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TO WHICH EXTEND IS THE “NEURAL CODE” A METRIC ?

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ABSTRACT

Here is proposed a review of the different choices to structure spike trains, using deterministic metrics. Temporal constraints observed in biological or computational spike trains are first taken into account. The relation with existing neural codes (rate coding, rank coding, phase coding, ..) is then discussed.

To which extend the “neural code” contained in spike trains is related to a metric appears to be a key point, a generalization of the Victor-Purpura metric family being proposed for temporal constrained causal spike trains.

KEY WORDS

Spiking network. Neural code. Gibbs distribution.

1 Global time constraints in spike trains

The output of a neural network is a set of events, defined by their occurrence times, up to some precision:

$$\mathcal{F} = \{\dots t_i^n \dots\}, t_i^1 < t_i^2 < \dots < t_i^n < \dots,$$

where t_i^n corresponds to the n th spike time of the neuron of index i , with related inter-spike intervals $d_i^n = t_i^n - t_i^{n-1}$. Such *spike train* writes $\rho_i(t) = \sum_{t_i^n \in \mathcal{F}_i} \delta(t - t_i^n)$, using the Dirac symbol $\delta(\cdot)$. See e.g. [1, 2, 3] for an introduction.

In computational or biological contexts, not all multi-time sequences correspond to spike trains since they are constrained by the neural dynamic, while temporal constraints are also to be taken into account: Spike-times are:

- [C1] bounded by a refractory period r , $r < d_i^{n+1}$,
- [C2] defined up to some absolute precision¹ δt , while
- [C3] there is always a minimal delay dt for one spike to influence another spike, and
- [C4] there is a maximal inter-spike interval D such that

$$\text{either } d_i^{n+1} < D \text{ or } t_i^{n+1} = +\infty$$

(i.e. either neuron fires within a time delay $< D$ or it remains quiescent forever).

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

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

The [C1] constraint is well-known, limiting the maximal rate. See e.g. [4] for an extended discussion on absolute / relative refractory periods.

¹Here, [C2] has the following precise meaning: Two spike-times are not synchronized if separated by more than δt . On the contrary, two spike-trains are synchronized if and only if they repetitively both spike in the same δt time window. Indeed, the fact that two isolated spike-times occur in the same δt time window is not significant.

The [C2] constraint seems obvious but is sometimes “forgotten” in model. In rank coding schemes for instance [5] it is claimed that “all” spike-time permutations are significant, which is not realistic since many of these permutations are indistinguishable, because of the bounded precision, as discussed in e.g. [6]. Similarly, a few concepts related to “reservoir computing” (e.g. [7]) assume implicitly an unrealistic unbounded time precision. [8].

Similarly, [C3] is also obvious and allows to avoid any spurious effects², and induce simplifications both at the modelization and simulation level [9]. Here we consider dt including for gap junctions [8].

The [C4] constraint is less obvious. The idea is that, in the absence of any input (isolated neuron), the potential decreases after a while and the neuron cannot fire anymore. This is true for usual deterministic models, unless a constant input current singular value is chosen. This seems true for cortical neurons, but likely not for all neurons in the brain [8].

As discussed in details in [10] whether the fact [C4] is verified or not, completely changes the nature of the dynamics. In the latter case, a neuron can remain silent a very long period of time, and then suddenly fire, inducing a complete change in the future state of the system. We distinguish situations with and without [C4] in the sequel.

Considering C[1-3] and optionally [C4], let us now review the related consequences regarding modeling

Simulation of time-constrained networks. The event-based simulation (see e.g. [11] for a review) of neural networks is strongly simplified by the fact that, thanks to [C2] and [C4] spike times and precisions are bounded, while thanks to [C3] spiking can not generate causal paradoxes. Here the specification allows to use “histogram based” methods and obtain³ with a small $O(1)$ complexity [8].

Furthermore, the simulation kernel is minimal (a 10Kb C++ source code), using a $O(D/dt + N)$ buffer size and about $O(1 + C + \epsilon/dt) \simeq 10 - 50$ operations/spike ($> 10^6$ spike/sec on laptop), for a size N network with C connections in average, while $\epsilon \ll 1$.

