

Accurate detection of spiking motifs in multi-unit raster plots

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Abstract. Recently, there has been growing interest in the hypothesis that within neural activity, information may be conveyed by precise spiking motifs. As a result, there have been several recent proposals for algorithms to detect such motifs in the Spiking Unit Activity (SUA) of populations of neurons. In this study, we introduce a detection model as an inversion of a generative model of raster plot synthesis. From this model, an optimal detection procedure is derived. This takes the form of a logistic regression coupled with a temporal convolution. Since this model is differentiable, we derive a supervised learning method in the form of gradient descent on the loss function of this auto-encoder model. We evaluate the ability of this model to detect spiking motifs in synthetic data. This learning method is able to recover the synthetically generated spiking motifs, and we plan to extend this method to neurobiological data as well.

Keywords: Neurobiology · spike trains · population coding · spiking motifs · heterogeneous delays · pattern detection.

1 Introduction

1.1 The age of large-scale neurobiological event-based data

Over the past decade, tremendous technological advances across multiple disciplines have dramatically expanded the frontiers of experimentally accessible neuroscience. These tools are now being used to probe the function, structure, and dynamics of neural networks at unprecedented levels of detail and precision. The staggering complexity of biological reality revealed by these technologies highlights the importance of neurobiological knowledge to provide a conceptual bridge between abstract principles of brain function and their biological implementation in neural circuits. As a consequence, there is a growing need to scale such analysis methods to larger amounts of data.

There are several approaches that try to solve this problem. One algorithm capable of accomplishing such a daunting task is the Rastermap algorithm [25]. Basically, it rearranges neurons in the raster map based on the similarity of their activity and applies a deconvolution strategy based on a linear model. However, this method has mainly been tested on calcium imaging data, which is known to

* Funded by A*MIDEX grant AMX-21-RID-025 “Polychronies”.

add some imprecision to the timing of the spiking activity observed in Spiking Unit Activity (SUA) recordings.

To overcome the limitations of models that either require spike times to be discretized, use a suboptimal least-squares criterion, or do not provide uncertainty estimates for model predictions or estimated parameters, Williams *et al* [36] addresses each of these shortcomings by developing a point process model that characterizes fine-scale sequences at the level of individual spikes and represents sequence occurrences as a few marked events in continuous time.

1.2 Decoding neural activity using spike distances

Overall, these methods rely on the definition of metrics to compute the distance between spike trains. One well-known measure is the Victor-Purpura distance, which overcomes inconsistencies experienced with a firing rate (Poisson model) of spike trains [34]. A further study attempts to refine the metric by including a time constant as a parameter which is then used to interpolate the distance between a coincidence detector and a rate difference counter [32]. Such distances have been extended to non-Euclidean metrics and to the use of morphological manipulations to compute a spike train dissimilarity [18]. These observations lead to the intuition that any distance may be the optimal solution of a generative model for these measures, possibly through non-linear relations.

Regarding spike timings, Levakova *et al* [20] have reviewed existing methods for estimating the latency of neural responses that include Bayesian binning. Alternatively, unitary event analysis can be performed using a statistical model of chance detection [11]. This has been used extensively to detect significant synchronous patterns above chance, especially in recordings of neuron pairs (see [30] for example). Including the possible existence to a temporal dithering of spike times improves the performance in the presence of patterns with different durations, such as surrogates generated to evaluate precisely timed higher order spike correlations [33].

1.3 Detecting spiking motifs with a heterogeneous delays SNN

These methods highlight the role of spike timing, and a striking example is given for the barn owl auditory system: When it hears the sound of a mouse, this sound generates a specific spiking response in both ears, and in particular, the precise timing between these signals can be used to determine the position of the prey [7]. More generally, there is now a large body of literature showing that the dynamics of the brain are often organized into stereotyped sequences (for a review, see [9]).

Here, we propose a new metric inspired by the *polychronization* model of Izhikevich [16]. This theoretical model is based on a random recurrent model of spiking neurons that includes synaptic delays chosen from a range of biologically realistic delays (from 0 to 20 ms) and whose weights are evolving with a Spike-Time Dependent Plasticity (STDP) learning rule. Delays are defined as the total time taken for a spike to travel from the soma of one presynaptic neuron to that

