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J. Stat. Mech. (2013) P03010

(http://iopscience.iop.org/1742-5468/2013/03/P03010)

Journal of Statistical Mechanics: Theory and Experiment
An IOP and SISSA journal

Towards a self-consistent description of irregular and asynchronous cortical activity

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Received 6 July 2012
Accepted 22 October 2012
Published 12 March 2013

Online at stacks.iop.org/JSTAT/2013/P03010
doi:10.1088/1742-5468/2013/03/P03010

Abstract. Experimental evidence shows that cortical activity exhibits correlated variability, often referred to as noise correlations. Reported correlation coefficients cover a wide range of values, from moderate to very small ones. There is an evident need of models and mathematical techniques with which to guide the interpretation of these results. However, the very existence of correlated variability is responsible for the technical difficulties that have prevented theory from making enough progress in determining how noise correlations are related to neuron and network properties. Here we review recent work that we have done to develop a program to study these issues. Given that noise correlations depend on the behavioral state, understanding how they are generated is a critical problem that has to be solved before biophysical models can be used to study behavioral tasks.

Keywords: neuronal networks (theory), population dynamics (experiment), neural code, computational neuroscience

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1742-5468/13/P03010+19$33.00

Contents

1. Introduction

The statistical properties of the firing activity of cortical networks depend on the behavioral state [1]–[4]. For instance, one of the phases of sleep is characterized by slow wave oscillation (<1 Hz) [5]. These oscillations persist when subjects awaken but remain quiet, but they disappear as they become active [6, 2]. At this point the cortical activity is characterized by spikes fired at seemingly random times, producing irregular firing patterns. This type of cortical activity—the activated state—is rather variable. If an experiment is repeated several times under the same conditions, the precise firing response of the neurons is different in each trial [7, 8]. This trial-to-trial variability is often referred to as 'noise', although its origin is not understood well. When two neurons are registered simultaneously it is noticed that the variability is correlated, however correlations are smaller in the activated state [2].

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Correlated variability appears in a variety of experiments [9]–[11] and is usually called noise correlation. Noise correlations vary within a wide range of values, depending on the experiment and on the behavioral state. Correlation coefficients of the spike-count (the number of spikes fired by a neuron during a time window of a given size) about 0.1–0.2 have been reported in sensory areas [10, 12], while values about 0.02–0.05 have been found in prefrontal areas when animals perform simple tasks [13] but also when they make perceptual decisions [14].

Two recent experiments found even lower values in sensory areas [15, 16]. Comparison of correlation coefficients obtained in different experiments has to be done cautiously because data are frequently registered under different conditions and correlations are defined differently. Correlations between *components* of the currents afferent to two neurons (i.e., the excitatory or the inhibitory parts of the current) have larger values [17]. Auto-correlations are also important; Poisson firing implies that the spike-count has a variance-to-mean ratio (Fano factor) equal to one, contradicting experimental observations (see, for instance, [8]).

Understanding this rather complex situation requires the development of models and mathematical techniques that could be used to study how neuron and network features affect the statistical properties of cortical activity. This has been one of the main objectives of our work. Regarding noise correlations, we aim to understand how they originate and propagate in cortical networks and ultimately how they are related to behavior.

From a technical perspective, we would like to find analytical methods to predict network activity properties such as population-averaged firing rates, Fano factors, correlation coefficients and auto- and cross-correlation functions. Briefly, the mathematical approach can be described as follows. One first characterizes input currents by their first- and second-order statistics. Then moments of the spiking activity of single cells and pairs of neurons receiving these currents, possibly filtered by synaptic receptors, are computed analytically. This gives a set of expressions for the firing activity moments that depend on moments of the current. Since in recurrent networks the afferent current is determined by the firing rate and spiking correlations of neurons in the network, these expressions form a set of self-consistency equations, the solution of which gives the model prediction of the cortical activity.

This program involves solving several problems: (i) predicting the firing rates of neurons receiving correlated currents [18, 19] evaluating correlation functions [20]; (ii) estimating the effect of synaptic filtering [21, 22]; (iii) defining the network features relevant to study noise correlations [15]; (iv) deriving the self-consistency equations for population-averaged quantities; and (v) developing methods to solve the self-consistency equations.

In this paper we will describe recent efforts that we have made to deal with these issues. To be useful, models should be realistic and, at the same time, be simple enough to be tractable; the choice of the relevant neuron and network features can determine the success of the approach to predict cortical activity. In the next section we discuss two of these features: strong synaptic couplings and dense network connectivity. We also define the activated state, the activity regime where we have focused our research work. The self-consistent approach used to solve the model is sketched in section 3. These ideas are applied to a network of binary neurons (section 4) and to a network of spiking neurons (section 5). After that we discuss how correlations could be related to behavior and give

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an example of how they can be modulated by internal processing (section 6). A discussion is given in section 7.

2. The recurrent network for cortical activity

Understanding the statistics of the neural activity in recurrent networks is a basic step that has to be taken before using neural network models to explain behavior. Network statistics may depend on anatomical features defining the network architecture as well as on the dynamics of the synaptic and neural components, such as synaptic filters and membrane properties. Solving the problem may be very complex. To make progress in the prediction of activity properties and to develop the theoretical techniques required for the analysis, one should find those features which plausibly are the determinants of the network behavior and use them in solvable models. Here this approach is reflected in the way the main features are selected, both at the neuron and network level. We will consider two simple model neurons, binary [23] and integrate-and-fire neurons [24, 25]. The network will be taken with a dense connectivity (otherwise current components correlations would not be present) and with strong synaptic connections (otherwise the activation of a large pre-synaptic population would be needed to produce a finite response).

In this section we first discuss these two basic requirements for the connectivity and the strength of the synaptic connections. After that we give a precise notion of asynchronous activity.

