Period Focusing Induced by Network Feedback in Populations of Noisy Integrate-and-Fire Neurons

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The population dynamics of an ensemble of nonleaky integrate-and-fire stochastic neurons is studied. The model selected allows for a detailed analysis of situations where noise plays a dominant role. Simulations in a regime with weak to moderate interactions show that a mechanism of excitatory message interchange among the neurons leads to a decrease in the firing period dispersion of the individual units. The dispersion reduction observed is larger than what would be expected from the decrease in the period. This “period focusing” is explained using a mean-field model. It is a dynamical effect that arises from the progressive decrease of the effective firing threshold as a result of the messages received by each unit from the rest of the population. A back-of-the-envelope formula to calculate this nontrivial dispersion reduction and a simple geometrical description of the effect are also provided.

1 Introduction

One of the most remarkable phenomena that takes place in natural information processing networks, such as the brain or a biochemical system, is the ability to maintain functionality even in the presence of significant levels of noise. Sources of noise are generally present in biological systems, and despite recent insight (Shimokawa, Rogel, Pakdaman, & Sato, 1999; Frank, Daffertshofer, Beek, & Haken, 1999), the role of noise regarding the processing of information has not yet been clarified. In early studies, it was assumed that fluctuations are an undesired, if unavoidable, element in such systems. Consequently, most models studied in connection with information processing assume that noise is but a small perturbation, whose effect on the functionality of the system is pernicious and therefore should be minimized. A remarkable exception to this trend is the work on stochastic resonance (Gammaitoni, Hanggi, Jung, & Marchesoni, 1998), where noise is a source of stability and organization in the dynamics.

The increasing amount of work devoted to characterizing synchronic firing also looks for information processing in spite of noise. The synchroniza-
tion of neural signals, supported by neural recordings, leads to a paradigm
of coherent perception and feature binding that can persist further in a noisy
environment than the stimulus-induced activity of the isolated units (von
der Malsburg, 1994; Gray, König, Engel, & Singer, 1989; Fujii, Ito, Aihara,
Ichinose, & Tsukada, 1996). Moreover, synchronic message interchange is a
cooperative phenomenon observed in populations of quite different living
units ranging from fireflies (Buck, 1988) to opera theater attendants (Néda,
Ravasz, Brechet, Vicsek, & Barabási, 2000). An analysis of cooperative be-

One of our goals in this work is to construct a simple discrete-probabilistic
model where the effects of noise and interactions can be investigated. The
model system should be able to reproduce a rich behavior with a small num-
ber of parameters, so that analytical estimations of relevant properties can
be easily derived. It is our belief that in biological information processing
systems, fluctuations should play an important role. Hence, the focus is on
the dynamics of systems with a large amount of randomness. The use of
discrete states and discrete times allows for a complete analysis of popula-
tion dynamics. Furthermore, computer simulations are feasible and stable
even for populations with a large number of units.

The system we investigate is a network of integrate-and-fire neurons
exchanging excitatory messages. The dynamics of each of these units are
stochastic, which implies that the firing period is defined only as an aver-
age quantity about which the actual interspike delay fluctuates. Two differ-
ent regimes are found depending on the degree of interaction among neu-
s. For strong interaction among network units, the system settles into
a regime where units fire regularly in groups (Rodríguez & López, 1999).
In this state, which closely resembles the one described in van Vreeswijk
and Abbott (1993), the strength of incoming messages is enough to produce
synchronization and even to override stochasticity.
The focus of this article is on a regime with smaller interaction, where neurons are observed to fire independently. Simulations show that the messages that arrive to any given neuron cover uniformly the time elapsed between the production of two consecutive spikes by that neuron. Although the system is far from synchronization, every neuron is generating spikes with a period that is more regular than it would be expected if the dynamics of messages received from the population were neglected. This narrowing of the period distribution (period focusing) can be accurately described within a mean-field model where the effect of the messages received is represented by a progressive lowering of the unit firing threshold.

2 Dynamics of the Neural Model

The neural model studied in this article is composed of a globally coupled network of nonleaky stochastic integrate-and-fire units. The dynamics are entirely discrete. Each of the units can exist only in one of a finite number of states, labeled \( l = 1, 2, \ldots, L-1 \), where all states beyond \( L-1 \) are metastable states that deterministically produce the release of a signal to the rest of the units (a spike) in the following time step. Transitions between states can take place only at discrete time steps. The discrete nature of the model makes it possible to carry out a detailed analysis of the phenomena that arise in the network as a result of interactions between the units.

