

Integrate-and-Fire Neuron Modeled as a Low-Rate Sparse Time-Encoding Device

Praveen K. Yenduri, Anna C. Gilbert and Jun Zhang

Abstract—Neurons as Time Encoding Machines (TEMs) have been proposed to capture the information present in sensory stimuli and to encode it into spike trains [1], [2], [3]. These neurons, however, produce spikes at firing rates above Nyquist, which is usually much higher than the amount of information actually present in stimuli. We propose a low-rate spiking neuron which exploits the sparsity or compressibility present in natural signals to produce spikes at a firing rate proportional to the amount of information present in the signal rather than its duration. We consider the IAF (Integrate-and-Fire) neuron model, provide appropriate modifications to convert it into a low-rate encoder and develop an algorithm for reconstructing the input stimulus from the low-rate spike trains. Our simulations with frequency-sparse signals demonstrate the superior performance of the *Low-Rate IAF* neuron operating at a sub-Nyquist rate, when compared with IAF neurons proposed earlier, which operate at and above Nyquist rates.

I. INTRODUCTION

IT is a common belief that neurons encode sensory information in the form of a sequence of action potentials (nerve impulses or “spike trains”). The fundamental unit of a “message” conveyed by a neuron is a single nerve impulse, propagating at high speed down its axon through well-understood electro-chemical processes [4]. These “spike trains” are interpreted by other neurons, leading to sensation and action. Fig. 1 illustrates a spike train produced by an auditory nerve cell. When we hear something, our brain is not actually interpreting the modulations in the acoustic waveform, but rather the spike trains generated, in response to the stimulus, by thousands of auditory nerves. In other words, spike trains form the language that the brain uses to communicate between neurons. Hence, understanding how a neuron encodes the stimulus or input signal into spike trains is of great interest.

Neurons generate spikes at relatively low rates, presumably due to a metabolic reason [5]. Metabolically efficient coding [6] is indicative of sparse encoding. Further, it has been observed that the process of spike encoding exhibits variability or randomness in response to identical inputs [7]. That is, for the same input stimulus, the neuron may produce different spike trains (as shown in Fig. 1). We are interested in developing a sparse encoding model of neuron that explains these observed features of spike trains.

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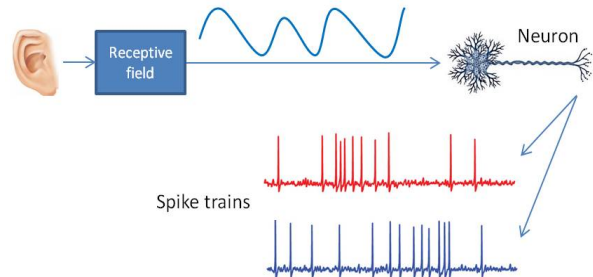


Fig. 1. Spike trains produced by an auditory neuron

Integrate-and-fire (or IAF, in short) models for neurons as generating time-stamp codes have been studied in [1] and [3]. Lazar et al. proved that a band-limited signal encoded by the precise spike timing of an IAF neuron can be reconstructed with reasonable accuracy from the spike train, when the average firing rate is above Nyquist rate [1]. When no other information is available about the input signal except its bandwidth, the signal has to be encoded at above Nyquist rate for successful recovery. However, most natural signals are often sparse or compressible in some orthonormal basis and hence the actual information present in the signal is usually much lower than the Nyquist rate.

From an information theoretic point of view, a sparse encoding neuron should be able to encode such signals using spike trains that have a rate proportional to the amount of information actually present in the signals. In other words, most natural signals live in a low dimensional space and an efficient encoder should be able to capture the low dimensional information from the high dimensional signal. In this paper, we develop an efficient model of a sparse encoding neuron, which we call the *Low-Rate IAF* neuron, by performing appropriate modifications to a conventional integrate-and-fire model. The Low-Rate IAF neuron exploits the sparsity or compressibility of input signals to encode them into spike trains with rates well below the Nyquist rate. We show that the low-rate spike trains contain enough information about the input stimulus to allow its recovery and develop a neural decoding algorithm based on spike times.

