

The Cauchy Problem for One-Dimensional Spiking Neuron Models

Romain Brette
Equipe Odysée (INRIA/ENS/ENPC),
Département d'Informatique,
Ecole Normale Supérieure,
45, rue d'Ulm,
F-75230 Paris Cedex 05, France.
`brette@di.ens.fr`

October 24, 2007

Abstract

I consider spiking neuron models defined by a one-dimensional differential equation and a reset — i.e., neuron models of the integrate-and-fire type. I address the question of the existence and uniqueness of a solution on \mathbb{R} for a given initial condition. It turns out that the reset introduces a countable and ordered set of backward solutions for a given initial condition. I discuss the implications of these mathematical results in terms of neural coding and spike timing precision.

Keywords: integrate-and-fire; Cauchy problem; spike timing precision; reliability; neuron models.

1 Introduction

The integrate-and-fire model was originally introduced by Lapique (1907) as a phenomenological description of the initiation of an action potential following current injection in a nerve. It consists of a simple linear electrical circuit and a threshold for spike initiation. Although the biophysics of action potential generation are known in much more details since the works of Hodgkin and Huxley (1952), variations of the integrate-and-fire model, also named *spiking neuron models* (Gerstner and Kistler, 2002), are still widely used in computational neuroscience, because of their relative simplicity. A

one-dimensional spiking neuron model is defined by a differential equation governing the dynamics of the membrane potential x :

$$\frac{dx}{dt} = f(x, t) \tag{1}$$

and a reset: when $x(t)$ reaches a threshold x_t (t for threshold, not to be confused with the time variable), then a spike is produced and $x(\cdot)$ is instantaneously reset to x_r . Up to a change of variables, one can set $x_t = 1$ and $x_r = 0$. The conditional reset makes this model a hybrid dynamical system. Surprisingly, we are still lacking some elementary mathematical information on this class of models. In particular, the question of whether there exists a unique solution for a given initial condition (the Cauchy problem) has never been answered. I will address this problem in this paper, starting with a few definitions. The present study only addresses one-dimensional models — higher-dimensional ones are important but much harder to tackle.

We assume that the differential equation (without reset) admits a flow on \mathbb{R} . I previously showed that two particular classes of spiking models have especially interesting properties (Brette and Guigon, 2003; Brette, 2004):

- *leaky models*, such that $\frac{\partial f}{\partial x} \leq \alpha < 0$;
- *reflecting models*, such that $f(0, t) > 0$ for all t .

Standard integrate-and-fire models are leaky (and $\frac{\partial f}{\partial x} = -g/C$, where g is the total conductance and C is the membrane capacitance), the quadratic model (Ermentrout and Kopell, 1986) is reflecting. In particular, these models have a unique firing rate (independent of initial condition). A typical integrate-and-fire model with synaptic conductances is governed by the following equation:

$$C \frac{dV}{dt} = -g_L(V - E_L) - \sum_i \sum_{t_i} g_i(t - t_i)(V - E_i)$$

which describes a leaky model (C is the membrane capacitance, V is membrane potential, g_L is the leak conductance, E_L is the leak reversal potential, i indexes the synapses, t_i indexes the timings of incoming spikes at synapse i , E_i is the reversal potential and $g_i(\cdot)$ is the post-synaptic conductance at synapse i).

An important mathematical object for these models is the *spike map* φ , which is defined such that a spike train produced by the model is the orbit of the first spike time under φ (Fig. 1). More precisely, $\varphi(t)$ is the minimal

$s \geq t$ such that the forward solution starting at $(t, 0)$ reaches 1 at time s . For leaky and reflecting models, the spike map is (strictly) increasing on its range but often discontinuous. General properties of the spike map are presented in more details in Brette (2004).

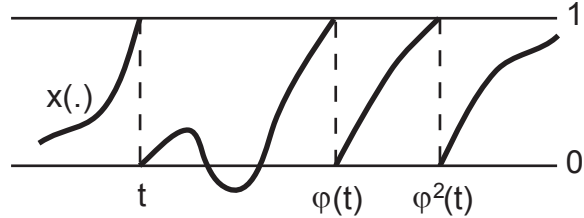


Figure 1: The spike map φ : $\varphi(t)$ is the time of the next spike for a trajectory starting from reset at time t .