Consider the dynamics of an isolated neuron. In the absence of coupling, each unit performs a random walk (Gerstein & Mandelbrot, 1964). At every time step, the state of the unit can be incremented with a probability \( p \), or it can remain unchanged with a probability \((1-p)\). The state of the \( i \)th unit in the network at time \( t \) is given by the variable \( a_i(t) \), whose domain is the state labels 1, 2, \ldots, \( L-1 \). When the state of the neuron reaches the level \( L \), the unit generates a spike with probability one. States with labels \( L \) and beyond are identified with the state of label 0. The spike is produced in the deterministic transition from state with label 0 to state with label 1.

To summarize, the dynamics are those of a stochastic oscillator characterized by a probability \( p \) and a threshold \( L \):

\[
a_i(t+1) = \begin{cases} 
a_i(t) + 1 & \text{with probability } p \\
a_i(t) & \text{with probability } (1-p) \\
1 & \text{if } a_i(t) < L \\
& \text{if } a_i(t) \geq L.
\end{cases}
\]

The time evolution of the probability distribution for an ensemble of \( N \)-independent oscillators starting at the origin \( (a_i(0) = 1; i = 1, 2, \ldots, N) \) at time 0 is given by the binomial distribution:

\[
P_B(l, t) = \binom{t}{l-1} p^{l-1}(1-p)^{t-l+1}, \quad l = 1, 2, \ldots, t+1.
\]
The time elapsed between the generation of consecutive spikes follows a
negative binomial distribution (Feller, 1971),

\[ P_{NB}(T; L, p) = \frac{(T - 2)}{L - 2} p^{(L-1)} (1 - p)^{(T-L)}, \quad T > 1. \]

(2.3)

For this distribution, we can derive the mean interspike delay and its stan-
dard deviation:

\[ \tau = 1 + \frac{L - 1}{p}, \]
\[ \sigma = \frac{\sqrt{(L - 1)(1 - p)}}{p}. \]

(2.4)

This model for the isolated neuron is compatible with many sources of
noise. The probabilistic drift given to the unit dynamics using the parameter
\( p \) could arise from any source (internal or external to the unit or the network),
provided that it is Poissonian. We should also point out that the model we
use in this work yields spike trains with a small coefficient of variation
(\( C_v \equiv \sigma/\tau \sim L^{-\frac{1}{2}} \) as \( L \to \infty \)), which cannot account for the behavior
observed in cortical neurons (\( C_v \sim 1 \)). It is understood that to reproduce
such a noisy train of spikes, both excitatory and inhibitory inputs need
need to be considered (Shadlen & Newsome, 1994). Research with an extended
model including both types of inputs is now in progress.

Although the model can be easily extended to consider continuous time,
we stay on the discrete-time domain since it has two main advantages.
First, it allows for a simpler explanation of the observed behavior, and, second, it leads to a simple and coherent procedure to update the dynamics
of the population. Complex differential equations are avoided in the model
interaction we have selected, and that is explained in what follows.

The interaction between units is a delayed spike transmission through
the neural connection, which produces a change in the state of the receiving
unit. More explicitly, a spike of unit \( j \) at time \( t - 1 \) affects the state of unit \( i \)
at time \( t \) according to the rule

\[ a_i(t) = a_i(t - 1) + \epsilon_{ij}(t), \]

(2.5)

where the magnitude \( \epsilon_{ij}(t) \) refers to the connection strength or, in other
words, the size of the message received by unit \( i \) from unit \( j \). Only integer
positive values are allowed for \( \epsilon_{ij} \). If after receiving the message associated
to a spike, the activity of unit \( i \) reaches a state at or above the threshold \( L \),
the unit fires and resets its state to 1 in the following time step, regardless
of the precise value of \( a_i(t) \) before receiving the message.

We focus here on an ensemble of \( N \) interacting units with global coupling
of equal strength \( \epsilon \) and with a fully connected architecture. Four parameters
are sufficient to characterize the ensemble: \( N \), the size of the ensemble, \( \epsilon \) the message strength, and \( L, p \) describing the evolution of the isolated units. In this article, we present the results in the limit of small \( \epsilon \). Since we can only reduce to 1 the size of \( \epsilon \) in our discrete model, results are given only for the case \( \epsilon = 1 \). Nonetheless, \( \epsilon \) is not dropped from any expression. In the presence of a nonzero coupling \( \epsilon \neq 0 \), besides the spontaneous evolution of the neural units, given by eq. 2.1, there is an additional step to account for interactions among units,

\[
a_t(t + 1) = a_t^*(t + 1) + \epsilon s_t(t),
\]

(2.6)

where \( a_t^* \) is the state of unit \( i \) after spontaneous evolution and \( s_t(t) \) the number of units, excluding neuron \( i \), that fired in the previous time step. Physically, the quantity \( s_t(t) \) represents the number of messages received by unit \( i \) at time \( t \). The maximum value this variable can take is \( V = N - 1 \). The quantity \( V \) is also the number of spikes that a test unit receives on average between two consecutive spikes. Therefore, \( \epsilon V \) represents the average total strength of the messages received by a single unit in the period between two consecutive spikes. In order to characterize the strength of interactions among the units, we introduce the parameter

\[
\eta = \frac{L - 1}{\epsilon V},
\]