²If a neuron instantaneously fire 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).

³Source code available at <http://enas.gforge.inria.fr>.

2 The maximal amount of information

Considering [C1-2], given a network of 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.

A rather simple reasoning [8] yields a rough *upper bound for the amount of information*:

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

Taking the numerical values into account it means for large T , about $1Kbits/neuron$.

In fact, the dynamics of a given network constraint very much the possible spike trains, and the real entropy is lower, when not strongly lower, than this bound.

In the particular case of fast-brain mechanisms where only “the first spike matters” [12], this amount of information is not related to the permutations between neuron spikes, i.e. of order of $o(\log(N!)) = N \log(N)$ but simply proportional to N , in coherence to what is found in [6].

This bound is coherent with results presented in [13] considering spike rate and using an information entropy measure. For instance, considering a timing precision of $0.1 - 1ms$ as set here, the authors obtain an information rate bounded around $500bits/s$ for a neural receptor.

Note that this is not bad, but good news. For instance, in statistical learning, this corresponds to a coding with large margins, thus as robust as support-vector machines, explaining the surprisingly impressive performances of fast-brain categorization [6].

3 Dynamics of time-constrained networks

A step further, taking [C1-3] into account, allows us to “discretize” the spike trains sequences: i.e. use “raster⁴”. The sampling period ΔT is taken smaller than r , δt and dt .

In simple models such as basic leaky integrate and fire neuron or integrate and fire neuron models with conductance synapses and constant input current, this discretization allows a full characterization of dynamics. Thus, it has been shown in these two cases that [14, 10]:

- [H1] *The raster plot is generically⁵ periodic, but, depending on parameters such as external current or synaptic weights, periods can be larger than any accessible computational time;*
- [H2] *There is a one-to-one correspondence between orbits⁶ and raster (i.e. raster plots provides a symbolic coding for dynamics).*

⁴ Formally, the spike train discretized raster, writes for $k \geq 0$:

$$w_i[k] = \#\{t_i^n, k \Delta T \leq t_i^n < (k+1) \Delta T\} \in \{0, 1\}$$

⁵ 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 thresholds.

⁶ Here we consider orbits, i.e. infinite trajectories, thus consider the system in its asymptotic stage.

The fact [H1] allows to clearly understand to which extends spike trains can code information: Periodic orbits give the code. When the input changes, the orbits are still periodic.

The fact [H2] means that, in these cases, the raster is a “symbolic coding” in the sense that no information is lost by considering spike times and not the membrane potential. Both facts also allow one to deeply understand the network dynamics: Fig. 1 sketches out some aspects.

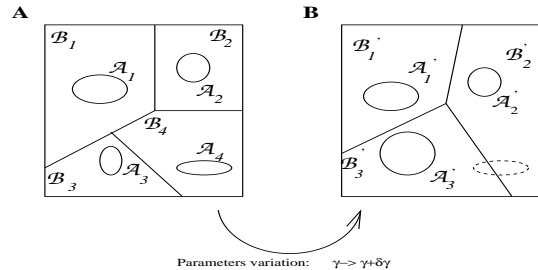


Figure 1. Describing the dynamic landscape of deterministic time-constrained networks. [A] The phase space is partitioned into bounded domains B_l and for each initial condition in B_l the initial trajectory is attracted to an attractor, here not a fixed point, as in, e.g. Hopfield networks, but a periodic orbit A_l . [B] If the parameters (input, weights) change, the landscape is modified and several phenomena can occur: change in the basins shape, number of attractors, modification of the attractor as for A_3 in this example; A point belonging to A_4 in Fig.1 A, can, after modification of the parameters, converge either to attractor A_2 or A_3 .

Remarks

Time is discretized, but without any constraint about the “sampling period”. A reasonable order of magnitude for the sampling period is dt since in the discretized model, a spike is propagated to efferent neurons at least one sampling period later. The [H1] and [H2] results are in fact true at any precision.

