

EMERGENT ASYNCHRONOUS, IRREGULAR FIRING IN A DETERMINISTIC ANALOG VLSI RECURRENT NETWORK

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Summary

We study the collective neural dynamics in an analog VLSI recurrent neural network with 21 (14 excitatory, 7 inhibitory) neurons and 129 synapses. All neurons have constant external afferent currents; the network is therefore a deterministic dynamical system with high feedback. The connectivity pattern is fixed but random, and we show how this 'quenched disorder' can support a markedly irregular collective neural firing pattern. The small electronic network exhibits a wide region in its parameter space in which the neural collective activity is stable and asynchronous. The amount and type of irregularity in neurons' firing provides in principle an attractive implementation of a distributed noise source, suited to drive the proposed stochastic learning scenario. The analysis of the experimentally observed network behaviour is complemented by a comparison with theoretical predictions.

Introduction

It has long been suggested that recurrent networks of model neurons can exhibit a highly irregular pattern in the spike emission times, even in the absence of noisy external inputs or inherently noisy elements (van Vreeswijk and Sompolinsky 1996).

We explore such a scenario and study the collective behavior of a small, analog VLSI recurrent, *deterministic* network of 21 (14 excitatory, 7 inhibitory), integrate-and-fire (IF) neurons with a constant decay of the depolarization in the absence of afferent spikes ('linear' IF neuron, introduced in (Mead 1989) and studied in (Fusi and Mattia 1999)). Spike transmission delays are negligible in the electronic network.

Under suitable coupling conditions a *fast* disorder in the time intervals between spikes results from the *quenched* disorder embedded in the irregular pattern of connections among the neurons in the network (while we remark that, despite the unavoidable electronic irregularities in the neurons' behavior, uncoupled neurons are essentially deterministic).

The network exhibits asynchronous collective neural states, for the stability of which the balance of excitation and inhibition creates favorable conditions.

In fact, IF neurons (whatever the leakage term) can operate in two essentially distinct dynamical regimes: a signal-dominated (supra-threshold) regime, in which the deterministic, average component of the afferent current induces a quite regular neural firing, and a noise-dominated, sub-threshold regime, in which the neuron depolarization would be prevented from reaching the emission threshold on the basis of the average afferent current, were it not for fluctuations that from time to time make the neuron fire.

The latter irregular firing regime can account for low rate, irregular spike emission reminiscent of what is commonly observed in electrophysiology.

For our deterministic network, in *weak coupling* conditions the neurons are essentially driven by the constant external currents and their inter-spike intervals (ISI) are quite regular (low *CV*, the coefficient of variation, which is the ratio between the standard deviation of the ISI and their mean). In moderately *strong coupling* conditions the neurons operate in a dynamical regime strongly influenced by the variability in recurrent input currents, and the *CV* increases (noise-dominated regimes). *Strong coupling* regimes (strong mutual excitation), can make the network undergo waves of synchronous firing; in this case, given the high variability in the (small) number and type of pre-synaptic contributions among the neurons, the synchronous firings can be separated in time by variable intervals, such that the *CV* of the single neurons still increases.

The emergent irregular firing temporal pattern has a major appeal in view of the stochastic scenario of Hebbian learning proposed in (Amit and Fusi 1994) and implemented in (Fusi et al. 2000).

Asynchrony in the emission pattern of the whole network is also a desirable feature allowing the system to quickly react to external stimuli (Treves 1993). In this regimes, in fact, there is always a pool of neurons close to the emission threshold, so that a rapid increase of the afferent current (representing a stimulation), is followed by a correspondingly fast activation of the network due to the above pool of neurons crossing together the threshold (see also (Mattia and Del Giudice 2001)).

We will therefore consider in what follows dynamical scenarios characterized by high *CV* and a low degree of synchrony (asynchronous collective states).

We also make contact with theoretical predictions obtained in an *extended* mean field framework, looking in particular at the power spectrum of the population emission rate.