Because equation (1) defines a flow, the spiking dynamical system always admits a semi-flow for positive time (i.e., unique forward solutions), but because of the resets, it may not admit a flow (i.e., unique solutions defined on \mathbb{R}). The question of existence and uniqueness of solutions on \mathbb{R} for a given initial condition (the Cauchy problem) is not only of mathematical interest, but it also has important implications in terms of neural coding. Indeed, consider that equation (1) reflects the synaptic integration of a number of input spike trains, which are then encoded in an output spike train via the reset mechanism (as in the example). The set of possible output spike trains in response to the given input spike trains corresponds to the set of solutions defined on \mathbb{R} (Fig. 2). In section 2, I solve the Cauchy problem by describing the structure of backward spiking trajectories. In section 3, I argue that the set of meaningful solutions on \mathbb{R} is in general not very large and I conjecture that for random realizations of input spike trains, the spiking dynamical system actually defines a single-valued function *input spike trains* \mapsto *output spike train*.

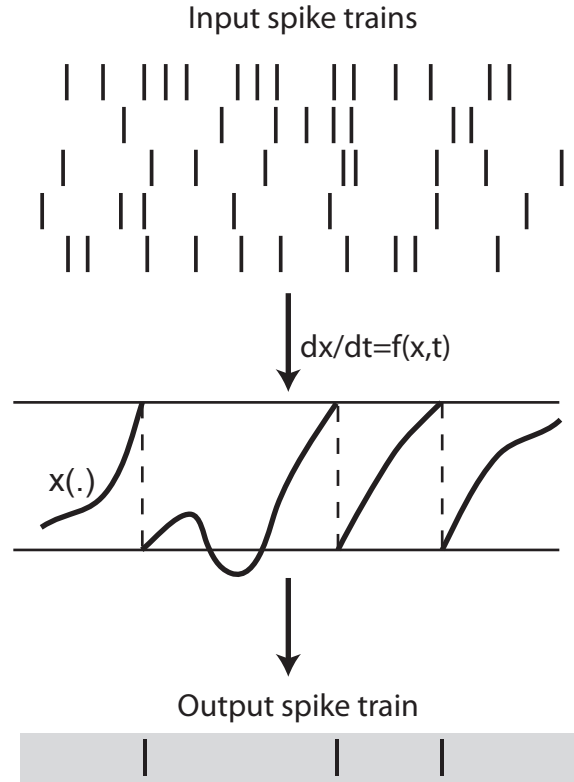


Figure 2: Encoding of input spike trains into a spiking output by an integrate-and-fire model. The output is defined via a differential equation and thus, depend on the initial state.

2 The Cauchy problem

Existence

Let us consider the set \mathcal{S} of solutions $x(\cdot)$ of the spiking dynamical system defined on \mathbb{R} , i.e.,

$$\mathcal{S} = \left\{ x(\cdot) \in X \mid \begin{array}{l} \forall t, \quad x(t) = 1 \Rightarrow x(t^+) = 0 \\ \text{and } x(t) \neq 1 \Rightarrow \frac{dx}{dt}(t) = f(x, t) \end{array} \right\}$$

where X is the set of right-continuous real functions. In the following, we assume that any finite interval contains a finite number of discontinuities (spikes), which is the case for example if f is bounded on compact sets (e.g., continuous)¹. We examine the solutions $x(\cdot) \in \mathcal{S}$ that satisfy a given initial condition $x(t_0) = x_0$. By construction, there is a unique solution on $[t_0, +\infty[$, which we shall call the *forward solution*². However, a backward solution on $] - \infty, t_0]$ does not necessarily exist. For example, consider the (continuous) solution $u(\cdot)$ to equation (1) such that $u(t_0) = x_0$; if there is an $s < t_0$ such that $u(s) = 1$ and $u(t) > 0$ on $[s, t_0]$, then clearly there can be no backward solution, and thus no solution on \mathbb{R} (Fig. 3A). The following theorem makes this remark more precise:

Theorem 1 (Existence). *Let (x_0, t_0) be an initial condition ($x_0 < 1$) and let $u(\cdot)$ be the (non-spiking) solution to equation (1) such that $u(t_0) = x_0$. There is a solution to the spiking dynamical system on \mathbb{R} with initial condition (x_0, t_0) if and only if $u(t) < 1$ for all $t < t_0$.*

Theorem 1 holds for any one-dimensional model (even non leaky and non reflecting).

