Contour integration and synchronization in neuronal networks of the visual cortex

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Abstract. The visual perception of contours by the brain is selective. When embedded within a noisy background, closed contours are detected faster, and with higher certainty, than open contours. We investigate this phenomenon theoretically with the paradigmatic excitable FitzHugh-Nagumo model, by considering a set of locally coupled oscillators subject to local uncorrelated noise. Noise is needed to overcome the excitation threshold and evoke spikes. We model one-dimensional structures and consider the synchronization throughout them as a mechanism for contour perception, for various system sizes and local noise intensities. The model with a closed ring structure shows a significantly higher synchronization than the one with the open structure. Interestingly, the effect is most pronounced for intermediate system sizes and noise intensities.

1 The introduction

Object representation in the brain relies on two properties: first, the detection of specific features (such as location and orientation) by individual neurons, and second, the integration of features of extended objects through dynamic association of neuronal assemblies [1]. Seminal experimental studies showed, for instance, that assembly coding allows for scene segmentation in the cat visual cortex [2, 3]: the response to individual objects in a scene, in that case a single moving bar, was characterized by synchronization among neuronal assemblies corresponding to the different parts of the scene, while correlations were absent in response to different objects, such as two moving bars with different orientations. When the stimulus is a static contour, the different sections of the contour map to different neurons in the visual cortex. It is hypothesized that these neurons fire synchronously when the contour is perceived. The potential beneficial role of synchrony in that context lies in the possibility that at the following stages of cortical processing the receiving or downstream neurons will be much more reactive to synchronous input than to temporally dispersed input. In this way synchrony can effectively impact the dynamics of further stages of information processing, and neurons that synchronize can have a higher saliency than the ones that do not. Experimental observations show that contours embedded within a noisy background are detected more efficiently if they are closed than if they are open. Here we study this phenomenon theoretically in a one-dimensional array of model neurons subject to noise, considering the effect of boundary conditions in the synchronization efficiency. We also show that noise has a beneficial role in this process by leading to a near zero-lag synchronization in the firing of all neurons in the array.

The effect of noise in brain activity has evoked a large interest in recent years. Stochasticity in neurons originates from different sources, including random synaptic input from other neurons, stochastic switching of ion channels, and quasi-random release of neurotransmitter by synapses. Despite (or maybe because of) the many noise sources in neuronal networks, the brain acts very reliably and needs only a very small amount of energy (about 12 W according to Ref. [4]). A growing number of scientific results suggests that noise plays a constructive role in brain activity. For instance, a noise-induced effect has been demonstrated in the visual processing area of the human brain [5]. In that experiment a periodic light signal was sent to one eye, whereas the other eye was subjected by noise, represented by light with fluctuating intensity. The result was that noise improved the processing of the periodic signal sent to the first eye.

Coherence resonance (CR), also known as stochastic coherence, is a noise-induced effect through which periodic oscillatory behavior arises and its coherece is optimized by noise. It has been found that at a certain noise intensity the system responds with a maximal periodicity, i.e. with an enhanced coherence. Both an increase and a decrease of the noise amplitude away from this optimal value lead to a decreasing of the coherence. CR has been observed in excitable systems like the Hodgkin-Huxley model [6], the FitzHugh-Nagumo systems [7], leaky integrate-and-fire models [8], the Plant/Hindmarsh-Rose neural model [9], and in dynamic systems which besides show jumps between several attractors [10]. Besides the neural context, CR can be found in climate [11] and laser models [12, 13].

Array-enhanced coherence resonance (AECR) [14] is an extension of the described noise-induced rhythm generation to an ensemble of many coupled excitable oscillators. Interestingly, the quality of the coherence in a large ensemble with diverse oscillators can be larger than in a single one with the same mean properties. The results presented below show that AECR provides a potential mechanism for contour perception, whose efficiency depends on the network topology, which should explain why a closed contour is better perceived than an open one.

