



Overview of facts and issues about neural coding by spikes

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ARTICLE INFO

Keywords:

Spiking neuron networks
Neural code
Time constraints
Spike train metrics

ABSTRACT

In the present overview, our wish is to demystify some aspects of coding with spike-timing, through a simple review of well-understood technical facts regarding spike coding. Our goal is a better understanding of the extent to which computing and modeling with spiking neuron networks might be biologically plausible and computationally efficient.

We intentionally restrict ourselves to a deterministic implementation of spiking neuron networks and we consider that the dynamics of a network is defined by a non-stochastic mapping. By staying in this rather simple framework, we are able to propose results, formula and concrete numerical values, on several topics: (i) general time constraints, (ii) links between continuous signals and spike trains, (iii) spiking neuron networks parameter adjustment. Beside an argued review of several facts and issues about neural coding by spikes, we propose new results, such as a numerical evaluation of the most critical temporal variables that schedule the progress of realistic spike trains.

When implementing spiking neuron networks, for biological simulation or computational purpose, it is important to take into account the indisputable facts here unfolded. This precaution could prevent one from implementing mechanisms that would be meaningless relative to obvious time constraints, or from artificially introducing spikes when continuous calculations would be sufficient and more simple. It is also pointed out that implementing a large-scale spiking neuron network is finally a simple task.

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1. Introduction

“Spikes are the neural code”: This claim is about 15 years old (Shadlen and Newsome, 1994; Rieke et al., 1996). It has been preceded by theoretical studies on the underlying mathematical processes (e.g. Gerstein and Mandelbrot, 1964) and followed by many developments regarding biological modeling or computational paradigms (e.g. Thorpe et al., 2001). However, the involvement of spikes in neural coding is still an open question. Several fundamental aspects of dynamics based on spike-timing have been very recently clarified, both at the neuron level (Touboul and Brette, 2008) and the network level (Cessac et al., 2008). Nevertheless, still a non negligible set of received ideas, such as the “in principle unlimited computational power [of spiking networks]” (e.g. Maass, 2009), or such general statements as the “mystery of the [spike based] neural code” (e.g. Rieke et al., 1996), are currently encountered in literature. Our purpose is to demystify some aspects of coding with spike-timing, through an overview of well-understood technical facts regarding spike coding. Let us first define the framework of the paper.

1.1. Neural coding by spikes

In a biological context, networks of natural neurons might be regarded as spiking neuron networks as soon as time becomes a central feature for exploring how the brain processes. Neurons have been considered to encode their outputs by their average firing rates until the seminal paper by Gray and Singer (1989) showed that correlations between spike-timings of primary visual cortex of the cat were related to the nature of stimuli. From now on, the precise timing of spike firings is regarded as an interesting alternative for understanding how the neurons work. However, the involvement of spikes in neural coding is still an open question. Therefore, artificial spiking neuron networks turn out to be helpful modeling tools in computational neuroscience. Brain imaging and efficient recording technologies (micro-electrodes, LFP or EEG recordings, fMRI) help to detect changes in the internal activity of brain, e.g. related to the perception of a given stimulus. Modeling and simulation are useful to validate – or invalidate – hypotheses proposed by neuroscientists, at different levels of observation: Microscopic models study the behavior of a single neuron or inter-

actions between two or a few neurons; mesoscopic models address one or several populations of neurons, in a cortical column or in a brain area, and deal with the emergence of a collective behavior out of the behavior of single neurons; macroscopic models aim to understand the observable behavior of the whole brain, through one or other cognitive process, by simulating large-scale interactions between distinct areas of the nervous system (see Meunier and Paugam-Moisy (2008) for an overview).

In a computational context, new paradigms for information processing and machine learning are often inspired by the most recent advances in understanding how the brain processes. For instance, spiking neuron networks are currently implemented through non specific network architectures, such as Echo State Networks (Jaeger, 2003) and Liquid State Machines (Maass et al., 2002) or other models (Paugam-Moisy et al., 2008) that are called “reservoir computing” (see Verstraeten et al. (2007) for a merge and definition of reservoir computing methods). In this framework, the reservoir is a network model of spiking neurons with random topology and sparse connectivity. An output layer, the so-called “readout neurons”, is driven by a supervised learning rule, generated from any type of classifier or regression algorithm. The distinction made between a readout layer and an internal reservoir is indeed induced by the fact that only the output of the neuron network activity is constrained, whereas the internal state is not controlled by an experimenter, so does the brain. Although the network architecture does not model any specific brain area nor structure of the nervous system, the inter-neuron connections and learning mechanisms are biologically inspired and based on coding by spikes (variations on weights and delays, synaptic plasticity, temporal Hebbian rule, etc.).

In both contexts, spike-timing is the central linchpin of the models. Therefore, an in-depth overview of realistic time constraints and relations between spikes and neural coding might be very informative for biologists and for computer scientists.

1.2. What is the paper about

Better understanding spiking neuron networks and the underlying neural code is the goal of the present overview. Both biological networks modeling and bio-inspired networks development should take into account the indisputable facts here unfolded. Sec-

tion 2 starts by clarifying the notions of “biological plausibility” and “simulation efficiency” that are the basis of our main concerns in this paper.

On the one hand, we claim that *understanding general time constraints in spiking neuron networks is a mandatory prerequisite*. Section 3 revisits this apparently obvious point and provides the reader with numerical evaluations. Several consequences for simulating spiking neuron networks on computer are then summarized. Our point of view has two major consequences. Firstly, the maximal amount of information present in a spike train is strongly bounded, implying that the “in principle unlimited computational power [of spiking neuron networks]” is a wrong idea: Section 4 makes explicit a bound about the maximal amount of information present in a “true” spike train, taking into account the general time constraints presented in Section 3. Secondly, these general time constraints give a way to study spiking neuron networks as discrete time systems, at least at a theoretical level. Strong results about the dynamics of spiking neuron networks may be thus derived: Section 5 reviews the results of a recent work about this topic and makes them accessible without a high mathematical background. In a nutshell, we claim that formalizing a small set of general time constraints, taken from biological evidence, leads to better understanding the temporal behavior of spiking neuron networks.

On the other hand, we introduce the idea that *defining the neural code contained in spike trains is related to the choice of a metric, “in the deterministic case”*, i.e. when the dynamics of the neuron network is defined by a non-stochastic mapping. Section 6 makes explicit the relation between spike trains and current neural codes (rate coding, rank order coding, phase coding, etc.) and shows that the most common spike metric can be generalized to our context, in including temporal aspects. This point of view has one major consequence, since it generalizes the over-used notion of “rate coding”. Considering convolution metrics, we make explicit the links between spike trains and continuous signals, in the linear case. Section 7 develops concrete methods to build such links. As a perspective of the present state-of-the-art, another major consequence is to give tracks for explicitly programming spiking neuron network parameters in order to obtain a given input/output relation. In a preliminary way, Section 8 discusses how, in our framework, the fact of introducing a metric makes possible to design new effective mechanisms based on variational methods in order to define the network behavior.

Finally, everybody who is interested by spiking neuron network models, either to simulate biological phenomena, or to get inspired for designing emerging computational paradigms, will gain to have such concepts “made simple”, i.e. demystified, as this overview aims to: Spikes do not provide with an unlimited computational power, but they are quite useful and not so unconnected to other methods.

2. Biological plausibility and computational efficiency

2.1. Spiking neuron and network models

A lot of *spiking neuron models* have been proposed in literature. Let us summarize the most popular ones. *Hodgkin and Huxley (1952)* have modeled the electro-chemical information transmission of natural neurons with electrical circuits: V is the membrane potential, C is the capacitance of the membrane, g_i denote the conductance parameter for a specific ion channel (sodium (Na), potassium (K), etc.) and E_i is the corresponding equilibrium potential. The variables m , h and n describe the opening and closing of the voltage dependent channels:

$$\begin{aligned} C \frac{dV}{dt} &= -g_{Na} m^3 h (V - E_{Na}) - g_K n^4 (V - E_K) - g_L (V - E_L) + I(t) \\ \tau_n \frac{dn}{dt} &= -[n - n_0(V)], \quad \tau_m \frac{dm}{dt} = -[m - m_0(V)], \\ \tau_h \frac{dh}{dt} &= -[h - h_0(V)] \end{aligned} \quad (1)$$

Most simple continuous-time models have been produced, such as the integrate-and-fire (IF) model (*Stein, 1965*) and its variants: Leaky integrate-and-fire (LIF), quadratic integrate-and-fire (QIF), exponential integrate-and-fire (EIF) and generalized integrate-and-fire (gIF) that will be discussed further in the section.

V being the membrane potential,

$$C \frac{dV}{dt} = -\frac{1}{R}(V(t) - V_{rest}) + I(t) \quad (2)$$

where spike firing time $t^{(f)}$ is defined by $V(t^{(f)}) = \vartheta$ with¹ $V(t^{(f)}) > 0$.

More recently, *Izhikevich (2003)* has defined a neuron model able to reproduce many realistic neural responses, like the Hodgkin–Huxley model, but with more simple equations:

$$\begin{aligned} \frac{dV}{dt} &= 0.04V(t)^2 + 5V(t) + 140 - w(t) + I(t) \\ \frac{dw}{dt} &= a(bV(t) - w(t)) \end{aligned} \quad (3)$$

with after-spike resetting: if $V \geq \vartheta$ then $V \leftarrow c$ and $w \leftarrow w + d$.

In a different way, the Spike Response Model (SRM), as defined by *Gerstner and Kistler (2002a)*, expresses the membrane potential V_i of neuron N_i as a time integral over the past, including a model of refractoriness. The SRM is a phenomenological model of neuron, based on the occurrence of spike firings. Let $\mathcal{F}_i = \{t_i^{(f)}; 1 \leq f \leq n\} = \{t | u_i(t) = \vartheta \wedge u_i'(t) > 0\}$ denote the set of all firing times of neuron N_i , and $\Gamma_i = \{j | N_j \text{ is presynaptic to } N_i\}$ define its set of presynaptic neurons. The state $V_i(t)$ of neuron N_i at time t is given by

$$\begin{aligned} V_i(t) &= \sum_{t_i^{(f)} \in \mathcal{F}_i} \eta_i(t - t_i^{(f)}) + \sum_{j \in \Gamma_i} \sum_{t_j^{(f)} \in \mathcal{F}_j} w_{ij} \epsilon_{ij}(t - t_j^{(f)}) \\ &+ \underbrace{\int_0^\infty \kappa_i(r) I(t - r) dr}_{\text{if external input current}} \end{aligned} \quad (4)$$

where the kernel functions η_i , ϵ_{ij} and κ_i respectively describe the potential reset, the response to a presynaptic spike and the response to an external current.

