Supplementary material 1

to "Correlated connectivity and the distribution of firing rates in the neocortex"

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The emergence of log-normal distribution in neural nets.

1. Introduction

The goal of this note is to formulate and address the seeming paradox that emerges in the studies of the distribution of synaptic strengths in the cortex and the distribution of spontaneous rates. The basic findings can be summarized as follows.

(1) The synaptic weights between pairs of cells chosen randomly are described by the log-normal distribution (LND, defined below) (Song et al., 2005).

(2) The spontaneous rates of cells are also distributed log-normally (LN) (Hromadka et al., 2008).

Simplistically, these two facts contradict to each other, because the spontaneous rates in a large network with LN weights distributed randomly and with no correlation are expected to have well-defined values, distributed narrowly, according to the Gaussian distribution. This statement will be addressed below in detail. Thus, if this statement were true, the experimental fact #2 appears to be in conflict with the fact #1. Since the random LN matrix with no correlations between elements appears to contradict these finding, correlations between network weights are expected. We address possible class of correlations that can make these experimental observations consistent with each other. Finally, we propose a non-linear multiplicative learning rule that can yield the proposed correlations.

The note is organized as follows. In Section 2 we describe the properties of the LND that will be useful in the further analysis. In Section 3 we describe the connection between the spontaneous firing rates and the principal eigenvector problem for synaptic weight matrix. In Section 4 we define the random matrices with uncorrelated elements that we call *regular*. In Section 5 we describe the properties of the principal eigenvectors of regular matrices. In this section we formulate the contradiction between two experimental finding listed above. In Section 6 we describe the properties of weight matrices that *do* have correlations between their elements of the type that yields LND for both synaptic weights and spontaneous rates. This section therefore resolves the paradox stated above. In Section 7 we introduce the type of Hebbian learning rules that yield correlations needed to resolve the paradox. Section 8 lists some motivations for the latter learning rule that make it biologically plausible. Finally in Section 9 we solve the equations of the learning rules.

2. The log-normal distribution

Consider a variable $x > 0$ whose logarithm $\xi = \ln x$ has a normal distribution, i.e.

$$\rho(\xi) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(\xi-\xi_0)^2/2\sigma^2} , \tag{1}$$

where σ and ξ_0 are the standard deviation and the mean respectively. The distribution function of x is obtained by assuming $\rho(x)dx = \rho(\xi)d\xi$ that leads to

$$\rho(x) = \rho[\xi(x)] \frac{d\xi(x)}{dx} = \frac{1}{x\sqrt{2\pi\sigma^2}} e^{-[\ln(x/x_0)]^2/2\sigma^2} , \tag{2}$$

where $x_0 = e^{\xi_0}$. The probability distribution (2) is called LND. By changing variables to ξ it is easy to calculate various moments of this distribution i.e.

$$\overline{x^n} \equiv \int_0^\infty x^n \rho(x)dx = x_0^n e^{\sigma^2 n^2/2} . \tag{3}$$

Important for us will be the first and the second moments:

$$\overline{x} = x_0 e^{\sigma^2/2} \tag{4}$$

and

$$\overline{x^2} = x_0^2 e^{2\sigma^2} . \tag{5}$$

The variance of the distribution (also called dispersion) is

$$D(x) = \overline{x^2} - \left(\overline{x}\right)^2 = x_0^2 e^{\sigma^2} \left(e^{\sigma^2} - 1\right) \tag{6}$$

It grows exponentially with increasing σ.

3. The spontaneous activity

We adopt here the simplest model for the network dynamics that is described by linear equations

$$f\left(t+\Delta t\right)=Wf\left(t\right)+i\left(t\right) \tag{7}$$

Here $f\left(t\right)$ is the column-vector describing the firing rates of N neurons in the network at time t. The input vector $i(t)$ represents the external inputs. The square weight matrix W describes the synaptic weights in the system.

In the absence of synaptic inputs we obtain

$$f(t+\Delta t)=Wf(t)\,. \tag{8}$$

Spontaneous firing rate is defined here as the average over time firing rate in the absence of external inputs:

$$f\equiv\overline{f(t)} \tag{9}$$

Spontaneous firing rate is therefore a right eigenvector of the synaptic weight matrix with the eigenvalue equal to one

$$f=Wf \tag{10}$$

It is therefore the eigenvector that does not decay over time. The other eigenvectors of W are expected to decay as a function of time. They are expected to have the eigenvalues whose absolute values are less that one.

Using another method one can motivate taking the principal eigenvalue of the weight matrix as the representation of spontaneous activity even when the external inputs cannot be neglected. Indeed, let us average equation (7) over time

$$f=Wf+i\,. \tag{11}$$

Here i is the averaged input into the network. Consider the set of right eigenvectors of matrix W that we denote $\vec{\xi}_\alpha$:

$$\sum_n W_{kn}\xi_{\alpha n}=\lambda_\alpha\xi_{\alpha k}\,. \tag{12}$$

Using this definition one can solve equation (11) for the vector of spontaneous activities $\vec{f}$:

$$f_n=\sum_{\alpha\beta}\frac{\xi_{\alpha n}}{1-\lambda_\alpha}\left(G^{-1}\right)_{\alpha\beta}\sum_k\xi^*_{\beta k}i_k\,. \tag{13}$$

Here $G_{\alpha\beta} = \sum_n \xi^*_{\alpha n} \xi_{\beta n}$ is the Gram matrix.

Clearly if one of the eigenvalues, say λ_α, approaches one, the term in the sum (13) corresponding to this eigenvalue will dominate the solution thus yielding

$$f_n \approx C\xi_{\alpha n}, \tag{14}$$

where C is some constant. Thus in the case when recurrent connections have sufficient strength so that one of the eigenvalues of the weight matrix is close to unity, the corresponding eigenvector represents the spontaneous activities in the network.

