

Modeling Networks with VLSI (linear) Integrate-and-Fire Neurons

Maurizio Mattia and Stefano Fusi

INFN, Sezione di Roma 1, Dipartimento di Fisica
Università di Roma, La Sapienza, P.le Aldo Moro 2, Rome Italy

Abstract. We analyse in detail all the statistical properties of a “canonical” integrate-and-fire VLSI neuron with a linear integrator [1]. We show that a network of such elements can maintain both stable spontaneous activity and selective delay activity, contrary to current opinion. The spike statistics appears to be qualitatively the same as in networks of conventional (exponential) integrate-and-fire neurons that in turn, exhibit a wide variety of characteristics observed in cortical recordings[2].

Introduction

The integrate-and-fire (IF) neuron has become popular as a simplified neural element in modeling the dynamics of large scale networks of spiking neurons. A simple version of IF neuron integrates the input current as an RC circuit (with a leakage current proportional to the depolarization) and emits a spike when the depolarization crosses a threshold. We will refer to it as to ‘*RC neuron*’. Networks of neurons schematized in this way exhibit a wide variety of characteristics observed in single and multiple neuron recordings in cortex in vivo. These networks can maintain stable spontaneous activity and when subjected to Hebbian learning, show a coexistence of selective delay activity distributions with the underlying spontaneous activity[2].

In VLSI the natural IF neuron has been canonized by Mead[1]. This VLSI implementation of the neuron has many desirable features: it operates with current generators and hence minimal currents and very low power consumption, an essential feature for integrating a large number of neurons on a single chip. It is also a natural candidate for working with transistors in a sub-threshold regime which brings another significant reduction in consumption[1]. One can also implement a VLSI dynamic synapse with similar attractive electronic characteristics[3].

Here we will concentrate on the statistical properties of the spikes generated by a VLSI neuron, as a function of the statistics of the input current, and on the effect on network dynamics of composing networks of VLSI neurons, keeping distributions of synaptic efficacies fixed. We ask the following question: given that the depolarization dynamics of the *VLSI neuron* is significantly different from that of the *RC neuron*, can the collective dynamics found in a network of *RC neurons* be reproduced in networks of neurons of the VLSI type? The collective behaviour we examine includes the coexistence of low rate, highly variable, spontaneous activity and selective delay activity stabilized by learning [2].

RC Neuron vs VLSI Neuron

The difference between the two types of neurons can be summarized as follows: the *RC neuron* below threshold, is an RC circuit integrating the input current with a decay proportional to the depolarization of the neuron $V(t)$: $\dot{V}(t) = -V(t)/\tau + I(t)$, where $I(t)$ is the net charging current, produced by afferent spikes. A spike is emitted when $V(t_0) = \theta$, followed by hyperpolarization.

The depolarization below threshold of the VLSI neuron is:

$$\dot{V}(t) = -\beta + I(t), \quad (1)$$

with the constraint that if $V(t)$ is driven below 0, it remains 0. The spiking condition remains unmodified. An absolute refractory period τ_{arp} after a spike is emitted, the depolarization is reset to 0.

The question about the collective behaviour of such ‘linear’ neurons is underlined by the following consideration: the linear integrator dynamics in the ‘positive drift’ regime (when on average the RHS of Eq.(1) is positive and the variance of the current is much smaller than the mean) leads to current to rate dynamics which is threshold-linear for a wide range of values of the input current [4, 6] and the coexistence of spontaneous activity with structured delay activity is not possible. Each of the two types of behaviour is implementable in a network with ‘linear’ neurons [6], but not both.

In contrast, if the statistics of the input current is such that the *VLSI neuron* can operate also is in its ‘negative drift’ regime the transduction of the neuron is non-linear and mean-field theory exhibits the coexistence of the two collective states.

Current-to-Rate Transduction Function

We derive the current-to-rate transduction function for a *VLSI neuron* with a noisy source $I(t)$. At any time t , the current is drawn randomly from a Gaussian distribution with mean $\mu_I(t)$ and variance $\sigma_I^2(t)$ per unit time, so that Eq. (1) can be rewritten as: $dV = \mu(t)dt + \sigma(t)z(t)\sqrt{dt}$, where $\mu(t) = -\beta + \mu_I(t)$, $\sigma(t) = \sigma_I(t)$ and $z(t)$ is a stochastic variable normally distributed with zero mean and unit variance.