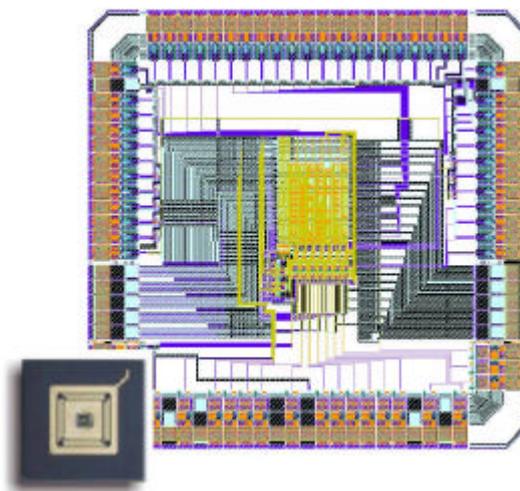


Figure 1: The LANN21b: picture and layout.

Methods

The network consists of 21 linear IF neurons (14 excitatory, 7 inhibitory), two neurons are connected with 30% probability (129 synapses overall). We used AMS CMOS 0.6 μm CUP technology with 3 metallic layers and 3 poly-silicon layers, realizing a 3 x 3

implies about a 60 seconds available time span for recording the network activity. The spike is encoded as the label of the emitting neuron and the attached time label.

A PC handles the communication with the I/O board. A high-level user interface has been developed for parameters setting, spikes recording and data analysis.

In order to fully characterize the response properties of the single neuron, we also performed a preliminary analysis of the firing of decoupled neurons in response to noisy input currents (a suitable noise generator was designed and built on purpose, mimicking a stationary gaussian noise source (D'Andreagiovanni 2001)). The experimental results, not discussed here, were in remarkable agreement with the theoretically predicted transfer function for a linear IF neuron with gaussian input (Fusi and Mattia 1999).

Results

We show in the following that there is a wide region in the network's parameters space in which the excitatory neural population, in the presence of recurrent inhibition and constant external input, exhibits a collective asynchronous activity. We further show a semiquantitative agreement with theoretical predictions on the detailed structure of the collective activity; this is non trivial, in view of the very small number of neurons on one side, and the large number of parameters characterizing the single neurons and synapses on the other side, with large variability among the single elements. The dynamical system appears to meet expectations in a remarkably robust way, a crucial ingredient if one wants to take further steps towards larger systems and their plastic reorganization as a result of interaction with their environment.

To characterize the dynamical regimes we are interested in, it is useful to adopt the simplifying assumption, that the afferent current to any neuron can be described as a stochastic gaussian process, fully described in terms of the mean and variance, μ and σ^2 . For a generic neuron, the validity of this *diffusion approximation* relies upon the independence of the afferent spikes, on the average value of the synaptic efficacies on its dendritic tree, compared to the emission threshold, the average number of synaptic afferents and the rate of incoming spikes. For such a small system like our neural chip, the validity of the above approximation can only be checked *a posteriori*.

Assuming μ and σ^2 fully describe the afferent currents, regimes with highly variable ISIs (high CV of the single neuron spike train) are characterized by low or negative μ and high σ^2 . For any emission rate ν , and for constant external input, we can in principle adjust the synaptic couplings in such a way to span a wide range of CV: on one extreme we have total input current with a very low σ^2 (which implies low efficacies), the constant external drive being just enough to make the neurons fire periodically at ν ; at the other end we can implement in principle a high coupling regime in which the fluctuations alone make the neuron fire irregularly at rate ν . In fact the dependence of μ and σ^2 on the (excitatory and inhibitory) synaptic couplings is such that σ^2 increases whenever any of the couplings is increased, while the balance between the excitatory and the inhibitory couplings controls μ .