Proof. If $u(\cdot)$ is such that $u(t) < 1$ for all $t < t_0$, then it is an admissible spiking solution on \mathbb{R} , therefore there is a spiking solution on \mathbb{R} . Assume there is $t_1 < t_0$ such that $u(t_1) = 1$, and suppose there is a spiking solution $x(\cdot)$ on \mathbb{R} such that $x(t_0) = x_0 = u(t_0)$ (Fig. 3B). On any interval where $x(\cdot)$ is continuous, the sign of $x(\cdot) - u(\cdot)$ cannot change, since trajectories cannot cross. When a spike occurs at time t , the difference changes by one: $(x(t^+) - u(t^+)) = (x(t) - u(t)) - 1$. It follows that at time t_1 , the value of $x(t_1)$ is at least $u(t_1) = 1$ plus the number of spikes in $[t_1, t_0]$, therefore

¹Consider a point t_1 such that $x(t_1) = 1$, and let $t_0 = \{\sup t < t_1 | x(t^+) = 0\}$. Because $x(\cdot)$ is right-continuous, we must have $t_0 < t_1$ (otherwise $x(t_1) = 0$). It follows that $x(\cdot)$ satisfies the differential equation in $]t_0, t_1[$, which implies that there is $x_0 \in [0, 1]$ and $t \in]t_0, t_1[$ such that $f(x, t) \geq 1/(t_1 - t_0)$. It follows that if the set $\{t \in [a, b] | x(t) = 1\}$ ($[a, b]$ is a given finite interval) has a cluster point then there is a sequence of points (x_n, t_n) in $[0, 1] \times [a, b]$ such that $f(x_n, t_n)$ tends to infinity.

²The uniqueness property comes from the fact that the differential equation defines a flow on \mathbb{R} : indeed suppose there are two different forward solutions $x_1(\cdot)$ and $x_2(\cdot)$ with identical initial conditions, and let $t^* = \sup\{t \geq t_0 | x_1(t) = x_2(t)\}$. Because of the flow property, t^* must be a discontinuity point for at least one of the solutions, so that $x_1(t^*) = x_2(t^*) = 1$. By construction, this must be a discontinuity point for both solutions, i.e., we must have $x_1(t^{*+}) = x_2(t^{*+}) = 0$, which is contradictory with the definition of t^* . This may not happen for backward solutions because $x(t^+) = 0$ implies either $x(t) = 1$ or $x(t) = 0$ (not only the former assertion).

$x(t_1) > 1$, which is a contradiction. Thus there can be no spiking solution $x(\cdot)$. \square

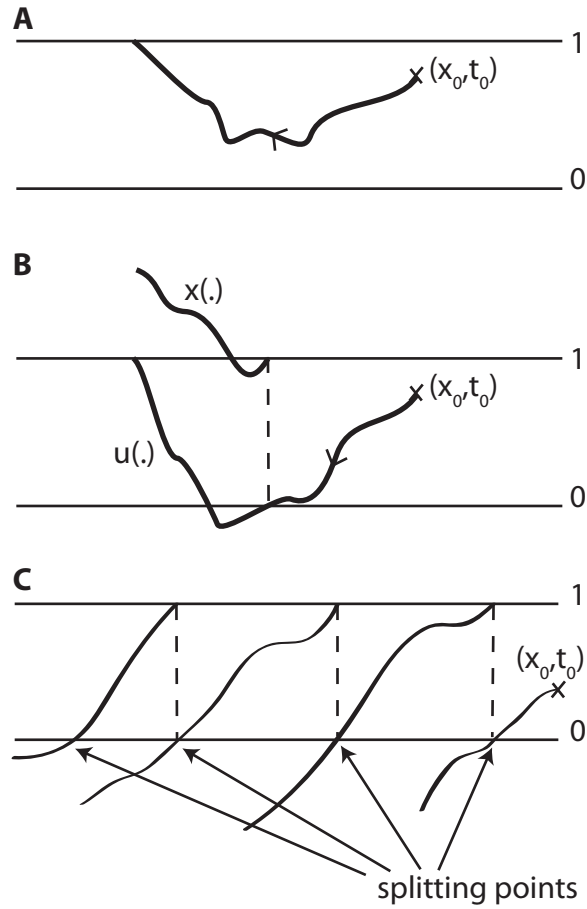


Figure 3: Backward solutions. A. Case with no backward solution from (x_0, t_0) . B. Graphical proof of theorem 1. C. Construction of backward trajectories by splitting at reset.