The remainder of the paper is organized as follows. The input signal model is described in Section II. A relevant background on time encoding through integrate-and-fire neurons, including the model proposed by Lazar in [3], is briefly presented in Section III. The proposed Low-Rate IAF neuron is presented in Section IV and is followed by a description of the reconstruction algorithm in Section V. A

set of numerical experiments compare the performance of Lazar's IAF neuron (from [3]) with the proposed Low-Rate IAF neuron in Section VI. We conclude with a discussion on future work in Section VII.

II. INPUT STIMULUS MODEL

The class of input signals is assumed to be band-limited with cutoff frequency W (in Hz) and periodic within a time period D . The Nyquist rate of the input signal space is thus $F_N = 2W$. W and D are related by

$$W = \frac{N}{2D}$$

where N is a positive integer that denotes the dimension of input space. If an input signal/stimulus $x(t)$ is sampled at Nyquist rate for a time duration of D , then the number of samples obtained is $N = F_N D$. Thus the signal $x(t)$, observed for a time duration D , can be represented as a vector x of length N in discrete domain, where

$$x[i] = x(i/F_N)$$

for $i = 1, \dots, N$. The signal $x(t)$ is further assumed to be S -sparse or compressible in frequency domain. A signal is called S -sparse in the frequency domain, if the DFT (discrete Fourier transform) of the signal samples at Nyquist rate has only S non-zero terms. That is, if X represents the DFT of vector x , then X has at most S non-zero elements. A signal is called S -compressible¹ in frequency domain, if the sorted list of its DFT coefficients has only S significant or dominant terms, compared to which the other terms are negligible. Thus, a compressible signal is one that is reasonably well approximated as a sparse signal.

The input signal can be expressed as a linear combination of complex exponentials as follows:

$$x(t) \approx \sum_{m=1}^S c_m \exp(j2\pi f_m t)$$

where $f_m, m = 1, \dots, S$ are the S dominant frequencies which lie in the interval $[-W, W]$ and c_m are the corresponding coefficients. We further assume that the input signal is real-valued, hence S is even and one set of frequencies are the negative of the other set. Thus, the input stimulus is a mixture of periodic waveforms, which is consistent with the brain mechanism of generating and entraining oscillations at multiple frequencies simultaneously.

III. TIME ENCODING WITH INTEGRATE-AND-FIRE NEURONS

In this section we review the time encoding machine (TEM) consisting of an integrate-and-fire (IAF) neuron [1], [2], [3]. Neurons encode continuous time sensory stimuli into discrete time events, i.e. the firing of action potentials at variable time points. Time encoding is an answer to

¹We call X , S -compressible, if it is well approximated as a S -sparse signal, $\|X - X_{(S)}\|_2 \leq C \cdot S^{-\alpha}$ for some constants C and $\alpha > 0$, where $X_{(S)}$ is the S -sparse signal that best approximates X .

one of the key questions arising in information processing, which is, how to represent a continuous signal as a discrete sequence. In conventional sampling, a band-limited signal is represented by set of amplitude samples spaced uniformly. If the uniform spacing is chosen to satisfy the Nyquist rate condition, the signal can be recovered perfectly, under no noise, through sinc interpolation. This is the well-known Shannon sampling theorem. In contrast, time-encoding of a real-valued band-limited signal is an asynchronous process of mapping the amplitude information into a strictly increasing sequence of time points. A time encoding machine (TEM) is a realization of such encoding. The reconstruction of input signal from the sequence of time points is referred to as time decoding.

A. Preliminaries

A typical IAF TEM neuron is schematically shown in Fig. 2. A constant bias b ($b > 0$ such that $x(t) + b > 0, \forall t$) is added to the input signal, which is then fed to the integrator. When the output of the integrator crosses a threshold δ , a spike is produced. The spike triggers a zero reset of the output of the integrator. The output of the TEM is thus a sequence of spikes at time points, $\{t_k\}$, that models the spike train produced by a neuron.