(2.7)

which measures the number of times each of the units in the ensemble has to send a message, on average, in order to induce a spike in a test neuron, assuming that no spontaneous evolution occurs in the test neuron. The inverse of this parameter represents the fraction of the evolution of a given unit that is accounted for by the messages received from the other neurons. The value of this parameter determines the regime in which the dynamics of the network takes place. For large \( \eta \to \infty \), the dynamics are dominated by the spontaneous evolution of the units. As \( \eta \) decreases and gets closer to 1, the relative importance of the coupling to the other units increases. We proceed now to examine the different regimes in detail.

3 The Limit of Large \( \eta \)

The dynamics of the network at the microscopic level (i.e., the level of each of the units) are complex and do not convey much relevant information. Borrowing the techniques for the analysis of collective behavior in complex systems from statistical mechanics, we focus on the mesoscopic level and describe the properties of ensembles of such networks. In particular, we focus on the statistics of spike production in the system. Presumably it is the production of spikes and their temporal structure the mechanism by which information is processed in the brain (Rieke, Warland, de Ruyter van
Steveninck, & Bialek, 1997). That is the reason for our focusing on this aspect of the dynamics.

Let us denote by $T_i$ the interval between the generation of two consecutive spikes by unit $i$, which has been arbitrarily singled out in the network. There are several different averages that will be performed. A first average is made over time for each of the units of the network. The mean firing interval for unit $i$ over time is $\tau_i$ and its standard deviation $\sigma_i$. These quantities give us an idea of the distribution of firing intervals of a particular unit in the network. The mean of the time-averaged firing interval over the ensemble of network units and over the different initial configurations for the network ensemble (average over the phases of the stochastic oscillators, assuming random initial phases) is noted as $\langle \tau_i \rangle_e$, $\phi_0$. Similarly, the mean of the standard deviation over the ensemble and initial phases is $\langle \sigma_i \rangle_e$, $\phi_0$.

Focusing on the regime in which most of the evolution can be accounted for by the spontaneous evolution of the units $\eta \to \infty$, we can give an estimate for the mean and standard deviation of the unit firing time by the following argument: In the absence of coupling between units, $\eta = \infty$, the average interspike period and its standard deviation are given by equations 2.4. Since, on average, during an interval between two spikes of unit $i$, all neurons fire once, the strength of the messages received by this unit in this interval is $V \epsilon$. Assuming all of these messages are effective in increasing the state of the unit in question, the ensemble should behave as a collection of independent stochastic oscillators with a renormalized threshold,

$$\tilde{L} = L - V \epsilon. \quad (3.1)$$

Under these assumptions, the estimated value for the mean and variance of the firing period is

$$\hat{\tau} = 1 + \frac{L - V \epsilon - 1}{p},$$

$$\hat{\sigma} = \frac{\sqrt{(L - V \epsilon - 1)(1 - p)}}{p}. \quad (3.2)$$

Since the stochastic evolution of every unit is affected by the same type of message perturbation from the ensemble, these quantities should be the same for all $N$ units in the system. The approximation given by the formulas equation 3.2 are valid only if the spikes from the neurons are well separated from each other. Quantitatively, this means that the average time per spike should be larger than the typical width of the firing-period distribution,

$$\frac{\hat{\tau}}{N} \gg \hat{\sigma}. \quad (3.3)$$

In terms of $\eta$, $N$, and $p$, condition 3.3 reads

$$N \ll \frac{\eta - 1}{1 - p}. \quad (3.4)$$
or, equivalently,

$$\eta \gg (1 - p)N + 1.$$  \hfill (3.5)

In Table 1 we compare the results of a simulation for different values of $\eta$ with the theoretical estimates. The results in the fourth and fifth column of Table 1 are the empirically measured mean firing time and dispersion for a unit. Between parentheses we display the standard deviation of these values when we average the individual firing times over the whole ensemble of units and the initial phases. It is worth remarking that these standard deviations are small, which confirms the hypothesis that a homogeneous state for the ensemble of units obtains. Columns 6 and 7 present the prediction given by equation 3.2. For the cases with $N = 11$ (where condition 3.5 translates into $\eta \gg 10$), both the mean and the standard deviation predicted are fairly close to the actual ones, which have been extracted from the simulations. For a number of oscillators $N = 101$, equation 3.5 would require $\eta \gg 100$. This condition is violated for the cases with $N = 101$ displayed in Table 1, and the simple estimation formulas, 3.2, fail to produce a good-quality prediction for the standard deviation. In all cases, although the prediction for the mean firing time is fairly accurate, the standard error is systematically overestimated in the renormalized independent oscillators picture. This means that the interplay of the spontaneous evolution and the mechanism of message exchanges leads to a narrower distribution for the firing period than the simple argument leading to the variance estimate of equation 3.2 predicts.