In order to understand [H1], it might be important to discuss how “obvious” it is. Time is discretized. If the bounded neuron state (membrane potential) would have been discretized also, we would have a finite state system. In that case, only fixed points and periodic orbits could occur and the result would have been obvious. As a consequence, [H1] reads: even if the neuron state takes continuous values, orbits are still generically periodic.

In a conductance based model, with the additional constraint that conductances depends on previous spikes without a finite horizon, [H1] still holds.

To which extends such a “canonical situation” extends to more complex models is an open question. We can easily conjecture [H1] is a model limitation for all integrate and fire models, defined with an instantaneous reset to a constant value.

However, since the period can be arbitrary large, these models are able to simulate more general models, such as Hodgkin-Huxley [15] neuron’s assemblies, during a bounded period of time: Periodic orbits approximate chaotic orbits (shadowing lemma). In this sense, they provide useful approximations of biological networks.

The previous conjecture can be explained as follows: Changing the initial value of the membrane potential, one may expect some variability in the evolution. But with the reset, all trajectories collapse on the same point and have obviously the same further evolution. Though this effect can be considered as pathological, it has a great advantage. After reset, the membrane potential evolution does not depend on its past value. This induces an interesting property used in all the Integrate and Fire models that we know: The dynamical evolution is essentially determined by the firing times of the neurons, instead of their membrane potential values.

4 Neural coding and temporal constraints

Let us now introduce the central idea of this review.

As an illustrative example, let us consider the temporal order coding scheme [5, 12] (i.e. rank coding): only the order of the events matters, not their absolute time values. This means that two spike trains $\mathcal{F}_1, \mathcal{F}_2$ with the same event ordering correspond to the same code. The key point here, is that rank coding defines a partition of spike trains set, each spike train with the same ordering being in the same equivalence class of the partition, i.e. corresponding to the same “code”. Choosing this code means we have structured spike trains using an “equivalence relation”.

The same view can be given for other coding: rate coding means that all spike trains with the same frequencies are in the same equivalence class, irrespective of their phase, etc..

Let us now introduce a “distance” $d(\cdot)$, which is 0 if \mathcal{F}_1 and \mathcal{F}_2 correspond to the same code, and 1 otherwise.

The fact that spikes precision is not unbounded leads to many indistinguishable orderings. This does not change the rank coding concept, while the partition is now coarser. Trains with two spikes with indistinguishable occurrence times are in the same equivalence class.

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, not discrete distances (i.e. with binary 0/1 values) but a “quantitative” distance. Two spike trains correspond exactly to the same neural code if the distance is zero and 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*. It is far for being new, but surprisingly enough not made explicit at this level of simplicity. In order to see the interest of this idea, let us briefly review the two main classes of spike train metrics.

As reviewed in details in [3, 16] spike trains deterministic metrics can be grouped in three classes:

- 0- “Binned” metric, with spikes grouping in bins (e.g. rate coding metrics), not discussed here.
- I- Convolution metrics, with a distance defined on some convolution of spike train, including raster-plot metric.
- II- Spike time metrics, such as alignment distances [17]

5 Using convolution metrics

Linear representation. A large class of metrics is defined through the choice of a convolution kernel K writing:

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

easily normalized between 0 (no spike) and, say, 1 (burst mode at the maximal frequency). The distance is then defined on the signal $\mathbf{s} = (\dots, s_i, \dots) \in \mathcal{R}^N$, e.g. using L^p norms. The “code” here corresponds to the linear representation metric. It allows us to link spike trains with a quantitative signal \mathbf{s} .

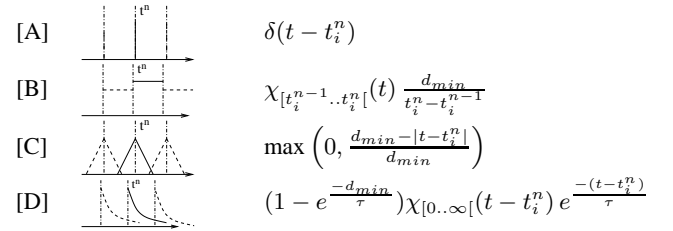


Figure 2. A few examples of spike train convolution: [A] The spike train itself, [B] A causal local frequency measure estimation (writing χ the indicatrix function), [C] A non-causal spike density, uniformly equal to 1 in burst mode, [D] A normalized causal exponential profile. Evoked post-synaptic potential profiles model 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.