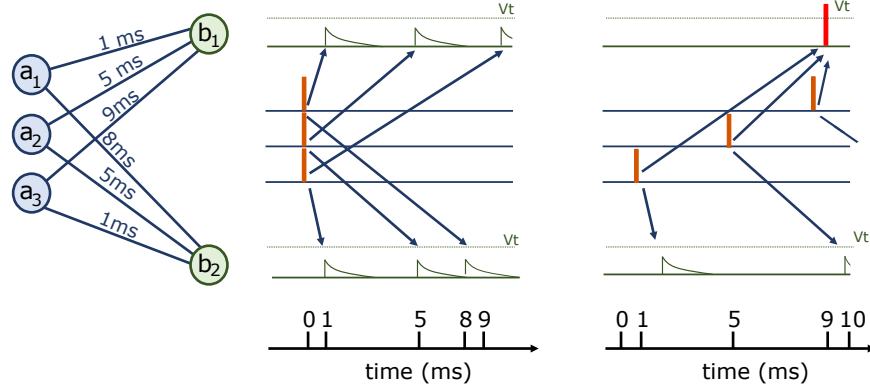


Fig. 1. Core Mechanism of Spike Motif Detection. (*Left*) In this toy example, three presynaptic neurons denoted a_1 , a_2 , and, a_3 are fully connected to two post-synaptic neurons b_1 and b_2 , with different delays of 1, 5, and 9 ms for b_1 and 8, 5, and 1 ms for b_2 , respectively. (*Middle*) If three synchronous pulses are emitted from presynaptic neurons, this will generate postsynaptic potentials that reach b_1 and b_2 asynchronously because of the heterogeneous delays, and they may not be sufficient to reach the membrane threshold (dashed line) in either of the postsynaptic neurons. (*Right*) If the pulses are emitted from the presynaptic neurons in such a way that, taking into account the delays, they reach the post-synaptic neuron b_1 at the same time (here, at $t = 10$ ms), the post-synaptic potentials V_i evoked by the three presynaptic neurons sum up, causing the voltage threshold to be crossed and thus the emission of an output spike which signals the detection of a spiking motif in the presynaptic population (red color).

of the efferent postsynaptic neuron. Note that only the weights are changed using the STDP rule, and that the set of delays is randomly set at initialization and then “frozen” for the rest of the simulation.

Due to the interplay between the delays and the STDP, the spiking neurons spontaneously self-organize into groups and exhibit reproducible time-locked firing patterns, which the author defines as “polychronous groups”. A key component of this model is the fact that neurons in a polychronous group fire at different times, but thanks to the effect of heterogeneous delays, spikes may converge synchronously on the soma of the postsynaptic neuron: This leads to the summation of the excitatory postsynaptic potentials evoked by each spike, and thus to the crossing of the voltage threshold and the discharge of a spike (see Figure 1). According to the STDP rule, the group of neurons involved in this polychronous activity will see their synaptic weight increase and thus consolidate the formation of that polychronous group. A limitation of this model is that these heterogeneous delays are fixed and can not evolve in time.

In this work, we propose to accurately detect spatio-temporal spiking motifs using a feed-forward, single layer heterogeneous delays spiking neural network (HD-SNN). The paper is organized as follows. We develop a theoretically defined

HD-SNN for which we can attune both the weights and delays. This will allow us to formalize the spiking neuron used to learn the model’s parameters in a supervised manner and test its effectiveness. In the results section, we will first evaluate the efficiency of the learning scheme. We will also study the robustness of the spiking motif detection mechanism and in particular its resilience to changing the dimensions of the presynaptic or postsynaptic populations, or the depth in the number of different possible delays. This will allow us to show how such a model can provide an efficient solution which may in the future be applied to neurobiological data.

2 Methods

Let us formally define the Heterogeneous Delays Spiking Neural Network (HD-SNN). First, we will define raster plots similar to those obtained from Spiking Unit Activity (SUA) recordings using an event-based and then binarized setting. We will then derive a generative model for raster plots using a HD-SNN, and derive a model for efficient detection of event-based motifs using a similar HD-SNN with “inverted” delays.

2.1 Raster plots: from event-based to binarized

In neurobiological recordings, any generic raster plot consists of a stream of *spikes*. This can be formalized as a list of neural addresses and timestamps tuples $\epsilon = \{(a_r, t_r)\}_{r \in [1, N_{ev}]}$ where $N_{ev} \in \mathbb{N}$ is the total number of events in the data stream and the rank r is the index of each event in the list of events. Each event has a time of occurrence t_r (these are typically ordered) and an associated address a_r in the space \mathcal{A} of the neural population. In a neurobiological recording like that of SUAs, this can be the identified set of neurons.