2.1. Strong coupling and densely connected networks

It would be technically convenient that correlations could be neglected in a theory of the activated (also called asynchronous) state, because in this case only the self-consistency equation for the population-averaged firing rates are needed and they could be solved easily.

However two characteristic features of cortical networks, (i) network connectivity is large (we will say that the network is densely connected) and (ii) synaptic couplings are strong, induce us to think that correlations should be included in the analysis. The existence of a network state characterized by weak correlations should be part of the solution of the model, not of its definition.

Network connectivity in the cortex is appreciable [26] and even weak correlation coefficients can have a large effect on the neuron firing rate [27, 18]. On the other hand, synaptic efficacy has to be strong to guarantee that the activation of a fraction of cells is enough to induce firing of the post-synaptic neurons. These facts greatly complicate the mathematical analysis of the statistics of the firing activity in recurrent networks. Perhaps for this reason most theoretical studies have neglected noise correlations by assuming that neurons are sparsely connected [28, 29, 53].

To define these two notions more precisely, let us consider a network with $N_{\rm p}$ populations and N cells in each of them. A given neuron is denoted as (αi), where $\alpha = 1, \ldots, N_{\rm p}$ is the population index and $i = 1 \ldots N$. Typically $N_{\rm p}$ is taken equal to three, and α takes the values E (excitatory population), I (inhibitory population) and X (external population).

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The synaptic connection from neuron (βi) to (αj) is denoted as $J_{ij}^{\alpha\beta}$. In the models considered here it is zero for unconnected neurons while for connected neurons it takes values that depend only on the two populations. Non-zero synapses are strong, i.e. a small population of $O(\sqrt{N})$ active cells produce an effect $O(N^0)$ on a post-synaptic neuron. This is achieved by scaling the synaptic efficacies as $j_{\alpha\beta}/\sqrt{N}$, where $j_{\alpha\beta}$ is $O(N^0)$ [23]. Denoting the connection probability between populations α and β by $p_{\alpha\beta}$, the probability of a non-zero value of the synaptic efficacy $J_{ij}^{\alpha\beta}$ is

$$P\left(J_{ij}^{\alpha\beta} = \frac{j^{\alpha\beta}}{\sqrt{N}}\right) = p_{\alpha\beta}. \tag{1}$$

The network is dense because $p_{\alpha\beta}$ is $O(N^0)$, hence a given neuron is connected, on average, to $O(N)$ cells.

2.2. The asynchronous state

We are interested in a network regime where, in the absence of stimulation, the population-averaged correlations are weak. More precisely, we want to see whether large densely connected networks of strongly coupled neurons can have a regime with population-averaged correlations behaving as $O(1/N)$. We take this property as the definition of the asynchronous state [30].

Let us make a remark on the apparent contradiction between the requirements imposed to the connectivity and the existence of an asynchronous state. An analytical proof that this is indeed possible was given in [15] for networks of binary neurons. Later, in section 4, we will review that work and in section 5 we will show how to deal with a model of spiking neurons. The strategy to address these problems is as follows: one first assumes that the dense network has an asynchronous steady state. Using this hypothesis one writes down expressions for the population-averaged firing rates, auto-correlations and pair-wise correlations (the macroscopic equations). Finally, one shows that these equations have a solution in which the network is indeed asynchronous, that is, correlations scale as $O(1/N)$.

3. Self-consistency analysis

In a cortical recurrent network the neurons' output firing activity contributes to the synaptic input of their post-synaptic cells. Since the activity of neurons in a homogeneous population must have the same statistics, its moments must satisfy self-consistency relationships. The goal is to obtain a set of equations mapping the input population-averaged values of the relevant dynamical variables of the network to their output values. To make this notion more explicit let us write the generic form of self-consistency equations for the first- and second-order statistics. The relevant variables are the steady state population-averaged firing rate ν_α, the auto-correlation function $a_\alpha(\tau)$ and the cross-correlation function $r_{\alpha\beta}(\tau)$. The self-consistency equations read $(\alpha, \beta = 1, \ldots, N_\mathrm{p})$

$$\nu_\alpha = G_\nu(\nu_\gamma, a_\gamma, r_{\gamma\delta}) \tag{2}$$

$$a_\alpha(\tau) = G_a(\nu_\gamma, a_\gamma, r_{\gamma\delta}) \tag{3}$$

$$r_{\alpha\beta}(\tau) = G_r(\nu_\gamma, a_\gamma, r_{\gamma\delta}), \tag{4}$$

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for each population α and pairs of populations α, β. Indices γ and δ in the arguments of the three functions run over the $N_{\rm p}$ neural populations. The dependence on ν_γ, a_γ and $r_{\gamma\delta}$ is through the input currents to the neurons. In a recurrent network the first- and second-order moments of the firing activity appear as input and output variables and the equations should be solved self-consistently.

Finding equations (2)–(4) is not easy, even for simple models such as networks of leaky integrate-and-fire (LIF) neurons. Even in cases where such equations can be obtained (e.g. recurrent networks of binary neurons [15] and of LIF neurons with slow synaptic filtering), extracting the self-consistent solution requires some care.

The problem is easier if pair-wise correlations are neglected. In this case only single neuron quantities are required. It is even simpler if one assumes a given fixed form for the auto-correlation function (e.g. Poisson firing) because the problem is reduced to finding the neuron firing rate in a completely uncorrelated noisy network. This is equivalent to a problem solved long ago [31] and the self-consistency procedure can then be carried out on a single equation for each population [28]. The next stage in difficulty is to include single neuron second-order statistics [32, 33]. This allows to find in a self-consistent way both the average firing rate and the Fano factor (see section 5.3).

If pair-wise correlations are taken into account, the first thing to do is to derive mathematical expressions for the firing rate and the auto-correlation function of individual cells and for the pair-wise cross-correlation functions, when neurons receive noisy correlated activity. After taking into account the dependence of the currents on the network firing activity and averaging over neurons (pairs of neurons for cross-correlations), one obtains the explicit form of equations (2)–(4).