4 The Limit of Intermediate $\eta$

The picture of renormalized independent oscillators can hold only in the limit of large $\eta$. The failure of this approximation as the relative importance of the interactions with other neurons is increased is made evident by the following observations. First, as $\eta$ decreases, the percentage of messages that are effective in contributing to the evolution of other units decreases. Second, the interactions between the different units induce correlations in their dynamics, which can no longer be considered as independent. Third,
the exchange of messages between the units has a regularizing effect that further reduces the dispersion of the firing period.

The first phenomenon is illustrated in Figure 1, which displays the number of messages in a system composed of 100 units that are effective in the evolution of a test unit as a function of $\eta$. The amount $V_{\text{eff}}^{\epsilon}$ represents the effective number of messages that a test unit receives from population between two consecutive spikes.

If all messages were effective, messages coming from spikes that occur in the instant preceding the firing of a test unit are effectively dissipated because they induce a transition that overshoots the threshold. At small values of this parameter, most of the oscillators reach their threshold by spontaneous evolution. The spikes of the units occur thus in isolation, and almost all the messages produced are effective in affecting the evolution of the remaining units under the threshold. As the strength of the interactions increases, some neurons start to fire simultaneously, and it becomes a relatively frequent event that a given oscillator fires only after receiving the messages coming from the spikes of other units.

The appearance of correlations in the dynamics can also be observed in the simulations. Intuitively, correlations appear because the firing of a neuron produces messages that increase the state of the remaining neurons and therefore increases the likelihood of neurons’ firing immediately after. In order to characterize this effect quantitatively, we measure the correlations
in $\theta(t)$, the number of messages received by a test unit at time $t$, which is placed in state $l = 1$ at $t = 0$. The correlation function of this quantity is

$$C_\theta(t, \tau) = \frac{\theta(t + \tau) - \overline{\theta(t + \tau)}}{\theta(t) - \overline{\theta(t)}}$$

where the bar indicates an ensemble average. These correlations for $t = 10$ are presented in Figure 2. The structure of the correlations exhibits two salient features: The positive component at short delays reflects the fact that spikes in a neuron or group of neurons favor the occurrence of other spikes, owing to the production of messages that increase the state of the other neurons. Similarly, a fluctuation where the number of spikes is lower than the average implies that fewer messages are produced, thus decreasing the likelihood of further spikes in the remaining neurons. There is an echo of
these correlations centered at a delay equal to the average period of the units, \( \tau \). The peak is wider due to the fluctuations arising from the spontaneous evolution of the units in that interval. In particular, the echo is less defined for \( p = 0.5 \), because the magnitude of the fluctuations is larger.

There are also long-range negative correlations. These are a consequence of the approximate conservation of the number of neurons that fire between two consecutive spikes of a given unit,

\[
\sum_{t=0}^{\tau} \theta(t) \approx \sum_{\tau=0}^{\tau} \theta(t),
\]  

(4.2)

which implies

\[
\sum_{\tau=0}^{\tau} C_{\theta}(t, \tau) \approx 0.
\]  

(4.3)

Since the correlations during an average firing period should average to approximately zero, there must be a negative contribution at longer delays to compensate the positive contribution of the peak of the correlations at short delays. Given that the direct influence of a given unit firing is short-ranged in time, the negative correlations are constant. The observation of these constant negative long-range correlations, which appear as a consequence of global conservation laws, has been previously reported in the literature (Bussemaker, Ernst, & Dufty, 1995; Suárez, Boon, & Grosfils, 1996).

This phenomenon can also be observed in the analysis of the accumulated number of messages received by the test unit in the interval \([0, T]\):

\[
\Theta(t) = \sum_{t'=0}^{t} \theta(t').
\]  

(4.4)

Figure 3 exhibits the roughly linear increase of \( \Theta(t) \) with the amount of time elapsed. The slope of this straight line can be easily deduced from the fact that the accumulated number of messages received by the test unit during the mean firing period, \( \tau \), should be

\[
\Theta(\tau) \approx V_{\text{eff}} \epsilon,
\]  

(4.5)

where \( V_{\text{eff}} \lesssim N - 1 \), the difference being attributable to the dissipated messages that only contribute to overshooting over the threshold of the unit. The average linear increase observed for the accumulated number of messages received by the test unit shows how far from synchronization the neurons in the ensemble are in the large \( \eta \) regime. Moreover, a simple description of the firing regime reached by the system is that neurons fire independently, covering uniformly the time frame between two consecutive spikes.
Figure 3: Results of simulations for an ensemble of 11 units, where the parameter \( \eta \) has the value of 4.634. The plots show the accumulated number of messages received by a test unit in an interval covering one firing period. Averages are performed over 50 initial phases and time evolution allowed up to 1000L. We show results for two probabilities, \( p = 0.5, 0.9 \).