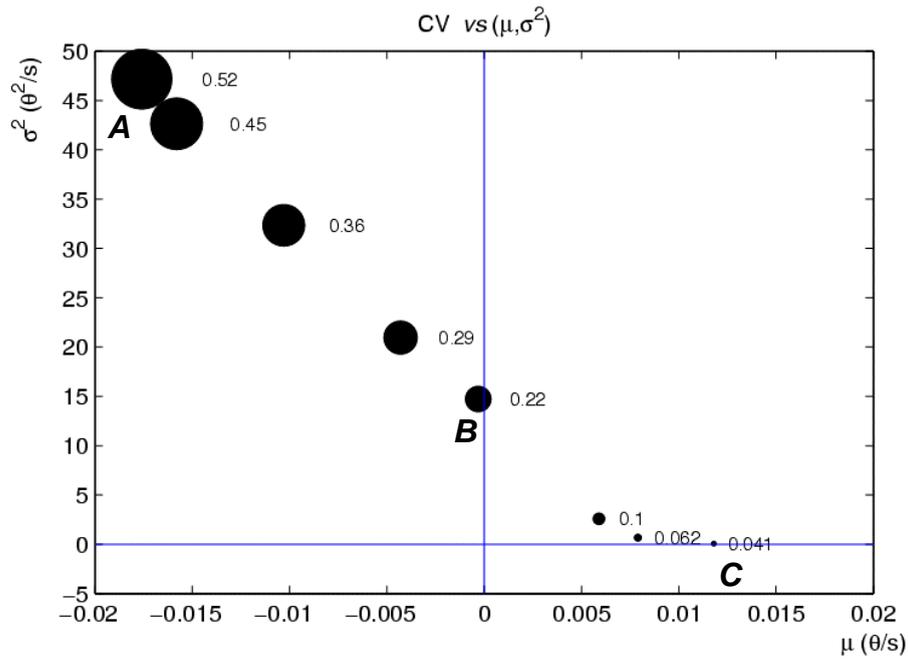


Figure 3. Average CV of the excitatory neurons for different values of (μ, σ^2) . The sizes of the circle markers are proportional to the average CVs (whose values are also reported next to the points on the plot). All the points (here and in the following Figures) refer to 60 seconds recordings, with a common average excitatory rate of 30 Hz, while the average inhibitory rate ranges from ~ 80 to ~ 120 Hz.

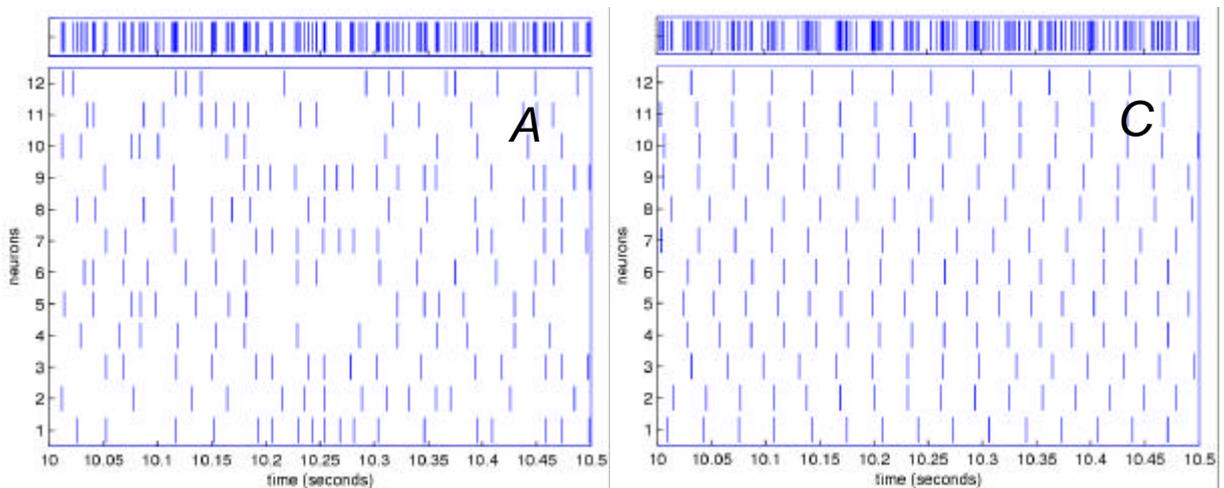


Figure 4. Lower panels: Raster plots of the spikes emitted in 500 milliseconds by 12 excitatory neurons. Plots are labeled as in Fig. 3. A: irregular-asyncronous ($\langle CV \rangle = 0.52$) state; C) regular-asyncronous ($\langle CV \rangle = 0.041$) state. Upper panel: Raster plot of the pooled activity. Notice that, despite the greatly different degree of regularity of the single spike trains for the two cases, the pooled activity is essentially asyncronous in both. It is also seen that network C shows burst-like, irregularly spaced short waves of activity.