The so-called “kernel methods” based on the Mercer theorem [3] are in direct links with linear representation since they are defined, as scalar products, writing:

$k(\mathcal{F}, \mathcal{F}') = \sum_i \sum_{n,m} \hat{K}_i(t_i^n - t_i^m) = \int_t s_i(t) s_i'(t)$ with direct correspondences for usual kernels with linear convolutions, e.g.:

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

This also includes distances based on inter-spike intervals as developed in e.g. [18].

Non static kernels of the form $K_i(t, t - t_i^n)$ or $K_i^n(t - t_i^n)$ can also be used (clock-dependent coding, raster plot, 1st spike coding, ..), while non-linear Volterra series allows to represent “higher order” phenomena (see e.g. [13]). Weighted spike trains (i.e. with quantitative values attached to each spike) are also direct generalizations of these.

These linear representations not only provide tools to compare different spike trains, but allows one to better understand the link between quantitative signals and spike times. For instance [1, 7], writing $s(t) = \sum_i \lambda_i s_i(t)$ allows to define some network readout to link spiking networks to “analog” sensory-motor tasks. Let us illustrate this aspect by the following two results.

Kernel identification. Given a causal signal \bar{s} generated by spike train \mathcal{F} the problem of identifying the related kernel is formally solved by the following program:

$$\min_K \int_{t>0} |s(t) - \bar{s}(t)|^2 \equiv \int_{\lambda} |K(\lambda) \rho(\lambda) - \bar{s}(\lambda)|^2$$
 using the Laplace transform Parseval theorem, thus:

$$K(\lambda) = [\bar{s}(\lambda) \rho(\lambda)^T] [\rho(\lambda) \rho(\lambda)^T]^{-1}$$

i.e. the spike train cross-correlation / auto-correlation ratio. Non-causal estimation would consider the Fourier transform. This setting corresponds to several identification methods [1, 3].

Spike deconvolution. A step further, if we know the convolution kernel K_i . It is obvious to formally write:

$$\rho_i = L_i * s_i \text{ with } L_i = \mathcal{F}^{-1} \left[\frac{1}{\mathcal{F}[K_i]} \right]$$

E.g.:
$$\begin{aligned} K_i &= \exp & L_i * s_i &= \frac{1}{\tau} s(t) + s'(t) \\ K_i &= \alpha & L_i * s_i &= \frac{1}{\tau^2} s(t) + \frac{2}{\tau} s'(t) + s''(t) \end{aligned}$$

well defined and allowing to reconstruct the spike-train from the continuous signal as illustrated in Fig. 3.

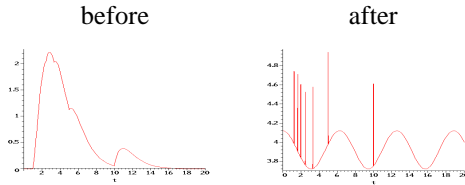


Figure 3. A small experiment of spike deconvolution. On the left the signal is the convolution of a spike-train using an $\alpha(t) = t/\tau e^{-t/\tau}$ profile, with addition of noise and of a spurious sinusoid has been added as an outlier to the signal. Spikes are not “visible” in the sense that they do not correspond to maxima of the signal because the spike responses are mixed. On the right the deconvolution is shown: the outlier is amplified, but spikes clearly emerges from the signal.

Signal reconstruction. In order to further understand the power of representation of spike trains in this case [19] has generalized the well-known Shanon theorem, as follows: A frequency range $[-\Omega, \Omega]$ signal is entirely defined by irregular sampling values s_i^n at “spike time” t_i^n

$$s_i(t) = \sum_n K_i^n(t - t_i^n) \text{ with } K_i^n(t) = s_i^n \frac{\sin(\Omega t)}{\pi t}$$

providing that $\max_n d_i^n \leq \frac{\pi}{\Omega}$. Thus providing an explicit signal “decoding”.