Events are generated by neurons which are defined on the one hand by the equations governing the evolution of its membrane potential dynamics on their soma and on the other hand by the integration of the synaptic potential propagating on their dendritic tree. A classical characterization consists in detailing the synaptic weights of each synaptic contact, the so-called weight matrix. As we saw above, one may add heterogeneous delays, i.e., the precise timing from one afferent neuron’s firing to its arrival in the soma. In such neurons, input presynaptic spikes ϵ will be multiplexed in time by the dendrites defined by this synaptic set (see Figure 1).

Let’s formalize such a layer of spiking neurons with heterogeneous delays (HD-SNN). Each neuron $b \in \mathcal{B}$ connects to presynaptic afferent neurons from \mathcal{A} . In biology, a single cortical neuron has generally several thousands of synapses. Each may be defined by its synaptic weight and also its delay. Note that two neurons may contact with multiple synapses, and thus different delays. Scanning all neurons b , we thus define the set of $N_s \in \mathbb{N}$ synapses as $\mathcal{S} = \{(a_s, b_s, w_s, \delta_s)\}_{s \in [1, N_s]}$, where each synapse is associated to a presynaptic address a_s , a postsynaptic address b_s , a weight w_s , and a delay δ_s .

This defines the full connectivity of the HD-SNN model. Of particular interest is to define the receptive field of a postsynaptic neuron $\mathcal{S}^b = \{(a_s, b_s, w_s, \delta_s) \mid b_s = b\}_{s \in [1, N_s]}$, or the emitting field of a presynaptic neuron $\mathcal{S}_a = \{(a_s, b_s, w_s, \delta_s) \mid a_s = a\}_{s \in [1, N_s]}$. Following this definition, an event stream which evokes neurons in the presynaptic address space is multiplexed by the synapses into a new event stream which is defined by the union of the sets generated by each emitting field from the presynaptic space: $\cup_{r \in [1, N_{ev}]} \{(b_s, w_s, t_r + \delta_s)\}_{s \in \mathcal{S}_{a_r}}$. In biology, this new stream of events is naturally ordered in time as events reach the soma of post-synaptic neurons. In particular, when post-synaptic neurons are activated on their soma by this spatio-temporal motif, the discharge probability will increase, notably when these spikes converge on the soma in a synchronous manner.

From the perspective of simulating such event-based computations on standard CPU- or GPU-based computers, it is useful to transform this event-based representation into a dense representation. Indeed, we may transform any event-based input as the boolean matrix $A \in \{0, 1\}^{N \times T}$, where N is the number of presynaptic neurons in \mathcal{A} and T is the number of time bins (see Figure 2a). In this simplified model, we will consider that heterogeneous delays are integers limited in range between 0 and D (that is, $\forall s \in [1, N_s], 0 \leq \delta_s < D$) such that the synaptic set can be represented by the dense matrix $K^b \in \mathbb{R}^{N \times D}$ giving for each neuron b the weights as a function of presynaptic address and delay (see Figure 2b). It is equal to zero except on synapses: $\forall s \in \mathcal{S}^b, K^b(a_s, \delta_s) = w_s$. Equivalently, one may define for each presynaptic neuron a the emitting kernel as the transpose kernel $K_a^T \in \mathbb{R}^{M \times D}$, where M is the number of postsynaptic neurons, whose values are zero except on synapses: $\forall s \in \mathcal{S}_a, K_a^T(b_s, \delta_s) = w_s$.

2.2 A generative model for raster plots

As described in Figure 1, a spiking motif can be detected using a properly tuned HD-SNN. Taking the argument the other way around, one may form a generative model for realistic raster plots in which spikes in the presynaptic address space are generated as the conjunction of spiking motifs defined in the postsynaptic space, knowing that both populations are connected by a set of weights and delays whose structure is stable relatively to the coding timescale. When connection weights are strong and sparsely distributed, this firing will robustly cause a specific temporal motif. Overall, these examples show that raster plots may be considered as a mixture of the effects of different elementary causes, and that each event triggers a specific spatio-temporal spiking motif.