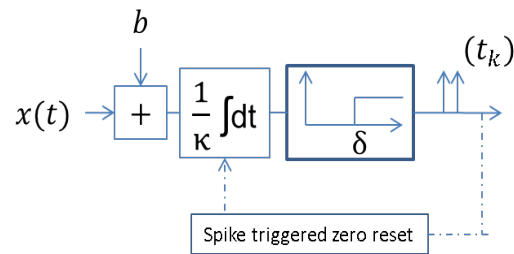


Fig. 2. Time encoding with an integrate-and-fire (IAF) neuron

Let K denote the number of spikes produced by the IAF neuron in the duration D for which the input stimulus is observed. From simple calculations we can easily derive,

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

for $k = 0, \dots, K - 1$, where t_0 is the time point at which we begin to observe the signal. If $|x(t)| \leq c, \forall t$, then the inter-spike-interval is bounded by,

$$\frac{\kappa\delta_k}{b+c} \leq t_{k+1} - t_k \leq \frac{\kappa\delta}{b-c}$$

It has been proved [1][2] that a successful recovery of x is possible when,

$$\frac{\kappa\delta}{b-c} < \frac{1}{2W}$$

that is, the maximum inter-spike-interval is smaller than the Nyquist period $T_N = 1/F_N = 1/2W$. Hence, the TEM IAF neurons encode all input signals at an average rate greater than the corresponding Nyquist rate.

B. Integrate-And-Fire Neurons with Random Thresholds

To model the variability or randomness characteristic of neuronal spike trains, neurons with random thresholds were proposed in [8]. An IAF neuron model with random thresholds is studied by Lazar in [3]. The model is identical to the TEM shown in Fig. 2, but with random thresholds δ_k . Every output spike not only resets the integrator output but also triggers the random selection of a new threshold δ_k . The random thresholds are assumed to be drawn from a Gaussian distribution with known mean δ and variance σ^2 .

For random thresholds TEM, let us define a measurement vector q and error vector ε of length K , as follows. For $k = 0, \dots, K - 1$,

$$q_k = \kappa\delta - b(t_{k+1} - t_k),$$

$$\varepsilon_k = \kappa(\delta_k - \delta).$$

Time-encoding can be expressed as the following system of equations,

$$GX = q + \varepsilon$$

where X is the N -point DFT of vector x and G (of size $K \times N$) is given as

$$G_{k,n} = \int_{t_k}^{t_{k+1}} e^{j2\pi \frac{n}{N} F_N s} ds$$

for $k = 0, \dots, K - 1$ and $n = -N/2, \dots, N/2$ (assuming N is even and with a slight abuse of notation).

A weighted least squares with ℓ_2 penalty is used for reconstructing an approximation \tilde{X} of X from q

$$\tilde{X} = \operatorname{argmin} \|q - GX\|^2 + K\lambda \|X\|^2.$$

Here, λ is a positive smoothing parameter that regulates the trade-off between faithfulness to the measurements and smoothness. The regularization is used to prevent over-fitting due to the noisy data.

For a successful recovery, the method requires that the average spike rate be above Nyquist rate [3]. In other words, we need the number of spikes $K > N$. Note that N is the number of samples at Nyquist rate and hence Lazar's TEM neuron is firing at rates above Nyquist. In the next section we develop a low-rate model of IAF neuron that fires at a sub-Nyquist rate.

IV. THE LOW-RATE INTEGRATE-AND-FIRE NEURON

We introduce appropriate modifications in the TEM IAF neuron and develop a low-rate IAF neuron model. The *Low-Rate* IAF neuron schematical is shown in Fig. 3. We use fixed thresholds (δ) as opposed to random thresholds used in Lazar's model. The randomness in inter-spike-interval exhibited in neuronal spike trains is produced by an additional component that switches off the IAF circuit for a random amount of time τ_k (with mean μ) after each spike (see Fig. 3). The process of switching off the IAF circuit mimics the "absolute refractory" period exhibited by a neuron. After a single impulse, a dormant period occurs during which no other impulse can be initiated [4], which is called the

"refractory" period. We model this refractory period as a random variable to account for the randomness in neuronal spike trains in response to identical inputs.

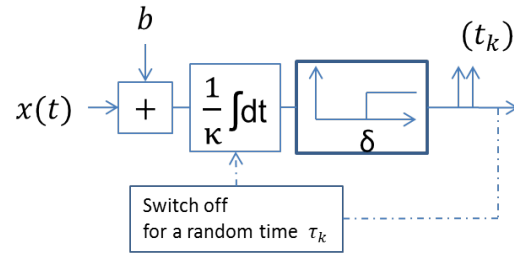


Fig. 3. Sparse time encoding with Low-Rate integrate-and-fire (IAF) neuron.