4. Regular matrices

Consider a square N by N matrix W. Consider an ensemble of matrices such that all matrix elements are random numbers that are produced from the same distribution. In addition assume that there are no correlations between different elements. This ensemble of matrices belongs to the class of *regular* matrixes. A more accurate definition of this class is given below. Here we will mention that regular matrices have an eigenvalue that in the limit of large N is much larger than other eigenvalues. Also, the eigenvector corresponding to this eigenvalue has elements that are very close to a constant in the limit of large N. This statement is true for an arbitrary distribution of the elements of the matrix. Regular matrices represent therefore the simplest class of random matrices with no correlations. They cannot yield a log-normal distribution of the eigenvector elements. Some other form of random matrices is therefore needed to satisfy both of the requirements postulated in the Introduction.

Definition: ***Regular Matrices***

Consider an ensemble of square matrices W_{ij} of different sizes, from one by one to infinity. This ensemble belongs to the class of regular matrices if the following four requirements are met

(i) The distribution of the matrix elements $\rho(W)$ is the same for every position in the matrices of the same size (assumption of uniformity).

(ii) The distribution of matrix elements is the same for matrices of different sizes in the ensemble, up to maybe a scaling factor. More precisely, for every N_1 and N_2 describing two different sizes of matrices in the ensemble, there exists a positive constant C such that $\rho_{N_1}(W) = C\rho_{N_2}(CW)$, where ρ_{N_1} and ρ_{N_2} are the distributions of elements of matrices of sizes N_1 and N_2.

(iii) Matrix elements in different columns are statistically independent. This implies that for any i and k

$$\rho(W_{ij}, W_{km}) = \rho(W_{ij})\rho(W_{km}) \tag{15}$$

if $j \neq m$, i.e. the matrix elements belong to different columns.

(iv) The matrix elements are positive on average, i.e.

$$\overline{W_{ij}} > 0 \tag{16}$$

We define the in-degree of the matrix as

$$d_i = \sum_j W_{ij} \,. \tag{17}$$

Define $\bar{d}$ and $\sigma(d)$ the average and the standard deviation of the in-degrees for the ensemble. Property (iv) in the definition of regular matrices leads immediately to

$$\bar{d} > 0 \tag{18}$$

It can be also be shown easily that due to central limit theorem and independence of elements in columns the coefficient of variation of in-degrees becomes infinitely small for an increasing size of the matrix, i.e. when $N \to \infty$

$$\frac{\sigma(d)}{\bar{d}} \equiv \varepsilon \equiv \frac{1}{\bar{d}N} \overline{\sum_i (d_i - \bar{d})^2} \to 0 \tag{19}$$

Smallness of the coefficient of variation is at the basis of perturbation theory used in this supplement.

Example 1: Binary Matrices

$W_{ij} = 0$ or 1. Assume that $p(W_{ij} = 1) = s$. The number $s \le 1$ is therefore the sparseness of the matrix. Assume that no correlations are present among matrix elements. For the average in-degree and the standard deviation we obtain after simple calculation

$$\bar{d} = sN \tag{20}$$

and

$$\sigma^2(d) = Ns(1-s) \,. \tag{21}$$

Parameter ε defined in (19) is then

$$\varepsilon = \sqrt{\frac{1-s}{Ns}} \propto \frac{1}{N^{1/2}} \to 0 \tag{22}$$

when $N \to \infty$. Since the CV of in-degrees vanishes for large N, the ensemble of such matrices belongs to the class of regular matrices.

Example 2: White-Noise Matrices.

Consider random matrices with uncorrelated matrix elements. We will assume that all elements have the same distribution. We call this type of matrices white-noise. Let us consider sparse matrices for which $\rho(w)$ is the conditional probability distribution for non-zero matrix elements. This distribution can be for example LN. The probability to have a non-zero element (sparseness) is defined by s as in the previous example. The CV of the in-degree for these matrices is

$$\varepsilon = \frac{\sigma(d)}{\bar{d}} = \frac{1}{\sqrt{Ns}} \frac{\sqrt{\overline{w^2} - s\bar{w}^2}}{\bar{w}}, \tag{23}$$

where $\bar{w}$ and $\overline{w^2}$ are the average and average square of the non-zero matrix elements. Since ε goes to zero in the limit of increasing matrix size this ensemble of matrices also belongs to the class of regular matrices. Equation (22) is a specific case of a more general expression (23). If for example the distribution of non-zero elements $\rho(w)$ is LN, such as (2), the CV of in-degree is

$$\varepsilon = \sqrt{\frac{e^{\sigma^2} - s}{Ns}}, \tag{24}$$

as follows from equations (4) and (5).

5. Principal eigenvector of the regular matrices

Here we will show that the principal eigenvector of the regular matrices has elements that are normally distributed. The CV of this distribution is equal to the parameter ε introduced by us in the previous section. Since $\varepsilon \to 0$ for large matrices [equation (19)], the elements of the eigenvector that represent the individual firing rates of neurons have Gaussian distribution with vanishing variance. This claim is valid even if the distribution of the matrix elements is LN, since it is true for any regular matrix (see example 2 above). Thus LN distribution of matrix elements in the absence of correlations yields the eigenvector with small variance in the individual elements (firing rates). Thus, experimental observation (2) (LN spontaneous firing rates) cannot follow from observation (1) (LN weights) in the absence of correlations. In the end of this section we discuss what type of correlations can resolve the paradox.

Consider a square N by N regular matrix W. That the matrix is regular, according to (16) requires that the average of the matrix element $\bar{W}$ is positive. Note that here by $\bar{W}$ we mean the average of all matrix elements: positive, negative, and equal to zero; whereas above we used the notation $\bar{w}$ for the average non-zero matrix element of a sparse matrix. It is instructive to first approximate W by the constant matrix, i.e. the one that contains the same value $\bar{W}$ at each position. Let us denote such a matrix by $W^{(0)}$:

$$W_{ij}^{(0)} = \bar{W} \text{ for any } i \text{ and } j. \qquad (25)$$

The principal eigenvalue and eigenvector of this matrix are easy to guess. Indeed, if $f_i = 1$ for any i, its easy to verify that

$$\sum_j W_{ij}^{(0)} f_j = N\bar{W} f_j . \qquad (26)$$

Thus a constant vector is an eigenvector of $W_{ij}^{(0)}$ with the eigenvalue equal to $N\bar{W}$. The other eigenvectors are orthogonal to it because $W_{ij}^{(0)}$ is symmetric. Therefore the sum of the elements of these other eigenvectors is zero. Hence their eigenvalues are also zeros. The constant vector is therefore a principal eigenvector of $W_{ij}^{(0)}$, i.e. its corresponding eigenvalue has a maximum absolute value.