2 The FitzHugh-Nagumo model

The FitzHugh-Nagumo (FHN) model is a paradigmatic model describing the behavior of firing spikes in neural activity [15]. The model was proposed in Refs. [16, 17] as a simplification of the famous model by Hodgkin and Huxley [16] and is a simple example of two-dimensional excitable dynamics. It describes qualitatively the response of an excitable nerve membrane to external stimuli. Important features are the inclusion of a refractory mechanism and the existence of different refractory states, as well as states of enhanced and depressed excitability depending on the external stimulation. Beside the paradigmatic description of the firing spikes of neural activity [15], the FHN model is representative for activator-inhibitor dynamics of excitable media in general [18]. The model reads:

$$\varepsilon \dot{x}_i = x_i - \frac{x_i^3}{3} - y_i + \xi_i(t) + D_{i-1}(x_{i-1} - x_i) + D_i(x_{i+1} - x_i) \tag{1}$$

$$\dot{y}_i = a - x_i \tag{2}$$

In a neural context, $x(t)$ represents the membrane potential of the neuron and $y(t)$ is related to the time-dependent conductance of the potassium channels in the membrane [15]. The dynamics of the activator variable x is much faster than that of the inhibitor y, as indicated by the small time-scale-ratio parameter ε and is fixed to $\varepsilon = 0.01$ throughout the following calculations. It is well known that for $|a| > 1$ the only attractor is a stable fixed point. For $|a| < 1$, the limit cycle generates a periodic sequence of spikes. The parameter a is the bifurcation parameter and is fixed below to $a = 1.05$, in order to tune the system to the excitable regime. The index i distinguishes the separate oscillators and runs from 1 to N, the total number of coupled elements. The Gaussian (white) noise sources $\xi_i(t)$ satisfy $\langle \xi_i(t)\xi_j(t')\rangle = \sigma_a^2 \delta(t - t')\delta_{i,j}$ with the noise intensity σ_a^2.

We model the neurons in the visual cortex by diffusively coupled FHN and consider in the present model only those neurons that map the visual contour. We assume a constant and equal external stimulus to all neurons mapping the contour, which leads to a constant reduction of the excitation threshold for all involved neurons. This assumption results in a permanent reduction of the parameter a in the model closer to the bifurcation point for all neurons, so that the external stimulus need not appear explicitly in the model equations. The neurons not involved in the contour mapping remain with high threshold of excitation and are ignored. All FHN elements are thus in a excitable state and remain in their rest state without spiking activity if no noisy stimulus is present. The noise is absolutely needed to overcome the excitation threshold and evoke spikes. We assume local Gaussian white noise subject to every neuron with the same intensity σ_a^2. The spikes are noise-evoked and mediated by the local nearest neighbor coupling with diffusive property and the coupling strength D_i. Note that the coupling is instantaneous, i.e. it does not include any explicit delay. Effective delay in the signal transmission will appear, however, due to the natural inertia of each neuron in the chain to react to an input (see sec. 4 below).

We consider three spatial architectures: the uncoupled situation ($D_i = 0.0$), a linear chain ($D_{1,\ldots,N-1} = 0.02$, $D_N = 0.0$, Fig 1 bottom), and a closed loop ($D_i = 0.02$, Fig 1 top).

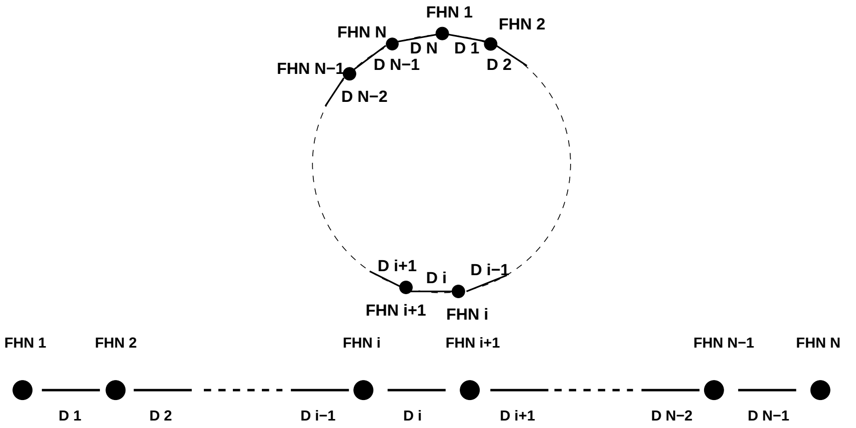

Fig. 1. Schemes of a closed loop and a linear open chain.