Structure of the set of solutions

When a backward solution exists, it is in general not unique. A construction of a set of backward solutions is sketched in Fig. 3C: every time a back-

ward trajectory reaches 0, it can split between a continuous and a spiking trajectory. The following theorem makes this statement more precise:

Theorem 2 (Structure of solutions on \mathbb{R}). *Assume the model is leaky or reflecting. Let (x_0, t_0) be an initial condition ($x_0 < 1$). There is a countable set of solutions to the spiking dynamical system on \mathbb{R} satisfying the initial condition. Let $N \in \mathbb{N} \cup \{\infty\}$ be the number of solutions. There is a decreasing sequence of times $s_{N-1} < \dots < s_2 < s_1 \leq t_0$ such that the set of spike times of every backward solution is $\{s_k, \dots, s_2, s_1\}$ for some $k \leq N - 1$.*

The integer N is called the degree of the initial condition (x_0, t_0) , and the solution with $N - 1$ spikes is called the maximal solution.

Note that a solution to a spiking dynamical system is uniquely defined by its set of spike times. We may rephrase theorem 2 as follows: if A and B are the sets of spike times of two spiking solutions with the same initial condition and $\inf A \leq \inf B$, then $B = A \cap [\inf B, +\infty[$.

Proof. Consider two spiking solutions $x(\cdot)$ and $y(\cdot)$ on \mathbb{R} such that $x(t_0) = y(t_0) = x_0$. We first note that if $x(t_1) = y(t_1)$ at some time t_1 , then the two solutions coincide on $[t_1, +\infty[$. Define $t_1 = \inf\{t \in \mathbb{R}, x(t) = y(t)\}$. One of the solutions must spike at time t_1 , say $x(\cdot)$, so that $x(t_1) = 1$ and $y(t_1) = x(t_1^+) = 0$. We will now consider the two hypotheses and show that $y(\cdot)$ can have no spike before t_1 .

Suppose the model is reflecting. Then the continuous solution $v(\cdot)$ such that $v(t_1) = y(t_1)$ is such that $v(t) < 0$ for all $t < t_1$, so that $y(\cdot)$ can have no spike before t_1 and coincides with $v(\cdot)$ on $] - \infty, t_1]$.

Suppose the model is leaky. We have $x(t_1) - y(t_1) = 1$. Suppose $y(\cdot)$ spikes before t_1 and let t_2 be the time of the last spike before t_1 . Because of the leak hypothesis, we must have $x(t_2^+) - y(t_2^+) > x(t_1) - y(t_1)$, i.e., $x(t_2^+) > 1$, which is impossible.

It follows that the set of solutions is totally ordered with respect to the inclusion of their sets of spike times, so that the number of (backward) spikes uniquely characterizes the solution. The existence of all intermediate numbers of spikes follows from theorem 1 (there is a continuous backward solution starting from every $(1, t_s)$ where t_s is a spike time of a spiking solution, such that $u(t) < 1$ for all $t < t_s$). The set of solutions can be constructed as follows: start from (x_0, t_0) and follow the differential equation backward until $x(t) = 0$ and the initial condition $(1, t)$ satisfies theorem 1. The continuous solution with initial condition $(0, t)$ is the spiking solution with one (backward) spike; continuing the solution $x(\cdot)$ from $(1, t)$ and reit-

erating the process gives spiking solutions with successive numbers of spikes (as shown in figure 3C). \square

Bounded solutions

A physiologically meaningful solution should be bounded, since the membrane potential is constrained by the reversal potentials of ions. We shall define a model as *silent* before some time t_0 if no solution on \mathbb{R} can spike before t_0 (in some sense, the stimulation starts after t_0). For non-silent models, the physiologically realistic solutions are the solutions with infinitely many spikes on \mathbb{R}^- :

Proposition 1 (Bounded solutions). *We assume the model is leaky and f is bounded. Then a solution is bounded if and only if it has infinitely many spikes on \mathbb{R}^- , unless the model is silent before some time t_0 . Consequently, there is a bounded solution on \mathbb{R} with initial condition (x_0, t_0) if and only if the condition has infinite degree.*

Thus, for a given equation (1), i.e., for a given set of inputs, the set of solutions with infinitely many spikes on \mathbb{R}^- defines the possible outputs of the neuron model. It follows from theorem 2 that, under the assumptions of the proposition above, there is at most one bounded spiking solution on \mathbb{R} for any given initial condition.