There exist many *models of networks* where the spiking nature of neurons activity is made explicit (see *Koch and Segev (1998)* and *Dayan and Abbott (2001)* for reviews), either from a biological point of view or for computer simulation, such as, for instance, biological models of cortical maps. For computational purpose, spiking neuron networks have been introduced more recently, firstly by simulating traditional neural networks (multi-layer perceptrons, Hopfield’s or RBF networks) at the end of the 90’s (*Maass, 1997a; Maass and Natschläger, 1997*), and then by defining specific models, such as reservoir computing (see Section 1).

Finally, let us define a *spike train* as the output of a spiking neuron network, i.e. a set of events defined by their occurrence times, up to some precision:

$$\mathcal{F} = \{\dots t_i^n \dots\} \quad \text{with } t_i^1 < t_i^2 < \dots < t_i^n < \dots, \quad \forall i, \quad \forall n \quad (5)$$

where t_i^n is the n th spike time of the neuron N_i , with related interspike intervals $d_i^n = t_i^n - t_i^{n-1}$.

¹ When V is not differentiable V' corresponds to the left derivative.

For more detailed introductions to models of spiking neurons and networks (see e.g. Maass and Bishop, 2003; Gerstner and Kistler, 2002a; Schrauwen, 2007; Paugam-Moisy and Bohte, 2010). By way of comparison, both neuron and network models may be evaluated with respect to (i) their biological plausibility and (ii) their efficiency for computer simulation.

2.2. Biological plausibility of neuron and network models

Biological plausibility at the neuron level is understood as the ability to reproduce what is observed at the cell level, often considering invitro experiments (Koch and Segev, 1998). The point of view is questionable as shown in recent experiments in V1 (Frégnac, 2003; Frégnac, 2004) where it appears that a single-cell observation highly differs between invitro and invivo conditions.

Biological plausibility at the network level is understood as the ability to reproduce what is observed regarding, e.g. the cortical map activity (Carandini et al., 2005). This includes predicting the response to specific stimuli, not only artificial ones, but also natural ones: this means, for V1, taking into account natural image sequences as inputs shifted by eye movements (Baudot, 2007), after the retinal and LGN processing (see e.g. Simoncelli and Olshausen (2001) for a discussion about information processing in these structures).

As far as this contribution is concerned, we consider a weaker notion of biological plausibility: A simulation is biologically plausible if it verifies an explicit set of constraints observed in biology (as pointed by Frégnac (2003)). More precisely, we are going to review and discuss a few time constraints, shared by all the neural dynamics, further called “general time constraints”. We develop their consequences at the simulation level. The time constraints are based on biological temporal limits and appear to be very precious quantitative elements, both for estimating the coding capacity of a system and for improving simulations.

2.3. Simulation efficiency of neuron and network models

The neuron model proposed by Hodgkin and Huxley (1952) is still considered as the reference for biological plausibility, but is unfortunately intractable when simulating large-scale neural networks. Compared to the neuron models governed by coupled differential equations, the SRM neuron is more intuitive to understand and more straightforward to implement.

Among the spiking neuron models, the punctual conductance-based generalized integrate-and-fire (gIF) is an adaptive, bi-dimensional, non-linear, integrate-and-fire model with conductance-based synaptic interactions (as e.g. in Destexhe (1997), Brette and Gerstner (2005), Rudolph and Destexhe (2007)). At the present state of the art, considering the gIF as a neuron model presents several advantages:

- It gives an effective description of the neuronal activity, with the ability to reproduce several important neuronal regimes (Izhikevich, 2004), well matching to biological data, especially in high-conductance states, typical of cortical invivo activity (Destexhe et al., 2003).
- Nevertheless, it consists of a simplification of Hodgkin–Huxley models, which is useful both for mathematical analysis and numerical simulations (Gerstner and Kistler, 2002a; Izhikevich, 2003).

Moreover, though these models have mainly been considered for studying the dynamics of a single neuron, they are easy to integrate into a network structure, including synaptic plasticity modeling (Markram et al., 1997; Pfister and Gerstner, 2006). See, e.g.

Rauch et al. (2003) for further elements in the context of experimental frameworks and Camera et al. (2008a,b) for a review.

However, in all the variants of integrate-and-fire models, it is assumed that an *instantaneous* reset of the membrane potential occurs after each spike firing, except for the Spike Response Model. The reset is a formal simplification and has a spurious effect: Information theory² is not applicable to unbounded frequencies. From the information theory point of view, it is a temptation to relate this spurious property to the *erroneous* fact that the neural network information is not bounded. In the biological reality, time synchronization is indeed not instantaneous, due to action potential time-course, synaptic delays, refractoriness, and so on...

Theoretically, networks of spiking neurons can perform very powerful computations with precise spike-timings. Spiking neurons are at least as computationally powerful as the sigmoid neurons traditionally used in artificial neuron networks (Maass, 1997b). This result has been shown using a SRM neuron and considering piece-wise linear approximations of the membrane potential profiles. In this context, analog inputs and outputs are encoded by temporal latencies of spike firings. It has been shown that any finite piece of orbit issued from a feed-forward or recurrent network of analog neurons can be simulated arbitrarily closely by a larger network of spiking neurons, the number of neurons depending on the length of this piece of orbit and on the required precision. The assertion holds even in the presence of noise. Such theoretical results highly motivate the use of spiking neuron networks for modeling and simulation purpose.

3. General time constraints in spike trains

Let us now consider spike trains, as defined by sequences of events in Section 2. In computational or biological contexts, not all sequences \mathcal{F} correspond to realistic spike trains since they are constrained by the neural dynamics. Furthermore, in computational or biological contexts, the following time constraints must be taken into account:

- [C1] Inter-spike intervals d_i^n are bounded by a refractory period r_i which implies $d_i^n > r_i$.
- [C2] Spike times are defined up to some absolute precision δt .
- [C3] There is always a minimal delay dt for a presynaptic spike to influence a post-synaptic neuron, thus having a *causal* effect on another spike.
- [C4] Considering a neuron i , without input (see below), there is a maximal, *finite*, inter-spike interval D such that $\forall n$ either $d_i^n < D$ or $t_i^n = +\infty$ (i.e. either a neuron fires within a time delay $< D$ or it remains quiescent forever).

[C1–3] are always verified. Mathematically, [C4] is only violated if D is infinite, which never occurs in real neurons, and can occur in non generic situations for gIF models (see below). The main content of this constraint is to avoid that there is a time horizon, which can be very long, after which, a silent neuron suddenly fires, with important consequences on dynamics.

For biological neurons, orders of magnitude are typically, in milliseconds:

r	δt	dt	D
1	0.1	$10^{-[1,2]}$	$10^{[3,4]}$

where, for C4, we assume that the neuron receives no external current. In the rest of the section, the “general time constraints” [C1–4]

² Shannon’s theorem, stating that the sampling period must be less than half the period corresponding to the highest signal frequency.

are analyzed and discussed, and the evaluations of numerical values for the temporal variables δt , dt and D are proposed.

The [C1] constraint is well-known as a straightforward limit for the maximal firing rate. See e.g. Koch (1999) for an extended discussion on absolute/relative refractory periods.

3.1. Spike time precision

The [C2] constraint might correspond to more than one definition. For instance, probabilistic interpretations often consider an additive perturbation in the dynamic evolution, to encounter for the fact that spike times are not precisely defined. On the other hand, deterministic interpretations may consider precision intervals. Here, we propose a simple deterministic specification:

Two spike times are different, e.g., not synchronized, if separated by more than δt .

Two spike times are non distinguishable if they are separated by less than δt .

“Non distinguishable” does not mean “equal”, but this means we can not state if equal or different. The [C2] constraint is sometimes forgotten in models. In rank coding schemes for instance (Gautrais and Thorpe, 1998) it is claimed that all spike-time permutations are significant. It is not realistic since many of these permutations are non distinguishable, because of the bounded precision, as discussed in Viéville and Crahay (2004). Similarly, network models related to reservoir computing (see Section 1) do not address this issue, although simulations indeed have to take it into account. As a consequence, an unrealistic unbounded time precision is implicitly assumed.

3.1.1. Spike time precision evaluation

Let us see how to estimate δt by means of a simple approximation method. Here, the spike time precision is evaluated, on the basis of the time at which the membrane potential reaches a maximum. The time at which the membrane potential crosses a given threshold during the rising phase could lead to a different evaluation. However, such “spiking threshold” is definitely an arbitrary concept, when considering the literature. Note that in Hodgkin-Huxley models the threshold is not sharply defined (Cronin, 1987); mathematically the “threshold” is defined by a manifold in the phase space, called the “separatrix”, depending on the activity variables. Up to our best knowledge, we do not see how to evaluate the spike time precision following this track, whereas the action potential maximum is a well defined cue. Since we are looking for a lower-bound, we simply make the reasonable assumption that spike time precision is not higher than the action potential maximum precision. Furthermore, since action potential shapes are rather stable, both measures should be strongly related.

Assuming that the spike time of a real neuron is defined by the time t_i when the membrane potential $V(t_i)$ reaches a maximum, we obtain around t_i , assuming differentiability of V :

$$V(t) = V(t_i) + \kappa(t - t_i)^2 + o(|t - t_i|^2)$$

writing $\kappa = d^2V/dt^2(t_i)$ the related curvature. As a rule of thumb for the spike-time precision δt , we thus obtain:

$$\delta t \simeq \sqrt{\frac{\langle \delta V \rangle}{\langle \kappa \rangle}}$$

the averages $\langle \rangle$ are to be taken over a set of measurements. Here δV is the voltage precision and κ can be measured on the action potential, around the maximum.

In order to roughly estimate spike time precision, we have considered electro-physiological data from a few dozen of spike pro-

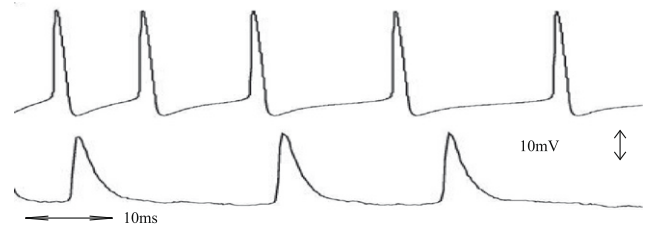


Fig. 1. Two examples of biological data: Spike profiles in the cat primary visual cortex. The peak curvature order of magnitude is between 30 and 100 mV/ms².