3 Comparison of the synchronization of an open and a closed contour

This section should shed light on the question of whether synchronization is better in a closed contour than in an open one. We measure the degree of synchronization R_{syn} as the ratio of the variance of the mean field to the mean variance of the individual elements [19]:

$$R_{syn} = \frac{\langle \bar{x}^2 \rangle - \langle \bar{x} \rangle^2}{\frac{1}{N}\sum_{i=1}^{N}(\langle x_i^2 \rangle - \langle x_i \rangle^2)} = \frac{\mathrm{Var}(\bar{x})}{\mathrm{Mean}_i(\mathrm{Var}(x_i))} \tag{3}$$

with the mean membrane potential $\bar{x}$

$$\bar{x} = \frac{1}{N}\sum_{i=1}^{N} x_i \; . \tag{4}$$

The fully desynchronized state results in a synchronization measure $R_{syn} = 0$, whereas the complete synchronization amongst all oscillators is becoming manifest by $R_{syn} = 1$. Values between 0 and 1 describe states of partial synchronization. The measure R_{syn} detect only zero-lag synchronization, i.e. delay free synchronization and express the average difference between the mean field and the dynamics of the individual oscillators. For small ensembles R_{syn} results in values larger than zero also if one compares completely independent elements, e.g. for only two oscillators each of them influences the mean field to 50%. To eliminate this effect of the system size, we considere the fully uncoupled ensemble as the baseline to compare open and closed structures.

We consider two main influences on R_{syn}: the noise intensity σ_a^2 and the system size N. First we discuss the synchronization measure R_{syn} as a function of the system size N for different fixed noise intensities σ_a^2 (Fig. 2). In the first case ($\sigma_a^2 = 0.01$) the noise intensity is sub-threshold and only few and irregular spikes were evoked. The dynamics is determined by the small noisy and uncorrelated sub-threshold fluctuations. Hence the coupling does not play a significant role and the loop and chain configuration are close to the reference of the uncoupled chain. An increased noise intensity leads to a spiking behavior and the coupling contributes to the dynamics. The next plot ($\sigma_a^2 = 0.025$) shows a clear difference between the loop, the chain and the uncoupled case. For intermediate system sizes the loop synchronizes the ensemble more effectively than the open chain. Further increase of the noise to $\sigma_a^2 = 0.2$ optimizes the synchronization. The difference between loop and chain is less pronounced, but the absolute synchronization quality is enhanced, especially for large system sizes, i.e. the zero lag synchronization becomes stronger. $\sigma_a^2 = 1.0$ is beyond the optimal noise intensity and the synchronization is less than in the optimal case over the complete range of N. Interestingly, in the non-optimal noise case but close to it, the closed loop configuration shows a significant better performance than the open chain for intermediate system sizes. Further increase of the noise intensity ($\sigma_a^2 = 5.0$) destroys the synchronization. The system is determined by the random fluctuations and the coupling is too small to smoothen the irregular spikes.

The previous plots of the synchronization measure R_{syn} as a function of the system size (Fig. 2) have shown a strong dependence of the performance on the noise intensity. The noise evoking a maximal difference between open and close contour differs from the overall optimal noise, and we see that intermediate system sizes demand a noise strength for optimization different than larger sizes. To investigate this issue further, we calculated R_{syn} as a function of the noise intensity σ_a^2 for two fixed system sizes ($N = 16$ and $N = 64$) and the same coupling, in the spirit of stochastic and coherence resonance as a noise-induced effect with a resonance like response curve. Besides the synchronization measure R_{syn}, we also computed the correlation coefficient $r_{i,j}$ and the mean correlation coefficient $\bar{r}$. The correlation coefficient $r_{i,j}$ is the value of the cross-correlation function at time delay $\tau = 0.0$ and reads:

$$r_{i,j} = \frac{\langle x_i x_j \rangle - \langle x_i \rangle \langle x_j \rangle}{\sqrt{\langle x_i^2 \rangle - \langle x_i \rangle^2}\,\sqrt{\langle x_j^2 \rangle - \langle x_j \rangle^2}} \tag{5}$$

and $\bar{r}$ is:

$$\bar{r} = \frac{2}{N(N-1)} \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} r_{i,j} \tag{6}$$