The time durations τ_k are assumed to be uniformly distributed with mean μ . The operational equation of time-encoding can be obtained as follows,

$$\int_{t_k + \tau_k}^{t_{k+1}} x(s) ds = \kappa\delta - b(t_{k+1} - t_k - \tau_k)$$

for $k = 0, \dots, K - 1$. Similar to Section III, we define measurement vector q and matrix G as follows,

$$q_k = \kappa\delta - b(t_{k+1} - t_k - \tau_k)$$

$$G_{k,n} = \int_{t_k + \tau_k}^{t_{k+1}} e^{j2\pi \frac{n}{N} F_N s} ds$$

for $k = 0, \dots, K - 1$ and $n = -N/2, \dots, N/2$.

In an actual implementation of the Low-Rate IAF neuron in hardware, the time durations τ_k can be generated using a pseudo-random number generator such as linear feedback shift register (LFSR). If the seed that is used to initialize the LFSR is assumed to be known, then τ_k can be computed by the reconstruction algorithm. An alternative is to actually measure τ_k using a time to digital converter (TDC). The measurements q_k can thus be computed by the reconstruction algorithm.

The low-rate neuron produces spikes at a sub-Nyquist rate determined by the parameters δ and μ . Let K denote the number of spikes produced in duration D , then $K < N$. We are interested in solving for X (the N -point DFT of input signal) given t_k for $k = 0, \dots, K - 1$, i.e., we want to solve the following linear system of equations for the case when $K < N$,

$$GX = q + \xi$$

where ξ is a noise vector, which can model additive noise at the input or a time jitter noise in measuring t_k . The problem is ill-posed in general, since it is under-determined and has infinitely many solutions. But under the assumption that X is sparse or compressible (as described in Section II), it may be possible to uniquely recover X . We develop a new recovery technique to reconstruct X , which is described in the next section.

V. THE RECONSTRUCTION ALGORITHM

Given the measurements $q = GX + \xi$ of a sparse or compressible signal X (of length N), with number of measurements $K < N$, the novel area of *Compressive Sensing* (CS) offers explicit constructions or distributions on matrices G and algorithms such as those proposed in [9],[10] and [11], to recover an approximation of X (denoted by \tilde{X}). One line of research assumes that the measurement matrix G satisfies a property called the restricted isometry (RIP) [11], and uses either greedy iterative algorithms ([9],[10],[12]) or convex optimizations to obtain \tilde{X} . Another line of research designs matrices G and algorithms jointly, optimizing for reconstruction time [13], storage requirements of G , or physical realizability [14] of measurement with matrix G . The matrix G produced by an IAF time-encoding system (whether deterministic or random) does not necessarily satisfy the RIP condition. Hence, following the second line of research, we co-designed the measurement system (i.e. the Low-Rate IAF neuron model) and the recovery algorithm, keeping in mind the physical realizability of the TEM as well as the TDM (time decoding machine). In this section, we describe the reconstruction algorithm developed for the Low-Rate IAF neuron model presented in Section IV. We begin by transforming $GX = q$ into a new system of equations $BX = y$ by doing the following.

From mean value theorem, we know that there exists $s_k \in (t_k + \tau_k, t_{k+1})$ such that

$$x(s_k)(t_{k+1} - t_k - \tau_k) = \int_{t_k + \tau_k}^{t_{k+1}} x(s) ds.$$

Thus we can define s_k for $k = 0, \dots, K - 1$ and the corresponding signal amplitudes as

$$y_k = x(s_k) = \frac{q_k}{(t_{k+1} - t_k - \tau_k)}.$$

We define a new measurement vector y in this manner. The N -point DFT X and measurement vector y can be related as

$$BX = y,$$

where the new measurement matrix B (of size $K \times N$) is given by

$$B_{k,n} = e^{j2\pi \frac{n}{N} F_N s_k}$$

for $k = 0, \dots, K - 1$ and $n = -N/2, \dots, N/2$. Note that B is not really a sub-DFT matrix, since $s'_k s$ do not have to lie on a Nyquist time grid.