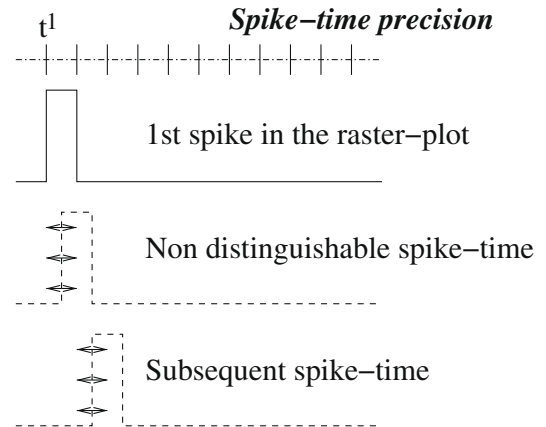


Fig. 2. Evaluating the information in a set of spike times (see text for details).

files in several spike trains (Carandini and Ferster, 2000; Koch, 1999), we have graphically estimated the values in a zoom of the figures provided in articles. We have obtained $\delta t \simeq 0.1$ ms, with a peak curvature order of magnitude $\langle \kappa \rangle = 100$ mV/ms², as illustrated in Fig. 1, by considering a voltage precision of average $\langle \delta V \rangle = 10$ μ V, i.e. at the order of magnitude of the membrane potential noise Koch (1999).

Furthermore, a similar order of magnitude is obtained in literature: The numerical precision in inter-neuron synchronization is estimated at about 1 ms (Crook et al., 1998), while Mainen and Sejnowski (1995) (e.g. in Fig. 2B) report sub-millisecond accuracy in vitro, but not exceeding 0.1 ms.

3.2. Spike time propagation

The [C3] constraint expresses the need for a delay of spike transmission. Such a constraint is obvious and has for consequence to avoid spurious effects³ in neural dynamics, and to induce simplifications both at the modeling and simulation levels (Morrison et al., 2005).

3.2.1. Spike time propagation evaluation

Synaptic delays. Delays from one spike to another involve the presynaptic axonal delay, the synaptic delay and the post-synaptic dendritic delay. Numerically, the values of delays observed in experiments (Koch, 1999; Burnod, 1993) are at least 0.5 ms, up to 40–50 ms for inter cortical maps transmissions. In Swadlow (1985, 1992) coherent values of 0.1–44 ms are reported. Then a

³ If a neuron instantaneously fires after receiving a spike, this can generate avalanche effects (another neuron instantaneously fires and so on) or even temporal paradoxes (another inhibitory neuron instantaneously fires inhibiting this one, thus not supposed to fire any more).

reasonable assumption is to consider that synaptic connections are delayed by $dt \gtrsim 0.1$ ms.

In this simple discussion, we are looking for a lower-bound. Hence, we do not consider the axonal arborization nor the presynaptic processing which generate a variety of altered and/or delayed sets of events, at least in biological systems. In such cases, larger delays can occur.

Gap-junction delays. A step further, many local inter-neuronal connections in the cortex are realized through electrical gap junctions (Galarreta and Hestrin, 2001), which is even predominant between cells of a same sub-population (Amitai et al., 2002). In such a case the transmission is mainly due to the spike potential raise, with a time constant of about 0.1–0.2 ms (see Lewis and Rinzel (2003) for a discussion about the electrical transmission). The delays of gap-junctions are much smaller ($dt \gtrsim 10 \mu\text{s}$) but still measurable (Lewis and Rinzel, 2003; Koch, 1999). Then a reasonable assumption is to consider that electrical connections are delayed by $dt \gtrsim 0.01$ ms.

3.3. Spike time upper-bound

The [C4] constraint, that states the existence of a time upper-bound for spike firing, is less obvious. The idea is that, as far as there is no input (i.e., the neuron is isolated from the network between two input spikes), the potential decreases towards a resting potential and the neuron cannot fire anymore.

As discussed in details in Cessac et al. (2008), the fact whether the constraint [C4] is verified or not completely changes the nature of the dynamics. This issue will be extensively reviewed in next section. Roughly speaking, if [C4] is violated, a neuron might remain silent a very long range of time, and then suddenly fire, inducing a drastic change in the further state of the system.

3.3.1. Spike time upper-bound evaluation

At the simulation level, [C4] is violated for deterministic neural models with constant internal current, that are able to integrate during an unbounded period of time, or to sustain sub-threshold oscillations.

This phenomenon is easy to illustrate by considering a LIF model, where g and i are constant:

$$\begin{cases} C \frac{dv}{dt} + gV = i, \\ V(t_0) = V_0, V(t_1) = \theta \end{cases} \Rightarrow t_1 = t_0 + \frac{C}{g} \log \left(\frac{i - gV_0}{i - g\theta} \right) \quad \text{with } i > g\theta > gV_0.$$

If the internal current verifies: $i > g(\theta - V_0 e^{-Dg/C}) / (1 - e^{-Dg/C})$, then [C4] is verified. Since $C/g \simeq 1 \dots 10$ ms, thus $e^{-Dg/C} \ll 10^4$, and it is sufficient to get $i > (1 + 10^{-4})g\theta$, i.e. a very small amount above $g\theta$. However, if $i \rightarrow g\theta$, then the firing period becomes unbounded, yielding a spurious event (which can affect the whole dynamic) at an unbounded time. At the level of networks it can be shown that this case is non generic for gIF models (it holds for a negligible set of synaptic weights and constant current values, Cessac, 2008; Cessac et al., 2008).

Thus, this case is easy to check and to avoid, and a maximal spontaneous firing period can be derived. Synaptic conductance based models (gIF – Destexhe, 1997) and spike response models (SRM – Gerstner and Kistler, 2002a) usually omit this constant current and their intrinsic “leak” guaranties that [C4] is not violated. On the contrary, with stochastic models, [C4] might be reconsidered, since there is always a “chance” to fire a spike, with a decreasing probability as time increases.

At the biological level,⁴ in vitro, a cortical pyramidal neuron that spikes regularly, without synaptic input, remains silent since

⁴ We are especially thankful to Dr. Thierry Bal, for a scientific discussion on this subject.

its membrane potential is close to the resting potential (Koch, 1999). In vivo, in the cortex, current observations (Dayan and Abbott, 2001) show that a neuron is always firing (unless it is dead). This is due to the large amount of neuromodulators, inducing depolarization on the one hand, and on the other hand a membrane potential getting close to the firing threshold. This behavior is thus realistic for cortical pyramidal neurons, but likely not for all neurons in the brain (Par et al., 1990; McCormick and Bal, 1997). However, the constraint [C4], for which isolated neurons are under consideration, does not apply in this situation. On the contrary, thalamic neurons can fire spontaneously after a long resting period (Par et al., 1990). Even in vitro, their internal currents such as IT (low threshold transient Ca^{2+} current) or IH (hyper-polarization-activated cation current) can induce spikes (due to oscillatory behaviors) (McCormick and Bal, 1997).

Under the assumptions C[1–3], and optionally [C4], let us now review the related consequences regarding modeling and simulation.

3.4. Time-constrained networks for improving simulation

Simulation efficiency is a twofold issue of precision and performance. See Brette et al. (2007) for a review on both event-based and clock-based simulation methods.⁵

Event-based simulation methods are technically restrictive: Models can be simulated if and only if the next spike-time can be explicitly computed in reasonable time. Therefore, not all neuron models can be a priori implemented on event-based simulators. An event-based simulation kernel is less easy to use than a clock-based one. In other words, event-based simulation methods may save precision and computation time, but not the labor time of the scientist.

From now on, taking into account our previous discussion, the event-based simulation of spiking neuron networks would be strongly simplified. Thanks to [C3], spike firing cannot generate causal paradoxes: Since there exists a minimal delay, it is not possible that an event instantaneously causes another event which is itself the first event cause, whereas this phenomenon could occur without [C3]. Thanks to [C3] again, parallel implementations of event-based simulation are possible (see e.g. Mouraud et al., 2006) since, in a time window shorter than dt we have the guaranty that events do not influence each others and thus can be processed in parallel. Thanks to [C2] and [C4], spike times and precisions are bounded, allowing us to use efficient “histogram based” methods,⁶ with a small $O(1)$ complexity. This implies that clock-based mechanisms may be easily added to event-based ones, since the kernel overhead for managing irregular events (and not only a regular clock) becomes negligible. See Cessac et al. (2009a) for an in-depth discussion.

⁵ Regarding precision, event-based simulations, in which firing times are not regularly discretized but calculated event by event at the machine precision level, provide (in principle) an unbiased solution. On the reverse, it has been shown that a regular clock-based discretisation of continuous neural systems may introduce systematic errors, with drastic consequences at the numerical level, even when considering very short sampling times. Furthermore, the computational cost is an order of magnitude better using event-based sampling methods, in theory, although this may be not always verified in practice. State-of-the-art simulators are essentially clock-based, while some of them integrate event-based as a marginal tool or in mixtures with clock-based methods.

⁶ See for instance <http://enas.forge.inria.fr>. In this implementation, the simulation core is a simple (about 10 Kb C++ source code) mechanism, using a $O(D/dt + N)$ buffer size and about $O(1 + C) \simeq 10$ –50 operations/spike ($>10^6$ spike/s on a laptop), for a size N network with C connections in average.

3.5. Studying spiking neuron networks as discrete time systems

Taking [C1–3] into account is a mean to “discretize” the spike train sequences and give us a way to study spiking neuron networks as discrete time systems. The consequences of this point of view are developed in the next two sections.

4. The maximal amount of information

Under the assumptions [C1–2], in a given network of N spiking neurons observed during a finite period $[0, T]$, the number of possible spikes is obviously limited by the refractory period r . Furthermore, the information contained in all spike times is strictly bounded, since two spike occurrences in a δt window are not distinguishable, and $\delta t < r$ numerically.

The following rough upper-bound for the amount of information can be stated:

$$N \frac{T}{r} \log_2 \left(\frac{T}{\delta t} \right) \text{ bits during } T \text{ seconds}$$

Taking into account the biological values, a straightforward numerical derivation leads to about 10 Kbit/s/neuron.

4.1. Information upper-bound evaluation

Let us consider a given neuron (the index number is omitted) and its first spike time t^1 . This time is going to be used as a reference. The next spike of the neuron, (i) either occurs no later than $t^1 + \delta t$ thus at a time not distinguishable from t^1 by an observer, (ii) or occurs at least δt later. In order to be meaningful, spikes must thus occur in distinct temporal boxes of width δt , the precise location of the box being fixed by the first time of occurrence, as schematized in Fig. 2. Since, numerically, there is a refractory period $r > \delta t$, the second and next spikes will never be mixed with their predecessors but are going to be subject to the same limitation.

Once a spike time has been set to t^i , the next spike time t^{i+1} must belong to the interval $[t^i, T]$. As a consequence, no more than one spike every r milliseconds can be introduced in a temporal histogram of δt box width, as illustrated in Fig. 2. In a $[0, T]$ time range, there are $T/\delta t$ choices for the first neuron spike, less than $T/\delta t - 1$ for the second neuron choice, etc. This means that for the T/r maximal number of spikes, they are less than $(T/\delta t)^{T/r}$ choices.

Assuming, as a maximal case, that each spiking pattern is independent, we obtain⁷ the proposed bound of $O\left(\frac{T}{r} \log_2 \left(\frac{T}{\delta t}\right)\right)$.

