Time Encoding with Integrate-and-Fire Neurons

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Abstract

Time encoding is a mechanism of mapping amplitude information into a time sequence. We show that time encoding with integrate-and-fire neurons provides, under natural conditions, an invertible representation of information, i.e., a sensory stimulus can be recovered from its multidimensional spike train representation loss-free.

1 Introduction

A key question arising in theoretical neuroscience is how to represent an arbitrary stimulus as a sequence of action potentials [1]. The temporal requirements imposed on this representation might dependent on the information presented to the sensory neurons. For example, the temporal precision of auditory processing involves measurements of interaural time delays with sub millisecond accuracy [5]. Rapid intensity transients appear to be a key stimulus feature for triggering precisely timed spikes [10]. The nervous system uses ensembles of neurons to encode information but direct experimental insights into the operation of biological neural networks is scarce [11].

In [7] the question of stimulus (signal) representation was formulated as one of time encoding, i.e., as one of encoding amplitude information into a time sequence. Formally, a time encoding of a bandlimited function $x(t), t \in \mathbb{R}$, is a representation of $x(t)$ as a sequence of strictly increasing times $(t_k), k \in \mathbb{Z}$ (see Figure 1). The bandlimited function models the stimulus whereas the time sequence models the spike train.

There are two natural requirements that a time encoding mechanism should satisfy. The first is that the encoding should be implemented as a real-time *asynchronous circuit*. Secondly, the encoding mechanism should be *invertible*, that is, the amplitude information can be recovered from the time sequence with arbitrary accuracy. A Time Encoding Machine (TEM) is the realization of such an encoding mechanism.

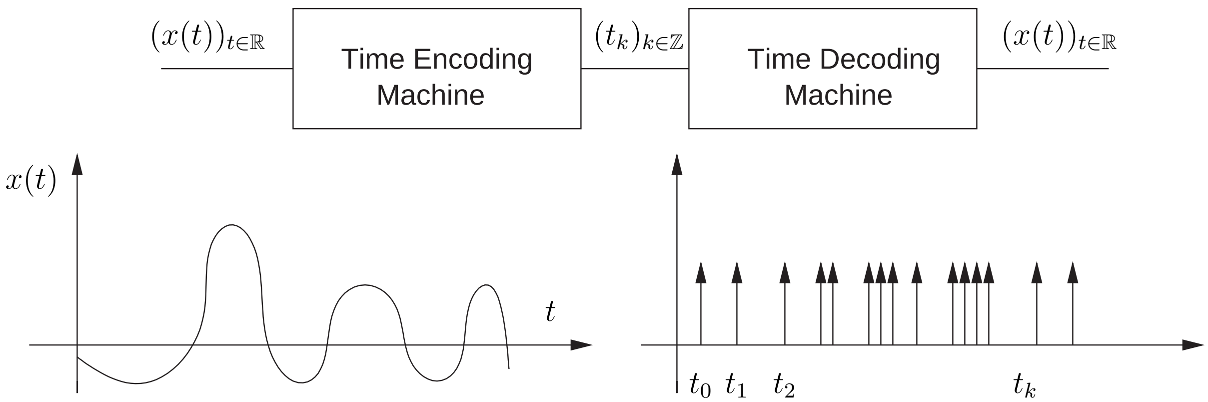

Figure 1: Time Encoding and Decoding.

The first example of a Time Encoding Machine satisfying the above requirements was given [7]. It consists of a feedback loop that contains an adder, a linear filter and a noninverting Schmitt trigger. Such a circuit models a neuron with feedback. The invertibility property of the TEM is due to a representation of the bandlimited function $x(t)$, $t \in \mathbb{R}$, as a discrete set of integral values $\int_{t_k}^{t_{k+1}} x(u)du$ evaluated on time intervals that satisfy in average the Nyquist rate. Hence, under simple conditions, bandlimited signals encoded with the Time Encoding Machine can be recovered loss-free from the time sequence at its output. A Time Decoding Machine (TDM) is the realization of an algorithm for stimulus recovery with arbitrary accuracy.

The average rate of $(t_k)_{k\in\mathbb{Z}}$ in [7] is proportional with the bandwidth of the stimulus. Clearly the output of a neuron can not support large spike averages and a natural physical limit has to be imposed in modelling of sensory neurons. The receptive fields arising in a number of sensory systems, including the retina [9] and the cochlea [5] have been modelled as a bank of filters, with each of the filters feeding a signal into an integrate-and-fire neuron. Such a model is a possible realization of time encoding with integrate-and-fire neurons. This model raises a number of questions. The one addressed in this paper is whether such a model is invertible and if so, what algorithm achieves perfect stimulus recovery.