We then calculated the principal eigenvector of W using $W^{(0)}$ as the starting point. We used the perturbation theory that is described in section 10. The result that we got for the eigenvector and the eigenvalue are:

$$f_i = 1 + \frac{d_i - \bar{d}}{\bar{d}} \qquad (27)$$

and

$$\lambda = \bar{d} + \frac{1}{N}\sum_i (d_i - \bar{d}) \qquad (28)$$

Here d_i is the in-degree defined by (17). The correction to the eigenvector in (27) is of the order of $\sigma(d)/\bar{d} = \varepsilon << 1$ for large regular matrices. Similar statement can be made about the correction to the principal eigenvalue in (28). CV of the in-degrees serves therefore as the 'smallness' parameter in the perturbation theory.

The paradox formulated

Our results show that two experimental constraints listed in the introduction cannot be simultaneously satisfied. The distribution of the elements of the eigenvector (27) is normal due to the central limit theorem, as a distribution of sums of independent random variables. The CV of the distribution is equal to the parameter $\varepsilon << 1$ for the regular matrices. This result holds even if distribution of the individual matrix elements is LN, since such matrices are also regular (24). Thus it is impossible for regular matrices to have both their matrix elements and the elements of the principal eigenvector to be LN. The latter will be distributed normally, with a small CV. We arrive at the conclusion that cortical connectivity must contain correlations of the type that makes them not regular.

Example 3: Suffix (Column) Matrices

Consider a set of matrices that are formed by products of white-noise matrix A_{ij} and the white-noise random vector v_j.

$$B_{ij} = A_{ij} v_j \qquad (29)$$

We will assume that all of the elements of the vector are drawn from the same distribution and that they are not correlated with elements of matrix A_{ij}. The ensemble of matrices B_{ij} is regular because the matrix elements located in different columns are not correlated. This is despite the presence of correlations between matrix elements in the same column induced by the common multipliers. We will also show that the distribution of the elements of the principal eigenvector is sharper that that of matrix with no correlations.

Consider the in-degree of matrix B_{ij}

$$d_i = \sum_j B_{ij} \tag{30}$$

The white-noise correlations between elements of v_j and A_{ij} can be described as follows:

$$\overline{v_i v_j} = \sigma^2(v)\delta_{ij} + \overline{v}^2 \tag{31}$$

$$\overline{A_{ij} A_{km}} = \sigma^2(A)\delta_{ik}\delta_{jm} + \overline{A}^2 \tag{32}$$

These relationships lead to the expression for the cross-correlations between matrix elements of B_{ij}.

$$\overline{B_{ij} B_{km}} = \sigma^2(A)\sigma^2(v)\delta_{ik}\delta_{jm} + \sigma^2(A)\overline{v}^2\delta_{ik}\delta_{jm} + \overline{A}^2\sigma^2(v)\delta_{jm} + \overline{A}^2\overline{v}^2 \tag{33}$$

Our argument will hinge on the following equation describing correlations between in-degrees which is an immediate consequence of Eq. (33).

$$\overline{d_i d_k} = N\sigma^2(A)\sigma^2(v)\delta_{ik} + N\sigma^2(A)\overline{v}^2\delta_{ik} + N\overline{A}^2\sigma^2(v) + N^2\overline{A}^2\overline{v}^2 \tag{34}$$

Because the average in-degree is

$$\overline{d} = N\overline{A}\overline{v} \tag{35}$$

the coefficient of variation (CV) for the in-degrees is

$$\varepsilon^2 = \frac{\overline{d^2} - \overline{d}^2}{\overline{d}^2} = \frac{\sigma^2(A)\sigma^2(v) + \sigma^2(A)\overline{v}^2 + \overline{A}^2\sigma^2(v)}{\overline{A}^2\overline{v}^2}\frac{1}{N} \tag{36}$$

Since $\varepsilon \to 0$ when $N \to \infty$, B is a regular matrix. We also note that

$$\frac{\sigma^2(B)}{\overline{B}^2} = \frac{\sigma^2(A)}{\overline{A}^2} + \frac{\sigma^2(v)}{\overline{v}^2} \tag{37}$$

For this reason the expression for ε can also be rewritten as follows

$$\varepsilon^2 = \frac{\sigma^2(A)\sigma^2(v) + \sigma^2(B)}{\overline{B}^2}\frac{1}{N}, \tag{38}$$

CV for a white noise matrix can be obtained from (38) by assuming that $\sigma^2(v) = 0$.

$$\varepsilon^2 = \frac{\sigma^2(W)}{\overline{W}^2}\frac{1}{N} \tag{39}$$

Therefore CV for a prefix matrix (38) is larger or equal than that of a white noise matrix with the same distribution of individual elements. Because both types of matrices are regular, their principal eigenvector has the elements given by Eq.

(27). Therefore the CVs of eigenvector elements and in-degrees are the same. Thus expressions (38) and (39) can be understood as the CVs of the eigenvector elements for these two types of matrices. The conclusion about larger CV of the prefix matrix than that of the white-noise matrix is misleading however because in the case of the prefix matrix there is substantial correlation between eigenvector elements. Because (38) describes variability when averaging includes different matrices it does not reflect these correlations. For example, imagine that A is a constant matrix. In this case the in-degrees will still have some variability when considering an ensemble of matrices of the same size. This variability is described accurately by (38). However is this case *all* of the in-degrees are the same for a single matrix which implies, according to (27), that all of the elements of the principal eigenvector are the same. This means that eigenvector elements have no difference for a single matrix.