4. Networks of binary neurons

Here we briefly review the work in [15] on the self-consistent equations for a network of binary neurons.

4.1. Microscopic equations

The dynamics of networks of binary neurons has been described several times [30, 23, 15]. Here we give the main expressions required for the discussion of the self-consistency problem.

The state of neuron (α, i) is denoted by $\sigma_i^\alpha = 0, 1$. The probability that a neuron changes its state from σ_i^α to $1 - \sigma_i^\alpha$ is $w(\sigma_i^\alpha)$. The state of the whole network at time t is the vector $\vec{\sigma} = \{\sigma_i^\alpha\}$. Following Glauber [34], the probability $P(\vec{\sigma}, t)$ that the network is in state $\vec{\sigma}$ at time t obeys the master equation

$$\frac{\mathrm{d}}{\mathrm{d}t}P(\vec{\sigma},t) = -P(\vec{\sigma},t)\sum_{\alpha i}^{N_{\rm p},N} w(\sigma_i^\alpha) + \sum_{\alpha i}^{N_{\rm p},N} P(\vec{\sigma}(i^*),t)w(1-\sigma_i^\alpha), \tag{5}$$

where $\vec{\sigma}(i^*)$ differs from state $\vec{\sigma}$ only in the state of neuron (α, i). The transition probabilities are

$$w(\sigma_i^\alpha) = \frac{1}{\tau_\alpha}[\sigma_i^\alpha - \Theta(h_i^\alpha)]^2 \tag{6}$$

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$$w(\sigma_i^X) = \frac{1}{2\tau_X}[1 - (2\sigma_i^X - 1)(2M_i^X - 1)], \tag{7}$$

where Θ is the Heaviside function and M_i^X is the mean activity of cell i in the external population X, a parameter of the model. The afferent current h_i^α to neuron (αi) is

$$h_i^\alpha = \sum_{\beta}^{E,I,X} \sum_{j}^{N} J_{ij}^{\alpha\beta}\sigma_j^\beta - \theta_i^\alpha, \tag{8}$$

where θ_i^α is a threshold parameter (neuron (αi) is not included in the sum). We are interested in the steady state first- and second-order firing statistics given by the mean firing rate m_i^α, the temporal variance of the activity a_i^α and the zero-lag cross-correlation function $r_{ij}^{\alpha\beta}$

$$m_i^\alpha = \langle\sigma_i^\alpha\rangle; \qquad a_i^\alpha = \langle(\delta\sigma_i^\alpha)^2\rangle; \qquad r_{ij}^{\alpha\beta} = \langle\delta\sigma_i^\alpha\delta\sigma_j^\alpha\rangle, \tag{9}$$

where $\langle\cdot\rangle$ denotes averaging over the stochastic process and $\delta y = y - \langle y\rangle$. From the master equation (5) we obtain

$$m_i^\alpha = \langle\Theta(h_i^\alpha)\rangle \tag{10}$$

$$m_i^X = M_i^X \tag{11}$$

$$(\tau_\alpha + \tau_\beta)r_{ij}^{\alpha\beta} = \tau_\alpha\langle\delta\sigma_i^\alpha\delta\Theta(h_j^\beta)\rangle + \langle\delta\Theta(h_i^\alpha)\delta\sigma_j^\beta\rangle\tau_\beta \tag{12}$$

$$(\tau_\alpha + \tau_X)r_{ij}^{\alpha X} = \langle\delta\Theta(h_i^\alpha)\delta\sigma_j^X\rangle\tau_X. \tag{13}$$

4.2. Population-averaged firing rates and correlations

Equations (10)–(13) are expressions for the microscopic quantities, that is, for the firing rates and auto-correlations of individual neurons and for pair-wise correlations. We are interested in computing the corresponding population-averaged quantities. To obtain them we have to perform two different averages: over the stochastic process and over neurons in the same homogeneous population. To compute the first of these averages we notice from equation (8) that each h_i^α is the sum of a large number of stochastic variables. Invoking the central limit theorem, the probability distribution of h_i^α could be approximated well by a Gaussian distribution for large networks, provided that those variables are independent or only weakly correlated [35]. This is the case in the asynchronous regime for which the average correlations are $O(1/N)$ (note that this is our working hypothesis, which has to be checked at the end). This means that the averages in the above equations can be obtained as integrals over correlated Gaussian variables. Consequently, they will be functions of the steady state values of the mean current and the zero-lag auto- and cross-correlations (μ_i^α, c_i^α and $c_{ij}^{\alpha\beta}$, respectively),

$$\mu_i^\alpha \equiv \lim_{t\to\infty}\langle h_i^\alpha(t)\rangle; \qquad c_i^\alpha \equiv \lim_{t\to\infty}\langle(\delta h_i^\alpha(t))^2\rangle; \qquad c_{ij}^{\alpha\beta} \equiv \lim_{t\to\infty}\langle\delta h_i^\alpha(t)\delta h_j^\beta(t)\rangle. \tag{14}$$

To average over neurons in a given population we use a technique, which is standard in the statistical physics of disordered systems [36], consisting in invoking the self-averaging property and, instead of averaging over neurons, averaging over different realizations of the synaptic efficacies, according to equation (1).