Proof. Consider a spiking solution $x(\cdot)$ with finitely many spikes on \mathbb{R} , so that there is no spike before t_0 . Since the model is not silent, some solution spikes at time $t_1 < t_0$. It follows from theorem 1 that the continuous solution $u(\cdot)$ with initial condition $(1, t_1)$ satisfies $u(t) < 1$ for all $t < t_1$. From the leak hypothesis, we know that $u(t) - x(t) > (u(t_1) - x(t_1)) \exp(\alpha(t_1 - t))$ for all $t < t_1$. Therefore $\liminf x = -\infty$.

Consider a spiking solution $x(\cdot)$ with infinitely many spikes on \mathbb{R}^- . Let (t_n) be the sequence of spikes and

$$m_n = \min_{t \in [t_n, t_{n+1}[} x(t)$$

The minimum m_n is either 0 or $m_n = x(s_n)$, where $s_n \in]t_n, t_{n+1}[$ and $f(s_n, m_n) = 0$. It follows from the leak hypothesis that $f(s_n, 1) \leq \alpha(1 - m_n)$ (and $\alpha < 0$). If $x(\cdot)$ is not bounded, then $\liminf m_n = -\infty$, which implies that $\liminf f(s_n, 1) = -\infty$. This implication contradicts the assumption that f is bounded. \square

3 Implications for neural coding

The set of admissible spike times

Our interest for solutions on \mathbb{R} can be rephrased as follows. Since an integrate-and-fire model transforms input spike trains into an output spike train through a dynamic state variable, its output for a given set of inputs depends on its state at some point (the initial condition). However, we have seen that not all states are possible if we consider that the neuron has a past; only initial conditions with an infinite degree lead to bounded solutions on \mathbb{R} , which constrains the possible outputs of the model.

What is the set Ω of times t such that there is a bounded solution spiking at time t , in other words, what is the set of admissible spike times? In terms of the spike map φ defined in section 1, and since a bounded solution has infinitely many spikes on \mathbb{R}^- (except for silent models), it can be written simply as:

$$\Omega = \bigcap_n \varphi^n(\mathbb{R})$$

This is the intersection of a decreasing sequence of sets. When φ is continuous, we simply have $\Omega = \mathbb{R}$, i.e., any spike time is admissible. This is so when $f(1, t) > 0$ for all $t \in \mathbb{R}$, as showed in Brette (2004). In terms of the membrane equation, that inequality means that the current at threshold is positive at all times, which is a very strong assumption. This is not a physiologically plausible situation for cortical neurons. In particular, recent physiological data indicate that the distribution of the membrane potential and of the membrane current (CdV/dt) are approximately Gaussian (Destexhe et al, 2003) and that spikes are triggered by fast fluctuations of that current, the average of which is far from threshold (Piwkoswka et al, 2007). In terms of spiking models, this fact means that most of the time $f(1, t) < 0$, and we know that $\varphi(\mathbb{R}) \subset \{t \in \mathbb{R} | f(1, t) \geq 0\}$ (Brette, 2004) — this result comes the simple fact that the derivative of a solution cannot be negative at spike time. Thus, $\varphi(\mathbb{R})$ is already a small set, which suggests that Ω is much smaller. In a previous paper (Brette and Guigon, 2003), I showed that such a construction generally leaves only a finite number of solutions for periodic inputs, and seems to leave a single solution for aperiodic inputs (realizations of noise), although this latter fact is still lacking a rigorous proof.