A pseudo-code of the reconstruction algorithm is presented in Table I. For a vector z , $\text{supp}(z)$ is defined as the set of indices of the non-zero elements of z and $z_{(s)}$ stands for the best s -term approximation² of z . For an index set $T \subset \{1, 2, \dots, N\}$, z_T stands for a sub-vector of z containing only those elements of z that are indexed by T . Similarly G_T

²The best s -term approximation of a vector z can be obtained by equating all the elements of z to zero, except the elements that have the top s magnitudes.

stands for a sub-matrix of G containing only the columns of G indexed by T .

The matrix B is similar to the matrix used in [14] and hence we use the algorithm developed in [14] to estimate the indices of the dominant terms in X , that is, we identify the dominant frequencies in X . The largest components in $B^H y$ provide a good indication of the largest components in X [14]. The algorithm applies this idea iteratively to reconstruct an approximation to the signal X . At each iteration, the current approximation induces a residual, which is the part of the signal that has not been approximated yet. The current approximation vector \tilde{X} is initialized to a zero vector and the residual is initialized to the measurement vector y . At the end of iterations, once the dominant frequencies are identified (denoted by index set T in Table I), their coefficients (i.e. the elements of \tilde{X}_T) are then estimated through performing a least squares with a truncated matrix G_T . We approximate $s_k = (t_{k+1} + t_k + \tau_k)/2$.

The reconstruction algorithm	
INPUT:	N (signal length), S (sparsity), $(s_k, y_k), k = 0, 1, \dots, K - 1$.
OUTPUT:	\tilde{X} (S -sparse approximation to X , length N)
$\tilde{X}^{(0)} = \underline{0}$, residual $r^{(0)} = y$	
for $i = 0, 1, 2, \dots$	
	$\tilde{X}^{(i+1)} = [\tilde{X}^{(i)} + B^H r^{(i)}]_{(S)}$
	$r^{(i+1)} = y - B\tilde{X}^{(i+1)}$
	until $\ r^{(i+1)}\ _2$ does not vary within a tolerance θ .
	$T = \text{supp}\{\tilde{X}\}$
	$\tilde{X}_T = (G_T^H G_T)^{-1} G_T^H y$ (Least Squares)
	$\tilde{X}_{T^c} = 0$

TABLE I
THE RECONSTRUCTION ALGORITHM

The computationally intensive step of least squares is performed only once in the algorithm. The least squares is implemented using the accelerated Richardson iteration [15] with runtime of $O(SK \log(2/e_t))$ where e_t is a tolerance parameter. The structure of the measurement matrix lends us to use the inverse NUFFT [16] with cardinal B-spline interpolation for forming the products of the form $B^H r$, in a runtime of $O(N \log N)$. Hence the total runtime of the algorithm is dominated by $O(IN \log N)$ where I is the number of iterations which has a gross upper bound of $\log N$. In practice, we find that the approximation $s_k \cong (t_{k+1} + t_k + \tau_k)/2$ is good when the threshold δ is small enough. It is possible to update $s_k, k = 0, \dots, K - 1$ using the current approximation \tilde{X} at the end of each iteration, by using Newton's method for example. More sophisticated methods might yield better results.

VI. RESULTS AND DISCUSSION

Lazar's TEM neuron and our Low-Rate IAF neuron are simulated in MATLAB, along with the reconstruction algorithms. We compared the performance of our Low-Rate neuron firing at sub-Nyquist spike-rate with TEM neurons

in [3] operating at and above Nyquist rate. We define the sparse-encoding ratio of Low-Rate IAF neuron as $\frac{K}{N}$, which implies that the firing rate of the neuron is $\frac{K}{N}F_N$. The input signal, as explained, is assumed to be a mixture of sinusoidal waveforms of S frequencies. Because we inject additive white Gaussian noise into the input signal, we use the traditional measure of signal-to-noise ratio (SNR) as the performance metric. The output SNR³ is defined as the ratio between the signal energy and the reconstruction error, whereas the input SNR is defined as the ratio between signal energy and noise energy.

