We consider the problem of reconstructing finite energy stimuli from a finite number of contiguous spikes. The reconstructed signal satisfies a consistency condition: when passed through the same neuron, it triggers the same spike train as the original stimulus. The recovered stimulus has to also minimize a quadratic smoothness criterion. We show that under these conditions, the problem of recovery has a unique solution and provide an explicit reconstruction algorithm for stimuli encoded with a population of integrate-and-fire neurons. We demonstrate that the quality of reconstruction improves as the size of the population increases. Finally, we demonstrate the efficiency of our recovery method for an encoding circuit based on threshold spiking that arises in neuromorphic engineering.

Index Terms— time encoding, spiking neurons, consistent recovery.

1. INTRODUCTION

Formal spiking neuron models, such as integrate-and-fire (IAF) neurons, encode information in the time domain [1]. Assuming that the input is bandlimited with known bandwidth, a perfect recovery of the stimulus from the train of spikes is possible provided that the spike density is above the Nyquist rate [2]. These results hold for stimuli encoded with neuron population models of a wide variety of sensory stimuli including audio [3] or video [4]. More generally, Time Encoding Machines (TEMs) encode analog amplitude information in the time domain using only asynchronous circuits [2]. Time encoding has been shown to be closely related to traditional amplitude sampling. This observation has enabled the application of a large number of results obtained in irregular sampling to time encoding.

A common underlying assumption of TEM models is that the input stimulus is bandlimited with known bandwidth. Although realistic for sensory stimuli, the bandlimitedness assumption has some caveats. Bandlimited functions require an infinite time support and real-time algorithms that operate on finite time intervals are computationally more demanding [5]. Often, a good estimate of the bandwidth is not available because of some nonlinear processing in the transduction pathway or elsewhere (e.g., contrast extraction in vision).

In this paper we investigate the problem of reconstructing stimuli from a population of spike trains on a finite time horizon. The only assumption about the input stimulus is that they have finite energy, i.e., belong to $L^2$ on some time interval $[0,T]$. The reconstruction problem is not one of perfect recovery. Rather signal recovery is consistent and satisfies an optimal smoothness criterion. The consistency condition requires that the reconstructed signal triggers exactly the same spike train when passed through the same neuron as the original stimulus. The maximal smoothness criterion ensures that the problem has a unique optimal solution. The method was introduced in [6, 7] in the context of generalized sampling.

The paper is organized as follows. A brief introduction of time encoding for bandlimited functions is provided in section 2. Section 3 formulates the problem of consistent reconstruction from a finite number of spikes and presents its solution for several types of spiking neuron models that arise in practice. Explicit reconstruction schemes are provided and examples are presented. Finally section 4 concludes our work.

2. TIME ENCODING OF BANDLIMITED STIMULI

Let $\Xi$ denote the space of bandlimited functions with finite energy and bandwidth $\Omega$. Let $u = u(t), t \in \mathbb{R}$, be a signal (stimulus) in $\Xi$. The stimulus biased by a constant background current $b$ is fed into an ideal IAF neuron with threshold $\delta$ and integration constant $\kappa$. Let $(t_k), k \in \mathbb{Z}$, denote the output spike train of the neuron.

A complete description of the encoding circuit above is provided by the $t$-transform. The latter can be written as

$$\int_{t_k}^{t_{k+1}} (b + u(s)) \, ds = \kappa \delta$$

or in inner product form

$$\langle u, g \ast 1_{[t_k, t_{k+1}]} \rangle = \kappa \delta - b(t_{k+1} - t_k) := q_k,$$  \hspace{1cm} (1)

where $g(t) = \sin(\Omega t)/\pi t, t \in \mathbb{R}$, is the impulse response of a low pass filter with bandwidth $\Omega$. Note that from the

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spike train \((t_k), k \in \mathbb{Z}\), a series of projections \(<u, \phi_k>\) with 
\(\phi_k = g * 1_{[t_k, t_{k+1}]} , k \in \mathbb{Z}\), can be obtained. Therefore, stim-
ulus recovery can be readily obtained from these projections; if these projections span the whole space \(\mathcal{Z}\) perfect recovery of the signal is possible. The recovery is in addition stable 
provided that the set \(\{\phi_k\}, k \in \mathbb{Z}\), forms a frame for \(\mathcal{Z}\) [8].