Note that we may simply consider that a spike train generated by a single neuron reduces to a sequence of T/r binary values: 0 if no spike occurs, 1 if one spike occurs in each temporal bin. Then the amount of information per neuron in the period $[0, T]$ is bounded by T/r . This point of view corresponds to neglecting the information brought by neuron relative spike times within the network.

4.2. Discussion

Note that the upper-bound we have derived is rough and does not take into account the constraints imposed by the dynamics at the network level. These constraints further reduce the available information. Actually, the dynamics of a given network does constraint very much the plausible spike trains, and the related information may be lower, or even strongly lower, than this bound.

In the particular case of fast-brain mechanisms, where only “the first spikes matter” (Thorpe and Fabre-Thorpe, 2001), this amount

of information is not related to the permutations between neuron spikes, i.e. of order $o(\log(N!)) = N \log(N)$ but simply proportional to N , in coherence to what is found in Viéville and Crahay (2004).

The latter bound is coherent with several results presented in Rieke et al. (1996) where the authors consider firing rates and use entropy as information measure. For instance, as observed in their study, by considering a timing precision of 1 ms, the authors obtain an information rate bounded around 1 bits/s for a neural receptor. This number has an order of magnitude coherent with our bound, although the network dynamics itself introduces more specific constraints. These constraints should yield an information rate lower than predicted by the previous bound. The reason of this discrepancy is that the dynamics looks like rich enough to maintain a high information rate.

This information bound is not bad, but good news. Since different information are necessarily represented by distinguishable spiking patterns, this result means that there is a well-defined margin between two different representations of information. The notion of neural coding with large margins is discussed in Viéville and Crahay (2004), and may explain the surprisingly impressive performance of fast brain categorization. This corresponds to introducing an incompressible margin, which guaranties a robust coding.

5. Dynamics of time-constrained networks

A step further, we have mentioned that taking [C1–3] into account is a mean to “discretize” the spike train sequences. The sampling period has to be taken smaller than r , δt and dt : Smaller than r in order to have either 1 or 0 spike during a sampling period; Smaller than δt in order that the sampling does not impair the spike-time precision; smaller than dt since, in a discrete time system, the information is propagated from one sampling period to another through recurrence relations.

A raster is formally defined as follows: To each neuron of index i , a binary variable $\omega_i(k) \in \{0, 1\}$ is associated such that the neuron fires during the k th sampling period if and only if $\omega_i(k) = 1$ and is silent otherwise.

5.1. Theoretical results

In models such as (i) basic leaky integrate-and-fire (LIF) or integrate and fire neuron models with conductance synapses and (ii) constant external current (gLIF), a full characterization of the network dynamics can be derived from such a discretization. Here, we consider models with constant parameters (weights, delays, etc.). In the present section, we state the results that have been proved in Cessac (2008) and Cessac et al. (2008) for both cases (LIF and gLIF) and we summarize their meaning and significance.

- [Fact 1] *The raster is generically⁸ asymptotically periodic, but, depending on parameters such as constant external current or synaptic weights, periods can be larger than any accessible computational time.*
- [Fact 2] *There is a one-to-one correspondence between orbits⁹ and raster (i.e. a raster provides a symbolic coding for the network dynamics).*

⁸ Considering a basic leaky integrate-and-fire neuron network the result is true except for a negligible set of parameters. Considering an integrate-and-fire neuron model with conductance synapses the result is true unless the trajectory accumulates on the threshold from below.

⁹ Here we consider orbits, i.e. infinite trajectories, thus consider this deterministic system, with constant input, in its asymptotic stage.

⁷ We are especially thankful to one reviewer of this paper, for enlightening remarks brought on this point.

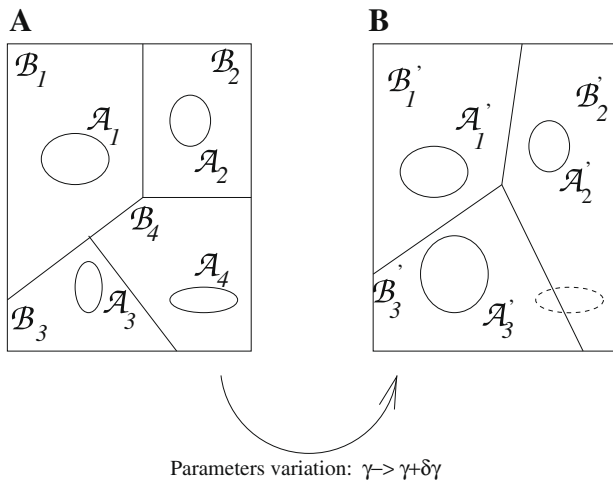


Fig. 3. Basins of attraction of a dynamic landscape, for deterministic time-constrained networks. (A) The phase space (in other words the space of the network states) is partitioned into bounded domains \mathcal{B}_i and for each initial condition in \mathcal{B}_i the initial trajectory is attracted, not towards a fixed point (as in Hopfield networks with asynchronous dynamics), but towards a periodic orbit \mathcal{A}_i . (B) If the parameters (external input, weights) change, the landscape is modified and several phenomena can occur: change in the attractor's shapes, number of attractors, as for \mathcal{A}_3 in this example; a point belonging to \mathcal{A}_4 in (A), can, after modification of the parameters, converge either to attractor \mathcal{A}'_2 or \mathcal{A}'_3 .

The first fact expresses that (stable) periodic orbits constitute somehow the “skeleton” (omega-limit set) of gIF-models dynamics. Especially the probability of spike blocs, containing information or neural code, can be computed from this periodic orbits skeleton. When the parameters vary, the orbits change accordingly but are still periodic (with possibly very large periods).

The second fact means that, in the LIF and gIF cases, the raster is a “symbolic coding” in the sense that no information is lost by considering the spike times instead of the membrane potential variations.

Both facts are good bases for deeply understanding the network dynamics: Fig. 3 sketches out some aspects, showing the global behavior of the system and illustrating that attractors are generically stable period orbits. More precisely, the dynamics is piecewise continuous, i.e. continuous except when a spike is fired. The network dynamics is locally contracting, this being due to the term of leak in the neuron dynamics (see Cessac (2008) and Cessac et al. (2008) for details). Furthermore, after each neuron has fired once the dynamics is no longer dependent on the initial conditions. Nevertheless, when the membrane potential is close to the threshold, a small perturbation may induce drastic changes in the dynamics, while it is otherwise damped. This behavior corresponds to a notion of “edge of chaos” which is precisely defined within this framework (Cessac, 2008; Cessac et al., 2008). However, this definition differs from the usual notion of chaos in differentiable systems (the terminology “stable chaos” has been proposed by Politi and Torcini (2009)).

5.2. Discussion

Time is discretized, but without any constraint about the “sampling period”. The two previous results hold at any finite precision. However, we wonder the extent to which the period of the periodic orbits does not depend on the sampling period, provided the sampling period is small enough. More generally, periodic orbits dependence with respect to the sampling period is still an open issue.

In order to understand the Fact 1, it might be important to discuss how “obvious” it is. Time is discretized. If the membrane po-

tential would have been discretized also, the question would have been reduced to studying a finite state system. In the latter case, only fixed points and periodic orbits could occur and the result would have been obvious. As a consequence, the Fact 1 reads: *Even if the neuron state is described by continuous values, orbits are still generically periodic.*

In a conductance based model, with the additional constraint that conductances depend on previous spikes within a finite horizon, it appears that the Fact 1 still holds, although this is even intuitively less obvious than the LIF case (Cessac et al., 2008).

To which extent such a “canonical situation” is still true for more complex models is an open question. We can easily conjecture that the Fact 1 is a model limitation for all integrate-and-fire models, providing they are defined with an instantaneous reset to a constant value. The question is still open for Spike Response Models.

The Fact 2 can be explained as follows: Changing the initial value of the membrane potential, one may expect some variability in the dynamics. But due to the reset, close-by distinct trajectories can be collapsed onto a same trajectory, after finite time. As a result, the membrane potential evolution only depends on the previous spike times, instead of the previous membrane potential values (Cessac, 2008).

Since periods exhibited by integrate-and-fire models can be arbitrary large, depending on parameters such as synaptic weights, it is likely that raster produced by these models can approach raster produced by more realistic models such as Hodgkin–Huxley neurons, for a finite horizon. However, this suggestion is a conjecture only. See, e.g. Fitzgibbon et al. (1996) for a discussion about the link between the standard Hodgkin–Huxley system and its hyperbolic approximation. This property is reminiscent of the shadowing lemma of dynamical systems theory (Katok and Hasselblatt, 1998), stating that chaotic orbits produced by a uniformly hyperbolic system can be approached arbitrary close by periodic orbits.

6. Neural coding and spike train metrics

In a biological as well as a computational context, the analysis of experimental data or simulation data often requires a comparison between two or several spike trains. Either the spike trains concern a given neuron and result from several repetitions of a same experiment, or the spike trains have been generated by different neurons during a given time range, in a unique experiment. In both cases, the idea is to look for invariants, or differences, in the underlying neural code. In the present section and the next two, we study the relation between neural coding and different spike train metrics.

As an illustrative example, let us consider the temporal order coding scheme (Gautrais and Thorpe, 1998; Thorpe and Fabre-Thorpe, 2001) (i.e. rank coding): Only the order of the events matters, not their specific time values. Two spike trains \mathcal{F}_1 and \mathcal{F}_2 with the same event ordering correspond to the same code. This assertion defines an *equivalence relation* which structures the set of all the spike trains into a partition: Every spike trains in a same equivalence class correspond to the same “code”. Other coding methods lead to similar definitions of metrics. For instance, rate coding means that all spike trains with the same frequency are in the same equivalence class,¹⁰ irrespective of their phase.

However, when we reconsider the question of neural coding under the light of the time constraints discussed in previous sections, the fact that spike time precision is not unbounded leads to many

¹⁰ Considering a classification where firing rates take continuous values, this class has uncountably many elements.

non-separable (i.e. non distinguishable) orderings. This fact has no consequences on the rank coding concept, while the partition is now coarser: Trains with two spikes occurring at non distinguishable times are in the same equivalence class.

Let us now introduce the notion of spike train metric. The basic idea consists in defining a distance $d(\cdot)$, such that $d(\mathcal{F}_1, \mathcal{F}_2) = 0$ if \mathcal{F}_1 and \mathcal{F}_2 correspond to the same code, and $d(\mathcal{F}_1, \mathcal{F}_2) = 1$ otherwise.

A step further, how can we capture the fact that, e.g. for rank coding, two spike times with a difference “about” δt are “almost” indistinguishable? The natural idea is to use a “quantitative” distance instead of a discrete distance (i.e. with binary 0/1 values): Two spike trains correspond to the same neural code exactly if the distance is zero, otherwise the distance increases with the difference between the trains.