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In summary, the way to proceed is to first use a Gaussian distribution for the synaptic currents h_i^α. Once this is done, the microscopic equations appear as integrals over Gaussian variables. Then, the macroscopic equations for the population-averaged firing rates and correlations are obtained by averaging the microscopic equations over the distribution of synaptic efficacies. This gives the following result for the population-averaged cross-correlations (for further details see [15]).

$$(\tau_\alpha + \tau_X) r_{\alpha X} = \left[\epsilon \tilde{J}_{\alpha X} a_X + \frac{1}{\epsilon} \sum_{\gamma=E,I} \tilde{J}_{\alpha\gamma} r_{\gamma X} \right] \tau_X \tag{15}$$

$$(\tau_\alpha + \tau_\beta) r_{\alpha\beta} = \epsilon \tilde{J}_{\alpha\beta} a_\beta \tau_\beta + \frac{1}{\epsilon} \left[\sum_{\gamma=E,I} \tilde{J}_{\alpha\gamma} r_{\gamma\beta} + \tilde{J}_{\alpha X} r_{X\beta} \right] \tau_\beta + \alpha \longleftrightarrow \beta. \tag{16}$$

Here $\epsilon = 1/\sqrt{N}$ was taken as a small parameter. We have defined the notation $\tilde{J}_{\alpha\beta} = (\partial m_\alpha / \partial \mu_\alpha) J_{\alpha\beta}$, where $J_{\alpha\beta} \equiv p j_{\alpha\beta}$ is $O(\epsilon^0)$ (in equation (1) we have taken $p_{\alpha\beta} = p$). Importantly, we have also used equations (8) and (14) to express the right hand side of these equations in terms of the population-averaged firing rate m_α, temporal variance of the spiking activity a_α, and cross-correlation $r_{\alpha\beta}$

$$m_\alpha = \frac{1}{N} \sum_i^N m_i^\alpha \tag{17}$$

$$a_\alpha = \frac{1}{N} \sum_i^N a_i^\alpha \tag{18}$$

$$r_{\alpha\beta} = \frac{1}{N^2} \sum_{i,j}^N r_{ij}^{\alpha\beta}. \tag{19}$$

Likewise, averaging the current moments in equation (14) we obtain the quantities μ_α, c_α and $c_{\alpha\beta}$. Using equation (8), the population-averaged current covariance between the total currents afferent to neurons in populations α and β can be expressed in terms of the spike statistics

$$c_{\alpha\beta} = \sum_\gamma^{E,I,X} J_{\alpha\gamma} a_\gamma J_{\gamma\beta}^t + \frac{1}{\epsilon^2} \sum_{\gamma\lambda}^{E,I,X} J_{\alpha\gamma} r_{\gamma\lambda} J_{\lambda\beta}^t. \tag{20}$$

The covariances between the components γ and λ of the currents afferent to neurons in populations α and β are

$$c_{\gamma\lambda}^{\alpha\beta} = \delta_{\gamma\lambda} J_{\alpha\gamma} a_\gamma J_{\lambda\beta}^t + \frac{1}{\epsilon^2} J_{\alpha\gamma} r_{\gamma\lambda} J_{\lambda\beta}^t. \tag{21}$$

Then, the total current covariance is decomposed in terms of the covariances between its excitatory, inhibitory and external components as

$$c_{\alpha\beta} = c_{EE}^{\alpha\beta} + c_{II}^{\alpha\beta} + c_{XX}^{\alpha\beta} + 2(c_{EI}^{\alpha\beta} + c_{EX}^{\alpha\beta} + c_{IX}^{\alpha\beta}). \tag{22}$$

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Notice that the terms in equations (20) and (21) containing a_γ are contributions from shared inputs while the terms containing $r_{\gamma\lambda}$ come from correlations between pre-synaptic inputs.

4.3. Correlation balance relationships in binary networks

A perturbation analysis in ϵ yields, to leading order, the solution of the self-consistent equations (15) and (16)

$$r_{EX} = \epsilon^2 A_E a_X + O(\epsilon^3) \tag{23}$$

$$r_{IX} = \epsilon^2 A_I a_X + O(\epsilon^3) \tag{24}$$

$$r_{EE} = \epsilon^2 (A_E^2 a_X - a_E^{(0)}) + O(\epsilon^3) \tag{25}$$

$$r_{II} = \epsilon^2 (A_I^2 a_X - a_I^{(0)}) + O(\epsilon^3) \tag{26}$$

$$r_{EI} = \epsilon^2 A_E A_I a_X + O(\epsilon^3), \tag{27}$$

where $a_E^{(0)}$ and $a_I^{(0)}$ are the $O(\epsilon^0)$ temporal variances of the spiking activity and

$$A_E = \frac{J_{EI}J_{IX} - J_{II}J_{EX}}{J_{EE}J_{II} - J_{EI}J_{IE}}; \qquad A_I = \frac{J_{IE}J_{EX} - J_{EE}J_{IX}}{J_{EE}J_{II} - J_{EI}J_{IE}}. \tag{28}$$

These equations explicitly show that correlations in the binary network are indeed small, in spite of the dense connectivity and strong couplings. In fact they are $O(\epsilon^2)$, in agreement with the initial assumption about correlations in the activated state (section 2.2). This result can be explained in terms of a dynamical phenomenon [15]. In short, they are the consequence of a mechanism consisting in the tracking of fluctuations in the population-averaged activities. The inhibitory firing rate $m_I(t)$ tracks the excitatory one $m_E(t)$ and both track the external firing activity $m_X(t)$. At large N both $m_E(t)$ and $m_I(t)$ are proportional to $m_X(t)$. We will refer to the result given in equations (23)–(27) by saying that in a recurrent network population-averaged correlations are balanced.

The covariance between the total currents afferent to a pair of neurons, equation (20), is also small. Indeed, one can show that the correlation balance equations imply that total current covariances are $O(\epsilon)$. This comes about from cancellations between recurrent feedback and contributions from the external input. This is easily checked by replacing the $O(\epsilon^2)$ correlation coefficients (equations (23)–(27)), A_E and A_I (equation (28)) in the expression of the population-averaged total current covariance (equation (20)).

In contrast, the current component covariances, equation (21), are $O(\epsilon^0)$. This is a crucial difference between sparse and dense networks, since for sparse networks correlations between current components are defined to be zero. The sparse and dense regimes also differ in their prediction on the width of the distribution of spiking correlation coefficients, which in densely connected networks is $O(\epsilon)$; since their mean is $O(\epsilon^2)$, this implies that negatively correlated pairs appear in about the same number as positively correlated ones [15].