Fig. 3 illustrates such a repertoire of dynamical scenarios: each point in the (μ, σ^2) is representative of a network with a chosen set of synaptic couplings. Starting from the extreme right, we go from an excitatory population with essentially periodic neurons

(very low CV, $\mu > 0$, low σ^2) to a network with a much higher average ISI variability (one order of magnitude in CV), negative μ and high σ^2 (strong coupling, strong recurrent inhibition). The above findings are further illustrated in Fig. 4 by the raster representations of the network activity, in which the qualitatively different ISI distributions can be perceived at a glance.

We remark that a global asynchronous, high total CV, neural activity can result from quite regular (low CV) spike trains of the single neurons, under an independence condition of the neurons' firings (see (Brunel 2000) for a general discussion of the different regimes of collective activity accessible to a sparsely connected network): indeed the spike train obtained by pooling all the excitatory spikes exhibits a remarkably Poisson-like ISI distribution (Fig. 5C) for a regime with a low average CV of the single spike trains (compare the raster plots in Fig. 4C). The CV of the pooled spike train is in fact 0.94. Theory provides general conditions for single point processes to produce, when pooled, a Poisson flux of events (Grigelionis' theorem, see (Gnedenko 1968)). Contrary to naive expectation, neural activity with higher average CV of the single spike trains produces pooled spike trains farther from the Poisson case (e.g. case A in Figs. 4 and 5). This is due to the fact that, as already mentioned, irregular single spike trains are brought about by higher couplings which, for such a small system, tend to favor the appearance of upsurges of activity: the pooled spike train exhibits 'bursty' features, which are reflected by the excess in the ISI distribution for very small ISI, while the Poisson fit is again good for higher intervals. The waves of almost synchronous firing of excitatory subpopulations do not reflect a globally synchronous activity. From the above discussion we conclude that for the whole region of the (μ, σ^2) plane explored in Fig. 3 the network is in a globally stable, asynchronous state.

