Emergence of Synchronous Oscillations in Neural Networks Excited by Noise.

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The presence of noise in non linear dynamical systems can play a constructive role, increasing the degree of order and coherence or evoking improvements in the performance of the system. An example of this positive influence in a biological system is the impulse transmission in neurons and the synchronization of a neural network. Integrating numerically the Fokker-Planck equation we show a self-induced synchronized oscillation. Such an oscillatory state appears in a neural network coupled with a feedback term, when this system is excited by noise and the noise strength is within a certain range.

I. INTRODUCTION.

Neural networks consist of many nonlinear components (neurons that beyond a threshold emit action potentials) which are interdependent (the output of a neuron is the input of another neuron in the network) and form a complex system with new emergent properties that are not hold by each individual item in the system alone. The emergent property of this dynamical system is that a set of neurons will synchronize and fire impulses simultaneously. In the context of neuroscience, this emergent property is used to implement quite sophisticated and highly specialized "logical" functionalities such as memorization with Hebbian learning, and recognition of patterns (or memories).

There at least two mechanisms by which such synchronous oscillations can take place:

- Synchrony can be a consequence of a common input produced by an oscillating neuron (or set of neurons) (pacemakers).
- Synchrony can also be a consequence of an emergent population oscillation within a network of cells. There is no external coordination when this oscillation is built up, it is self-organized and its properties must be related to the structural way in which the networks are connected.

Each neuron can receive input from neighboring neurons of the network and from external impulses. These neural networks are also excited by electrical noise which is ubiquitous in the neuronal system and seem to be able to operate in such a noisy environment in a robust way. The main sources of noise are related to the synaptic connections and voltage-gated channels [1, 2, 3, 4]. The role of noise in the functioning of the non-linear nervous system is poorly understood but there are evidences of positive interactions of noise and nonlinearity in neuronal systems [5, 6, 7, 8, 9, 10].

In the present work we will investigate the relevance of noise in the synchronization of a neural network. In order to do so we will integrate numerically the Fokker-Planck equation associated to the stochastic system. This has the advantage of giving better accuracy in the tails of the distribution than solving the stochastic differential equations. Integrating numerically this equation one can obtain a quick overview of the system dynamics and the time evolution of the probability density. We will show that noise can help the system building a synchronous oscillation.

The starting point is the equation of motion of the single neuron, see section II. Then, in section III we describe the ensemble of neurons excited by noise using the Fokker-Planck equation, which we integrate numerically in different scenarios. We first show a noise induced transition in the distribution for a certain range of noise intensity (see subsection III A). Next we introduce different situations where synchrony is attained in the presence of noise: first exciting the ensemble of neurons with an oscillating external input (see subsection III B), then introducing only a feedback term (see subsection III C) and finally reinforcing the external excitation with the internal feedback (see subsection III D). In all these scenarios there exist a defined range of noise intensity where the synchronization is maximized.

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II. FITZHUGH-NAGUMO EQUATION FOR A SINGLE NEURON.

The impulse transmission in a neuron can be essentially described with the Hodgkin-Huxley model, \[1\]. The FitzHugh-Nagumo (FHN) model (\[12, 13\]) is a simplified variant of the previous model accounting for the essentials of the regenerative firing mechanism in an excitable nerve cell, namely, it has a stable rest state, and with an adequate amount of disturbance it generates a pulse with a characteristic magnitude of height and width.

In the FHN model all dynamical variables of the neuron are reduced to two quantities: the voltage of the membrane $u$ (fast variable) and the recovery variable $v$ which corresponds to the refractory properties of the membrane (slow variable):

$$
\dot{u} = c(-v + u - u^3/3 + I_1(t) + \sqrt{2D}\xi(t)) \tag{1}
$$

$$
\dot{v} = u - bv + a \tag{2}
$$

$$
<\xi(t)\xi(t')> = \delta(t-t') \tag{3}
$$

The neuron is excited by an external input $I_t = I_1(t) + \sqrt{2D}\xi(t)$. Here we have added white Gaussian noise $\xi(t)$ to the standard FHN equation obtaining a Stochastic Differential Equation (SDE). For all the cases described below we will study this system for $c = 10$, $a = 0.7$, and $b = 0.8$. The neuron is said to "fire" or emit a "spike" when $u > 0$. This impulse is then transmitted along the axon and elicits the emission of neurotransmitters which in turn excite other neurons.

Let us first consider the deterministic system ($D = 0$) with constant excitation $I_t = A$. A typical feature of a neuron system is that the information is encoded in the firing rate. For constant input there is a threshold amplitude (in this case $A = 0.35$) beyond which the output is a periodic oscillating system (a train of spikes with $u > 0$), whose frequency (and not the amplitude) depends on the amplitude $A$ of the exciting force. In Fig. 1-left we show the projection onto the phase space of two of these attractors excited by different inputs of constant amplitude. All the orbits are attracted to this periodic attractor. Such attractors will also be seen later in the extension to a noisy system. If the excitation is below the threshold then the system goes to the stable rest state (there is no oscillation in this case).