Raster-plot metrics. A step further, it is easy to see, that representing the spike time by a “raster⁴” corresponds to

non-static convolution kernel. Spike trains can be represented as the real number in $[0..1[$ which binary representation corresponds to the spike-train, inducing new metrics. A useful related metric is of the form, for $\theta \in]0, 1[$:

$$d_\theta(\omega, \omega') = \theta^T, T = \arg\max_t \omega^t = \omega'^t$$

thus capturing the fact that two rasters are equal up to a certain rank. Such metrics are used to analyze the dynamics of spiking networks and are typically used in the context of symbolic coding in dynamical systems theory[14, 10].

6 Using alignment metrics

The original alignment metric. The second family of metrics we want to review directly considers spike times [17, 16].

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 the other. 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 spikes trains with the same number of spikes, there is always a time-constant τ small enough such that the distance is equal to $\sum_n |t_i^n - t_i'^n|/\tau$.

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

Although computing such 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 number of spikes). This is due to the fact that, 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. It allows to calculate iteratively the minimal distance 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}' .

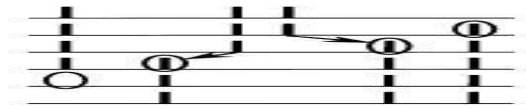


Figure 4. An example of minimal alignment from the upper to the lower spike train, using from top to bottom an insertion, a rightward shift, a leftward shift and a deletion respectively.

When considering spike trains with more than one unit, one point of view is to sum the distances for each alignment unit-to-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 on the power of the number of units [20].

This family of metrics include alignment not only on spike times, but also on inter-spike intervals, or metrics sensitive to motifs of spikes, etc.. They have been fruitfully applied in a variety of neural systems, to characterize neuronal variability and coding [16]. For instance, neurons that act as a coincidence detector with integration time (or temporal resolution) τ , spike trains will have similar post-synaptic effects if they are similar for this metric.

A generalized alignment metric. Let us remark, here, that the previous metric generalizes to metric whith:

- [causality] At a given time the cost of previous spikes alignment decreases with the obsolescence of the spike, say, with an exponential time-constant τ' .
- [non-linearity] The cost of a shift can be defined very small, say quadratic, when lower that the time precision and then, say, linear with the time difference.

This leads to an iterative definition of the distance $d_{n,n'}$ defined previously: $d_{n,n'}$ =

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

with, e.g., $\phi(d) = ((d\tau/\delta t)^2 \wedge d)$, again implementable in quadratic time. It corresponds to the original alignment metric iff $\phi()$ is the identity and $\tau' = +\infty$.

This modified metric illustrates how versatile is this class of distance to represent the differences between spike trains, considering temporal properties only.

Spike training. As a formal application, let us consider a neuron spike response model [21] of the form:

$V_i(t) = \nu(t - t_i^{n-1}) + \sum_{jm} w_{ij} \alpha(t - t_j^m)$, $t_i^{n-1} < t \leq t_i^n$, the spike time being defined by $V_i(t_i^n) = \theta$, where θ is the spiking threshold, thus as an implicit equation.

Previous metrics on spike times allows to optimize the neural weights in order to tune spike-times, deriving, e.g., rules of the form:

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

where $\bar{\mathcal{F}} = \{\dots, \bar{t}_i^n, \dots\}$ is the desired spike train

Such mechanisms of optimization is also applicable to time-constants, delays or thresholds. Using spike train metrics open the door to the formalization of such adaptation rules, in order to “compute with spikes”.

7 Discussion

Although probabilistic measures of spike patterns such as correlations [21] or entropy based pseudo-distances (e.g. mutual information) provides a view of spike trains variability which is enriched by the information theory conceptual framework, it may be difficult to estimate them in practice, since such measures are robust only if a large amount of samples is available. On the contrary, deterministic distances allow to characterize aspects of spike coding, with efficient methods and without this curse of sampling size.

This review highlights some of these methods and propose to consider that “choosing a coding” means “defining a metric”, in the deterministic case. Making explicit that spikes do not contain that much information.

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