Thus, I conjecture that a leaky spiking model defined by equation 1, where f is determined by a given realization of random inputs, has a single solution on \mathbb{R} with probability 1, which determines its unique output to the given inputs. In this way, spiking neuron models encode their inputs

into specific sequences of precisely timed spikes. This conjecture is consistent with the experimental finding that cortical neurons respond reliably to time-varying currents injected in vitro at the soma (Mainen and Sejnowski, 1995). An interesting way to phrase this conjecture is to state that the transformation *input spike trains* \mapsto *output spike train* defined by the leaky spiking model is a function (restricted on some input set of full measure). I give a sketch of the proof of a weak version of this conjecture in appendix B. I must emphasize that the conjecture is loosely defined, in that the precise hypotheses for the random inputs is to be found. In particular, it would not apply in general to periodic inputs (see e.g. Brette and Guigon, 2003), but I predict that it would include stationary shot noise and diffusion processes for both current and conductance inputs (i.e., additive or multiplicative).

Numerical example

In order to illustrate this conjecture in a realistic setting, I compute the degrees of initial conditions for the following integrate-and-fire model:

$$C \frac{dV}{dt} = -g_L(V - E_L) - g_e(t)(V - E_e) - g_i(t)(V - E_i)$$

where the parameter values are taken from Brette and Gerstner (2005), and g_e and g_i are excitatory and inhibitory fluctuating synaptic conductances (mimicking synaptic activity in vivo), with parameter values typical of a low rate high-conductance state (Table 1, first line of HC set in Brette and Gerstner, 2005). The slope factor Δ_T is zero (the spike threshold is sharp). From the membrane equation, we can see that the membrane current at threshold is normally distributed with mean μ and standard deviation σ as follows:

$$\begin{aligned} \mu &= g_L(E_L + E_e + 3E_i - 5V_T) = -43.6mV \times g_L \\ \sigma &= g_L \sqrt{\frac{1}{4}(V_T - E_e)^2 + (V_T - E_i)^2} = 35.2mV \times g_L \end{aligned}$$

Then the probability that the current be positive at threshold is

$$\frac{1}{\sqrt{2\pi}} \int_{-\mu/\sigma}^{+\infty} \exp\left(-\frac{x^2}{2}\right) \approx 0.11$$

Thus, the current at threshold is negative almost 90% of the time. This fact implies that at least 90% of points $(1, t)$ have degree zero. Given that the correlation time constant of synaptic currents is much shorter than the typical duration of an interspike interval, we might expect that the probability

of that a point has degree at least n decreases geometrically as p^n . Fig. 4 shows the distribution of degrees for random initial conditions, which agrees with our prediction with $p = 0.6$, and more than 95% of points have degree zero. For example, 99.999% of points have degree less than 10. In other words, the 10th spike of any solution occurs in an extremely small area of the time axis, i.e., the timing of spikes is very precise.

The algorithm to calculate the degrees is described in appendix A.

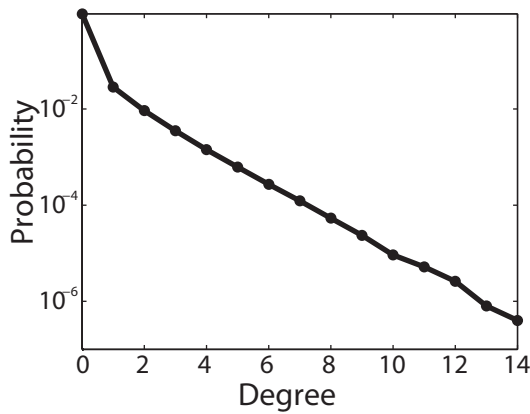


Figure 4: Distribution of the degrees of initial conditions for a leaky integrate-and-fire model with fluctuating synaptic conductances. The degrees were computed for 10^7 sample random points $(1, t)$. More than 95% points have degree zero. The probability of positive degrees n scales as 0.6^n .

4 Discussion

In this paper, I have considered the problem of solutions on \mathbb{R} with a given initial condition for one-dimensional spiking models, i.e., the problem of backward solutions, since forward solutions always uniquely exist for a given initial condition. It appears that, contrary to the case of the non-spiking differential equation, neither existence nor uniqueness is granted for the spiking model. Theorem 1 gives a simple necessary and sufficient condition for existence, and theorem 2 shows that one can construct all solutions by discarding an initial part of a unique maximal solution. In particular, for any initial condition, there is at most one solution with infinitely many spikes on \mathbb{R}^- , which is the unique bounded solution under the assumptions

of proposition 1. In appendix A, I describe an algorithm to calculate the number of spiking solutions and the maximal solution for a given initial condition. Finally, I showed that, from previous studies on the reliability of spike timing (Brette and Guigon, 2003), we would expect the set of bounded solutions to be a singleton in many cases (or perhaps a set of null measure). This would make the transformation *input spike trains* \mapsto *output spike train* a function. This point is still lacking a sound mathematical proof in general cases, but the result of appendix B is probably a good starting point.