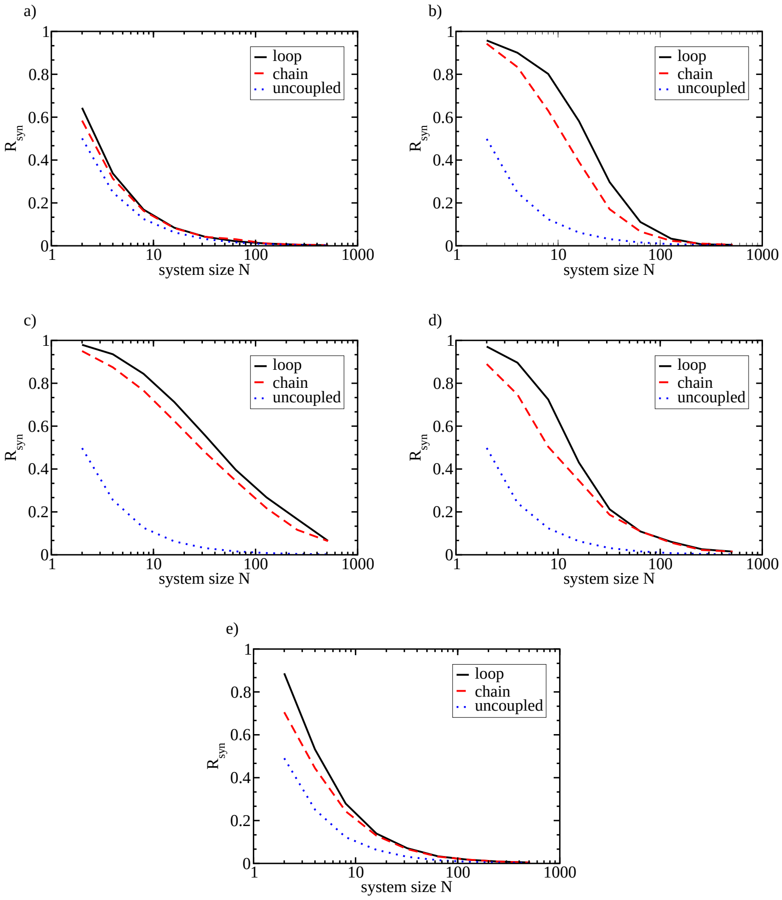

Fig. 2. Synchronization measure R_{syn} versus system size N. The plots differ by the noise intensities: a) $\sigma_a^2 = 0.01$, b) $\sigma_a^2 = 0.025$, c) $\sigma_a^2 = 0.2$, d) $\sigma_a^2 = 1.0$, e) $\sigma_a^2 = 5.0$. Each plot compares the synchronization in a closed loop, an open chain and in the fully uncoupled case as the reference.

All these measures (R_{syn}, $r_{i,j}$, and $\bar{r}$), plotted in Fig. 3, quantify the level of zero-lag synchronization, and express the same behavior.

Figure 3 reveals a typical resonance-like behavior. Too small noise leaves the oscillators near the stable fixed point without crossing the threshold. Too large noise dominates the overall dynamics and the coupling can not provoke synchronization. Only intermediate noise is able to improve the synchronization amongst the neurons in combination with the coupling. For the two system sizes considered, the closed contour of the loop surpasses the synchronization results of the open chain. In the case of intermediate size $N = 16$, the relative advantage