To describe the distribution of the principal eigenvector elements in individual matrices we introduce the following measure:

$$\Delta^2 \equiv \overline{\left(d_i - \frac{1}{N}\sum_j d_i \right)^2} \tag{40}$$

that describes the variance of in-degrees with respect to the mean in-degree calculated for the *same* matrix. Opening the brackets and using (34) we obtain

$$\Delta^2 = (N-1)\sigma^2(A)\overline{v^2} \,. \tag{41}$$

Therefore this measure of variance goes to zero when elements of matrix A are all the same yielding no difference between elements of the eigenvector as suggested in the end of the last paragraph. The coefficient of variation for Δ is

$$\frac{\Delta^2}{\overline{d^2} - \overline{d}^2} = \frac{\sigma^2(A)\sigma^2(v) + \sigma^2(A)\overline{v}^2}{\sigma^2(A)\sigma^2(v) + \sigma^2(A)\overline{v}^2 + \overline{A}^2\sigma^2(v)} \frac{N-1}{N} < 1 \,. \tag{42}$$

That this ratio is below one explains our observation made in the main paper that the distribution of spontaneous firing rates (elements of the principal eigenvector) for prefix matrix is narrower than for a white-noise matrix with the same distribution of individual matrix elements.

6. Irregular matrices

Consider a regular matrix A_{ij}. Consider then another matrix B_{ij} that is produced by multiplying all rows of A_{ij} by the elements of random vector v_i whose mean value is larger than zero:

$$B_{ij} = v_i A_{ij} \tag{43}$$

These matrices can also be called *prefix* or *row* matrices. We assume here that A_{ij} and v_i are not correlated. The matrix B_{ij} may or may not belong to the class of regular. Indeed, the in-degrees of B_{ij} are

$$b_i = \sum_j B_{ij} = v_i d_i , \tag{44}$$

where d_i is the in-degree of the regular matrix A. Since the latter are distributed with low CV [cf. (19)] the distribution of b_i is dependent upon the distribution of the elements of vector v_i that we denote $\rho(v)$. If the CV of $\rho(v)$ is small, matrix B is regular. If, on the other hand, the CV of $\rho(v)$ does not vanish in the limit of large matrices ($N \to \infty$) matrix B is not regular. It remains to be seen or proven that any irregular matrix can be decomposed into the product of the form (43). We will not prove or disprove this statement in this note.

Eigenvectors of irregular matrices

Consider now the eigenvector problem for matrix (43). It is formulated as follows

$$v_i \sum_j A_{ij} f_j = \lambda f_i \tag{45}$$

If one introduces the notation

$$y_i = f_i / v_i \tag{46}$$

the eigenvector equation (45) can be rewritten as follows

$$\sum_j A_{ij} v_j y_j = \lambda y_i \tag{47}$$

Thus y_i is the eigenvector of the matrix $C_{ij} = A_{ij} v_j$. Here A_{ij} is random regular while v_i is the random vector. In Example 3 above we showed that matrix C_{ij} is regular. Since C_{ij} is regular its principal eigenvector is approximately constant, as follows from (27)

$$y_i \approx 1 \tag{48}$$

and

$$f_i \approx v_i \tag{49}$$

This approximate equation becomes more and more precise in the limit $N \to \infty$, as follows from (27). We conclude that the distribution of the components of the principal eigenvector matches that of the outer product vector v_i.

Example 4: Lognormal Irregular Matrices

Consider a matrix whose element have log-normal distribution. For simplicity we will represent the matrix elements in the exponential form

$$A_{ij} = e^{\xi_{ij}} \tag{50}$$

where ξ_{ij} has a normal distribution. If we assume that all ξ_{ij} are taken from the same distribution and are uncorrelated, matrix A is regular. We will now consider a vector v_i, whose components are also LN distributed i.e.

$$v_i = e^{\eta_i} \tag{51}$$

where η_i are normally distributed and are not correlated with each other. They are also not correlated with the elements of the matrix ξ_{ij}. Let us now construct an irregular matrix B_{ij} using the (43) as a prescription:

$$B_{ij} = v_i A_{ij} = e^{\eta_i + \xi_{ij}} . \tag{52}$$

Because each element of B is an exponential of the sum of two normally distributed quantities, it is LN. Also, according to (49) the principal eigenvector of B is LN distributed:

$$f_i \approx v_i = e^{\eta_i} \tag{53}$$

The approximate equality here becomes asymptotically exact in the limit $N \to \infty$ as commented earlier. Thus we arrive at the matrix for which two statements are true, at least, in the limit $N \to \infty$

(1) The elements of matrix B are LN

(2) The components of its principal eigenvector are LN

Since we have suggested a relation between the eigenvector problem and the spontaneous rates in Section 3, these two features may match the corresponding experimental observations listed in the Introduction. Thus, it is possible that cortical networks and the spontaneous activity are produced by irregular matrices, for example, having strong correlations between the outgoing connections, as suggested here.

7. The learning rule

Here we propose the learning rule that can yield the irregular matrices in the final stable state. We propose the non-linear multiplicative learning rule for the recurrent synaptic matrix W_{ij}

$$W_{ij}(t+\Delta t) = \varepsilon_1 f_i^{\alpha} W_{ij}^{\beta}(t) f_j^{\gamma} + (1-\varepsilon_2) W_{ij}(t) . \qquad (54)$$

Here we introduced three exponents α, β, and γ that describe the non-linearity. It is reasonable to assume that these exponents are positive. The two constants that describe the rates of modification of the components of the weight matrix are ε_1 and ε_2. The former parameter describes the rate of acquiring the new values, while the latter determines the rate of 'forgetting' of the current values of synaptic strengths. The spontaneous rates of the neurons are contained in the components of the vector f_i, which is given by the principal eigenvector of the weight matrix

$$\sum_j W_{ij}(t) f_j = \lambda f_j \ . \qquad (55)$$

We assume that the average value for the spontaneous rates is determined by e.g. metabolic constraints

$$\sum_i f_i / N = \overline{f} \qquad (56)$$

The average spontaneous rate $\overline{f}$ is assumed to be constant and independent on time.