The framework I presented applies to realizations of random processes which satisfy the hypotheses of this study (e.g. the leak hypothesis), including current noise and conductance (multiplicative) noise. Also, although the non-spiking dynamical system was defined with a differential equation, the results can be extended to realizations of discontinuous random processes because the core assumption is the existence of a flow for the process. The leak hypothesis can also be expressed without derivatives by writing the integral formulation of the hypothesis.

A more complete mathematical theory of spiking neuron models should include a special treatment of *divergent models*. Divergent models are spiking models in which spikes are generated when the membrane potential diverges to infinity, that is, when the threshold is $+\infty$. There are presently three such models in the literature: the quadratic model (Ermentrout and Kopell, 1986), the exponential model (Fourcaud-Trocmé et al, 2003) and the quartic model (Touboul, 2007). In particular, an augmented exponential model has been shown to be a good integrate-and-fire approximation for detailed biophysical models (Brette and Gerstner, 2005) and for real cortical neurons (Pospischil et al, 2007). Future work should focus on the specificities of these models. Finally, the present study only applies to one-dimensional models. Higher-dimensional models (even bidimensional) are much harder to tackle, because many arguments for the one-dimensional case relied on the property that solutions of the differential equation cannot cross. It would be very interesting to extend these results to bi-dimensional models (e.g., with a second adaptive equation).

Acknowledgments

This work was partially supported by the EC IP project FP6-015879, FACETS, and the EADS Corporate Research Foundation.

References

- [1] Brette R (2004) Dynamics of one-dimensional spiking neuron models. *J Math Biol* 48(1): 38–56
- [2] Brette R, Gerstner W (2005) Adaptive exponential integrate-and-fire model as an effective description of neuronal activity. *J Neurophysiol* 94: 3637–3642.
- [3] Brette R, Guigon E (2003) Reliability of spike timing is a general property of spiking model neurons. *Neural Comp* 15(2): 279–308
- [4] Destexhe A, Rudolph M and Paré D (2003) The high-conductance state of neocortical neurons in vivo. *Nat Rev Neurosci* 4: 739–751
- [5] Ermentrout B, Kopell N (1986) Parabolic bursting in an excitable system coupled with a slow oscillation. *SIAM J Appl Math* 46: 233–253
- [6] Fourcaud-Trocmé N, Hansel D, van Vreeswijk C and Brunel N (2003) How Spike Generation Mechanisms Determine the Neuronal Response to Fluctuating Inputs. *J Neurosci* 23(37): 11628–11640
- [7] Gerstner W, Kistler WM (2002) *Spiking Neuron Models*. Cambridge University Press.
- [8] Hodgkin A, Huxley A (1952) A quantitative description of membrane current and its application to conduction and excitation in nerve. *J Physiol (Lond)* 117: 500–544
- [9] Lapicque L (1907) Recherches quantitatives sur l’excitation électrique des nerfs traitée comme une polarisation. *J Physiol Pathol Gen* 9: 620–635
- [10] Mainen ZF, Sejnowski, TJ (1995) Reliability of spike timing in neocortical neurons. *Science* 268: 1503–1506
- [11] Piwkowska Z, Pospischil M, Brette R, Sliwa J, Rudolph-Lilith M, Bal T and Destexhe A (2007) Characterizing synaptic conductance fluctuations in cortical neurons and their influence on spike generation. arXiv:0706.1306v1
- [12] Pospischil M, Piwkowska Z, Bal T and Destexhe A (2007) Which model best captures the spiking response of cortical neurons to excitatory inputs? Preprint
- [13] Touboul J (2007) Bifurcation analysis of a general class of non-linear integrate-and-fire neurons. Submitted

A Numerical calculation of the maximum degree of an initial condition

In this appendix, I briefly explain how to calculate numerically the maximum degree of an initial condition in the case of the numerical example of section 3. For a given initial condition, we compute the backward (continuous) trajectory $u(\cdot)$ by numerically integrating the differential equation and use the following lemma:

Lemma 1. *Suppose that the model is leaky, not silent and that $f(x, t) > 0$*

if $x > x_m$ for some value x_m . Let $u(\cdot)$ be the continuous solution of the differential equation with initial condition (x_0, t_0) ($x_0 < 1$).