On average, one neuron from the ensemble fires every \((\eta - 1)/p\) time units. This result will be understood more precisely with the mean-field approach presented in the next section.

The characteristic form of the dispersion (with a narrowing around the firing period) is due to the presence of short-time positive correlations and long-time negative correlations.

We emphasize that the focus of this article is on a regime (intermediate and large values of \( \eta \)) where these correlations need not be explicitly considered in estimating the mean and standard deviation of firing periods. For small values of \( \eta \), correlations are of crucial importance to understand the temporal firing patterns that appear in the system (van Vreeswijk & Abbott, 1993; Rodríguez & López, 1999). An analysis of the strong interaction regime is outside the scope of this work.

Another important phenomenon observed in the simulations is the interplay between the intrinsic fluctuations of the oscillations and the dynamic exchange of messages between the units, which leads to a reduction of the dispersion of the firing period. Qualitatively this effect can be understood as follows: Assume that, owing to a fluctuation in the spontaneous evolution, one of the units in the network takes longer to fire than average. During the longer spontaneous evolution, this unit will also tend to receive a larger number of messages. Thus, the contribution from the messages received from other units in the ensemble tends to reduce the duration of the interspike interval. In the opposite case, when the spontaneous evolution is faster than the average, which would lead to a shorter firing period, the unit...
receives on average fewer messages from the other neurons, which results in a delay in the production of a spike. The net result is a narrowing of the distribution of firing times. This effect can be studied in a mean-field model of the neural ensemble, which we describe in detail in the following section.

5 Mean-Field Theory of the Oscillator Ensemble

The narrowing of the firing period distribution caused by the interplay between fluctuations in the evolution of the oscillators and the accumulated effect of messages received by a given neuron can be studied in greater detail within the framework of mean-field theory (see Figure 4). Consider a test neuron that is singled out from the ensemble. The spontaneous evolution

Figure 4: Comparison between the distributions for the time when the threshold is reached in the model with a renormalized threshold (continuous curve) and the mean-field model (histogram), for \( L = 31, N = 16, p = 0.5, \eta = 2 \). The horizontal line corresponds to the renormalized threshold (see eq. 3.1), and the staircase line corresponds to the effective threshold (see equation 5.2) in the mean-field model. A number of typical trajectories of the neuron in the space of activation states are drawn. The mean-field distribution has been obtained in a simulation, where a gaussian smoothing term that reflects the effect of fluctuations of the effective threshold has been used.
of this test unit is governed by the dynamics specified in equation 2.1. The effect of the messages from the remaining oscillators can be accounted for by a progressive lowering of the threshold. Assuming that we measure time from the instant that the test neuron has reached the threshold and is about to fire (i.e., \( a_{\text{test}}(t = 1) = 1 \)), the mathematical expression for the effective threshold for \( t > 0 \) is

\[
\tilde{L}(t) = L - \Theta(t),
\] (5.1)

where \( \Theta(t) \) (see equation 4.4) is the accumulated number of messages received by the test unit in the interval \([0, t] \). \( \Theta(t) \) is a fluctuating quantity, and, in principle, it depends on the actual state of the test neuron. The results of the simulations presented in Figure 3 indicate that for large and intermediate values of \( \eta \), the fluctuations of \( \Theta(t) \) are actually small and can in a first approximation be neglected. Furthermore, the increase with time of the cumulative number of messages received by the test neuron is approximately linear, which indicates that the firing probability density of the remaining neurons in the network is roughly constant and independent of the state of the test oscillators (i.e., correlations can be neglected). This is the case because for \( \eta \gg 1 \), the feedback effect from the network is not sufficient to induce synchronization among the units. These then behave approximately as if they were independent integrate-and-fire oscillators with a threshold that is decreasing in time with a constant rate \( \alpha \). As \( \eta \) approaches one, the feedback effect of the network becomes stronger, and correlations between the neurons are no longer negligible. In fact at \( \eta = 1 \), the oscillators fire periodically within synchronization clusters (van Vreeswijk & Abbott, 1993; Rodríguez & López, 1999). The theoretical analysis of such regime, where the simplifying assumptions we make in the formulation of this mean-field theory are no longer valid, is more involved and outside the scope of this article.