We can also discriminate between correlation coefficients of pairs of neurons with a direct recurrent connection and pairs with only indirect connections. The effect of a direct connection is $O(\epsilon)$, which is small when compared with the net effect of shared inputs or with the net effect of firing correlations between inputs, which are both $O(\epsilon^0)$. However,

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because of the cancellation between these two contributions, correlations are affected by the presence of a direct connection (Supplementary online material in [15]).

Networks of inhibitory neurons are described in the same way, arriving to balance equations for the correlation coefficients r_{II} and r_{IX} similar to equations (23)–(27):

$$r_{IX} = \epsilon^2 A'_I a_X + O(\epsilon^3) \tag{29}$$

$$r_{II} = \epsilon^2 (A'^2_I a_X - a_I^{(0)}) + O(\epsilon^3), \tag{30}$$

where $A'_I = -J_{IX}/J_{II}$. The population-averaged covariance between the total currents afferent to inhibitory neurons in the recurrent network is related to the spiking activity moments by

$$c_{II} = \sum_{\gamma}^{I,X} J_{I\gamma} a_\gamma J^t_{\gamma I} + \frac{1}{\epsilon^2} \sum_{\gamma\lambda}^{I,X} J_{I\gamma} r_{\gamma\lambda} J^t_{\lambda I}. \tag{31}$$

Again, replacing here the $O(\epsilon^2)$ correlation coefficients given by equations (29)–(30) we obtain $c_{II} \sim O(\epsilon)$. Writing the total current covariance in terms of the covariances between its external and recurrent components

$$c_{II} = c^{II}_{II} + c^{II}_{XX} + 2c^{II}_{IX}, \tag{32}$$

we notice that, similarly to what happens with the total current covariance in the network with excitatory and inhibitory populations (equation (22)), the $O(\epsilon)$ behavior of c_{II} comes from cancellations between recurrent feedback and contributions from the external input.

5. Networks of LIF neurons

5.1. LIF neurons

The equation for the membrane potential of a leaky integrate-and-fire neuron (αi) is

$$\tau_{\rm m} \frac{\mathrm{d}}{\mathrm{d}t} V_i^\alpha(t) = -V_i^\alpha(t) + \tau_{\rm m} I_i^\alpha(t), \tag{33}$$

where $\tau_{\rm m}$ is an effective membrane time constant and $I_i^\alpha(t)$ is the synaptic current. In this model a spike is emitted when V_i^α reaches a threshold value θ. Then the potential is reset to a value H. We set the resting potential at 0 mV. In the network, each neuron obeys an equation like the one above. $I_i^\alpha(t)$ contains the contribution of the spikes produced by the cells pre-synaptic to neuron (αi), filtered with a characteristic synaptic time constant $\tau_{\rm s}$

$$\tau_{\rm s} \frac{\mathrm{d}}{\mathrm{d}t} I_i^\alpha(t) = -I_i^\alpha(t) + \sum_{(\gamma j,k)} J_{ij}^{\alpha\gamma} \delta(t - t^\gamma_{j,k}), \tag{34}$$

here $t^\gamma_{j,k}$ is the arrival time of the kth spike from pre-synaptic neuron (γj).

Since the number of input spikes is large and the effect of one spike on a post-synaptic neuron is small we can replace the point process by a Gaussian one [31]. The filter equation becomes

$$\tau_{\rm s} \frac{\mathrm{d}}{\mathrm{d}t} I_i^\alpha(t) = -I_i^\alpha(t) + \mu_\alpha + \sigma_\alpha \eta_i^\alpha(t) \tag{35}$$

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where μ_α is the mean current, $\sigma_\alpha^2/2\tau_s$ is the current variance and η_i^α is a Gaussian noise with unit variance.

Later, in section 5.5, we will need the firing rate of a LIF neuron receiving a deterministic constant current I_0. This is

$$\nu_i^{\alpha(0)}(I_0) = \frac{1}{\tau_m}\left[\ln\left(\frac{\tau_m I_0 - H}{\tau_m I_0 - \theta}\right)\right]^{-1} \tag{36}$$

for $I_0 > \theta/\tau_m$ and zero otherwise.

5.2. Spiking first- and second-order statistics

We denote the spike train produced by neuron (αi) as

$$\rho_i^\alpha(t) = \sum_k \delta(t - t_{i,k}^\alpha) \tag{37}$$

where $t_{i,k}^\alpha(t)$ indicates the time when the neuron emitted its kth spike. The firing rate of this neuron is given by

$$\nu_i^\alpha(t) = \left\langle \sum_k \delta(t - t_{i,k}^\alpha) \right\rangle, \tag{38}$$

and the firing auto- and cross-correlation functions are

$$C_i^\alpha(t_1, t_2) = \left\langle \left(\sum_k \delta(t_1 - t_{i,k}^\alpha) - \nu_i^\alpha\right)\left(\sum_l \delta(t_2 - t_{i,l}^\alpha) - \nu_i^\alpha\right)\right\rangle \tag{39}$$

$$C_{ij}^{\alpha\beta}(t_1, t_2) = \left\langle \left(\sum_k \delta(t_1 - t_{ik}^\alpha) - \nu_i^\alpha\right)\left(\sum_l \delta(t_2 - t_{jl}^\beta) - \nu_j^\beta\right)\right\rangle. \tag{40}$$