We study now the response of the system to a time varying force of the type $I_t = A\cos(2\pi ft) + \sqrt{2D}\xi(t)$, with $A = 0.15$, $f = 0.55$ and various noise intensities $D$. For a given initial condition $(u(t_0), v(t_0)) = (0,0)$, we perform a Monte Carlo simulation: integrate the SDE for different noise realizations and average over the ensemble to obtain $\langle u(t) \rangle$. We can evaluate the spectrum and the Signal-to-Noise-Ratio (SNR). The system shows a maximal susceptibility to the external periodic forcing for $D \approx 0.005$, see Fig. 2. This feature will also survive when we consider an ensemble of neurons and will be decisive for the behavior of the network.

The enhancement of the system response due to noise is a characteristic trace of stochastic resonance (for a comprehensive review on prominent references see \[14, 15\]). Noise can induce hopping from the resting state to excited state and vice-versa. The mean time that it takes a neuron to move from one state to the other for a given noise intensity is called mean escape time. Stochastic resonance takes place when there exists some kind of synchronization between the forcing time and the mean escape time, i.e. when there exists a time-scale resonance condition. For instance, for the double-well potential, this happens when the mean escape time is comparable with half the period of the periodic forcing.
FIG. 1: Phase space projection of two supra-threshold trajectories for the FHN excited with constant amplitude $I_t = A$. 

FIG. 2: The signal to noise ratio shows the presence of stochastic resonance in the SDE of a FHN system excited by $I_t = A \cos(2\pi ft) + \sqrt{2D}\xi(t)$ when $A = 0.17$ and $f = 0.55$. 

III. NEURON ENSEMBLE AND FOKKER-PLANCK EQUATION.

In the previous section we have introduced the behavior of a single neuron described by an FHN oscillator excited by constant force or by a periodic force plus noise. But what happens when we consider an ensemble of such excitable elements?. In order to describe this set of oscillators we will use the Fokker-Planck (FP) equation, which is a partial differential equation, describing the time evolution of the probability density associated to a SDE. If one needs to obtain global information from a system of independent neurons excited by noise, one can either run a Monte Carlo simulation for the SDE for all the initial conditions (one per neuron of the network) and group the solution in histograms or solve the FP equation for the density in phase space with a given initial condition [16]. Integrating the FP equation we get better accuracy in the tails, where the probability is very low, than running the Monte Carlo simulation. These tails will be particularly important in the FHN stochastic equation since the supra-threshold excursions in the attractor region, that are relevant for the network excitation, are of low probability.

We integrate numerically the Fokker-Planck equation of the previously described FHN system:

\[
\frac{\partial \rho}{\partial t} = - \frac{\partial}{\partial v} (u - bv + a) \rho - \frac{\partial}{\partial u} (v - w_u^3/3 + I_1(t)) \rho + DC^2 \frac{\partial^2 \rho}{\partial u^2}
\]  

(4)

using an alternating semi-implicit scheme, to obtain the time evolution of the probability density \( \rho(x, v, t_0) \) for any given initial condition. This equation gives the distribution of the state of our network of neurons, the neurons can be excited or at rest depending on the input current and noise. If we monitor the activity of this network from outside, as it is done when performing an electro-encephalograph, we measure the average response of this network \( < u > \). We will see that this value can be at rest or oscillate with different frequencies depending on the input current \( I(t) = I_1(t) + \sqrt{2D} \xi(t) \), with \( \xi(t) \) white Gaussian noise. The connectivity of the network is implicitly given in the structure of \( I_1(t) \).

For the rest of the work we will integrate this partial differential equation with the following values: \( \Delta u = 0.03 \), \( \Delta v = 0.013 \), absorbing boundaries at \( u = \pm 4.5, v = \pm 2.34 \) and \( \Delta t = 0.01 \) for various noise intensities \( D \). Our initial condition is a Gaussian distribution centered close to the equilibrium point (non firing condition), representing a network with all the neurons at rest. The Gaussian initial condition has mean values \( < u > = -1.0 \) and \( < v > = -0.55 \) and variances \( \sigma_u^2 = 0.05, \sigma_v^2 = 0.013 \).