Before providing biological motivation for the learning rule (54) in the next section we will show that this rule will yield the irregular matrix of the form (52). To this end we consider the final stationary state described by the condition

$$W_{ij}(t+\Delta t) = W_{ij}(t) \equiv W_{ij} \qquad (57)$$

Putting this condition into (54) we obtain for the stationary value W_{ij} the following equation

$$\varepsilon_2 W_{ij} = \varepsilon_1 f_i^{\alpha} W_{ij}^{\beta} f_i^{\gamma} \qquad (58)$$

This equation has two solutions:

$$W_{ij} = 0 \qquad (59)$$

and

$$W_{ij} = (\varepsilon_1 / \varepsilon_2)^{1/(1-\beta)} f_i^{\alpha/(1-\beta)} f_j^{\gamma/(1-\beta)} . \qquad (60)$$

Which one of the solutions has to be chosen? From the form of the equation (54) it follows that a weight cannot become zero if originally it was above zero. Conversely a synaptic weight that is zero will remain equal to it forever. Thus, the connectivity matrix is preserved during the process described by (54). An element of connectivity matrix C_{ij} is equal to one if there is a synapse from cell j to cell i and zero otherwise. It is thus equal to the transposed adjacency matrix as defined in the graph theory. Two solutions (59) and (60) can be combined into one formula using the connectivity matrix:

$$W_{ij} = (\varepsilon_1 / \varepsilon_2)^{1/(1-\beta)} f_i^{\alpha/(1-\beta)} f_j^{\gamma/(1-\beta)} C_{ij} \tag{61}$$

The synaptic matrix itself depends on the spontaneous rates in the stationary state, which complicates the solution. From the formulation of the eigenvector problem

$$\sum_j W_{ij} f_j = \lambda f_j \tag{62}$$

we obtain the following equation for f

$$f_i = \frac{1}{\lambda^M} \left(\frac{\varepsilon_1}{\varepsilon_2} \right)^{\frac{1}{1-\alpha-\beta}} \left(\sum_j C_{ij} f_j^{\frac{\gamma}{1-\beta}} \right)^M \tag{63}$$

Here

$$M = \frac{1-\alpha}{1-\alpha-\beta} \tag{64}$$

Matrix $C_{ij} f_j^{\frac{\gamma}{1-\beta}}$ is regular. Because of this, the sums in (63) are normally distributed with a low CV. If the in-degree of this matrix is d_i

$$d_i = \sum_j C_{ij} f_j^{\frac{\gamma}{1-\beta}} = \bar{d} + \Delta_i \tag{65}$$

The random variable Δ_i is normally distributed and $\sigma(\Delta_i)/\bar{d} = \varepsilon << 1$. For the logarithm of the spontaneous rates we can write

$$\ln f_i = C + M \ln\left(1 + \frac{\Delta_i}{\bar{d}}\right) \tag{66}$$

Here C is some constants. Due to the smallness of parameter $\varepsilon = \sigma(\Delta_i)/\bar{d}$ we can expand the logarithm and write

$$\ln f_i = \tilde{C} + M \frac{\Delta_i}{\bar{d}} \tag{67}$$

The logarithm of the spontaneous rate is therefore normally distributed. Of course the standard deviation of this distribution may be small:

$$\sigma(\ln f) = M\varepsilon \tag{68}$$

because $\varepsilon << 1$. However with $\alpha + \beta \to 1$ the exponent M may become large so that the distribution of f becomes LN. Note that the distribution of the non-zero synaptic weights is also LN as the distribution of the product of LN variables (61) .

8. Motivation for the learning rule.

The standard Hebbian learning rule would look like this:

$$W_{ij}(t+\Delta t) = \varepsilon_1 f_i \; f_j \; + (1-\varepsilon_2) W_{ij}(t) \tag{69}$$

There are several ways in which our rule (54) is more biologically plausible than (69).

(1) The learning rule that we postulated (54) preserves connectivity matrix. This means that the sparse matrix of synaptic weight will remain sparse, with the same connectivity. The learning rule (69) produces a full matrix. Since cortical connectivity is sparse (Song et al., 2005), our rule is more biologically plausible.

(2) Our learning rule suggests that the uptake of proteins controlling the synaptic strength occurs at the rate dependent of the number of existing proteins. This is consistent with the models in which the uptake occurs into spatially localized clusters in PSD, which would make the rate of synapse growth larger for a larger synapse (Shouval, 2005).

9. Variance of the log-normal distribution.

Eq. (68) for the variance of the logarithm of the firing rates $\sigma^2(\ln f)$ can be rewritten as follows

$$\sigma^2(\ln f) = M^2\varepsilon^2 \tag{70}$$

where

$$\varepsilon = \varepsilon\left[\sigma^2(\ln f)\right] \tag{71}$$

is the CV of the in-degrees of matrix $C_{ij} f_j^{\frac{\gamma}{1-\beta}}$. Because the matrix itself depends on f the CV of in-degrees is determined by the distribution of the components f_i, which is emphasized by the last equation. The exact form of dependence in (71) is easy to derive using (24)

$$\varepsilon^2 = \frac{e^{\sigma^2(\ln f)\left(\frac{1-\beta}{\gamma}\right)^2} - s}{Ns} \tag{72}$$

where s is the sparseness of the connectivity matrix C_{ij}, which is by definition

$$s \equiv \frac{1}{N^2}\sum_{ij} C_{ij} \tag{73}$$

i.e. the fraction of its non-zero elements. The full form of the equation which determines $\sigma^2(\ln f)$ is

$$\sigma^2(\ln f) = \frac{M^2}{Ns}\left[e^{\sigma^2(\ln f)\left(\frac{1-\beta}{\gamma}\right)^2} - s\right] \tag{74}$$

This equation should be solved iteratively to find the variance of the logarithm of the firing rates. The solution becomes large when $M = (1-\beta)/(1-\alpha-\beta) \to \infty$, i.e. when $\alpha+\beta \to 1$.

The variance of the logarithm of non-zero weight matrix elements is then given by

$$\sigma^2(\ln W) = \sigma^2(\ln f)\frac{\alpha^2+\gamma^2}{(1-\beta)^2} \tag{75}$$

The latter relationship is found from (61).