This is the idea we wanted to highlight here. This proposal is not a mathematical “axiomatic”, but a simple modeling choice. The principle is far from being new, but rather surprisingly it has not been made explicit at this level of simplicity. In order to see the interest of the idea, let us briefly review the main classes of spike train metrics.

As reviewed in details in Schrauwen (2007) and Victor (2005), spike trains metrics can be categorized in three classes:

- 0 – “Bin” metrics, based on grouping spikes into bins (e.g. rate coding metrics): Not discussed.
- I – Convolution metrics, including the raster-plot metric: Discussed in Section 7.
- II – Spike time metrics, such as alignment distances (Victor and Purpura, 1996): Discussed now.

6.1. The original alignment metric

The first family of metrics we want to review is defined on spike times themselves (Victor and Purpura, 1996; Victor, 2005).

The distance between two finite spike trains $\mathcal{F}, \mathcal{F}'$ is defined in terms of the minimum cost of transforming one spike train into another. Two kinds of operations are defined:

- spike insertion or spike deletion, the cost of each operation being set to 1,
- spike shift, the cost to shift from $t_i^n \in \mathcal{F}$ to $t_i^m \in \mathcal{F}'$ being set to $|t_i^n - t_i^m|/\tau$ for a time-constant τ .

For small τ , the distance approaches the number of non-coincident spikes, since instead of shifting spikes it is cheaper to insert/delete non-coincident spikes, the distance being always bounded by the number of spikes in both trains.

For high τ , the distance basically equals the difference in spike number (rate distance), while for two spike trains with the same number of spikes.

Here, two spike times are comparable if they occur within an interval of 2τ , otherwise they had better to be deleted/inserted.

Although computing such a distance seems subject to a combinatorial complexity, it appears that quadratic algorithms are available (i.e. with a complexity equal to the product of the numbers of spikes). This is due to the fact that, as illustrated in Fig. 4, in a minimal path, each spike can be either deleted or shifted once to coincide with a spike in the other spike train. Also, a spike can be inserted only at a time that matches the occurrence of a spike in the other spike train. Thus, the minimal distance can be calculated iteratively by considering the distance $d_{n,n'}(\mathcal{F}, \mathcal{F}')$ between a spike train composed of the first n spikes of \mathcal{F} and the first n' spikes of \mathcal{F}' .

When considering spike trains with more than one unit, an approach consists to sum the distances for each alignment unit-to-

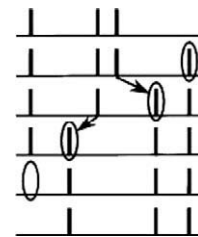


Fig. 4. An example of minimal alignment from the upper to the lower spike train. Successive operations are, from top to bottom: an insertion, a rightward shift, a leftward shift and a deletion.

unit. Another point of view is to consider that a spike can “jump”, with some cost, from one unit in \mathcal{F} to another unit in \mathcal{F}' . The related algorithmic complexity is no more quadratic but to the power of the number of units (Aronov, 2003).

This family of metrics include alignments not only on spike times, but also on inter-spike intervals, or metrics which are sensitive to patterns of spikes, etc. Such metrics have been fruitfully applied to a variety of neural systems, in order to characterize neuronal variability and coding (Victor, 2005). For instance, in a set of neurons, that act as coincidence detectors, with integration time (or temporal resolution) τ , spike trains will have similar post-synaptic effects if they are similar w.r.t. this metric.

6.2. Generalization of the alignment metric

Here, let us remark that the previous metric can be generalized as follows:

- [causality] At a given time, the cost of the alignment of previous spikes decreases with the obsolescence of the spike, say, with an exponential profile parametrized by a time-constant τ' . When $\tau' \rightarrow \infty$, the original alignment metric is retrieved.
- [non-linearity] The cost of a shift is not necessarily a linear function of $\frac{|t_i^n - t_i^m|}{\tau}$, as in the original metric, but any suitable non-linear function $\phi\left(\frac{|t_i^n - t_i^m|}{\tau}\right)$.

For instance, we may choose a small quadratic profile when lower than the time precision (accounting for additive noise, but implementing the fact that spike time differences are negligible), and then, a linear profile.

This leads to an iterative definition of the previous distance $d_{n,n'}$, now generalized, and defined as follows: On one hand, $d_{n,0} = n$ and $d_{0,n'} = n'$ (due to the fact that the distance between any spike train and the empty spike train corresponds to the cost of deleting all spikes). On the other hand, by induction, we can write, generalizing the standard alignment metric (the two 1st lines corresponding to spike insertion, and the 3rd line including a spike shift, as detailed in Aronov (2003)):

$$d_{n,n'} = \min \left(\begin{array}{l} e^{-\frac{t_i^n - t_i^{n-1}}{\tau'}} d_{n-1,n'} + 1, \\ e^{-\frac{t_i^m - t_i^{m-1}}{\tau'}} d_{n,n'-1} + 1, \\ e^{-\frac{\max(t_i^n, t_i^m) - \min(t_i^{n-1}, t_i^{m-1})}{\tau}} d_{n-1,n'-1} + \phi\left(\frac{|t_i^n - t_i^m|}{\tau}\right) \end{array} \right),$$

with, e.g., $\phi(d) = \min(d, (d\tau/\delta t)^2)$, again implementable in quadratic time. It corresponds to the original alignment metric if and only if $\phi(\cdot)$ is the identity function and $\tau' = +\infty$, still calculable with a quadratic complexity.

This modified version of the metric illustrates how this class of distances not only “statically” represents the underlying neural code as a metric, but also is relevant in temporal paradigms. This

property results from having integrated the previously discussed “general time constraints” in the formalism.

6.3. Limitations of alignment metric and polychronization

A spiking neuron network can *polychronize*, i.e., exhibit reproducible time-locked but not synchronous firing patterns within 1 ms precision. Polychronization could be viewed as a generalization of the notions of synchronization and synfire chains. Due to the interplay between the delays and a form of synaptic plasticity (implementable by way of STDP), the spiking neurons spontaneously self-organize into groups and generate patterns of stereotypical polychronous activity.

In Izhikevich (2007), it has been shown that the number of co-existing polychronous groups far exceeds the number of neurons in the network, resulting in an unprecedented memory capacity of the system. The author speculates on the significance of polychrony to the theory of neuronal group selection and cognitive neural computations.

In Paugam-Moisy et al. (2008), the network processing and the resulting performance is explained by the concept of polychronization. The model emphasizes that polychronization can be used as a tool for exploiting the computational power of synaptic delays and for monitoring the topology and activity of a spiking neuron network (Martinez and Paugam-Moisy, 2008).

Taking such complex aspects of the neural code into account cannot be performed by any available metrics. New metrics, taking into account long term interactions, have to be developed and this is a challenging issue.

7. Convolution metrics for linking spike trains and continuous signals

Spike trains define “times”, not directly “values”. However, many signals such as sensory input or motor output is intrinsically defined by continuous quantitative values. A link between spike trains and continuous signals is thus to be made, and “rate coding” is almost often considered to build this link. In this section, we are going to see that rate coding is a particular case of convolution metrics. All convolution metrics share interesting properties, with a good capacity to reconstruct the signal from the spikes, to decode the spikes from the signal, to identify the kernel linking both of them, etc. In order to be concise, we overview these links in the form of a commented formulary.

7.1. Linear representation

A large class of metrics is defined through the choice of a convolution kernel K_i applied to a spike train function written $\rho_i(t) = \sum_{t_i^n \in \mathcal{F}_i} \delta(t - t_i^n)$, where $\delta(\cdot)$ is the Dirac distribution. Note that, in most case, K_i is related to a linear response of the neuron (or synapse) to spike trains inputs, thus introducing a natural notion of causality and action/reaction. This is a possible way of considering “the code”. A neuron responds in an appropriate and adapted way to specific spike sequences.

For a given spike train \mathcal{F}_i , the convolution equation is:

$$s_i(t) = \sum_{t_i^n \in \mathcal{F}_i} K_i(t - t_i^n) = K_i * \rho_i(t) \in [0, 1],$$

The signal s_i is easily normalized between 0 (no spike) and, say, 1 (burst mode at the maximal frequency). A few examples of convolution kernels are given in Fig. 5.

The distance between two spike trains is then defined by applying some L^p norm to the continuous signal $s = (\dots, s_i, \dots)$, at the network level. The “code” here corresponds to the linear represen-

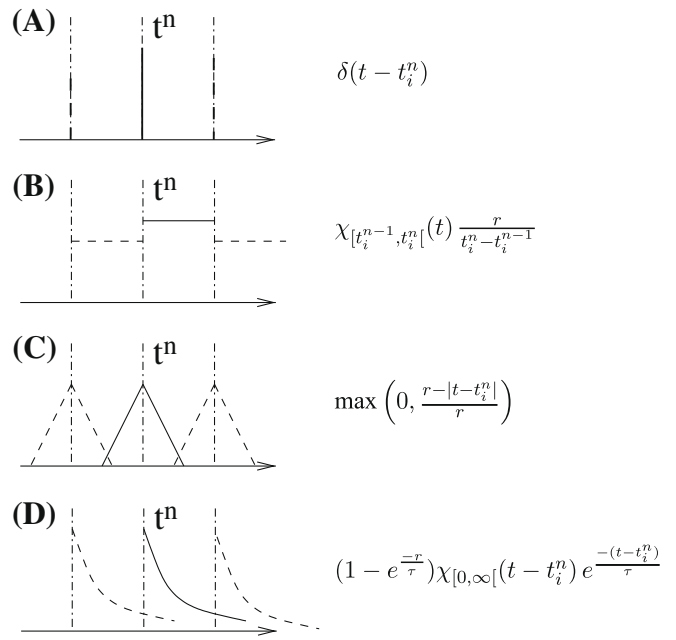


Fig. 5. A few examples of spike train convolution: (A) The spike train itself. (B) A causal local frequency measure estimation (writing χ the indicatrix function). (C) A non-causal spike density, uniformly equal to 1 in burst mode. (D) A normalized causal exponential profile, parameterized by a decay time τ . Evoked post-synaptic potential profiles are nothing but such causal convolution (using e.g. double-exponential kernels to capture the synaptic time-constant – weak delay – and potential decay). Similarly, spike trains representations using Fourier or Wavelet Transforms are intrinsically related to such convolutions.

tation metric: The codes are similar if the related continuous signals are similar. It allows us to link spike trains with a continuous signal s .