The auto-correlation function $C_i^\alpha(t_1, t_2)$ gives the excess joint probability with respect to independent events that the neuron fires at times t_1 and t_2. Similarly $C_{ij}^{\alpha\beta}(t_1, t_2)$ is the excess joint probability with respect to independent spiking that neurons (αi) and (βj) fire at times t_1 and t_2. Although these are covariances, here we will refer to them as correlations. We are interested in a steady state of the network activity. When this regime is reached the firing rate becomes independent of time and the correlation functions depend only on the time difference. We then define the steady state auto- and cross-correlation functions

$$a_i^\alpha(\tau) \equiv \lim_{t\to\infty} C_i^\alpha(t, t+\tau) \tag{41}$$

$$r_{ij}^{\alpha\beta}(\tau) \equiv \lim_{t\to\infty} C_{ij}^{\alpha\beta}(t, t+\tau). \tag{42}$$

We aim to study population-averaged moments of the firing activity, which we define as

$$\nu_\alpha = \frac{1}{N_\alpha}\sum_i^{N_\alpha} \nu_i^\alpha \tag{43}$$

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$$a_\alpha(\tau) = \frac{1}{N_\alpha} \sum_i^{N_\alpha} a_i^\alpha(\tau) \tag{44}$$

$$r_{\alpha\beta}(\tau) = \frac{1}{N_\alpha N_\beta} \sum_{i,j}^{N_\alpha, N_\beta} r_{ij}^{\alpha\beta}(\tau) \tag{45}$$

(N_α and N_β are large). Finally, current auto- and cross-correlation functions (covariances) are defined as

$$c_i^\alpha(t_1, t_2) = \langle \delta I_i^\alpha(t_1) \delta I_i^\alpha(t_2) \rangle \tag{46}$$

$$c_{ij}^{\alpha\beta}(t_1, t_2) = \langle \delta I_i^\alpha(t_1)\ \delta I_j^\beta(t_2) \rangle, \tag{47}$$

and their steady state population-averaged values are $c_\alpha(\tau)$ and $c_{\alpha\beta}(\tau)$.

5.3. Single neuron self-consistency analysis of recurrent LIF networks

In the simplified situation in which pair-wise correlations are neglected, the self-consistency problem contains only the equations for the firing rate and auto-correlations. In this case the neuron's firing is not Poissonian and the Fano factor is not necessarily equal to one. These temporal correlations in the spike trains emitted by the neurons are seen by the post-synaptic cells as correlated input currents.

The effect of input correlations on the firing rate has been studied in [18, 19]. Although the current consists of spikes, if the number of action potentials is large and the effect of individual events is small, then the point process can be replaced by a continuous Gaussian process; this is the diffusion approximation [31]. Clearly, in this approximation only the first- and second-order moments of the current affect the neurons' firing rates. The basic result is that spiking correlations contribute to firing through an additional term to the current variance. The output firing rate has the same functional form as in the uncorrelated case (studied in [31]), but with the white noise variance replaced by an effective variance (for details see [19]).

We studied this self-consistency problem in [32, 33]. Apart from the mathematical formulation that we have just sketched, we were interested in explaining why in working memory tasks cortical activity is rather irregular both before a first stimulus is presented and during the delay period [37, 38]. Models typically fail to explain the irregularity during the delay period (experiments show that it is larger than during the fixation period). The reason for this failure is that even if models succeed in describing the activity during the pre-stimulation period as a regime dominated by current fluctuations, they erroneously predict that during the delay period the network is in a mean-driven regime. This yields regular firing activity.

The model in [33] proposed that local inhibition (inhibition selective to the stimulus) should be included together with selective excitation, both forming selective microcolumns. Since local inhibition can balance selective excitation, application of a stimulus puts the network in a fluctuation-driven regime that persists during the delay period. Experimental evidence about the existence of selective inhibition [39] makes plausible the idea that selective inhibition could be a solution to the problem.

The model proposed in [33] succeeds in finding a higher irregularity during the memory period. However it does not avoid another drawback, common to most working memory

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models (see e.g. [40]). If the potentiation parameter (the coupling between neurons in the same selective population) is too weak the network lacks bistability, whereas if it is too strong the network jumps to the persistent activity state spontaneously. The range of values of the potentiation parameter for which bistability is robust is too narrow and setting its value requires some degree of tuning.

There have been other attempts to deal with this problem. It is possible that other biophysical mechanisms, such as short-term synaptic plasticity [41, 42], contribute to the increase in the irregularity of the regime of persistent activity. Another proposal includes a Hopfield memory structure besides the random excitatory connections, but still obtains low coefficients of variations [43]. However, the question of whether the higher irregularity of the persistent state can be explained in terms of purely static synaptic properties still remains open. It has recently been observed that inhibitory spike timing-dependent plasticity increased the irregularity in a memory model [44], but this issue has not been studied in multi-stable networks.

5.4. LIF neurons with a slow synaptic filter

In section 5.3 we have discussed a self-consistent analysis neglecting pair-wise correlations. Several technical issues prevent us, for the moment, from finding a general self-consistent solution for all values of the model parameters. The large connectivity, and the presence of correlated current components and of synaptic filtering are the main factors responsible for these difficulties.

However the full input–output mapping in equations (2)–(4) can be obtained when there is at least one slow synaptic filter. This is a realistic condition, the cortical state we are describing is characterized by a high conductance [45], which implies a short effective membrane time constant (i.e., $\tau_{\rm m} \sim 5$ ms), as has been observed *in vivo* [46]. On the other hand, $GABA_A$ receptors have a characteristic time of about 10 ms [47, 48]. Hence, there is at least one receptor type with a characteristic time-scale longer than the integration time of the membrane. Since we are considering a version of the LIF model based on currents, this condition is implemented by choosing a synaptic characteristic time longer than the effective membrane time constant ($\tau_{\rm s} > \tau_{\rm m}$).

5.5. Self-consistency equations for recurrent LIF networks

Here we write down the set of self-consistent equations for networks of LIF with one slow filter. We start by presenting the equations for the firing rate and auto-correlation function of a LIF neuron [18, 21, 49, 20, 33, 19, 22] and the spiking activity cross-correlation function of a pair of LIF neurons [20], when neurons receive correlated noise[1].