10. Perturbation theory solution for the principal eigenvector of the regular matrix.

Here we will prove equations (27) and (28) that are used to demonstrate the smallness in the variation of the components of the principal eigenvector of the regular matrices. To this end we represent a regular matrix W_{ij} as a sum of a constant matrix $W_{ij}^{(0)} = \bar{W} > 0$, whose elements are all the same, and the correction ΔW_{ij}

$$W_{ij} = W_{ij}^{(0)} + \Delta W_{ij} \tag{76}$$

This equation may be understood as the definition of the correction matrix ΔW_{ij}. Despite the fact that the individual elements of ΔW_{ij} are large, we will assume that the effects of adding this correction on the eigenvector and eigenvalue are small. We will show that this actually is true in the end of calculation. This may be viewed as a circular argument. Indeed, to obtain smallness of the correction we assume that the correction is small. However, we know that there is only one solution. The uniqueness of the solution is provided by the Perron-Frobenius theorem for non-negative matrices. Therefore, obtaining solution that is self-consistent, i.e. does not contradict to itself, is sufficient.

To perform the perturbation theory analysis we will represent the principal eigenvector of the matrix W_{ij} as a sum of the solution of the 'unperturbed' problem $f_i^{(0)}$ and the correction

$$f_i = f_i^{(0)} + \delta_i \tag{77}$$

where $f_i^{(0)} = const$ as we argued before, and the small correction $\delta_i << f_i^{(0)}$. The correction can always be made perpendicular to $f_i^{(0)}$ by including the non-perpendicular component of δ_i into $f_i^{(0)}$. Since $f_i^{(0)} = const$ we conclude that

$$\sum_j \delta_j = 0 \tag{78}$$

The vector $f_i^{(0)}$ is the solution to the 'unperturbed' eigenvector problem

$$\sum_j W_{ij}^{(0)} f_j^{(0)} = \lambda^{(0)} f_i^{(0)}, \tag{79}$$

where, according to (26)

$$\lambda^{(0)} = N\bar{W}. \tag{80}$$

The vector f_i is the solution to the full problem

$$\sum_j W_{ij} f_j = \lambda \ f_i \tag{81}$$

where

$$\lambda = \lambda^{(0)} + \Delta\lambda \tag{82}$$

Equations (77), (81), and (82) can be combined as follows

$$\sum_j (W_{ij}^{(0)} + \Delta W_{ij})(f_j^{(0)} + \delta_j) = (\lambda^{(0)} + \Delta\lambda)(f_i^{(0)} + \delta_i) \tag{83}$$

In the expanded form this reads:

$$\begin{aligned} &\sum_j W_{ij}^{(0)} f_j^{(0)} + \sum_j W_{ij}^{(0)} \delta_j + \sum_j \Delta W_{ij} f_j^{(0)} + \sum_j \Delta W_{ij} \delta_j = \\ &= \lambda^{(0)} f_i^{(0)} + \lambda^{(0)} \delta_i + \Delta\lambda f_i^{(0)} + \Delta\lambda \delta_i \end{aligned} \tag{84}$$

The first term in the l.h.s. cancels with the first term in the r.h.s. because of (79). The second term in the l.h.s. is zero, because $W_{ij}^{(0)}$ is a constant matrix and δ_j satisfies (78). The forth term in l.h.s. is much smaller than the third, and, therefore can be neglected. The same is true about the fourth term in the r.h.s. in comparison with the third term there. We therefore arrive at a much shorter equation:

$$\sum_j \Delta W_{ij} f_j^{(0)} = \lambda^{(0)} \delta_i + \Delta\lambda f_i^{(0)} \tag{85}$$

This equation is approximate. However, it is asymptotically correct, when $\delta_i << f_i^{(0)}$.

We will now multiply both sides of the equation by $f_i^{(0)}$ and sum over i. Because $\delta_i \perp f_i^{(0)}$ the first term in the r.h.s. gives no contribution. We obtain for the correction to the eigenvalue

$$\Delta\lambda = \sum_{ij} f_i^{(0)} \Delta W_{ij} f_j^{(0)} / \sum_i \left| f_i^{(0)} \right|^2 = \frac{\vec{f}^{(0)T} \Delta \hat{W} \vec{f}^{(0)}}{| \vec{f}^{(0)} |^2} \tag{86}$$

Let us estimate this correction. Because the elements of vector $\vec{f}^{(0)}$ are all the same, we can write

$$\Delta\lambda = \frac{1}{N} \sum_i (d_i - \bar{d}) \tag{87}$$

where

$$d_i = \sum_j W_{ij} \tag{88}$$

are the in-degrees of matrix $\hat{W}$. The average over the ensemble value of the correction is zero. The variance of the correction is

$$\overline{\Delta\lambda^2} = \frac{1}{N} \overline{\left(d_i - \bar{d}\right)^2} = \frac{\sigma^2(d)}{N} \tag{89}$$

The relative correction to the eigenvalue can be estimated to be

$$\frac{\Delta\lambda}{\lambda^{(0)}} = \frac{\sigma(d)}{\bar{d}}\frac{1}{\sqrt{N}} = \frac{\varepsilon}{\sqrt{N}} << 1 \quad (90)$$

i.e. is small because both the CV of the in-degrees of the regular matrix ε is small and the matrix is large.