A. Neural network excited only by noise.

Let us first consider the ensemble of independent neurons when the only input current is the noisy term \( I_2(t) = \sqrt{2D} \xi(t) \). For low noise intensities, \( D = 0.001 \), after a transient time, the probability of these large excursions is almost non-existent. See Fig. 3-left where the density is peaked on top of the stable fixed point. For bigger noise intensities, \( D = 0.005 \), after the transient time, there is a certain probability for a neuron to be excited, even in the absence of external forcing. In Fig. 3-right we show the stationary distribution for \( D = 0.005 \) that has non-vanishing tails on the supra-threshold area. We can talk of noise induced transition in the density distribution in the sense that the stationary distribution changes with noise. We will see that this strong dependence on the noise intensity will survive if we take into account additional influences, such as external driving or feedback, and will be determinant for tuning the system response.
FIG. 3: Stationary distribution of the neural network distribution excited only by noise with intensity $D = 0.001$ (left) and $D = 0.005$ (right). The tails of the distribution extend to the supra-threshold area, lying on top of the attractor. There is a significant increment in the probability for a neuron to be excited (supra-threshold area) when $D = 0.005$. 
B. Periodic force excitation.

Next we study the system excited by noise for $D = 0.005$, and an external periodic force $I_1(t) = A \cos(2\pi ft)$ (induced for instance by an external pacemaker) with frequency $f = 0.55$ (period $T = 1/f$), and $A = 0.15$. After the transient time the density moves along the phase space plane (over a slightly different attractor) in a periodic way, with the period of the exciting force, see Fig. 4. This periodic oscillation is sustained as long as it is excited by the external periodic force. We have studied the time evolution of the 1st moment $<u(t)> = \int_{-\infty}^{\infty} u \rho(u,v,t) du dv$ for different noise intensities when the pseudo-stationary solution is reached As in the single neuron case introduced in section III A we also find here the stochastic resonance phenomenon in the signal to noise ratio of the spectral analysis $<u(t)>$, see Fig. 5.

FIG. 4: Pseudo-stationary distribution (periodic in time) for the neural network excited by an external periodic force $I_1(t) = A \cos(2\pi 0.55t)$ and noise. Shown at time $t = 100, 120, 140$ for $D = 0.005$ and $A = 0.15$. 
FIG. 5: Signal to noise ratio from the spectral density for $I_c = A \cos(2\pi 0.55t)$ with $A = 0.15$ and various noise intensities. The response of the system to the forcing is maximized at $D = 0.005$. 
What happens when our neural network has no external driving force but instead is coupled internally via some kind of feedback term? We will see that this network can exhibit autonomous stochastic resonance: for a certain range of noise intensities a self-organized and robust coherent oscillation appears in the absence of external periodic forcing.

Let us first find the simplest possible model which includes the basic features of a neural network in the brain. The current flowing into each neuron is due to the interactions with other cells and the response of the neuron is expected to depend on the sum of the active synapses (sum of firing neurons where the dendrites are connected to). We simulate now this input current \( I(t) \) as the sum of two terms. The first one \( I_1(t) = A \cdot n(t) \) is proportional to the number of excited neurons in the network \( n(t) = \int_0^\infty \rho(u,v; t-\Delta T) dudv, \) and is the same for each neuron (mean field approximation). This term is evaluated at time \( t-\Delta T \) but it acts at time \( t \). We are tacitly assuming that our neural network is fully connected, and that there is some transmission delay (synaptic communications between neurons depend on propagation of action potentials often over appreciable distances), where the delay \( \Delta T \) corresponds to the time that this process takes before acting back on the network. The second term \( I_2(t) = \sqrt{2D\xi(t)} \) is stochastic, as above, and represents the deviations with respect to this global term for each neuron input. Finally we have a network of neurons described as an ensemble of FHN oscillators coupled via a nonlocal feedback term.

We have mentioned before that the neuron dynamics is such that, for constant input above the threshold of excitation the system oscillates whereas for input below the threshold the system is at rest. We first study this system for \( \Delta T = 0.2 \) and a strong feedback term \( A = 0.9 \). In Fig. 6 (left) we show the response of the system \( < u(t) > = \int_{-\infty}^\infty u \rho(u,v,t) dudv \) for different noise intensities \( D \). For low noise intensities \( (D = 0.001) \) the feedback term \( I_1(t) \) alone is below the threshold of excitation. The response of the system is enhanced by stochastic resonance, reaching the maximal amplitude and level of synchronization for \( D = 0.005 \). Beyond this noise intensity the response to the feedback is lower but still beyond the level of excitation so that a smaller amplitude oscillation is sustained for \( D = 0.02 \). The maximum value of \( n(t) \), \( n_{\text{max}} \), gives a measurement of the synchronization of the network, for the cases shown \( n_{\text{max}} = 0.05 \) for \( D = 0.001 \), \( n_{\text{max}} = 0.95 \) for \( D = 0.005 \) and \( n_{\text{max}} = 0.8 \) for \( D = 0.02 \).

If the amplitude of feedback excitation \( A \) is weaker, such as \( A = 0.5 \), the enhancement effect is even clearer, see Fig. 6 (right). The feedback is only able to overcome the threshold of oscillation in a narrow region of the noise intensity \( D \), where stochastic resonance is at its maximum.