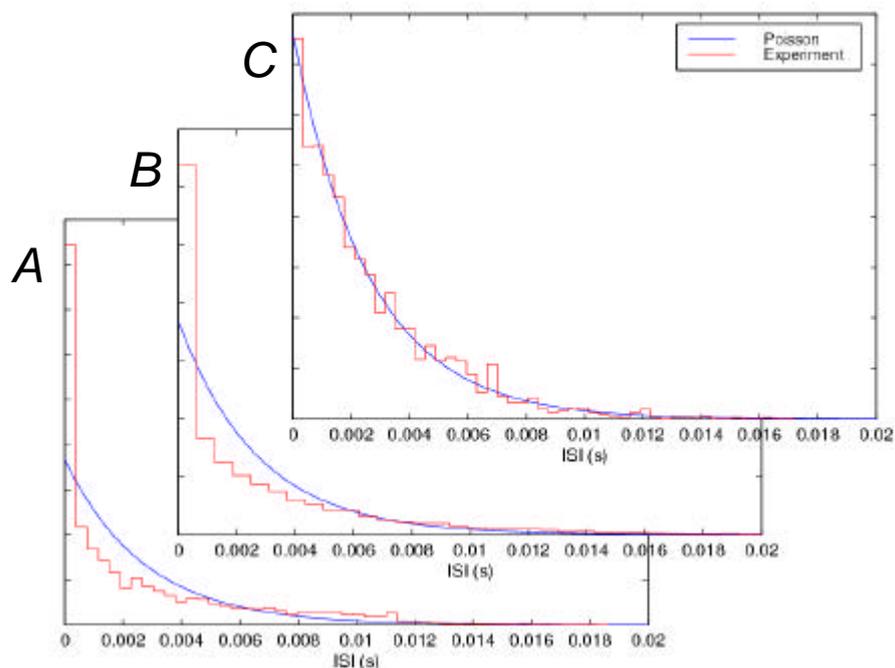


Figure 5: Inter-spike interval (ISI) distributions (red) of the pooled activity of the excitatory neurons for the three representative points in Fig. 3. Blue lines are the ISI distributions for Poisson processes with the same frequencies. It is seen that the network whose excitatory population is in a signal-dominated regime (C, $\mu > 0$) exhibits a ISI distribution very close to a Poisson one, while noise dominated regimes show a significant excess with respect to the Poisson case for very low ISI (see text).

For such stable, asynchronous states, a dynamical mean field approach has been recently taken to predict several features of the collective dynamics of interacting IF neurons (Mattia and Del Giudice 2001); we examine in the following the frequency content of the collective neural activity in various regimes, in the light of the mentioned theoretical approach.

We start from the leftmost representative point *A* in Fig. 3, for which the network is noise-dominated, stable and asynchronous for the excitatory population, and signal-dominated (though non synchronous) for the inhibitory population. For a single population in a stable asynchronous state, under the assumption that the diffusion approximation and the hypotheses underlying the mean field treatment hold, and that spikes are transmitted with negligible delays (which is the case for the neural chip) the theory developed in (Mattia and Del Giudice 2001) predicts for the power spectral density $P(\omega)$ of the noise-dominated collective activity the following simple features: for not too high CV of the single neuron the low frequency part of the spectrum has a dip which can be described in terms of an effective refractory period, while for higher ω the spectrum settles on the constant, white noise value v/N (where v is the average emission rate of the population and N is the number of neurons in the population: $v = (\text{total number of spikes in } dt) / (N dt)$ for $dt \gg 0$). The signal-dominated activity of an inhibitory population exhibits different features: the low- ω dip is larger, and a high peak appears at $\omega/2\pi \approx v$, with damped lower peaks at multiples of this value; the asymptotic constant value of $P(\omega)$ is still v/N .

In this case (noise-dominated excitatory population), the inhibitory-to-excitatory synapses are very large, while the excitatory-to-inhibitory ones are very small. In this condition we can safely consider the excitatory population as an input-output system (the input being the sum of the constant external current and the current contributed by the inhibitory population), whose transfer function is known from the theory, and is predicted to be constant (because of negligible delays) for high enough ω . The power spectrum of the drift-dominated inhibitory population exhibits a peak in correspondence with the mean rate of the population v_I , which therefore produces, via the essentially constant transfer function, a peak at v_I (and multiples thereof) in the power spectrum of the excitatory activity (notice that on the other hand, since the excitatory activity is noise-dominated, there is no peak at v_E).

Fig. 6A shows the experimental estimate of $P(\omega)$ for the two populations, which are remarkably consistent with theoretical expectations.

An excess is appreciable in the asymptotic value of the excitatory spectrum. This can be understood considering the low-ISI large peak in the ISI distribution which is systematically present in noise-dominated cases (compare Figs. 5A,B): in fact the latter implies a large zero-lag peak in the autocorrelation function of the collective activity, which is in turn the integral of the power spectrum. An excess with respect to the pure white noise theoretical expectation is therefore to be attributed to the extra contribution to the constant component of the power spectrum, due to the waves of partial synchronization which characterize the regimes under consideration. This suggests that inspecting the high- ω region of the power spectrum of the collective activity could be an effective way to assess the asynchronous nature of the network state.

For the case C the power spectrum of both the excitatory and the inhibitory activity have the expected asymptotic value for a population driven by white noise¹. The signal-

¹ According to the view adopted in (Mattia and Del Giudice 2001) this is to be interpreted as a 'self-stimulation' of the network, because of the finite-size fluctuation of its activity in an asynchronous state.

dominated excitatory activity is very weakly coupled to the inhibitory one, and the power spectrum is consistent with theoretical expectation for a single excitatory population for $\mu > 0$, with peaks at multiples of the mean rate.