**Theorem 1.** The bandlimited stimulus \(u = u(t), t \in \mathbb{R}\), can be perfectly recovered from the spike train \((t_k), k \in \mathbb{Z}\), if the 
density of the spike train \(D\) satisfies the condition \(D > \Omega/\pi\). 
If this condition holds, the recovered signal takes the form 
\[
u(t) = \sum_{k \in \mathbb{Z}} c_k \psi_k(t),
\]
with \(\psi_k(t) = g(t - s_k), s_k = (t_k + t_{k+1})/2\) and the coefficients \(c_k = |c|_k\) are given in vector form by 
\[
c = G^+ q,
\]
where \(G^+\) denotes the pseudoinverse of \(G\), \([q]_k = q_k\), and the 
matrix \(G\) has entries \([G]_{ki} = \langle \phi_k, \psi_i \rangle, k, l \in \mathbb{Z}\).

**Proof:** The proof is based on density results for frames of 
complex exponentials and frame theory. See [3] for details. □

The key condition for perfect recovery in Theorem 1 calls 
for the spike density to be above a certain threshold which 
depends on the bandwidth of the signal. Thus, there is a deep 
connection between time encoding and traditional amplitude 
sampling. Extensions to encoding bandlimited stimuli as well 
as space-time (video) signals with a population of neurons in 
cascade with receptive fields have also been reported [3,4].

The perfect recovery results mentioned above are based on 
the premise that the bandwidth of the encoded stimulus is 
known. In sensory systems, however, it is common to find that 
the bandwidth of the signal that enters the soma of the neuron is 
unknown. Furthermore, stimuli have limited time support 
and the neurons respond with a 
finite number of spikes.

### 3. RECOVERY OF FINITE-LENGTH STIMULI

Let \(u\) be a signal of finite length and energy, i.e., \(u \in L^2([0, T])\). In what follows we assume that the input stimulus 
\(u\) is fed to a population of \(N\) neurons. Let \(t^j_k\) denote the \(k\)-th
spike of the neuron \(j\), with \(k = 1, 2, \ldots, n_j\), where \(n_j\) is the 
number of spikes that the neuron \(j\) produces, \(j = 1, 2, \ldots, N\). 
As in section 2 the spiking of the neuron can be associated 
with the projection (measurement) of the stimulus on a set 
of functions. Through the use of the \(t\)-transform we can determine both the sampling functions and the result of the 
projection based only on the knowledge of the spike times.

**Definition 1.** A reconstruction based on the spike times 
\((t^j_k), j = 1, 2, \ldots, N, k = 1, 2, \ldots, n_j\) is called consistent 
provided that the reconstructed stimulus \(\hat{u}\) triggers exactly 
the same spike train as the original stimulus \(u\).

**Remark 1.** The consistency condition was introduced in the 
context of signal independent sampling in [9] and requires 
that the reconstructed signal provides the same samples as 
the original one when sampled with the same device, i.e,
\[
\langle u, \phi_k^j \rangle = \langle \hat{u}, \phi_k^j \rangle = q_k^j,
\]
for all \(j = 1, 2, \ldots, N\) and \(k = 1, 2, \ldots, n_j\). Note however that 
in the neural context, the sampling functions \(\phi_k\) are signal 
dependent.

Since we have a finite number of spikes, the sampling 
functions cannot form a frame for \(L^2([0, T])\) [8] and therefore 
perfect recovery is not possible. We seek instead a con-
sistent reconstruction which is also optimal in the sense of a 
certain criterion. We choose the plausible criterion of maxi-
mum smoothness which is equivalent to minimizing \(\|\hat{u}''\|^2\). If 
a reconstruction \(\hat{u}\) satisfies the above, it is called the optimal 
consistent reconstruction of \(u\).