If $p(v, t)$ is the probability density that at time t the neuron has a depolarization v , it obeys the Fokker-Plank equation (see e.g. [5]). This equation must be completed by restricting the process to the interval $[0, \theta]$, which is done by imposing appropriate boundary conditions: at $v = 0$ a reflecting barrier, since no process can pass below 0 and at $v = \theta$ an absorbing barrier that resets processes crossing the threshold to 0. Formally, this is equivalent to the conditions that $p(v, t) = 0$ at $v = \theta$ (see e.g. [5]), and that no process is lost when absorbed at θ or reflected at $v = 0$. This implies that the rate at which processes are crossing the threshold must be the same as the rate at which they re-enter from 0, i.e.:

$$\sigma^2 \partial_v p|_{v=\theta} = -2\nu(t) \quad [\sigma^2 \partial_v p - 2\mu p]|_{v=0} = -2\nu(t) \quad (2)$$

where $\nu(t)$ is the probability per unit time of crossing the threshold θ .

If $\tau_{arp} > 0$, then the realizations that drive the neuron above the threshold θ must be delayed before coming back to the reset value. This is obtained by imposing that the neuron, after crossing the threshold, has to walk on a fictitious interval (which can be arbitrarily set to $[\theta, \theta + 1]$) at constant drift, in such a way that the process of getting from θ to $\theta + 1$ takes a time equal to τ_{arp} . At the end of the interval the depolarization is reset to 0. In terms of a diffusion process we have that, for $v > \theta$, $-\mu_{arp}\partial_v p = \partial_t p$ where $\mu_{arp} = 1/\tau_{arp}$.

The complete set of boundary conditions is now given by:

$$\sigma^2 \partial_v p|_{v=\theta} = -2\nu(t) \quad [\sigma^2 \partial_v p - 2\mu p]|_{v=0} = -2\nu'(t) \quad \mu_{arp} p|_{v=\theta+1} = \nu'(t)$$

In the case of a steady statistics of the input current (i.e. $\mu(t) = \mu, \sigma(t) = \sigma$ for any t) the asymptotic solution ($p(v) = \lim_{t \rightarrow \infty} p(v, t)$) of Fokker-Planck equation is:

$$p(v) = \frac{\nu}{\mu} \left[1 - \exp\left(-\frac{2\mu}{\sigma^2}(\theta - v)\right) \right] \quad \text{for } v \in [0, \theta]$$

and $p(v) = \nu\tau_{arp}$ for $v > \theta$. ν is determined by imposing that the integral of $p(v)$ over $[0, \theta + 1]$ is 1:

$$\nu = \Phi(\mu, \sigma) = \left[\tau_{arp} + \frac{\sigma^2}{2\mu^2} \left(\frac{2\mu\theta}{\sigma^2} - 1 + e^{-\frac{2\mu\theta}{\sigma^2}} \right) \right]^{-1}$$

which gives the mean rate of the *VLSI neuron* as a function of the mean and the variance of the input current.

Inter-Spike Interval Distribution. The probability density of the inter-spike intervals is computed following [5]: the first passage time T is a random variable with a p.d.f. $g(v_0, T)$ that depends on the initial value v_0 (i.e. the hyperpolarization) and satisfies a backward Kolmogorov diffusion equation (see e.g. [5]). The Laplace transform $\gamma(v_0, s)$ of the $g(v_0, T)$, calculated in $v_0 = 0$ is

$$\gamma(0, s) = \frac{ze^{\theta C}}{z \cosh(\theta z) + C \sinh(\theta z)}$$

where $C \equiv \mu/\sigma^2$ and $z \equiv \sqrt{\mu^2 + 2s\sigma^2}/\sigma^2$.

Positive and Negative Drift Regimes

If the total mean drift μ is positive and σ is small, Φ is essentially linear over a wide range of μ (see Fig.3):

$$\nu = \Phi(\mu, \sigma) \simeq \mu [\theta + \tau_{arp}\mu]^{-1}$$

The non-linearity shows only at high frequencies, comparable to $1/\tau_{arp}$. In this case the random walk is dominated by the drift which is the deterministic part of the current, and the neuron fires quite regularly (see Figs.1,2). The probability density $p(v)$ is almost uniform (see Fig.2) because the neuron tends to go from 0 to θ at constant speed.

In contrast, in the ‘negative drift’ regime, the neuron spends most of the time fluctuating near the reflecting barrier, and emits only when, by chance, a large