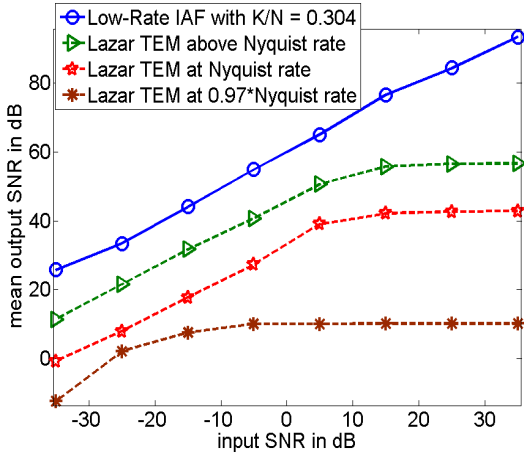


Fig. 4. Output SNR vs input SNR for signals with $S = 10$

In the first experiment, we choose $S = 10$ and compare the recovery performance of Lazar’s TEM neuron and Low-Rate IAF neuron. The sparse-encoding ratio of Low-Rate neuron is chosen as $K/N = 0.3052$. Fig. 4 plots the mean output SNR vs. input SNR. We see that the Low-Rate IAF neuron (even when operating at about one third the Nyquist rate in this example) outperforms the TEM neurons (which are not sparse encoders) operating at and above Nyquist rates. Moreover, we see that Lazar’s reconstruction degrades significantly when the average firing rate of TEM neurons is reduced to about $0.97F_N$.

In the next experiment, we choose $S = 60$. Mean output SNR vs. input SNR is plotted in Fig. 5 for Low-Rate IAF neuron operating at different rates and Lazar’s TEM neuron operating at about twice the Nyquist rate. To match the performance of Lazar’s TEM neuron at twice the Nyquist rate, we need to set the firing rate of the Low-Rate IAF neuron to about 0.38 times the Nyquist rate. Fig. 5 demonstrates that an increase in sparse-encoding ratio K/N improves the performance of the Low-Rate IAF neuron.

VII. CONCLUSION AND FUTURE WORK

We proposed a model for a sparse encoding neuron, called the Low-Rate IAF (integrate-and-fire) neuron, which is an adaptation of the TEM IAF model proposed by Lazar [1],

³Output SNR(dB) = $20 \log(\|X\|_2 / \|X - \tilde{X}\|_2)$, where X is the input signal and \tilde{X} is the output of the algorithm

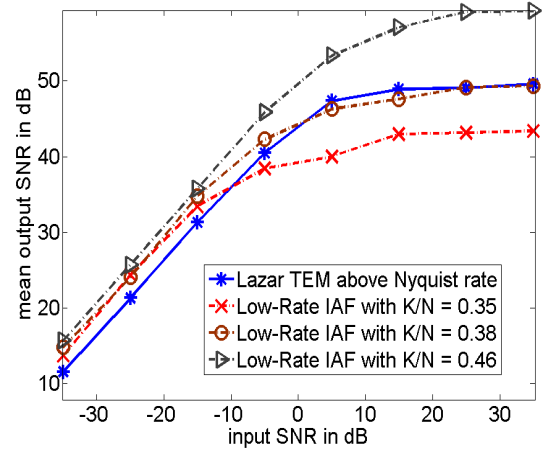


Fig. 5. Output SNR vs input SNR for signals with $S = 60$

[2], [3]. Lazar’s TEM model produces spikes above Nyquist rate, which is usually much higher than the amount of information actually present in the input sensory stimuli. By exploiting the sparsity, the Low-Rate IAF neuron encodes input stimulus into spike trains with average firing rate well below Nyquist rate, while using the spike timing information in a smart manner to improve the performance of stimulus recovery. The developed reconstruction algorithm is computationally efficient and can be tailored for practical hardware implementations. A number of other time-encoding neuron models, including many other IAF architectures, have been proposed in the literature. The methodology of low-rate or sparse encoding, along with the developed reconstruction algorithm, can be extended to these neuron models. This direction will be explored in the future. We are also interested in investigating the application of our Low-Rate neurons in developing a sparse encoding model for videos. The classification of input stimuli from low-rate spike trains is another potential future direction.

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