If the neural dynamics is faster than the synaptic characteristic time ($\tau_{\rm s}$) then, during a time interval T shorter than $\tau_{\rm s}$ the afferent current ($I(t)$) will be reasonably constant. Therefore, at that time-scale neuron (αi) will fire with a constant rate $\nu_i^{\alpha(0)}(I)$ (given in equation (36)). If the current distribution in the steady state $P(I)$ is known, then the probability density that the neuron emits a spike can be computed by averaging the firing

[1] The firing rate of conductance-based LIF neurons with short effective membrane time constant was obtained in [49].

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rate produced by a current frozen at the value I, $\nu_i^{\alpha(0)}(I)$, with $P(I)$ [21, 22]

$$\nu_i^\alpha = \int \mathrm{d}I\, P(I)\nu_i^{\alpha(0)}(I). \tag{48}$$

Since in the diffusion approximation the current distribution is a Gaussian, we only need to know the mean and variance of $I(t)$.

The steady state auto-correlation function, $a_i^\alpha(\tau)$, between the spiking activity of neuron (αi) at time t_1 and the same neuron at time t_2 can be approximated in a similar way [20]

$$a_i^\alpha(\tau) \equiv \lim_{t_1\to\infty} C_i^\alpha(t_1, t_1+\tau) = \int \mathrm{d}I_1\, \mathrm{d}I_2\, P_a(I_1, I_2; \tau)\nu_i^{\alpha(0)}(I_1)\nu_i^{\alpha(0)}(I_2), \tag{49}$$

where $P_a(I_1, I_2; \tau)$ is the joint probability that the afferent current to neuron (αi) at the times t_1 and $t_2 = t_1 + \tau$ are, respectively, I_1 and I_2. It depends on the means μ_i^α and the auto-correlations $c_i^\alpha(\tau)$ of the currents.

Finally, the steady state cross-correlation function $r_{ij}^{\alpha\beta}(\tau)$ between the spiking activity of neuron (αi) at time t_1 and neuron (βj) at $t_2 = t_1 + \tau$ is, in the same approximation,

$$r_{ij}^{\alpha\beta}(\tau) \equiv \lim_{t_1\to\infty} C_{ij}^{\alpha\beta}(t_1, t_1+\tau) = \int \mathrm{d}I_1\, \mathrm{d}I_2\, P_\mathrm{c}(I_1, I_2; \tau)\nu_i^{\alpha(0)}(I_1)\nu_j^{\beta(0)}(I_2). \tag{50}$$

$P_\mathrm{c}(I_1; I_2; \tau)$ is the joint current probability density of having an input current I_1 to neuron (αi) at time t_1 and an input current I_2 to neuron (βj) at t_2. This equation can be understood as follows. The first neuron receives a current I_1 at time t_1, while the second receives the current I_2 at time t_2. Since current fluctuations are slow, at those times the neurons fire with probabilities $\nu_i^{\alpha(0)}(I_1)$ and $\nu_j^{\beta(0)}(I_2)$, respectively. Equation (50) simply states that the two-point correlation function of the output spike trains is the average of the product of the instantaneous firing rates of the two neurons evaluated at times t_1 and t_2. This average of instantaneous firing rates over synaptic currents approximates the average over stochastic realizations of the spikes in equation (40). P_c depends on the current cross-correlation function $c_{ij}^{\alpha\beta}(\tau)$.

In these expressions the effect of input correlations on ν_i^α, $a_i^\alpha(\tau)$ and $r_{ij}^{\alpha\beta}(\tau)$ is taken into account by the dependence of $\nu_i^{\alpha(0)}$ on the effective current variance and by the dependence of P_a and P_c on current correlations coefficients [18, 20, 19, 22, 33].

The self-consistency equations are obtained by expressing the current moments in terms of the moments of the spiking activity ν_i^α, $a_i^\alpha(\tau)$ and $r_{ij}^{\alpha\beta}(\tau)$. The relationship between population-averaged current and firing activity moments is similar to equation (20), although now there appear convolutions due to synaptic filtering. The current correlation still has two terms, one coming from the contribution of shared inputs—containing the spiking auto-correlation—and the other reflecting the presence of pair-wise correlations in the network.

In the above presentation we assumed that the total current came from a single, slow synaptic channel. In general there are several synaptic types and some of them can be fast. However the above equations can be generalized provided that there is at least one slow filter [21, 22]. The presence of a fast channel only affects the form of the firing response to a constant current, $\nu_i^{\alpha(0)}(I)$. If the fast channel is characterized by a variance σ_f, then

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the effective constant current has the form $I = \mu + \sigma_f z$, where z is a Gaussian current fluctuation and $\nu_i^{\alpha(0)}(I)$ is given by an expression derived in [31].

5.6. Correlation balance relationships in LIF networks

An analysis of the self-consistency equations (48)–(50) shows the existence of balance relationships for correlations in the LIF network [50]. Simulations for the case in which the synaptic characteristic times of excitatory and inhibitory currents are the same confirm that spiking correlations coefficients scale as $1/N$ [51]. However one can expect that the cancellation of current correlations do not take place under some conditions; for instance, inhibitory tracking of excitatory fluctuations becomes more difficult as the difference between the inhibitory and excitatory synaptic time constants increases. This is seen in the simulated model and in a recent study of the effect of $GABA_B$ receptors on the slow oscillations in rodent cortical slices [52].