The so-called “kernel methods” based on the Mercer theorem (Schrauwen, 2007) are in direct links with the linear representation since they are defined, as scalar products, writing:

$$k(\mathcal{F}, \mathcal{F}') = \sum_i \sum_{n,m} \hat{K}_i(t_i^n - t_i^m) = \int_t s_i(t) s_i'(t) dt,$$

where \hat{K}_i is the corresponding Mercer’s Kernel, a symmetric function of $\mathcal{F}, \mathcal{F}'$. There is direct correspondences for usual kernels with linear convolutions, e.g.:

	Triangular	Exponential	Gaussian
$K_i(t)$	$\sqrt{\frac{\lambda}{2}} \mathcal{H}\left(t\left(\frac{\lambda}{2} - t\right)\right)$	$\sqrt{2\lambda} \mathcal{H}(t) e^{-\lambda t}$	$\sqrt{\frac{2\lambda}{\sqrt{\pi}}} e^{-2\lambda^2 t^2}$
$\hat{K}_i(d)$	$\max\left(1 - \frac{\lambda}{2} d , 0\right)$	$e^{-\lambda d }$	$e^{-\lambda^2 d^2}$

where \mathcal{H} is the Heaviside function. Distances based on inter-spike intervals are also included, as developed in e.g. Kreuz et al. (2007).

Non static kernels of the form $K_i^t(t - t_i^n)$ (i.e. depending on t) can also be used (clock-dependent coding, raster, 1st spike coding, etc.), while non-linear Volterra series are useful for representing “higher order” phenomena (see e.g. Rieke et al., 1996).

These linear representations not only provide tools to compare different spike trains, but also help to better understanding the link between continuous signals and spike times. For instance (Dayan and Abbott, 2001; Maass, 1997a), writing $s(t) = \sum_i \lambda_i s_i(t)$ is a mean to define some network readout to link spiking networks to “analog” sensory-motor tasks. Let us illustrate this aspect by the following results.

7.2. The link with raster representation

A step further, it is easy to see that representing the spike time by a raster, as defined previously, corresponds to a non-stationary convolution kernel.

A given raster can be represented by a real number in $[0, 1]$, the binary representation of its decimal part being the spike train itself. Using this representation, a useful related metric is of the form, for $\theta \in]0, 1[$:

$$d_\theta(\omega, \omega') = \theta^T, T = \operatorname{argmax}_t \omega^t = \omega'^t,$$

thus capturing the fact that two rasters are equal up to a certain rank. Such metrics can be applied to analyze the dynamics of spiking neuron networks and they are typically used in the context of symbolic coding in dynamical systems theory (Cessac, 2008; Cessac et al., 2008).

7.3. Kernel identification

Given a causal signal \bar{s}_i generated by a spike train \mathcal{F}_i at the unit level, the problem of identifying the related kernel is formally solved by the following paradigm:

$$\min_{K_i} \int_{t>0} |s_i(t) - \bar{s}_i(t)|^2 dt \equiv \int_{\lambda} |K_i(\lambda)\rho_i(\lambda) - \bar{s}_i(\lambda)|^2 d\lambda,$$

using the Laplace transform Parseval theorem (here, λ is the Laplace domain variable and $K_i(\lambda)$, $\rho_i(\lambda)$ are the Laplace transforms of the corresponding function), thus:

$$K_i(\lambda) = [\bar{s}_i(\lambda)\rho_i(\lambda)^T][\rho_i(\lambda)\rho_i(\lambda)^T]^{-1}$$

i.e. the spike train cross-correlation versus auto-correlation ratio. Non-causal estimation would consider the Fourier transform instead. This setting corresponds to several identification methods (Dayan and Abbott, 2001; Schrauwen, 2007).

The paradigm has to be used, for instance, for identifying the average synaptic response profile from the observation of the input spike train and synaptic evoked potential output. Given the observation of a spike train function ρ_i and the related response \bar{s}_i , the related kernel may be estimated from the previous formula.

7.4. Spike deconvolution

A step further, if the convolution kernel K_i is known analytically, it is obvious to formally write $\rho_i = L_i * s_i$ with $L_i = F^{-1} \left[\frac{1}{F[K_i]} \right]$, writing $F[\cdot]$ the Fourier transform e.g. for synaptic responses:

$$K_i(t) = e^{-t} \rightarrow (L_i * s_i)(t) = \frac{1}{\tau} s(t) + s'(t)$$

$$K_i(t) = \frac{t}{T} e^{-t} \rightarrow (L_i * s_i)(t) = \frac{1}{\tau^2} s(t) + \frac{2}{\tau} s'(t) + s''(t)$$

that is well-defined. Then the spike train can be easily reconstructed from the continuous signal, as illustrated in Fig. 6.

The good news is that the inverse convolution filters L_i are not singular so that the deconvolution is well-defined and in explicit form. However, this requires the use of derivative filters, known as being sensible to noise. Unpublished numerical investigations have shown that as soon as the error on the kernel profiles is higher than 10–20%, several spikes are lost in the deconvolution.

7.5. Signal reconstruction

In order to further understand the power of representation of spike trains, Lazar (2005) has generalized the well-known Shannon's theorem, as follows: A frequency range $[-\Omega, \Omega]$ signal is entirely defined by irregular sampling values s_i^n at spike times t_i^n

$$s_i(t) = \sum_n K_i^n(t - t_i^n)$$

with

$$K_i^n(t) = s_i^n \frac{\sin(\Omega t)}{\pi t},$$

provided that $\max_n d_i^n \leq \frac{\pi}{\Omega}$, where d_i^n is the inter-spike interval.

This supplies an explicit signal “decoding”, since given any signal s it provides an explicit formula to represent this signal by a convolution kernel K and a spike train.

8. Implementing spiking neuron networks

The main objective is now to capitalize on the previous statements for giving tracks for explicitly programming spiking neuron network parameters in order to obtain a given input/output relation. After a reminder on some theoretical results proving that

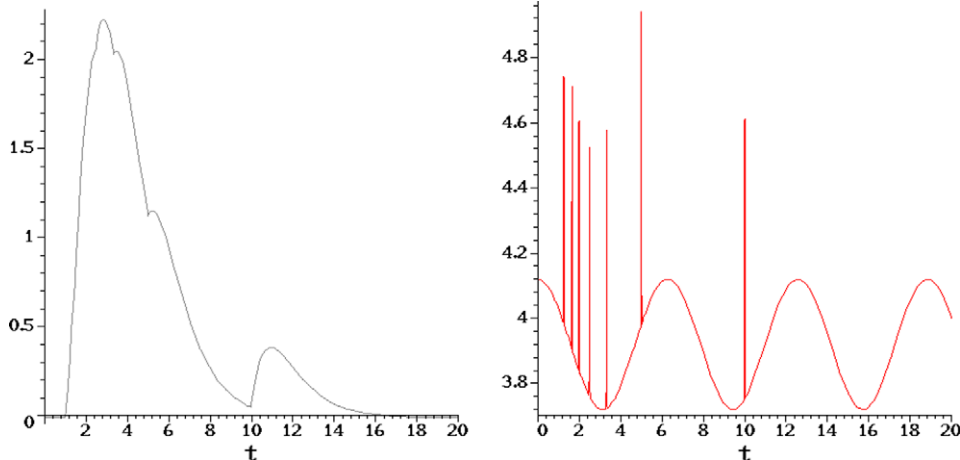


Fig. 6. A small experiment of spike deconvolution. Left: The signal is the convolution of a spike train using an $\alpha(t) = t/\tau e^{-t/\tau}$ profile, with addition of additive Gaussian noise (20% magnitude w.r.t. to the signal) and of a spurious sinusoid which has been added as an outlier to the signal. Spikes are not “visible” in the sense that they do not correspond to maxima of the signal because the spike responses are mixed. Right: The deconvolution is shown: The outlier is amplified, but spikes clearly emerge from the signal.

spiking neuron networks are computationally powerful in many ways, we discuss how, in our framework, the fact of introducing a metric makes possible to design new effective mechanisms based on variational methods for defining the network behavior.

8.1. Calculability of neural networks

Let us now consider the *calculability* of neuron network models. It is known that recurrent neuron networks based on rate coding are universal approximators (Schäfer and Zimmermann, 2006), as multi-layer feed-forward networks are (Hornik et al., 1989). This means that neuron networks are able also to simulate dynamical systems, not only to approximate measurable functions on a compact domain, as originally stated (see, e.g., Schäfer and Zimmermann (2006) for a detailed introduction on these notions). Spiking neuron networks have been proved to be also universal approximators (Maass, 2001). See Paugam-Moisy and Bohte (2010) for a review on calculability and learnability results for spiking neuron networks.

8.2. Learning the parameters of a spiking neuron network

In a biological context, learning is mainly related to synaptic plasticity (Gerstner and Kistler, 2002b; Cooper et al., 2004) and STDP (see e.g., Toyozumi et al. (2007) for a recent formalization), as far as spiking neuron networks are concerned. This unsupervised learning mechanism is known to reduce the variability of neuron responses (Bohte and Mozer, 2007) and related to the maximization of information transmission (Toyozumi et al., 2005) and mutual information (Chechik, 2003). It has also other interesting computational properties such as tuning neurons to react as soon as possible to the earliest spikes, or segregate the network response in two classes, depending on the input to be discriminated, and more general structuring effect such as the emergence of an orientation selectivity (Guyonneau et al., 2004).

In the present study, the point of view is quite different: We consider supervised learning while, since “each spike may matter” (Guyonneau et al., 2004; Delorme et al., 2001), we want not only to statistically reproduce the output spike-timing pattern, but also to reproduce events, either approximately or even exactly.

The motivation to explore this track is twofold. On the one hand we want to better understand what can be learned at a theoretical level by spiking neuron networks, by tuning weights and delays. The key point is the non-learnability of spiking neurons (Maass and Schmitt, 1999; Šíma and Sgall, 2005), since it is proved that the problem is NP-complete, when considering the estimation of both weights and delays. Here we show that we can “elude” this caveat and propose an alternate efficient estimation, inspired by biological models.

We also have to notice that the same restriction not only applies to simulation but also, as far as this model is biologically plausible, holds at the biological level. It is thus an issue to wonder if, in biological neuron networks, delays are really estimated during learning processes, or if a weaker form of weight adaptation, as developed now, is considered.

On the other hand, the computational use of spiking neuron networks in the framework of reservoir computing or beyond (Schrauwen, 2007), as far as applications using such network are concerned, requires efficient tuning methods not only in “average”, but in the deterministic case.

8.3. Weight training from spike times

As a first illustration, let us review Schrauwen (2007) and consider a SRM₀ neuron, with a simplified equation (only the last spike of neuron N_i , no external current):

$$V_i(t) = v(t - t_i^{n-1}) + \sum_{jm} w_{ij} \alpha(t - t_j^m) \quad \text{for } t_i^{n-1} < t \leq t_i^n,$$

the spike time being defined by $V_i(t_i^n) = \theta$, where θ is the spiking threshold.

Previous metrics on spike times give us a way to optimize the neural weights in order to tune spike times, deriving, e.g., rules of the form:

$$\Delta w_{ij} \equiv \sum_n (t_i^n - \bar{t}_i^n) \frac{\partial V_i}{\partial w_{ij}}(t_i^n) / \frac{\partial V_i}{\partial t_i^n}(t_i^n).$$

Such mechanisms of optimization are also applicable to time-constants, delays or thresholds. Unfortunately, the method cannot be easily used in practice, since the equation is numerically unstable (Schrauwen, 2007). However, spike train metrics leads to the formalization of such adaptation rules, in order to “compute with spikes”.