- The degree of (x_0, t_0) is zero if and only if there is a time $t < t^*$ such that $u(t) = 1$.
- The degree of (x_0, t_0) is positive if and only if there is a time $t < t^*$ such that $u(t) = x_m$ and there is no $s \in [t, t_0]$ verifying $u(s) = 1$. (then $u(s) < x_m$ for all $s < t$).

In the case of an integrate-and-fire model with synaptic conductances, x_m is the minimum of all reversal potentials. In the case of the numerical example of section 3, $x_m = E_i$. We follow the trajectory $u(\cdot)$ backward until it reaches 1 or x_m . If it reaches 1, the algorithm stops and the degree is zero. If it reaches x_m , we know that the degree is positive. The degree is at least 2 if and only if the backward trajectory can split at some time $s \in [t, t_0]$ such that $(1, s)$ has positive degree, and the splitting point is unique by theorem 2. It is such that $u(s) = 0$ and $(1, s)$ has positive degree. If there is no such point, then the degree is 1 and the algorithm stops. If there is a splitting point s , then the degree of (x_0, t_0) is the degree of $(1, s)$ plus one, and is defined recursively.

Proof. The first point of the lemma is simply theorem 1. Suppose that the degree of (x_0, t_0) is positive. Then $u(s) < 1$ for all $s < t_0$, and, according to prop 1, $u(\cdot)$ is not bounded on \mathbb{R}^- . It follows that there is a $t < t_0$ such that $x(t) = x_m$. Conversely, if there is a $t < t_0$ such that $x(t) = x_m$, then $u(s) < x_m$ for all $s < t$ because of the hypothesis on f so that $u(\cdot)$ defines a valid spiking solution on $] -\infty, t_0]$ if there is no $s \in [t, t_0]$ verifying $u(s) = 1$. Therefore the degree of (x_0, t_0) is positive. \square

The computation of the degrees can be accelerated thanks to the following lemma:

Lemma 2. *Let (x_0, t_0) be an initial condition with degree zero, and $u(\cdot)$ the corresponding continuous solution. Then any point (x, t) such that $t > t_0$ and $x > u(t)$ (above the graph of $u(\cdot)$) has degree zero.*

In particular, if one follows the (forward) continuous solution $u(\cdot)$ starting from an initial condition $(1, t_0)$ such that $f(1, t_0) < 0$, then all points $(1, t)$ such that $t > t_0$ and $u(t) < 1$ have degree zero. With balanced synaptic input and short time constant, this condition is fulfilled most of the time and the remaining set is already rather small.

Proof. Consider the backward spiking solution $x(\cdot)$ starting from (x, t) . Following the trajectories backward, since the difference $x(\cdot) - u(\cdot)$ increases by 1 at every spike and never changes sign otherwise, it must remain positive. In particular, we will have $x(s) > 1$ when $u(s) = 1$, so that (x, t) has degree zero. \square

B Geometric distribution of degrees in a simplified model

In this appendix, I briefly show for a simplified integrate-and-fire model with synaptic conductances that the degrees of initial conditions $(1, t)$ are geometrically distributed. In particular the probability of finding a point $(1, t)$ with infinite degree is zero, which proves a weak version of the conjecture for this model. I consider the same model as in the numerical example of section 3, except that $g_e(\cdot)$ and $g_i(\cdot)$ are (possibly rectified) white noise processes with positive mean (preferably in Stratonovich sense). With this assumption, spiking solutions are Markov processes. I also assume that $E_i = E_L =$ reset value (shunting inhibition). I normalize the potential so that the reset is zero and the threshold is one.

Consider a backward trajectory starting from $(1, t_0)$. If it hits 1 then the degree is 0. If it hits 0 at time s then it must be negative for $t < s$, so that its degree is at least 1 and the (possible) splitting point is at time s . Applying the same process from $(1, s)$, one can see that the probabilities of the two outcomes are independent from the two outcomes for the first trajectory. Therefore, the distribution of the degrees is geometric.