In summary, in the regime of intermediate and large \( \eta \), we can assume that in equation 5.1, the quantity \( \Theta(t) \) can be replaced by its average \( \overline{\Theta(t)} \), which increases approximately in a linear fashion with time, \( \overline{\Theta(t)} \approx at \),

\[
\tilde{L}(t) \approx L - \overline{\Theta(t)} \approx L - at.
\] (5.2)

The speed of the lowering of the threshold \( \alpha \) is determined in a self-consistent manner by requiring that, on average, during the period between two consecutive spikes of the test neuron, the remaining neurons have fired. The distribution of firing periods predicted by this model is given by the expression

\[
P_{\text{mf}}(\tau) = \sum_{l=L_0}^{L_\alpha} \binom{\tau - 2}{l - 1} p^{l-1} q^{\tau-1-l} + \binom{\tau - 2}{L_l - 2} p^{L_l-1} q^{\tau-L_l},
\] (5.3)
The quantities $L_l$ and $L_u$ are the lower and upper limits of the states that are swept through by the lowering of the threshold at each time step, respectively,

\[
L_l = \lceil \tilde{L}(\tau) \rceil, \\
L_u = \begin{cases} 
\lfloor \tilde{L}(\tau - 1) \rfloor & \text{if } \tilde{L}(\tau - 1) \text{ is not integer}, \\
\lfloor \tilde{L}(\tau - 1) \rfloor - 1 & \text{if } \tilde{L}(\tau - 1) \text{ is integer}.
\end{cases}
\]  

The first term in equation 5.3 represents the contribution from the states that are swept through by the lowering of the threshold. The second term corresponds to the instances in which the oscillator reaches the threshold by spontaneous evolution. From the distribution of the firing period given by equation 5.3, we can estimate the expected period and its standard deviation:

\[
\langle \tau \rangle_{mf} = \sum_\tau \tau P_{mf}(\tau) \\
\sigma_{mf} = \sum_\tau (\tau - \langle \tau \rangle_{mf})^2 P_{mf}(\tau).
\]  

(5.5)

Analytical expressions for these quantities can be obtained if some simplifying assumptions are made. The details of the derivation of the approximate expressions for the mean and the standard deviation of the firing period are given in appendix A. The resulting expressions are

\[
\tau_{mf} = \hat{\tau} \\
\sigma_{mf} = \frac{p}{p + \alpha} \hat{\sigma} = \frac{\eta - 1}{\eta} \hat{\sigma}.
\]  

(5.6)

where $\hat{\tau}$ and $\hat{\sigma}$ are given by equation 3.2, where the mean speed for the lowering of the threshold is

\[
\alpha = \frac{V \epsilon}{\tau_{mf} - 1} = \frac{p}{\eta - 1}.
\]  

(5.7)

It is clear from equation 5.6 that whereas the firing period is the same as in the model with a renormalized threshold, the width of the distribution is reduced by the factor

\[
\frac{\eta - 1}{\eta} < 1.
\]  

(5.8)

The results can be given a graphical interpretation (see Figure 6), whose justification can be found in appendix B. A summary of results is presented in Table 2.
Table 2: Comparison Between Mean-Field Theory and Simulation (Exact) Results.

<table>
<thead>
<tr>
<th>L</th>
<th>N</th>
<th>(\eta)</th>
<th>(\langle t_t \rangle_{e,0})</th>
<th>(\sigma_{t_t} \rangle_{e,0})</th>
<th>(\langle t \rangle_{mf})</th>
<th>(\sigma_{mf})</th>
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<tr>
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<td>11</td>
<td>99.9</td>
<td>1099.9 (0.11)</td>
<td>10.9 (0.08)</td>
<td>1099.89</td>
<td>10.94</td>
</tr>
<tr>
<td>500</td>
<td>11</td>
<td>49.9</td>
<td>544.3 (0.08)</td>
<td>7.6 (0.07)</td>
<td>544.33</td>
<td>7.54</td>
</tr>
<tr>
<td>1000</td>
<td>101</td>
<td>9.99</td>
<td>1000.0 (0.03)</td>
<td>9.5 (0.03)</td>
<td>999.92</td>
<td>9.48</td>
</tr>
<tr>
<td>500</td>
<td>101</td>
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<td>444.56 (0.02)</td>
<td>5.7 (0.02)</td>
<td>444.42</td>
<td>5.61</td>
</tr>
</tbody>
</table>

Note: \(p = 0.9\) in all cases.

We have observed in our study that the quality of the mean-field approach varies with the stochastic character of units. The larger the randomness of the spontaneous advance in the unit activity, the better the results the mean-field model gives. That is, the quality of the agreement between values measured in simulations and those given by the model is retained for smaller values of \(\eta\). In Figure 5 we present results as a function of \(\eta\) for three different values of the randomness parameter \(p\). The reason to choose the dispersion reduction magnitude of Figure 5 will be made clear in the next section.