8.4. Weak estimation of delayed network parameters

As pointed out previously, the non-learnability of spiking neurons is known (Maass and Schmitt, 1999; Šíma and Sgall, 2005), i.e. the previous estimation is proved to be NP-complete. This means that in order to “learn” the proper parameters we would have to “try all possible combinations of delays”. This is intuitively due to the fact that each delay has no “smooth” effect on the dynamics but may change the whole dynamics in an unpredictable way.

This is the way proposed to elude this NP-complete problem by considering *another* estimation problem. Here we do not estimate *one* delay (for each synapse) but consider connection weights at several delays and then estimate a balancing of their relative contribution. This means that we consider a *weak* delay estimation problem.

The alternative approach is to estimate delayed weights, i.e. a quantitative weight value W_{ijd} at each delay $d \in \{1, D\}$, using e.g. a model of the form:

$$V_i[k] = \gamma_i V_i[k-1](1 - Z_i[k-1]) + \sum_{j=1}^n \sum_{d=1}^D W_{ijd} Z_j[k-d] + I_{ik}.$$

where $V_i[k]$ stands for the i th neuron potential, at the discrete time k , γ_i is a leak, $Z_i[k] = 1$ if the neuron fires, else 0 and I_{ik} is an additional current. This form of equation is directly related to the piece of theory reviewed in Section 5. It is now reused, not at a theoretical level, but at a computational level.

Obviously, the case where there is a weight W_{ij} with a corresponding delay $d_{ij} \in \{0, D\}$ is a particular case of considering several delayed weights, since we can write:

$$W_{ijd} = W_{ij} \delta(d - d_{ij}),$$

$\delta()$ being the Kronecker symbol in this case. In other words, with our weaker model, we are still able to estimate a neuron network with adjustable synaptic delays.

We thus do not restrain the neural network model by changing the problem, but we enlarge it. Actually, the present estimation gives a smooth approximation of the previous NP-complete problem.

It has been made explicit in Rostro-Gonzalez et al. (2009) that the parameter estimation of such a neural network in order to generate a given spike train, is a Linear (L) problem if the membrane potentials are observed, and a Linear Programming (LP) problem if only spike times are observed, with a glF model. Such L or LP adjustment mechanisms are distributed and have the same structure as an Hebbian rule. A step further, this paradigm is easily generalizable to the design of input–output spike train transforma-

tions. This means that a practical method is available to “program” a spiking neuron network, i.e. to find a set of parameters for exactly reproducing the network output, given an input.

Finally, we have shown, in a preliminary way, how the fact of introducing a metric in our framework makes possible to design new effective mechanisms based on variational methods in order to define the network behavior.

9. Conclusion

This article has proposed an overview of a set of indisputable facts that could help better understanding the extent to which computing and modeling with spiking neuron networks might be biologically plausible and computationally efficient. The links between spike trains and neural coding have been highlighted, with the help of several metrics and under a set of time constraints as hypotheses. Altogether, there are pragmatical and practical facts to better understand the extent to which computing and modeling using spiking neuron networks can be useful, and how to implement such networks in a pertinent way.

Probabilistic measures of spike patterns, such as correlations (Gerstner and Kistler, 2002b) or a more sophisticated formalism (Cessac et al., 2009b) related to entropy based pseudo-distances (e.g. mutual information) highlight a view of spike trains variability which is enriched by the information theory conceptual framework. Nevertheless, it may be difficult to estimate such measures in practice, since they are robust only if a large amount of samples is available. On the contrary, distances give a mean to characterize several aspects of spike coding, with efficient methods and without this curse of the sampling size.

The underlying hypothesis adopted here appears to be that “every spike may matter”. We know it is true in some biological contexts such as fast-brain mechanisms (Guyonneau et al., 2004; Delorme et al., 2001), or when observing sparse responses to natural stimuli (Baudot, 2007). Surprisingly it has been observed that such a sparse response indeed corresponds to a situation where the neural sub-system (the V1 area in this case) is not involved in an artificial paradigm, whereas submitted to a realistic stimulus. The meaning is not that all of this is limited to situations where all spikes are the same. On the contrary, the introduction of a metric allows to formalize the idea of “approximate” correspondences between two spike trains. This is a weaker notion than the probabilistic ones, but still useful.

Regarding *understanding spiking neuron networks*, as pointed out in the introduction, we are very cautious with respect to biological plausibility and prefer to simply consider that “a simulation is biologically plausible if it verifies an explicit set of constraints observed in biology”. This means that the causal associations enlightened by the simulation are consistent with the related existing biological knowledge. This is an humble position, but the key point is that such an approach is still interesting even if the results that are produced this way remain falsifiable. Several facts proposed in the present overview verify this assertion: for instance, the maximal amount of information in a spike is lower than the proposed bound. Would it be not the case, the assumptions would have to be reworked. Another key point is that, for the class of models under consideration, the orbits are periodic. This is indeed questionable, but facts are stubborn, and this result shows how the related spiking neuron models with constant reset are limited (see Kirst et al. (2009) for a recent investigation on this point).

A step further, in a nutshell, this review has proposed to consider that “choosing a neural coding” means “defining a metric”. This point of view has provided the reader with a synthetic insight of several methods applied to spiking neuron networks, from links

between spike trains and continuous signals to advice for programming spiking neuron networks. To the best of our knowledge, only polychronization mechanisms are not easily representable with the tools we made use of, and it would be an interesting issue to study the link between these non-local temporal interactions inside spiking neuron networks and the underlying neural code.

Acknowledgments

Partially supported by the ANR MAPS and the MACCAC ARC projects.

References

- Amitai, Y., Gibson, J., Beirleiner, M., Patrick, S., Ho, A., Connors, B.W., Golomb, D., 2002. The spatial dimensions of electrically coupled networks of interneurons in neocortex. *Journal of Neuroscience* 22, 4142–4152.
- Aronov, D., 2003. Fast algorithm for the metric-space analysis of simultaneous responses of multiple single neurons. *Journal of Neuroscience Methods* 124 (2).
- Baudot, P., 2007. Nature is the code: high temporal precision and low noise in v1. Ph.D. Thesis.
- Bohte, S.M., Mozer, M.C., 2007. Reducing the variability of neural responses: a computational theory of spike-timing-dependent plasticity. *Neural Computation* 19 (2), 371–403.
- Brette, R., Gerstner, W., 2005. Adaptive exponential integrate-and-fire model as an effective description of neuronal activity. *Journal of Neurophysiology* 94, 3637–3642.
- Brette, R., Rudolph, M., Carnevale, T., Hines, M., Beeman, D., Bower, J.M., Diesmann, M., Morrison, A., Goodman Jr., P.H., Harris, F.C., Zirpe, M., Natschläger, T., Pecevski, D., Ermentrout, B., Djurfeldt, M., Lansner, A., Rochel, O., Vieville, T., Muller, E., Davison, A.P., Boustani, S.E., Destexhe, A., 2007. Simulation of networks of spiking neurons: a review of tools and strategies. *Journal of Computational Neuroscience* 23 (3), 349–398.
- Burnod, Y., 1993. *An Adaptive Neural Network: The Cerebral Cortex*, second ed. Masson, Paris.
- Camera, G.L., Giugliano, M., Senn, W., Fusi, S., 2008a. The response of cortical neurons to in vivo-like input current: theory and experiment. *Biological Cybernetics* 99 (4–5), 279–301.
- Camera, G.L., Giugliano, M., Senn, W., Fusi, S., 2008b. The response of cortical neurons to in vivo-like input current: theory and experiment: II. Time-varying and spatially distributed inputs. *Biological Cybernetics* 99 (4–5), 303–318.
- Carandini, M., Ferster, D., 2000. Membrane potential and firing rate in cat primary visual cortex. *The Journal of Neuroscience* 20 (1), 470–484.
- Carandini, M., Demb, J.B., Mante, V., Tollhurst, D.J., Dan, Y., Olshausen, B.A., Gallant, J.L., Rust, N.C., 2005. Do we know what the early visual system does? *Journal of Neuroscience* 25 (46), 10577–10597.
- Cessac, B., 2008. A discrete time neural network model with spiking neurons. Rigorous results on the spontaneous dynamics. *Journal of Mathematical Biology* 56 (3), 311–345.
- Cessac, B., Viéville, T., 2008. On dynamics of integrate-and-fire neural networks with adaptive conductances. *Frontiers in neuroscience* 2 (2).
- Cessac, B., Rochel, O., Viéville, T., 2009a. Introducing numerical bounds to improve event-based neural network simulations. Tech. Rep. RR-6924, INRIA, HAL.
- Cessac, B., Rostro-Gonzalez, H., Vasquez, J., Viéville, T., 2009b. How gibbs distribution may naturally arise from synaptic adaptation mechanisms: a model based argumentation. *Journal of Statistical Physics* 136 (3), 565–602.
- Chechik, G., 2003. Spike-timing-dependent plasticity and relevant mutual information maximization. *Neural Computation* 15 (7), 1481–1510.
- Cooper, L., Intrator, N., Blais, B., Shouval, H., 2004. *Theory of Cortical Plasticity*. World Scientific Publishing.
- Cronin, J., 1987. *Mathematical Aspects of Hodgkin–Huxley Theory*. Cambridge University Press.
- Crook, S., Ermentrout, G., Bower, J., 1998. Spike frequency adaptation affects the synchronization properties of networks of cortical oscillations. *Neural Computation* 10 (4).
- Dayan, P., Abbott, L.F., 2001. *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. MIT Press.
- Delorme, A., Perrinet, L., Thorpe, S., 2001. Network of integrate-and-fire neurons using rank order coding b: spike timing dependant plasticity and emergence of orientation selectivity. *Neurocomputing* 38, 539–545.
- Destexhe, A., 1997. Conductance-based integrate and fire models. *Neural Computation* 9, 503–514.
- Destexhe, A., Rudolph, M., Paré, D., 2003. The high-conductance state of neocortical neurons in vivo. *Nature Reviews Neuroscience* 4, 739–751.
- Fitzgibbon, W., Parrott, M., You, Y., 1996. Finite dimensionality and upper semicontinuity of the global attractor of singularly perturbed Hodgkin–Huxley systems. *Journal of Differential Equations* (1).
- Frégnac, Y., 2003. Association field in visual cortical neurons: from subthreshold visual synaptic integration to apparent-motion perception. In: *European Conference on Visual Perception*, Paris.