The following notation will be used throughout this 
section. The vector \(q\) is a column vector defined as \(q = \left[q_1^1, \ldots, q_N^N\right]^T\) with \(q^j = \left[q^j_1, \ldots, q^j_{n_j-1}\right]^T, j = 1, 2, \ldots, N\). 
The vectors \(p, r, c\) are of the same dimensions and similarly 
defined. The matrix \(G\) is a block square matrix defined 
as 
\[
G = \begin{bmatrix}
G_{11} & \cdots & G_{1N} \\
\vdots & \ddots & \vdots \\
G_{N1} & \cdots & G_{NN}
\end{bmatrix}
\]
and \(G_{ij} = [G^{|j|}]_{i,j}, i, j = 1, \ldots, N, k = 1, \ldots, n_k - 1, l = 1, \ldots, n_j - 1\).

#### 3.1. Representation with a Population of LIF Neurons

Consider \(N\) leaky integrate-and-fire (LIF) neurons where neu-
ron \(j\) has threshold \(\delta^j\), bias \(b^j\), resistance \(R^j\) and capacitance 
\(C^j\). Neuron \(j\) fires a spike when it’s membrane potential hits 
its threshold and then it resets its membrane potential to 0. 
The \(t\)-transform of the population can be written as 
\[
\int_{t^j_k}^{t^j_{k+1}} \left[u(s) + b^j\right] e^{-\frac{t^j_{k+1} - s}{R^jC^j}} ds = C^j \delta^j
\]
or in inner product form as 
\[
\langle u, \phi_k^j \rangle = q_k^j,
\]
with 
\[
\phi_k^j = e^{-\frac{t^j_{k+1} - t}{R^jC^j}} 1_{[t^j_k, t^j_{k+1}]}(t)\]
\[
q_k^j = C^j \delta^j - b^j R^j C^j \left(1 - \exp \left(-\frac{t^j_{k+1} - t^j_k}{R^jC^j}\right)\right),
\]
for all \(j = 1, 2, \ldots, N\) and all \(k = 1, 2, \ldots, n_j - 1\). We have the following:

**Theorem 2.** Assume that at time 0 the membrane potential o 
of all neurons is at the rest value 0. The optimal consistent

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reconstruction \( \hat{u} \) is unique and can be written as

\[
\hat{u}(t) = a_0 + a_1 t + \sum_{j=1}^{N} \sum_{k=1}^{n_j-1} c_k^j \psi_k^j(t),
\]

where

\[
\psi_k^j(t) = \int_{t_k^j}^{t_{k+1}^j} |t - s|^3 \exp \left( -\frac{(t_k^j - s)^2}{2} \right) ds.
\]

The reconstruction coefficients are given in matrix form by

\[
\begin{bmatrix}
  a_0 \\
a_1 \\
c
\end{bmatrix} = \begin{bmatrix}
p & r \\
0 & G \\
0 & r^T
\end{bmatrix}^+ \begin{bmatrix}
q \\
0 \\
0
\end{bmatrix},
\]

(6)

\[
p_k^j = R^j C^j \left( 1 - e^{-\frac{t_{k+1}^j - t_k^j}{\tau}} \right)
\]

\[
r_k^j = R^j C^j \left( t_{k+1}^j - R^j C^j - (t_k^j - R^j C^j) e^{-\frac{t_{k+1}^j - t_k^j}{\tau}} \right)
\]

\[G_{kl}^{ij} = \langle \phi_k^i, \psi_l^j \rangle.\]

**Proof:** The unique representation result of (4) together with (5) and (6) are a direct consequence of the main result of [6].

To get some intuition, note that the quadratic criterion \( \|\hat{u}\|^2 \) can be written in a bilinear form as \( \langle \mathcal{D} * \hat{u}, \hat{u} \rangle \), where \( \mathcal{D} \) is the fourth order differential convolution kernel

\[
\mathcal{D} = \frac{d^4}{dt^4} \delta(t).
\]

Then, the reconstruction functions of (5) can be obtained as

\[
\psi_k^j = \phi_k^j * f,
\]

(7)

where \( f(t) = |t|^3 \), is a Green’s function for \( \mathcal{D} \), i.e., it satisfies

\[\mathcal{D} * f(t) = \delta(t).\]