6 Discussion

The dynamics of the population of neurons studied in this work give rise to a rather complex structure for the correlations. Nonetheless, in the regime where synchronization does not obtain, these dynamics can be described using a simple mean-field model. In this approach, the effect of the ensemble of neurons on a probe unit is reduced to a “rain” of messages with constant speed. Despite its simplicity, this model accounts for the bulk part in the observed decrease of dispersion with respect to the trivial renormalized threshold picture. The results displayed in Table 2 give a first idea of the excellent agreement between period dispersions calculated with the mean-field approach and the ones measured in numerical simulations. Down to \(\eta = 9.99\), discrepancies between the results for the dispersion are within the variability of simulations that start from different initial conditions or focus on a different probe unit in the ensemble. A combined reading of the results in Tables 1 and 2 gives a quantitative measure of the impact in the dynamics of the simple mechanism included in the mean-field approach at intermediate values of \(\eta\). For instance, at \(\eta = 4.99\), the 19% reduction of dispersion with respect to the renormalized threshold model observed in the simulation is correctly computed in the mean-field approach, which predicts a 20% reduction (see Figure 5).

It is useful to take the renormalized threshold model as a reference, since it accounts for trivial effects that arise from the interaction among units in the ensemble. The sudden lowering of the threshold included in this
model leads to a shorter firing period and therefore to a certain reduction of the dispersion. This reduction is explained by the decrease in the number of random steps the neuron takes, on average, before it produces a spike. What is left out of this picture is a dynamical effect that arises from the rhythm at which messages are received by units interacting with the rest of the ensemble. This dynamical effect leads to a sharper focusing of the firing period of the units. Every neuron in the ensemble fires with a period that has a lower dispersion than what it would in isolation, even if, in both cases, the unit had the same intrinsic randomness (measured as the average number of random steps it has to perform to reach the firing threshold). Firing dispersion reductions of around 50% have been measured in the performed simulations for values $\eta \sim 2$ (see Figure 5). Up to that amount, the reduction is well explained by the mean-field approach. For values of $\eta$ smaller than 2, the ensemble dynamics becomes gradually different. When the parameter $\eta$ is exactly equal to 1, the dynamics are entirely dominated by the interactions (van Vreeswijk & Abbott, 1993; Rodríguez & Lopez, 1999).

In summary, the results displayed in Figure 5 clearly show that the main part of the observed dispersion reduction can be explained by a simplified
model where the threshold decreases at constant speed as a consequence of the messages received from the ensemble. Although more complex correlations are present in the original model, as discussed in section 5, they have a minor effect for large and intermediate values of $\eta$. The mean-field model is realistic, yet simple enough to give a clear picture of the phenomenon at hand. First, it allows for a simple geometrical construct explaining the origin of dispersion reduction and therefore of period focusing. Second, it provides a back-of-the-envelope formula to calculate the amount of dispersion reduction. This formula can be derived using simple geometrical considerations (see appendix B) and in its more general form, equation B.11, may be useful to analyze results in several situations. In particular, consider a network in which each neuron receives excitatory signals from various random sources and messages from the other units in the network. As a consequence of the message exchange mechanism, the period of each neuron becomes more sharply focused than in isolation, even with a properly renormalized firing threshold. If $\alpha$ denotes the speed at which the neuron is receiving the messages and $p$ the mean speed at which the unit travels toward the threshold with a dispersion proportional to $\sqrt{1 - p/p}$, then the dispersion reduction factor can be calculated directly as the ratio $p/(p + \alpha)$, as given by equation 5.6.

Appendix A: Mean-Field Formulas

Let us study in detail the mean-field model in which the effect of the ensemble of firing neurons on a test neuron is represented by a smoothly decreasing effective threshold,

$$\tilde{L}(t) = L - \alpha t,$$

where $\alpha$ is to be determined in a self-consistent fashion. Explicit formulas for the continuous version of this problem (without the self-consistent condition for $\alpha$) can be found in Buonocore, Nobile, and Ricciardi (1987). The state of the test neuron at time $t$ is

$$a(t) = 1 + \sum_{\tau=1}^{t} \xi_{\tau}. \tag{A.2}$$

The variables $\{\xi_{\tau}\}_{\tau=1}^{t}$ are independent and identically distributed random variables, corresponding to dichotomic noise

$$\xi_{\tau} = \begin{cases} 0 & \text{with probability } (1 - p) \\ 1 & \text{with probability } p \end{cases} \tag{A.3}$$

with the properties

$$\langle \xi_{\tau} \rangle = p$$
\[ \langle \xi_t^2 \rangle = p \]
\[ \dot{\xi}_t = \xi_t - \langle \xi_t \rangle = \xi_t - p \]
\[ \langle \dot{\xi}_t \dot{\xi}_t \rangle = p(1 - p) \delta_{tt'} . \]  
(A.4)

The instantaneous distance between the threshold and the state of the neuron is
\[ d(t) = \tilde{L}(t) - a(t) = L - \alpha t - 1 - \sum_{\tau=1}^{T} \xi_{\tau} . \]  
(A.5)

The time at which the neuron reaches the threshold is
\[ 0 = L - \alpha T - 1 - \sum_{\tau=1}^{T} \xi_{\tau} . \]  
(A.6)