We will now use the result (90) to find the correction to the eigenvector. Let us estimate various terms in equation (85) that we will recite here for convenience

$$\sum_j \Delta W_{ij} f_j^{(0)} = \lambda^{(0)}\delta_i + \Delta\lambda f_i^{(0)} \quad (91)$$

The first term is of the order of $\sigma(d) f_j^{(0)}$ while the last term in the r.h.s. is equal to

$$\lambda^{(0)} \frac{\varepsilon}{\sqrt{N}} f_i^{(0)} = \bar{d}\,\frac{\sigma(d)}{\bar{d}}\frac{1}{\sqrt{N}} f_i^{(0)} = \frac{\sigma(d)}{\sqrt{N}} f_i^{(0)} \quad (92)$$

The last term in (91) therefore can be neglected. For the correction to the eigenvector we obtain

$$\delta_i = \frac{1}{\lambda^{(0)}} f_i^{(0)} \sum_j \Delta W_{ij} = f_i^{(0)} \frac{1}{\bar{d}}\left(d_i - \bar{d}\right), \quad (93)$$

which is the same as equation (27). Equation (93) also implies that

$$\frac{\delta_i}{f_i^{(0)}} \sim \frac{\sigma(d)}{\bar{d}} \sim \varepsilon << 1 \quad (94)$$

i.e. correction to the eigenvector is small.

We now have to show that the neglected term in equation (84), i.e. the fourth term in the l.h.s. is much smaller than the third term in the limit of large matrices

$$s_3 \equiv \sum_j \Delta W_{ij} f_j^{(0)} >> s_4 \equiv \sum_j \Delta W_{ij}\delta_j \quad (95)$$

Because the expectation value for s_3 is zero while s_4 may be positive on average we will compare their squares. We obtain

$$\overline{s_3^2} = \sum_{jk} \overline{\Delta W_{ij}\Delta W_{ik}} = N\sigma^2(W) \sim N \quad (96)$$

In deriving this we used property (iii) in the definition of regular matrices (statistical independence of elements in different columns) which leads to

$$\overline{\Delta W_{ij}\Delta W_{ik}} = \sigma^2(W)\delta_{jk} \quad (97)$$

We also assumed that $f_j^{(0)} = 1 \sim \sigma(W)$ for simplicity.

Estimation of s_4 requires somewhat larger effort. Using (93) we can write

$$\overline{s_4^2} \equiv \overline{\left(\sum_j \Delta W_{ij} \delta_j\right)^2} \approx \frac{1}{\bar{d}^2} \sum_{jklm} \overline{\Delta W_{ij} \Delta W_{jk} \Delta W_{il} \Delta W_{lm}} . \quad (98)$$

Because $\overline{\Delta W_{ij}} = 0$ and elements in different columns (with different second indices) are independent, the sum in this equation breaks into the sum of products of pairs:

$$\overline{s_4^2} \approx \frac{1}{\bar{d}^2} \left[\sum_{\substack{jl \\ j \neq l}} \overline{\Delta W_{ij} \Delta W_{jj}} \cdot \overline{\Delta W_{il} \Delta W_{ll}} + \sum_{\substack{jk \\ j \neq k}} \overline{\Delta W_{ij} \Delta W_{jj}} \cdot \overline{\Delta W_{jk} \Delta W_{jk}} + \right.$$
$$\left. + \sum_{\substack{kj \\ j \neq k}} \overline{\Delta W_{ij} \Delta W_{kj}} \cdot \overline{\Delta W_{jk} \Delta W_{ik}} + \sum_j \overline{\Delta W_{ij} \Delta W_{jj} \Delta W_{ij} \Delta W_{jj}} \right] \quad (99)$$

Because the largest sums in this equation include N^2 terms we can estimate $\overline{s_4^2}$ as follows

$$\overline{s_4^2} \sim \frac{N^2}{\bar{d}^2} \sim 1 << \overline{s_3^2} \sim N . \quad (100)$$

Thus the forth term in equation (84) is much smaller than the third term on average for very large matrices.

Supplementary material 2

to “Correlated connectivity and the distribution of firing rates in the neocortex”

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The effects of exponential input-output relationship in the firing of neurons.

In this supplement we will consider a recurrent network of neurons for which the firing rate is an exponential function of the input current, i.e.

$$f = f_0 e^{I/\lambda} \tag{101}$$

Here f_0 and λ are constants. A simple explanation of lognormal spontaneous firing rates would be that the input current I for these neurons has a normal distribution as a result of uncorrelated synaptic strengths of many input synapses. As a result the firing rates, as exponentials of the input current, have lognormal distribution. Here we will show that the hypothesis of exponential input-output relationship cannot yield large variance in the logarithm of firing rates for the recurrent network of neurons. We will show that large variance in the logarithm will have to lead to instability in the recurrent network of such neurons. This is based on the extremely strong positive gain in the recurrent network provided by the exponential input-output relationship (101).

We will start by deriving the stability condition for the recurrent network. We will see below that the stability condition cannot be satisfied when the standard deviation of the logarithm of the spontaneous firing rates is substantial, i.e. is close to 1 as required by experimental observations. To proceed with the analysis of stability we introduce the variables for firing rates and weights

$$f_i = e^{\xi_i} \tag{102}$$

$$w_{ij} = e^{\eta_{ij}} \tag{103}$$

Here indexes i and j label neurons in the networks. The stability condition can especially easily be derived in the case when all neurons have essentially the same firing rates, i.e. $\overline{\delta\xi^2} \ll 1$. Here $\overline{\delta\xi^2}$ is the standard deviation of the logarithm of the firing rates. We will see from this stability condition that it is violated when $\overline{\delta\xi^2} \sim 1$. The latter case is therefore not essential for the stability analysis. Later we will however derive the stability condition for $\overline{\delta\xi^2} \sim 1$ case for the sake of completeness.

1) The case of small deviations $\overline{\delta\xi^2} << 1$.