Moreover, the set \( \{1, t\} \) forms a basis for the kernel of the quadratic criterion and the entries of \( p \) and \( r \) are given by

\[
p_k^j = \langle 1, \phi_k^j \rangle, \quad r_k^j = \langle t, \phi_k^j \rangle.
\]

(8)

Now \( \hat{u} \) satisfies (3) since from (6) we have that

\[
\begin{bmatrix}
p & r & G
\end{bmatrix} \begin{bmatrix}
a_0 \\
a_1 \\
c
\end{bmatrix} = \begin{bmatrix}
q \\
0 \\
0
\end{bmatrix}.
\]

(9)

Finally, since each neuron starts from its reset level the reconstructed signal will generate exactly the same spike times. Thus, the reconstruction is consistent.

**Fig. 1.** Consistent reconstruction from a finite number of spikes with an ensemble of LIF neurons.

An example of the performance of the consistent recovery algorithm is shown in Fig. 1. The input stimulus was a bandlimited function with \( \Omega = 2 \pi 100 \text{ rad/sec} \) restricted to the time interval [0, 200] msec. Four different LIF neurons encoded the stimulus. As it can be seen, the signal-to-noise ratio increases with the number of neurons, i.e., the number of spike trains, used for recovery. This is consistent with the evolutionary intuitive argument that increasing the number of neurons leads to an improved representation of the sensory world.

### 3.2. Representation with an ON-OFF AER Neuron

In this section we consider a silicon neuron model that has been used in the context of address event representation (AER) for silicon retina and related hardware applications [10]. The spiking mechanism is threshold based and simple reset mechanisms are included (see Fig. 2). The ON-OFF AER generates a spike whenever a change \( \delta \) is detected. The \( t \)-transform of the ON-OFF AER neuron amounts to

\[
u(t_k^j) = u(0) + \delta \cdot \left( k - \sum_{l=1}^{n_2} 1_{\{t_l < t_k^j \}} \right) = q_k^j
\]

\[
u(t_k^j) = u(0) - \delta \cdot \left( k - \sum_{l=1}^{n_1} 1_{\{t_l < t_k^j \}} \right) = q_k^j
\]

As in the previous examples, the above equalities can also be expressed in inner product form of (3) with \( \phi_k^j(t) = \delta(t - t_k^j) \) for all \( j, j = 1, 2 \) and all \( k, k = 1, \ldots, n_j \). Note that in this case, the spiking of the silicon neuron acts as an irregular sampler on the input stimulus. We have the following theorem:

**Theorem 3.** The optimal consistent reconstruction \( \hat{u} \)

\[
\hat{u}(t) = a_0 + a_1 t + \sum_{j=1}^{N} \sum_{k=1}^{n_j} c_k^j \psi_k^j(t),
\]

(11)

\[\frac{\text{Amplitude}}{\text{Time [sec]}}\]

\[\begin{bmatrix}
1 \text{ Neuron SNR=14.9dB} \\
2 \text{ Neurons SNR=26.2dB} \\
3 \text{ Neurons SNR=31.4dB} \\
4 \text{ Neurons SNR=35.1dB}
\end{bmatrix}\]

\[\frac{\text{Amplitude}}{\text{Time [sec]}}\]
We presented a new framework for the recovery of stimuli encoded into a finite number of spikes. The framework assumes that a parametric description of the encoding mechanism is available. Assuming that the recovered signals satisfy a quadratic smoothness criterion, we derived a consistent reconstruction algorithm. We demonstrated that the algorithm performs well in practice and that it is suitable when certain signal characteristics are unknown. Our work further enhances the view of neural encoding as a set of projections of the stimulus on a family of sampling functions; it thereby builds a strong connection between representation in the spike domain and traditional sampling theory. The effects of noise as well as recovery algorithms for stimuli encoded with more complex neural circuits will be presented elsewhere.

4. CONCLUSIONS

We presented a new framework for the recovery of stimuli encoded into a finite number of spikes. The framework assumes that a parametric description of the encoding mechanism is available. Assuming that the recovered signals satisfy a quadratic smoothness criterion, we derived a consistent reconstruction algorithm. We demonstrated that the algorithm performs well in practice and that it is suitable when