Taking the ensemble average of this equation, we obtain
\[ \langle T \rangle = \frac{L - 1}{\alpha + p} . \]  
(A.7)

The speed of the lowering of the threshold, \( \alpha \), is such that during the interval \( \langle T \rangle \), the test neuron has received messages with a total strength \( V \epsilon \):
\[ \alpha \langle T \rangle = V \epsilon . \]  
(A.8)

Therefore, the average interspike interval in this model is
\[ \tau_{mf} \approx 1 + \langle T \rangle = 1 + \frac{L - V \epsilon - 1}{p} , \]  
(A.9)

where the extra one corresponds to the deterministic time step in which the neuron is discharged.

The value from the dispersion of the period can be found by rewriting equation A.6 using equation A.4 and the definition \( \hat{T} = T - \langle T \rangle \):
\[ (\alpha + p) \hat{T} = - \sum_{\tau=1}^{T} \dot{\xi}_{\tau} . \]  
(A.10)

Taking the square of both sides of the equation, using the properties of the dichotomic noise, equation A.4, and the definition of \( \eta \), equation 2.7, we obtain, after some manipulation,
\[ \sigma_{mf}^2 \approx \langle \hat{T}^2 \rangle = \left( \frac{p}{\alpha + p} \right)^2 \hat{\sigma}^2 = \left( \frac{\eta - 1}{\eta} \right)^2 \hat{\sigma}^2 , \]  
(A.11)

where \( \hat{\sigma} \) is given by equation 3.2.
Figure 6: Graphical interpretation of the mean-field model, with $L = 31, N = 16, p = 0.5$. The continuous distribution curve represents the probability density for the time at which the neuron reaches the renormalized threshold. The histogram corresponds to simulations with the mean-field model, including a gaussian smoothing term that reflects the effect of fluctuations of the effective threshold.

Appendix B: Graphical Interpretation of the Mean-Field Theory

The mean-field model presented in section 5 can be derived from a simple graphical construct. The effective threshold is assumed to decrease linearly, according to equation A.1. The random walk of the neuron in the space of excitation states is replaced by a linear increase in the excitation state with gaussian fluctuations around this average evolution. The variance of these fluctuations increases linearly with time:

$$\langle a(t) \rangle \approx pt \quad \text{(B.1)}$$
$$\sigma_a^2(t) \approx \chi^2 t. \quad \text{(B.2)}$$

This replacement is valid asymptotically, when the binomial distribution describing the evolution of an ensemble of random walkers is well approximated by a normal distribution. In Figure 6, $\chi$ has been chosen so that at a given instant, 90% of the trajectories are within the region delimited by
the curves \( pt \pm \chi \sqrt{t} \). The time when, on average, the neuron reaches the
threshold is the abscissa of point A in Figure 6:

\[
\hat{\tau} = \tau_{mf} = \frac{L - 1}{\alpha + p},
\]

(B.3)

From the geometrical construct in Figure 6, it is apparent that the ratio be-
tween the standard deviation estimated by the effective threshold model
(section 3) and that predicted by the mean-field model (section 5) is approx-
imately given by

\[
\frac{\sigma_{mf}}{\hat{\sigma}} \approx \frac{\tau'_{2} - \tau'_{1}}{\tau_{2} - \tau_{1}}.
\]

(B.4)

The values \( \tau_{1}, \tau_{2} \) can be obtained from the abscissas of points B and E,
respectively, in Figure 6:

\[
p\tau_{1} + \chi \sqrt{\tau_{1}} = L - 1 - \alpha \hat{\tau}
\]

(B.5)

\[
p\tau_{2} - \chi \sqrt{\tau_{2}} = L - 1 - \alpha \hat{\tau}.
\]

(B.6)

From these equations, using equation B.3, we obtain

\[
p(\tau_{2} - \tau_{1}) = \chi (\sqrt{\tau_{1}} + \sqrt{\tau_{2}}).
\]

(B.7)

Similarly, from the expressions for the abscissas of points C and D and
equation B.3,

\[
(p + \alpha)(\tau'_{2} - \tau'_{1}) = \chi \left( \sqrt{\tau'_{1}} + \sqrt{\tau'_{2}} \right)
\]

(B.8)

Given that the relation

\[
\sqrt{\tau_{1}} + \sqrt{\tau_{2}} \approx \sqrt{\tau'_{1}} + \sqrt{\tau'_{2}}
\]

(B.9)

obtains, at least in an approximate manner, we have

\[
p(\tau_{2} - \tau_{1}) \approx (p + \alpha)(\tau'_{2} - \tau'_{1}),
\]

(B.10)

which leads to the desired relation

\[
\sigma_{mf} \approx \frac{p}{\alpha + p} \hat{\sigma}.
\]

(B.11)

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References


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