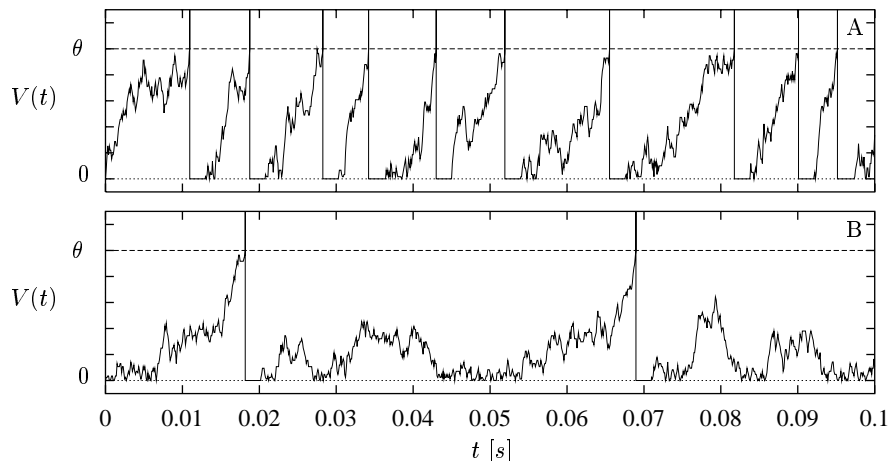


Fig. 1. Simulation of depolarization dynamics at positive (A) and negative drift (B). Parameters: (A) $\mu = 102\theta/s$, $\sigma = 5.3\theta/s^{1/2}$, producing a mean firing rate $\nu = 94Hz$; (B) $\mu = -10.1\theta/s$, $\sigma = 3.8\theta/s^{1/2}$, mean rate $\nu = 8.1Hz$. $\tau_{arp}=2ms$ in both cases. At positive drift the process is dominated by the deterministic part of the input current. The noisy linear ramp is clearly visible. At negative drift the depolarization fluctuates under threshold, waiting for the large fluctuation of the input current to drive $V(t)$ above threshold.

fluctuation in the input current drives the depolarization above the threshold (see Fig.1). Since the fluctuations are random and uncorrelated, the neuron fires irregularly and the ISI distribution is wide (see Fig.2). In this regime the process is essentially dominated by the variance of the afferent current.

In principle it is possible to have such a regime also for $\mu > 0$, provided σ is large enough. This would require a fine tuning of the parameters.

Network Dynamics: Double Fixed Point

The extended mean-field theory approach [2] allows to study the dynamics of a network of identical neurons randomly interconnected, provided that one knows the current-to-rate transduction function. In the most general case the afferent current to any neuron is composed of two parts: one from spikes emitted by other neurons in the same network, and the other from outside. If the mean number of afferent connections is large and the mean charging current produced by the arrival of a single spike (the mean synaptic efficacy) is small, then the current $I(t)$ is Gaussian and: $\mu(t) = a_\mu\nu(t) + b_\mu(t)$, $\sigma^2(t) = a_\sigma\nu(t) + b_\sigma(t)$, where the a s and b s are constants depending on the statistics of the connectivity, the synaptic efficacy, the decay β and the external afferents (see e.g. [2]). In order to have a fixed point, the self-consistency equation must be satisfied: $\nu = \Phi(\mu(\nu), \sigma(\nu))$. If the Φ function is linear in ν , as in the case of a neuron operating in a ‘positive drift’ regime, then only one stable fixed point is possible [6].

The non-linearity in the ‘negative drift’ regime is sufficient to allow for a double fixed point (see Fig.4).

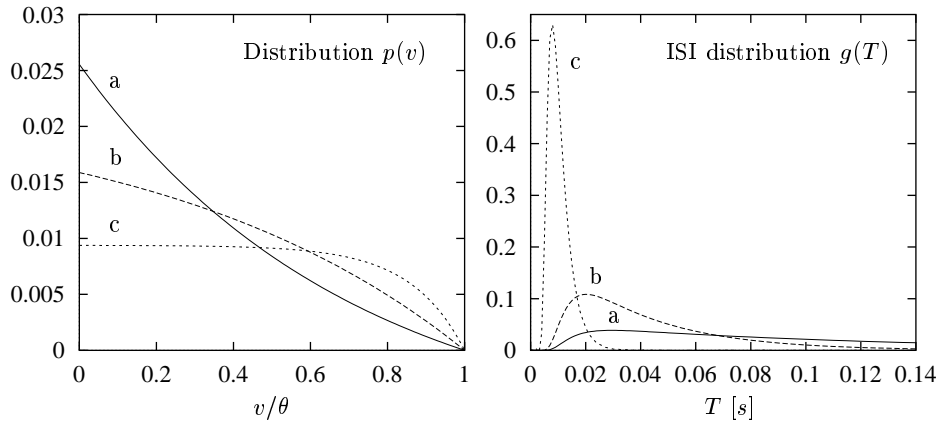


Fig. 2. Probability density function $p(v)$ (left) and ISI distribution $g(T)$ (right) at (a) negative, (b) intermediate and (c) positive drift. Parameters: (a) $\mu = -10.1\theta/s$, $\sigma = 3.8\theta/s^{1/2}$; (b) $\mu = 10.0, \theta/s$, $\sigma = 4.0\theta/s^{1/2}$ and (c) $\mu = 102\theta/s$, $\sigma = 5.3\theta/s^{1/2}$. At negative drift $p(v)$ is concentrated well below the threshold, near to the reset potential. As μ increases the curve changes concavity and tends to a uniform distribution. The ISI distribution is widespread for negative drift and tends to a peaked distribution as μ goes to positive values. The variability is clearly much higher in the negative drift regime.