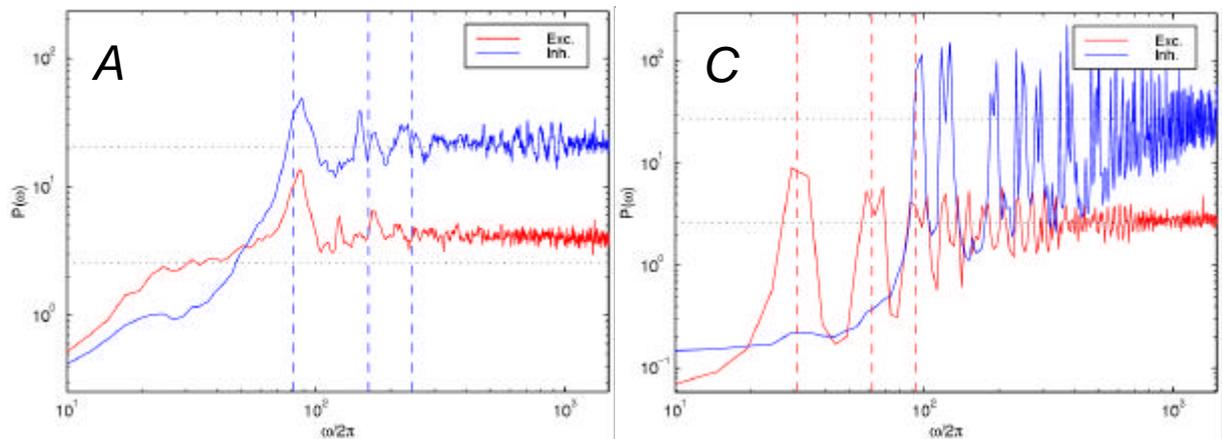


Figure 6. Power spectrum of the collective activity of the excitatory (red) and inhibitory (blue) populations. Horizontal dotted lines mark the n/N value. Dashed vertical lines mark the excitatory (red) and inhibitory (blue) mean rates and their multiples. $n_E @ 30$ Hz in both cases.

Conclusions

We have shown that a very small and simple analog VLSI recurrent network of IF neurons exhibits stable, asynchronous collective states in a wide range of parameters, with no need of fine tuning or external noise. Despite the small size of the system, knowledge gained through large scale simulations, and theoretical approaches valid for large systems, appear to provide surprising insight into the behaviour of the electronic network.

The results shown are therefore encouraging, in view of the ability of such electronic systems (small, inhomogeneous, noisy as they are) to serve as a useful testing ground for real-time implementations of models with interesting computational capabilities.

With the biological counterpart of the implemented neural models in mind, we underline as an interesting feature the fact that, as mentioned in the Introduction, globally stable asynchronous states endow the network with the ability to quickly react to sudden changes in the external input. The white noise like spectral structure exhibited by the neural activity in our chip offers support to this view.

Besides, the observed collective irregular firing patterns are particularly appealing in view of the scenario proposed in (Amit and Fusi 1994) of stochastic, spike driven, slow learning, in which the synaptic plasticity supposedly underlying the learning process is implemented as a sequence of stochastic transitions, induced by appropriate pre- and post-synaptic neural activities among otherwise stable synaptic states. It was argued in (Amit and Fusi 1994) and in (Brunel et al. 1998) that such a slow, stochastic synaptic modifications allow an optimal use of synaptic resources to associatively store in memory a set of stimuli. One interesting option for the noise source supporting the above stochastic mechanism would be the variability of the neurons' firing (as proposed in (Fusi et al. 2000)), a pervasive feature of neurons as observed *in vivo*.

In fact, the same neural chip considered in the present work has been used in (Chicca and Fusi) to directly test (in the simpler case of a purely excitatory population) how the irregular firing exhibited by the small network is able to support slow stochastic synaptic dynamics in a robust way.

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