Notice that not every single neuron is necessary oscillating with the same phase since the density distribution is diffused along the attractor, see the density plots at different times in Fig. 7.

![FIG. 6: Time evolution of the network output <u(t)> for different noise intensities showing and enhancement of the response for D = 0.005, when A = 0.9 (left) and when A = 0.5 (right). A self-sustained global oscillation is excited by the internal feedback and noise. If the feedback level is weak only for noise levels in the region of stochastic resonance (D = 0.005) can this oscillation emerge.](image)

Next we keep the noisy input constant and increase the delay time \( \Delta T \) up to 20% of the neuron cycle. We calculate \( n(t) \) the fraction of the population that is excited at a given time, shown in Fig. 8. As we increase the delay the synchronization level decreases significantly, the global excitement of the network is lower and the feedback input is lower. Because of the frequency dependence of the response of the FHN equation on the input, the frequency of oscillation decreases (up to 20%) with increasing delay. Following this model we would expect that two equal
networks, strongly connected through paths with long conduction delays, would oscillate with lower frequencies and less synchrony than those connected with short conduction delays.

This is indeed found in the brain, where the oscillatory activity of connected networks oscillates with lower frequencies in the case of connections that go along longer distances. For instance while local sensory integration evolves with a fast gamma (25-70 Hz) dynamics, multisensory integration evolves with an intermediate beta (12-18Hz) dynamics, and long-range integration during top-down processing evolves with a temporal dynamics in a low theta/alpha (4-12Hz) frequency range \[17\]. Many authors have studied the role of time-delays and nonlocal excitatory coupling in the generation of synchronous rhythm in the brain, although the detailed mechanisms behind this fact are still under investigation \[18, 19, 20\].

FIG. 7: Neural network distribution at different times when a self-oscillatory state is excited by a weak feedback term (\(A = 0.5\)) and noise (\(D = 0.005\)): t=10.24,20.48,30.72 and 40.96.
FIG. 8: (Left) Fraction of neurons above the threshold \( n(t) = \int_0^\infty \rho(u, v, t - \Delta T) dudv \) as a function of time for different delays \( \Delta T \), when the response of the system is at its maximum due to stochastic resonance \( (D = 0.005) \). For longer conduction delays the synchronization level and the oscillation frequency decrease. (Right) Maximum value of \( n_{\text{max}} \) (synchronization level) as a function of delay \( \Delta T \).
D. Periodic force and feedback, reinforcement of an external stimulus.

If we study the system excited by noise with $D = 0.005$, the feedback term described above with $A = 0.5$ and an external periodic force $I(t) = A \cos(2\pi ft)$ with frequency $f = 0.55$ (period $T = 1/f$), we observe that after the transient time the density moves along the attractor in the phase space plane in a periodic way, with the period of the exciting force. We can see that two different behaviors coexist in a single network: an almost Gaussian distribution is moving along the attractor trajectory, whereas a secondary maximum is stable and localized at the non-firing position. The fraction of neurons above the threshold, $n = \int^\infty_0 \rho(u,v,t-\Delta T)du \, dv$, oscillates now between 0% and 90%, the remaining 10% is at rest whereas without the feedback term the maximum $n$ is 60%. In this case the feedback term and the noise helps the network to synchronize giving a very strong response to a signal, in other words: such feedback structures helps the system in amplifying a signal.

These recurrent neuronal circuits where synaptic output is fed back as part of the input stream, exist naturally in cerebral structures as amplifier structures. Neural connectivity is highly recurrent (for instance Layer IV is believed to be the cortical signal amplifier of thalamic signals).

![Density for feedback with $\Delta T = 3/4T = 3.00$ and periodic excitation with $A = 0.5$, shown at at times $t = 35.84$ and $t = 40.96$. The network is strongly synchronized, all the neurons evolve in a similar state.](image)

IV. CONCLUSION

The Fokker-Planck equation has been used to explore the time evolution of the probability density of a neural network excited by noise. Integrating numerically this equation one can obtain a quick overview of the system dynamics, its moments and spectral density, the attractors and most probable states of the neuron ensemble. We can explore different basic mechanisms that show new emergent properties depending on the connectivity of the network and the noise intensity.

An intermediate level of noise alone, combined with nonlocal excitatory interactions, can give rise to coherent, strongly synchronized, oscillations. There are several competing mechanisms: noise, dispersion, nonlinearity and nonlocal interactions (the feedback term) [21]. The balanced combination of all of them leads to the formation of a global oscillatory and robust state.

This dynamics also helps the system to follow any external weak excitation, such as a periodic force. If the parameters are properly chosen as much as 95% of the neural population can be synchronized improving the sensibility of the system to weak external signals. If the delay time or if the noise is out of the adequate range the global oscillations process does not take place.
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