Formally, spiking motifs may be activated independently and at random times, such that we write this activity as $B(b, t) = 1$ if b is activated at t and else $B(b, t) = 0$. This defines $B \in \{0, 1\}^{M \times T}$ as the raster plot corresponding to the temporal activation of the spiking motifs, where M is the number of different spiking motifs (see Figure 2c). The probability of firing of a neuron a at a given time t can be understood as a Bernoulli trial whose (only) parameter is a bias $p(a, t) \in [0, 1]$. Assuming that this bias is conditioned by the presence of spiking motifs on *all* efferent postsynaptic neurons with the corresponding delays, it can be shown that the logit (inverse of the sigmoid) of this probability bias

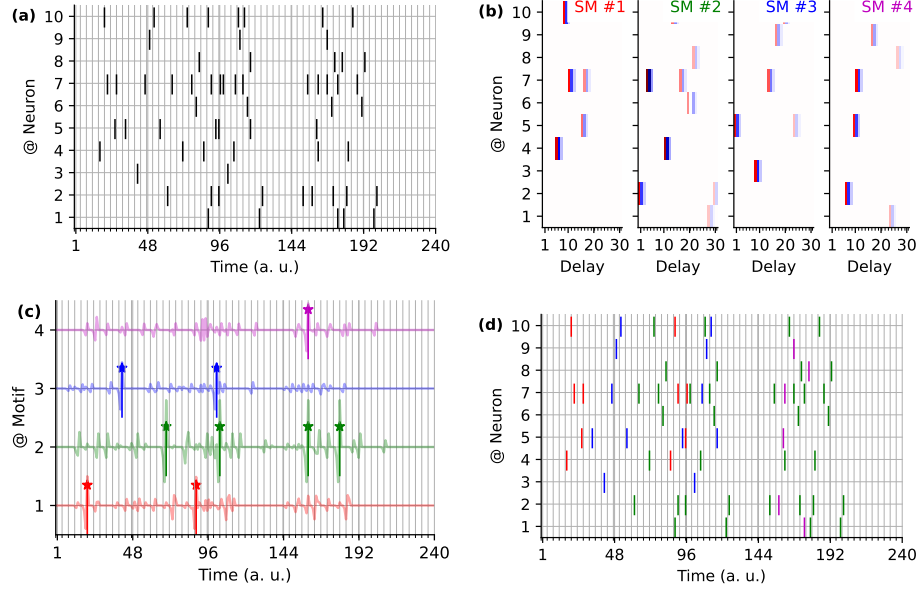


Fig. 2. Generating raster plots and inferring spiking motifs. **(a)** As an illustration for the generative model, we draw a multiunit raster plot synthesized from 4 different spiking motifs and for 10 neurons. **(b)** We show these motifs, each identified at the top by a different color. The evidence of activation (red) or deactivation (blue) is assigned to each presynaptic neuron and 31 different possible delays. **(c)** The activation in time of the different motifs (denoted by stars) is drawn at random and then used to generate a raster plot on the multi-unit address space (see panel a). By inverting this model, an inference model can be defined for their efficient detection, outputting an evidence value (continuous line) from which the identity and timing of SMs can be inferred (vertical bars). **(d)** The original raster plot can be annotated with each identified spiking motif.

can be written as the sum of the logit of each of these factors, whose values we will define as the corresponding weights in the kernel. We can thus write the probability bias $p(a, t)$ as the accumulated evidence given these factors as

$$p(a, t) = \sigma(K_{\mathcal{A}}(a) + \sum_{b \in \mathcal{S}_a, 0 \leq \delta \leq D} B(b, t + \delta) \cdot K^b(a, \delta))$$

where σ is the sigmoid function. We will further assume that kernel's weights are balanced (their mean is zero) and that $K_{\mathcal{A}}$ is a bias such that $\forall a, t, \sigma(K_{\mathcal{A}}(a))$ is the average background firing rate. Finally, we obtain the raster plot $A \in \{0, 1\}^{N \times T}$ by drawing spikes using independent Bernoulli trials $A \sim \mathcal{B}(p)$. Note that, depending on the definition of kernels, the generative model can model a discretized Poisson process, generate rhythmic activity or more generally propagating waves. This formulation thus defines a simple generative model for raster plots as a combination of independent spiking motifs.

2.3 Detecting spiking motifs

Assuming that we know the spiking motifs (as defined by the kernel K), the generative model defined above allows to determine an inference model for detecting sources \hat{B} when observing a raster plot A . Indeed, by using this forward model, it is possible to estimate the likelihood $p(b, t)$ for the presence of a spiking motif of address b and at time t by using the transpose convolution operator. This consists in using the emitting field \mathcal{S}_a of presynaptic neurons in place of the receptive field \mathcal{S}^b of postsynaptic neurons. It thus comes that when observing A , then one may infer the logit of the probability as the sum of evidences:

$$p(b, t) = \sigma(K_B(b) + \sum_{a \in \mathcal{S}^b, 0 \leq \delta \leq D} A(a, t - \delta) \cdot K_a^T(b, \delta))$$

This also takes the form of a temporal convolution. This assumption holds as long as the kernels are uncorrelated, a condition which is met here numerically by choosing a relatively sparse set of synapses (approximately 1% of active synapses). Finally, we compute \hat{B} by selecting the most likely items, allowing to identify the spiking motifs in the input raster plot (see Figure 2d).