- Frégnac, Y., 2004. From synaptic rumours to low-level perception: an intracellular view of visual cortical dynamics. *Progress in Biochemistry and Biophysics* 31, 6–8.
- Galarreta, M., Hestrin, S., 2001. Electrical synapses between gaba-releasing interneurons. *Nature Reviews Neuroscience* 2, 425–433.
- Gautrais, J., Thorpe, S., 1998. Rate coding vs. temporal order coding : a theoretical approach. *Biosystems* 48, 57–65.
- Gerstein, G.L., Mandelbrot, B., 1964. Random walk models for the spike activity of a single neuron. *Biophysical Journal* 4, 41–68.
- Gerstner, W., Kistler, W., 2002a. *Spiking Neuron Models*. Cambridge University Press.
- Gerstner, W., Kistler, W.M., 2002b. Mathematical formulations of Hebbian learning. *Biological Cybernetics* 87, 404–415.
- Gray, C.M., Singer, W., 1989. Stimulus specific neuronal oscillations in orientation columns of cat visual cortex. *Proceedings of the National Academy of Sciences USA* 86, 1698–1702.
- Guyonneau, R., vanRullen, R., Thorpe, S., 2004. Temporal codes and sparse representatives. *Journal of Physiology (Paris)* 98 (4–8), 487–497.
- Hodgkin, A., Huxley, A., 1952. A quantitative description of membrane current and its application to conduction and excitation in nerve. *Journal of Physiology* 117, 500–544.
- Hornik, K., Stinchcombe, M., White, H., 1989. Multilayer feedforward networks are universal approximators. *Neural Networks* 2, 359–366.
- Izhikevich, E., 2003. Simple model of spiking neurons. *IEEE Transactions on Neural Networks* 14 (6), 1569–1572.
- Izhikevich, E., 2004. Which model to use for cortical spiking neurons? *IEEE Transactions on Neural Networks* 15 (5), 1063–1070.
- Izhikevich, E.M., 2007. *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting*. The MIT Press.
- Jaeger, H., 2003. Adaptive nonlinear system identification with Echo State Networks. In: Becker, S., Thrun, S., Obermayer, K. (Eds.), *NIPS*2002, Advances in Neural Information Processing Systems*, vol. 15. MIT Press, pp. 593–600.
- Katok, A., Hasselblatt, B., 1998. *Introduction to the Modern Theory of Dynamical Systems*. Kluwer.
- Kirst, C., Geisel, T., Timme, M., 2009. Sequential desynchronization in networks of spiking neurons with partial reset. *Physical Review Letters* 102 (068101).
- Koch, C., 1999. *Biophysics of Computation: Information Processing in Single Neurons*. Oxford University Press, New York.
- Koch, C., Segev, I. (Eds.), 1998. *Methods in Neuronal Modeling: From Ions to Networks*. The MIT Press.
- Kreuz, T., Haas, J.S., Morelli, A., Abarbanel, H.D., Politi, A., 2007. Measuring spike train synchrony and reliability. In: *Computational Neurosciences meeting (CNS)*.
- Lazar, A., 2005. Multichannel time encoding with integrate-and-fire neurons. *Neurocomputing* 65, 401–407.
- Lewis, T.J., Rinzel, J., 2003. Dynamics of spiking neurons connected by both inhibitory and electrical coupling. *Journal of Computational Neuroscience* 14 (3), 283–309.
- Maass, W., 1997a. Fast sigmoidal networks via spiking neurons. *Neural Computation* 9, 279–304.
- Maass, W., 1997b. Networks of spiking neurons: the third generation of neural network models. *Neural Networks* 10, 1659–1671.
- Maass, W., 2001. On the relevance of time in neural computation and learning. *Theoretical Computer Science* 261, 157–178 (extended version of ALT'97, in *LNAI* 1316, 364–384).
- Maass, W., 2009. Motivation, theory, and applications of liquid state machines. In: Cooper, B., Sorbi, A. (Eds.), *Computability in Context: Computation and Logic in the Real World*. Imperial College Press.
- Maass, W., Bishop, C.M. (Eds.), 2003. *Pulsed Neural Networks*. MIT Press.
- Maass, W., Natschläger, T., 1997. Networks of spiking neurons can emulate arbitrary hopfield nets in temporal coding. *Neural Systems* 8 (4), 355–372.
- Maass, W., Schmitt, M., 1999. On the complexity of learning for spiking neurons with temporal coding. *Information and Computation* 153, 26–46.
- Maass, W., Natschläger, T., Markram, H., 2002. Real-time computing without stable states: a new framework for neural computation based on perturbations. *Neural Computation* 14 (11), 2531–2560.
- Mainen, Z., Sejnowski, T., 1995. Reliability of spike timing in neocortical neurons. *Science* 268 (5216), 1503–1506.
- Markram, H., Lübke, J., Frotscher, M., Sakmann, B., 1997. Regulation of synaptic efficacy by coincidence of postsynaptic ap and epsp. *Science* 275 (213).
- Martinez, R., Paugam-Moisy, H., 2008. Les groupes polychrones pour capturer l'aspect spatio-temporel de la mémorisation. In: Perrinet, L., Dauce, E. (Eds.), *Proc. of the 2nd French Conference on Computational Neuroscience*, Marseille, pp. 265–268. <<http://2008.neurocomp.fr>>.
- McCormick, D.A., Bal, T., 1997. Sleep and arousal: thalamocortical mechanisms. *Annual Review of Neuroscience* 20, 185–215.
- Meunier, D., Paugam-Moisy, H., 2008. Neural networks for computational neuroscience. In: *Proc. of European Symp. On Artificial Neural Networks – ESANN'2008*. *Advances in Computational Intelligence and Learning*, pp. 367–378.
- Morrison, A., Mehring, C., Geisel, T., Aertsen, A., Diesmann, M., 2005. Advancing the boundaries of high connectivity network with distributed computing. *Neural Computation* 17 (8), 1776–1801.
- Mouraud, A., Paugam-Moisy, H., Puzenat, D., 2006. A distributed and multithreaded neural event-driven simulation framework. In: *Int. Conf. on Parallel and Distributed Computing and Networks*. ACTA Press, pp. 393–398.
- Par, D., Bouhassira, D., Oakson, G., Datta, S., 1990. Spontaneous and evoked activities of anterior thalamic neurons during waking and sleep states. *Experimental Brain Research* 80 (1).
- Paugam-Moisy, H., Bohte, S., 2010. Computing with spiking neuron networks. In: Rozenberg, G., Back, T., Kok, J. (Eds.), *Handbook of Natural Computing*. Springer-Verlag.
- Paugam-Moisy, H., Martinez, R., Bengio, S., 2008. Delay learning and polychronization for reservoir computing. *Neurocomputing* 71, 1143–1158.
- Pfister, J.-P., Gerstner, W., 2006. Triplets of spikes in a model of spike timing-dependent plasticity. *Journal of Neuroscience* 26, 9673–9682. <<http://icwww.epfl.ch/gerstner/PUBLICATIONS/Pfister06b.pdf>>.
- Politi, A., Torcini, A., 2009. Stable chaos. <<http://lanl.arxiv.org/abs/0902.2545>>.
- Rauch, A., La Camera, G., Luscher, H.-R., Senn, W., Fusi, S., 2003. Neocortical pyramidal cells respond as integrate-and-fire neurons to in vivo-like input currents. *Journal of Neurophysiology* 90 (3), 1598–1612.
- Rieke, F., Warland, D., de Ruyter van Steveninck, R., Bialek, W., 1996. *Spikes, Exploring the Neural Code*. The MIT Press.
- Rostro-Gonzalez, H., Cessac, B., Vasquez, J.C., Viéville, T., 2009. Back-engineering of spiking neural networks parameters. In: *Computational Neurosciences Meeting (CNS)*.
- Rudolph, M., Destexhe, A., 2007. How much can we trust neural simulation strategies? *Neurocomputing* 70 (10), 1966–1969.
- Schäfer, A.M., Zimmermann, H.G., 2006. Recurrent neural networks are universal approximators. *Lecture Notes in Computer Science* 4131, 632–640. <<http://www.springerlink.com/content/5635187408g7k2x3/fulltext.pdf>>.
- Schrauwen, B., 2007. *Towards applicable spiking neural networks*. Ph.D. Thesis, Universiteit Gent, Belgium.
- Shadlen, M.N., Newsome, W.T., 1994. Noise, neural codes and cortical organization. *Current Opinion in Neurobiology* 4 (4), 569–579. <<http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=owner&owner=jtouboul>>.
- Šima, J., Spall, J., 2005. On the nonlearnability of a single spiking neuron. *Neural Computation* 17 (12), 2635–2647.
- Simoncelli, E., Olshausen, B., 2001. Natural image statistics and neural representation. *Annual Review of Neuroscience* 24 (1), 1193–1216.
- Stein, R.B., 1965. A theoretical analysis of neuronal variability. *Biophysics Journal* 5, 173–194.
- Swadlow, H., 1985. Physiological properties of individual cerebral axons studied in vivo for as long as one year. *Journal of Neurophysiology* 54, 1346–1362.
- Swadlow, H., 1992. Monitoring the excitability of neocortical efferent neurons to direct activation by extracellular current pulses. *Journal of Neurophysiology* 68, 605–619.
- Thorpe, S., Fabre-Thorpe, M., 2001. Seeking categories in the brain. *Science* 291, 260–263.
- Thorpe, S., Delorme, A., VanRullen, R., 2001. Spike based strategies for rapid processing. *Neural Networks* 14, 715–726.
- Touboul, J., Brette, R., 2008. Dynamics and bifurcations of the adaptive exponential integrate-and-fire model. *Biological Cybernetics* 99 (4–5), 319–334. doi:10.1007/s00422-008-0267-4. PMID:19011921, <<http://www.ncbi.nlm.nih.gov/pubmed/19011921>>.
- Toyoizumi, T., Pfister, J.-P., Aihara, K., Gerstner, W., 2005. Generalized bienenstock-cooper-munro rule for spiking neurons that maximizes information transmission. *Proceedings of the National Academy of Science* 102, 5239–5244.
- Toyoizumi, T., Pfister, J.-P., Aihara, K., Gerstner, W., 2007. Optimality model of unsupervised spike-timing dependent plasticity: synaptic memory and weight distribution. *Neural Computation* 19, 639–671.
- Verstraeten, D., Schrauwen, B., Dhaene, M., Stroobandt, D., 2007. An experimental unification of reservoir computing methods. *Neural Networks* 20 (3), 391–403.
- Victor, J., 2005. Spike train metrics. *Current Opinion in Neurobiology* 15 (5), 585–592.
- Victor, J., Purpura, K., 1996. Nature and precision of temporal coding in visual cortex: a metric-space analysis. *Journal of Neurophysiology* 76, 1310–1326.
- Viéville, T., Crahay, S., 2004. Using an Hebbian learning rule for multi-class svm classifiers. *Journal of Computational Neuroscience* 17 (3), 271–287. <<http://journals.kluweronline.com/article.asp?PIPS=5384399>>.