5.7. Other approaches to deal with self-consistent solutions of networks of spiking neurons

Recently there have been other efforts to describe the activity of networks of spiking neurons self-consistently [53]–[56]. As we have described in previous sections, we have studied a network of spiking neurons by assuming that neurons interact strongly, equation (1), and are densely connected. Another possibility is to assume neural interactions are very weak. For example, in [53] a neuron is connected to $N_c \to \infty$ neurons and $J \sim O(1/N_c)$ (or, equivalently, $N_c \gg 1$ is kept fixed but $J \to 0$). In this case the network is, at leading order, decorrelated by construction; for instance

$$C_{ij}^{\alpha\alpha}(t_1, t_2) = \delta_{ij}\delta(t_1 - t_2)\nu_i^{\alpha}(t_1). \tag{51}$$

Correlations can only appear as finite size corrections. To obtain them, Toyoizumi *et al* wrote up a master equation for the probability of a given state of the network and from it they derived a set of self-consistent equations. The solution of these equations yields finite size corrections to cross-correlations behaving as $1/N_c$. However, the strongly and the weakly interacting regimes give quite different predictions. To explain the large correlations between the current components using a weakly coupled network requires the adjustment of N_c. In contrast, in the strongly coupled regime these are always finite. These two regimes also differ in their prediction about the presence of negatively correlated neuron pairs. In the strongly coupled regime there are almost as many negatively as positively correlated neuron pairs because the width of the distribution of correlation coefficients is $O(N^{-1/2})$.

Another way to deal with the self-consistency problem is to consider a large but finite size network and set the model parameters at their physiological values. Finding a solution requires the use of some approximation. This has been done in [54]–[56] to study networks of LIF neurons using the linear response approximation. Their results confirmed the existence of cancellations, responsible for decorrelation. The work in [54, 55] addressed the issue of how different connectivity motifs contribute to spiking correlations: when the model parameters are kept finite and fixed, not only direct common inputs and direct connections between a pair of neurons but also more complex motifs with unidirectional chains and indirect common inputs contribute to the correlation.

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The self-consistency problem is still the subject of very active research. The work in [15] made the interesting proposal that the activity of cortical networks could be described as a strong coupling and densely connected regime, obtaining observable predictions on neural correlations. The properties of this regime have not been yet fully explored and the emergence of a time-scale related to tracking has still to be clarified. It is not clear that linear systems can do it. On the other hand, linearization makes the problem tractable and within certain limits (see e.g. [54] for a discussion on limitations of this approach) it can provide useful information on correlations in neural networks.

6. Noise correlations and behavior

We have seen that a cortical state characterized by irregular and very weakly correlated firing can emerge in spite of the existence of strong and dense connections [15, 51, 50]. However population-averaged correlation values larger than those predicted by these networks have been observed. If recurrent networks have very small current correlations, how do the observed correlations originate?

In fact, it has been argued that correlated activity is needed to explain experimental results in perceptual decision-making tasks [57]. In these experiments the activity of individual neurons contains information about the subject's decision [58, 59]. In the absence of correlations one would conclude that decisions are processed by rather small neural populations. But this is unlikely because neurons with activity correlated to behavior are found easily. The alternative explanation is that decision making is processed by larger and correlated neural populations [57].

Motivated by these issues we have recently studied [14] noise correlations between pairs of neurons recorded simultaneously while monkeys performed a decision-making task consisting in detecting a somatosensory stimulus [60, 59]. The subject reported his decision by pushing one of two buttons after a delay period. The stimulus was present in only fifty per cent of the trials and when it was applied its amplitude could be below or above the subject's detection threshold. Importantly, the stimulation time was chosen randomly. The uncertainty present in this task makes it very difficult for the subject to know whether, in a given trial, the stimulus has been applied or not.

We found that noise correlations (and firing rates) are modulated through all stages of the task, in a way that depends on the reported decision. The answer to the question of whether correlations can be small is affirmative. Correlation coefficients become on the order of 0.05 towards the end of the delay period, when supposedly the decision has already been taken, and also—in some trials—during the pre-stimulation period. On the other hand, they can become larger (on the order of 0.2–0.3) during other stages of the task, e.g. during the stimulation period and, most remarkably, during the pre-stimulation period, at the time when the conditions of the experiments make it possible to *infer* that the stimulus could have been applied. Data analysis and modeling work are consistent with the hypothesis that the registered prefrontal areas can have rather small noise correlations, however these correlations can be modulated by an internally generated signal, common to a population of neurons in the decision pool. Changes in neuronal excitability, due to the signal, increase correlation coefficients above the baseline value $\sim$0.05. This signal fluctuates slowly and greatly influences the decision reported by the subject.

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7. Discussion

The analysis of noise correlations can be an important approach to study how the brain processes information. They are modulated by behavior [1]–[4] and in perceptual decision-making tasks they fluctuate according to the subject's decision [14]. Understanding how information processing in the brain is related to correlated variability requires the development of models and analytical tools. These could allow us to explore systematically how neuron and network properties affect correlations.

Here we have reviewed our work on the design of mathematical techniques to study network activity. We have first found the response of single neurons and of pairs of neurons to correlated input currents [18, 20, 22]. Then we have used these results to write self-consistency equations from which a solution for firing rates and correlations can be derived. An important ingredient in the theory is the fact that network connectivity has to be dense [15].

We have described how, under some conditions, a recurrent network can cancel correlations induced by common inputs. This is an unexpected result which is difficult to infer given the complexity of neural phenomena. The next stage is to investigate how correlations are produced. There are many possible factors which can contribute to correlated variability. The existence of a variety of temporal scales in the cortical network can spoil the tracking mechanism responsible for the cancellation of correlations [51]. Besides, correlations could originate from changes of excitability in the neural population produced by trial-to-trial fluctuating signals. Yet another issue one would like to know is how the cancellation of correlations affects macroscopic signals.

Future work should address these and other questions; to make progress, analytical methods should still be improved and extended to deal with more realistic systems.

Acknowledgments

Most of the work reviewed here was done in collaboration with F Carnevale, J de la Rocha, J Manrique, R Moreno-Bote and A Renart, to whom I am also indebted for many stimulating discussions. Funding was provided by the Spanish MICINN FIS 2009-09433.

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