One may naturally extend this algorithm when the spiking motifs (that is, the weights) are not known, but that we know the timing and identity of the spiking motifs. Indeed, the equation above is differentiable. Indeed, the activation function of our spiking neural is a sigmoid function implementing a form of Multinomial Logistic Regression (MLR) [10]. The underlying metric is the binary cross-entropy, as used in the logistic regression model. In particular, if we consider kernels with similar decreasing exponential time profile, one can prove that this detection model is similar to the method of [2]. In our specific case, the difference is that the regression is performed in both dendritic and delay space by extending the summation using a temporal convolution operator.

3 Results

To quantify the efficiency of this operation, we generated $M = 144$ synthetic spiking motifs as random independent kernels over $N = 128$ presynaptic inputs and $D = 31$ possible delays. We drew random independent instances of B with a length of $T = 1000$ time steps and an average of 1.0 spikes per neuron. This allowed us to generate raster plots, which we use to infer \hat{B} . We compute accuracy as the rate of true positive detections (both for inferring the address and its exact timing) and observe on average $\approx 98\%$ correct detections.

We extended this result by showing how accuracy evolves as a function of the number of simultaneous spiking motifs, holding the frequency of occurrence constant. We show in Fig. 3 (left) that the accuracy of finding the right spiking motif is still above 80% accuracy with more than 1364 overlapping spiking motifs. This observation illustrates quantitatively the capacity of the HD-SNN in representing a high number of simultaneous patterns. Furthermore, we show in Fig. 3 (middle) that (with $M = 144$ spiking motifs fixed) the accuracy increases

significantly with increasing temporal depth D of the spiking motif kernel, quantitatively demonstrating the computational advantage of using heterogeneous delays. These results were obtained under the assumption that we know the K . However, this is generally not the case, for example, when considering the raster plot of a population of neurons.

Finally, we evaluated the performance of the supervised learning scheme in inferring the connection kernel when the address and timing of spiking motifs are known. The kernel was initialized with random independent values, and we used stochastic gradient descent with a learning rate of $1e-4$ over $1e4$ trials (i.e., over rasters as defined above with $T = 1000$ and $N = 128$). Qualitatively, the convergence was monotonous, and the correct values of the $M = 144$ spike motifs were quickly recovered. Quantitatively, the correlation between the true and learned kernel weights showed that all kernels were correctly recovered (see Figure 3, right). Performing inference with the learned weights was as efficient as with the true kernels, and showed no significant difference (not shown).

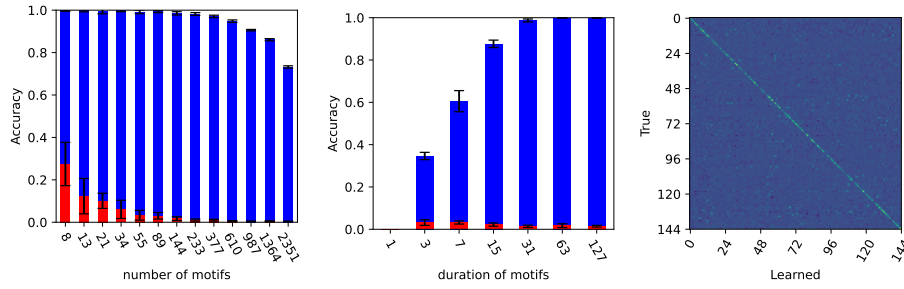


Fig. 3. Detecting spiking motifs using spiking neurons with heterogeneous delays. Accuracy of detection for the classical correlation (red) and the HD-SNN method (blue) as a function of **(Left)** the number M of kernels, **(Middle)** the temporal depth D of kernels among $M = 144$ kernels. **(Right)** Correlation matrix of true vs learned kernels.

4 Discussion

4.1 Synthesis and Main Contributions

In summary, in this paper we have introduced a heterogeneous delay SNN model that we have evaluated for the detection of spiking motifs in a synthetic model of neurobiologically-inspired raster plots.