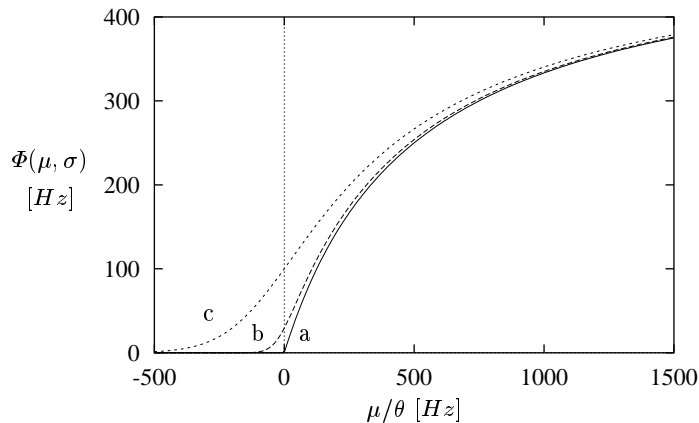


Fig. 3. Current-to-rate transduction function $\Phi(\mu)$ for different variances of afferent current: (a) $\sigma = 0$, (b) $\sigma = 5.6\theta/s^{1/2}$ and (c) $\sigma = 11\theta/s^{1/2}$. The firing rate in the region around $\mu = 0$, in the so called *negative drift regime*, is sensible to changes in the variance: the $\phi(\mu)$ passes from a threshold-linear function at $\sigma = 0$ to a non-linear function when $\sigma > 0$. If $\mu \gg \sigma$, the transduction function is almost independent on σ . The non-linearity that appears for large μ is due to τ_{arp} : Φ tends to the asymptotic frequency $1/\tau_{arp}$.

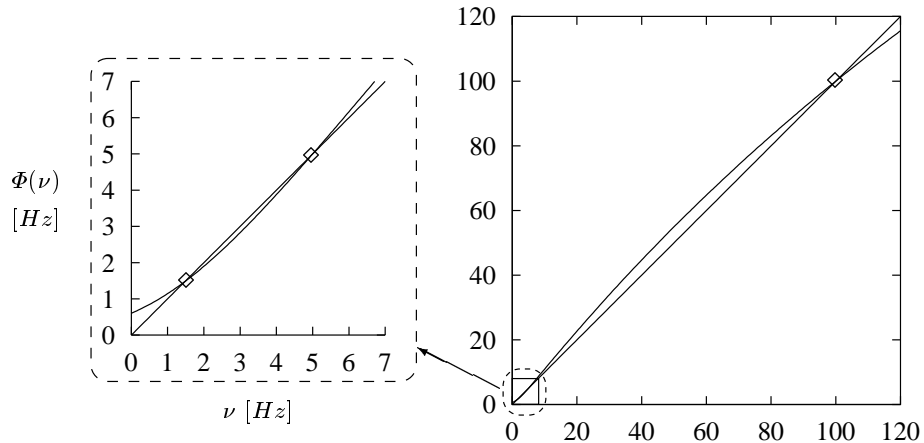


Fig. 4. Fixed points (\diamond) of network dynamics: graphical solution of the self-consistency equation: solid line = mean firing rate $\Phi(\nu)$; dashed line = ν . The dashed rectangle on the left is an enlargement of the low frequency region. Drift and variance: $\mu(\nu) = (-2.55 + 1.5\nu)\theta/s$ and $\sigma(\nu)^2 = (1.88 + 0.03\nu)\theta/s$. There are 3 intersections between $\Phi(\nu)$ and ν : two correspond to stable fixed points ($\nu = 1.5Hz$ at negative drift and $99Hz$ at positive drift) and one to an unstable fixed point ($5.0Hz$).

Conclusions

Considering fully the statistical properties, the collective dynamics of a network of *RC neurons* can be reproduced in a network of *VLSI (linear) neurons*. The existence of a reflecting barrier in 0 turned out to be fundamental in order to have the *VLSI neuron* operating in ‘negative’ drift regime and not only in ‘positive’ drift regime. The coexistence of two stable fixed points (spontaneous activity and selective activity) is strictly related to the presence of the reflecting barrier and to the existence of a not negligible variance in the input current. All the results of this paper have been tested by extensive simulations [7] and will be published in a future work.

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