For the recurrent current and the variance of the recurrent current we obtain

$$\overline{I} = wsNf + I_0 \tag{104}$$

$$\overline{\delta I^2} = w^2 sNf^2 A \tag{105}$$

Here w, s, N, I_0, and A are the average synaptic strength, sparseness of the network, number of neurons, external offset current, and a numerical coefficient of the order of one. For the lognormal distribution of synaptic weights it can be derived that

$$A = e^{\overline{\delta\eta^2}} - s \tag{106}$$

Experimental evidence suggests that $\overline{\delta\eta^2} \approx 1$ for cortical networks. Equations (104) and (105) are typical for the sum of independent random variables in which case both the average and the variance are proportional to the number of terms in the sum, i.e. N. The variance in the logarithm of the firing rates can be related to the variance of recurrent current through the input-output relationship (101)

$$\overline{\delta\xi^2} = \frac{\overline{\delta I^2}}{\lambda^2} = \frac{w^2}{\lambda^2} Nsf^2 A \tag{107}$$

Stability condition for the recurrent network reads

$$\frac{df}{dI} = \frac{f}{\lambda} < \frac{1}{d\overline{I}_{rec} / df} = \frac{1}{wsN} \tag{108}$$

Note that here one can disregard the difference between the current on the input of each neuron and the average current because of the condition $\overline{\delta\xi^2} << 1$. The gain in the input-output relationship λ can be excluded from the last equation using equation (107). After this substitution we arrive at the final result of this subsection, which expressed by the stability condition of the recurrent network in terms of the parameters of the lognormal distribution

$$\overline{\delta\xi^2} < \frac{A}{Ns}. \tag{109}$$

Therefore, for large networks ($N >> 1$) stability condition is impossible to satisfy if the logarithm of the firing rates has substantial variance i.e. $\overline{\delta\xi^2} \sim 1$. Experimental observations of large variance of the logarithm are therefore hard to reconcile with the exponential input-output relationship (101).

2) The case of substantial variance $\overline{\delta\xi^2} \sim 1$.

We will argue here that condition similar to (109) has to be satisfied in this case as well. The exact form of the condition is

$$\overline{\delta\xi^2} < \frac{e^{\overline{\delta\eta^2}+\overline{\delta\xi^2}} - s}{Ns} \tag{110}$$

It is possible to satisfy this inequality if $\overline{\delta\xi^2} << 1$ and if $\overline{\delta\xi^2} \approx \ln Ns >> 1$. We note however that the latter case is not consistent with experiments in which $\overline{\delta\xi^2} \approx 1$ is observed.

Our analysis is essentially based on the following equations that can be easily confirmed for lognormal variables

$$\bar{f} = \overline{e^{\xi}} = e^{\bar{\xi}+\overline{\delta\xi^2}/2}. \tag{111}$$

$$\overline{\delta f^2} = e^{2\bar{\xi}+\overline{\delta\xi^2}}(e^{\overline{\delta\xi^2}} - 1) \tag{112}$$

The coupled dynamics of the network current and the variance of the firing rates can be described by the following equations

$$\overline{\delta\xi^2(t+1)} = \frac{Ns}{\lambda^2} e^{2\bar{\eta}+2\overline{\xi(t)}} e^{\overline{\delta\eta^2}+\overline{\delta\xi^2(t)}} (e^{\overline{\delta\eta^2}+\overline{\delta\xi^2(t)}} - s) \tag{113}$$

$$\overline{I(t+1)} = Nse^{\bar{\eta}+\overline{\xi(t)}} e^{\overline{\delta\eta^2}/2+\overline{\delta\xi^2(t)}/2} + I_0 \tag{114}$$

Here we assumed that the network weights described by the variables η do not change with time and the weight matrix is uncorrelated. In the equilibrium we have

$$\overline{\delta\xi_0^2} = \frac{Ns}{\lambda^2} e^{2\bar{\eta}+2\bar{\xi}} e^{\overline{\delta\eta^2}+\overline{\delta\xi_0^2}} (e^{\overline{\delta\eta^2}+\overline{\delta\xi_0^2}} - s) \tag{115}$$

Dividing (113) by (115) we obtain

$$\frac{\overline{\delta\xi^2(t+1)}}{\overline{\delta\xi_0^2}} = e^{2\overline{\xi(t)}-2\bar{\xi}} e^{\overline{\delta\xi^2(t)}-\overline{\delta\xi_0^2}} \frac{e^{\overline{\delta\eta^2}+\overline{\delta\xi^2(t)}} - s}{e^{\overline{\delta\eta^2}+\overline{\delta\xi_0^2}} - s} \tag{116}$$

Using the relationship

$$\overline{\xi(t)} = \overline{I(t)}/\lambda + \ln f_0 \tag{117}$$

and introducing small deviations from the equilibrium

$$\overline{\delta\xi^2(t)} = \overline{\delta\xi_0^2} + \Delta(t) \tag{118}$$

$$\overline{I(t)} = \bar{I} + \Delta I(t) \tag{119}$$

we obtain the following linear system of equations for the small deviations

$$\Delta I(t+1) = \kappa \Delta I(t) + \frac{\kappa\lambda}{2}\Delta(t) \tag{120}$$

and

$$\Delta(t+1) = \overline{\delta\xi_0^2}\frac{2}{\lambda}\Delta I(t) + \overline{\delta\xi_0^2}\frac{2e^{\overline{\delta\eta^2}+\overline{\delta\xi_0^2}} - s}{e^{\overline{\delta\eta^2}+\overline{\delta\xi_0^2}} - s}\Delta(t)\,. \tag{121}$$

Here the coefficient

$$\kappa = \sqrt{\frac{\overline{\delta\xi_0^2}Ns}{e^{\overline{\delta\eta^2}+\overline{\delta\xi_0^2}} - s}}\,. \tag{122}$$

It can be shown that in the large-N limit the eigenvalues of the system (120) and (121) are below 1 in absolute value if $\kappa < 1$, i.e. when condition (110) is satisfied. Because $\overline{\delta\xi_0^2} \equiv \overline{\delta\xi^2} \approx 1$ experimentally and $Ns >> 1$ the condition $\kappa < 1$ is difficult to satisfy. The hypothesis of exponential firing rates (101) is therefore not compatible with the lognormal distribution produced by the recurrent networks because of the lack of stability.

References

Hromadka T, Deweese MR, Zador AM (2008) Sparse representation of sounds in the unanesthetized auditory cortex. PLoS Biol 6:e16.

Shouval HZ (2005) Clusters of interacting receptors can stabilize synaptic efficacies. Proc Natl Acad Sci U S A 102:14440-14445.

Song S, Sjostrom PJ, Reigl M, Nelson S, Chklovskii DB (2005) Highly nonrandom features of synaptic connectivity in local cortical circuits. PLoS Biol 3:e68.