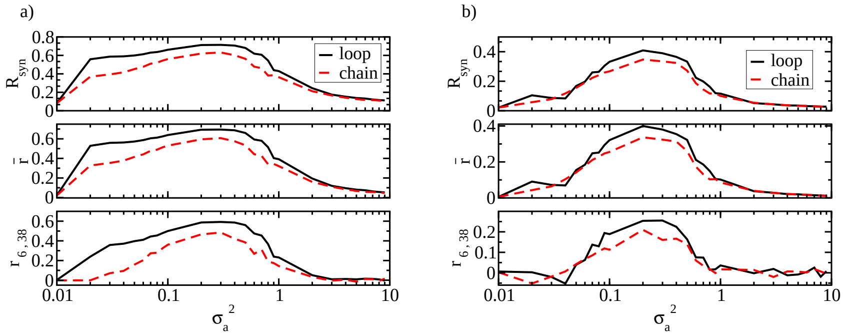

Fig. 3. Synchronization measure R_{syn} and correlation coefficient versus noise intensity σ_a^2. The left plot depicts a small ensemble ($N = 16$) and the right one shows the behavior of a larger system ($N = 64$).

of the loop to the chain is most striking before and after the absolute maximum located at $\sigma_a^2 \approx 0.3$, and the bell-shaped resonance curve is relatively broad compared to the narrower one for the large ensemble. For $N = 64$ the overall maximal synchronization is reached at $\sigma_a^2 \approx 0.1$, i.e. for a smaller noise intensity.

4 Near zero-lag synchronization by additive uncorrelated noise

The measures used above take into account only zero-lag synchronization. Local coupling and the limited transmission velocity of the signal leads normally to a time lag along the signal chain, as can be seen in Fig. 4(a). In contrast to this, experimental measurements show that synchronization with cell assemblies does not exhibit a significant time lag [2, 3]. We therefore study in what follows the time-lag in the cross-correlation function as a function of the noise intensity.

Specifically, we investigated an ensemble of $N = 64$ FHN oscillators in the loop configuration, for varying additive noise intensity σ_a^2. The results for the open chain are not shown but they are comparable. We calculate the cross-correlation functions of various pairs of elements, noted in the legend of each diagram (Fig. 5), choosing oscillator #6 as a reference, without loss of generality. The pair 6-6 is the auto-correlation function of the time series of oscillator #6, and the pair 6-38 depicts the cross-correlation function for two oscillators separated the maximal spatial distance in the system of 64 coupled FHNs. The rasterplots corresponding to the cross-correlation functions Fig. 5 are plotted in Fig. 4, and give a snapshot of the spiking activity in the three situations: insufficient noise, optimal noise and too large noise intensity.

In the case of small noise nucleation occurs rarely and each excitation travels from its nucleating oscillator to all the others. The locations of the noise-induced nucleation events are fully random, The finite traveling time of the signal pro-

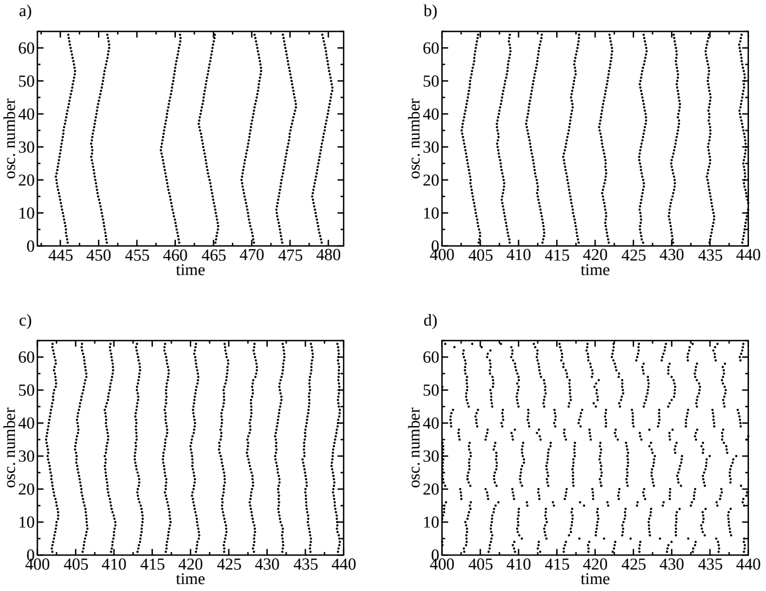

Fig. 4. Raster plots to illustrate the behaviour of the spiking dynamics. The noise intensity increases from top to bottom and left to right: a) $\sigma_a^2 = 0.04$, b) $\sigma_a^2 = 0.06$, c) $\sigma_a^2 = 0.2$, and d) $\sigma_a^2 = 1.0$. Compare with the cross-correlation functions in Fig. 5.

duces a time delay of the spike time of elements far from the nucleation site. Hence a growing spatial distance between neurons increases the time delay of the signal response, as one can see in the raster plot Fig. 4(a), and in the corresponding cross-correlation functions in Fig. 5(a). Small noise results in a non-zero-lag synchronization, with the lag time depending on the spatial distance.

