1988 *Physica* **149A** 447
- [18] Koch C and Segev I (eds) 1989 *Methods in Neural Modeling* (Boston, MA: MIT Press)
- [19] Abbott L F 1991 *Network* **2**, 245
- [20] Bressloff P C and Taylor J G 1993 *J. Phys. A: Math. Gen.* **26**, L165
- [21] Bressloff P C and Taylor J G 1993 *Phys. Rev. E* **47** 2899
- [22] Bressloff P C 1995 *Phys. Rev. E* submitted