We highlight some innovations in the contributions of this paper. First, the generic heterogeneous model is formalized from first principles for optimal detection of event-based spatiotemporal motifs. The model is evaluated on realistic data, while models like the tempotron are tested on simplified problems [12]. We have shown that the model accurately detects the exact identity and timing

of spiking motifs, even when many are superimposed, provided that the spiking motifs are known. Compared to methods that use a correlation-based heuristic [6,37], our method is found to be more efficient.

Second, compared to other event-based methods such as HOTS [19], the weights are explicable. They are directly related to the logit (inverse sigmoid of the probability) of detecting each spatiotemporal spike motif. Finally, another novelty is that while, for example, the polychronization model [16] learns only the weights using STDP, this model learns the weights and the delays simultaneously.

4.2 Main limits

We have identified several limitations of the model, which we will now discuss. First, the entire framework is based on discrete time binning. This is incompatible with the continuous nature of biological time. We took advantage of this binning to efficiently implement the framework on conventional hardware, particularly GPUs, and in particular to leverage one-dimensional temporal convolutions. However, it is possible to extend the HD-SNN formalism to a purely event-based SNN framework [8] by analytically including a precision term in the temporal value of the input spikes. As a result, promising speedups and energy gains for such computations could be achieved with such a purely event-based scheme.

Another limitation is that this model is purely feed-forward. Thus, the spikes produced by the postsynaptic neurons are generated solely on the basis of information contained in the classical receptive field. However, it is well known that neurons in the same layer can interact via lateral interactions, for example in V1, and that this can be the basis for computational principles [5]. Furthermore, neural information is modulated by feedback information, e.g. to distinguish a figure from its background [31], and it has been shown that feedback may be essential for building realistic models of primary visual areas [3], especially to explain non-linear mechanisms [4]. It is currently not possible to implement these recurrent connections in our implementation (lateral or feedback), mainly due to our use of convolutions. However, the generic theoretical model is able to incorporate them by inserting new spikes into the list of spikes reaching presynaptic addresses. While theoretically possible, in practice this must be properly tuned so that these recurrent connections do not amplify neuronal activity out of homeostatic state (by extinction or explosion).

For the implementation of predictive or anticipatory processes, such recurrent activity would be essential. This is essential in a neural system because it contains multiple different delays that require temporal alignment [14]. This has already been modeled to explain the flash-lag illusion [17]. As noted above, this could be implemented using generalized coordinates (i.e., variables such as position supplemented by velocity, acceleration, jerk, ...), and “neurobiologically, using delay operators just means changing synaptic connection strengths to take different mixtures of generalized sensations and their prediction errors” [29]. Our proposed heterogeneous delay model provides an alternative and elegant implementation solution to this problem.

4.3 Perspectives

The coding results were obtained under the assumption that we know the kernel K , or using supervised learning by knowing the identity and timing of spiking motifs. However, this is generally not the case, e.g. when observing the neurobiological raster plot of a population of neurons. One perspective would be to extend the model to a fully self-supervised learning paradigm, i.e. without any labeled data [1]. This type of learning is thought to be prevalent in the central nervous system and, assuming the signal is sparse [24], one could extend these Hebbian sparse learning schemes to spikes [27,23].

We expect that this would be particularly useful for exploring neurobiological data [22]. Indeed, there is a large literature showing that brain dynamics often organize into stereotyped sequences such as synfire chains [15], packets [21], or hippocampal sequences [26,35] (for a review, see [9]). These motifs are stereotyped and robust, as they can be activated in the same motif from day to day [13]. In contrast to conventional methods used to process neurobiological data, such an event-based model would be able to answer key questions regarding the representation of information in neurobiological data. Furthermore, it would open possibilities in the field of machine learning, especially in computer vision, to address current key concerns such as robustness to attacks, scalability, interpretability, or energy consumption.

Inspired by the k-means algorithm, it is possible to develop a self-supervised learning algorithm for the automatic detection of spiking motifs. For this, we can initialize K at random and define an auto-encoder scheme that infers the sources \hat{B} for each input A and then resynthesizes the corresponding raster plot. A natural metric is again binary cross-entropy, as used in the logistic regression model. Since the model is differentiable, we can optimize K using gradient descent. We can add a homeostatic regularization on the average firing rate of B to ensure that each motif was *a priori* equally activated [28]. Our preliminary results show that it is possible to retrieve spiking motifs embedded in synthetic data. However, further analysis is needed to improve the convergence of the algorithm and to apply such algorithms to real neurobiological data. In particular, it seems promising to use a sparseness constraint in the inference mechanism to remove spurious correlations in the inference.

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