In the situation of optimal and intermediate noise intensity ($\sigma_a^2 \approx 0.2$), multiple nucleation points appear almost simultaneously in the rasterplot [Fig. 4(c)]. The cross-correlation functions for all pairs, independently of their spatial separation, show maximal correlation at zero lag. Thus an optimal noise intensity in combination with local coupling leads to a zero-lag synchronization of all neurons in the ensemble [Fig. 5(c)]. As we noted there is no input signal in the model, thus the effect is fully noise driven.

Finally, too strong noise destroys the effect. In that case, noise is strong enough to evoke spikes everywhere at random times. The formation of small local synchronized cluster destroys the long range correlation completely, i.e. the zero-lag and the non-zero lag synchronization. Only very adjacent pairs like 6:9, 6:6 (trivially) and 6:3 show correlations [Fig. 5(d)].

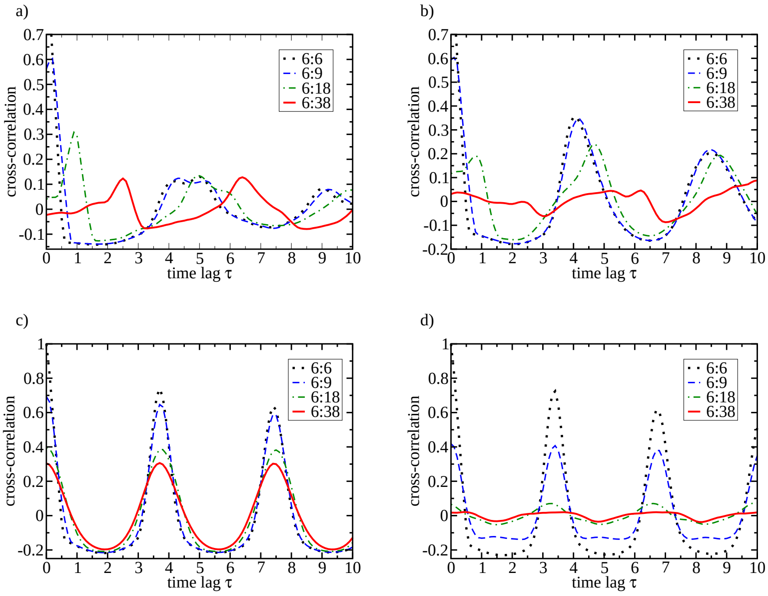

Fig. 5. Cross-correlation functions for different noise intensities and oscillator pairs of the closed contour of $N = 64$ FHNs. The noise intensity increases from top to bottom and left to right: a) $\sigma_a^2 = 0.04$, b) $\sigma_a^2 = 0.06$, c) $\sigma_a^2 = 0.2$, and d) $\sigma_a^2 = 1.0$.

5 Conclusion

We compared the synchronizability of open and closed structures of noisy neuronal networks, and relate it with the efficiency of contour perception in the visual cortex. For small and intermediate sized neuronal networks, a closed contour can be recognized better than a equally sized open contour. The effect shows a resonance-like relation between synchronization and the noise intensity. Furthermore, noise compensates the time lag in the signal transduction caused by the finite value of the signaling velocity. Note that the coupling in our model is instantaneous, so that the signaling velocity is not caused by axonal conduction delays, but by the inertia of each neuron to react to an input. In the case of insufficient noise, a clear time-lag can be seen in the cross-correlation function, increasing with the spatial distance between the neurons. An optimal non-zero noise enhances the correlation and synchronization amongst the neuron ensemble, and shifts the maximal of the cross-correlation function to zero-lag as one can see in experimental measurements [2, 3].

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