Using the theory of frames ([3], [4]) we shall derive a channelization of the bandwidth of the stimulus that leads to a multidimensional time encoding representation of the stimulus $(t_k^m)_{k\in\mathbb{Z}}, 1 \le m \le M$, where M is the number of channels. By choosing M, the transfer function of the filters describing the filter bank, and the parameters of the integrate-and-fire neuron model, the average spike rate at the output of each integrate-and-fire neurons can be controlled. We shall demonstrate that time encoding based on filter banks and integrate-and-fire neurons provides, under certain natural conditions, an equivalent representation of information, i.e., the stimulus $(x(t))$, $t \in \mathbb{R}$, can be recovered loss-free from its multidimensional spike train representation (t_k^m), $k \in \mathbb{Z}$ and $m = 1, 2, ..., M$. If the m'th integrate-and-fire neuron is characterized through an arbitrary, possibly time varying threshold $\delta^m(t)$, $k \in \mathbb{Z}$ and $m = 1, 2..., M$ that satisfies a simple upper bound condition the stimulus can be perfectly recovered if $(t_k, \delta^m(t_k^m))$ is known for all $k \in \mathbb{Z}$ and $m = 1, 2..., M$.

This paper is organized as follows. A canonical model for using integrate-and-fire neurons for time encoding and stimulus recovery is introduced in section 2. Perfect stimulus recovery is detailed in Section 3. The analysis and synthesis of time encoding and decoding is presented in sections 3.1 and 3.2, respectively. Section 4 concludes the paper.

2 A Canonical Model for Time Encoding

The canonical model for time encoding and decoding consists of an information representation (analysis) subsystem and an information recovery (synthesis) subsystem. These are shown in Figures 2 and 4, respectively. The representation subsystem consists of a generic filter bank followed by a cascade of TEMs. The recovery subsystem consists of a cascade of TDMs followed by appropriately chosen filters.

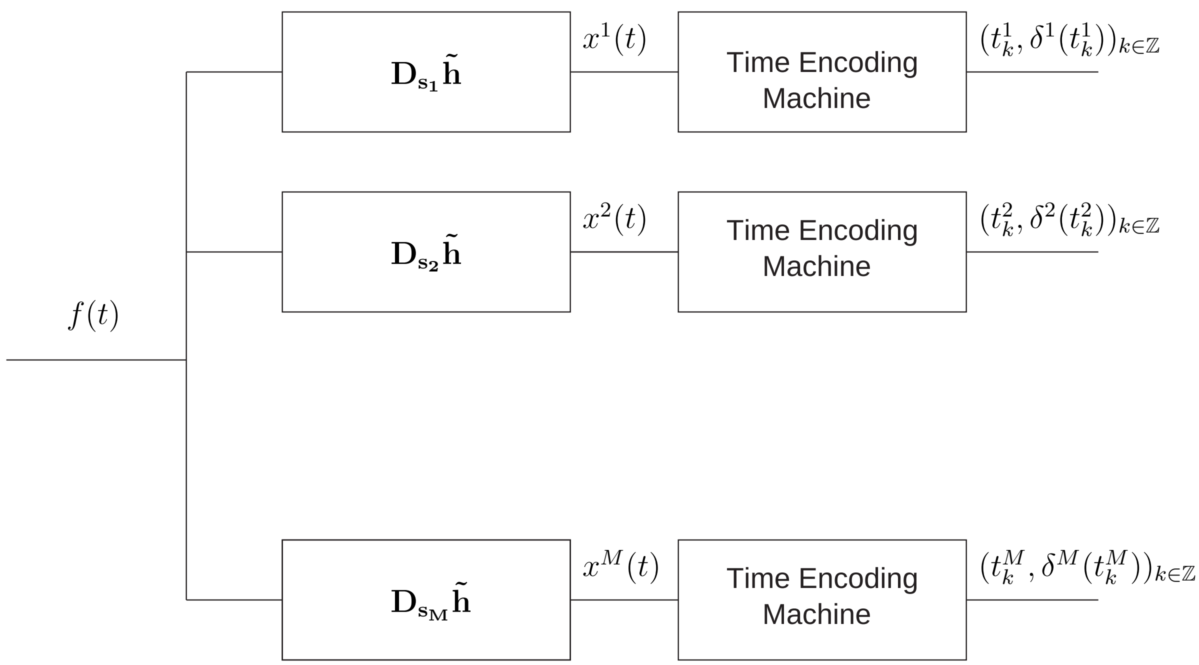

Figure 2: Wavelet Time Encoding.

The filter banks can be designed using various methodologies. The one considered here is based either on the wavelet transform or the Gabor transform ([**?**], [4], [**?**]). The conditions for invertibility on the generated filter banks are quite standard. Informally, they only require that overall no signal frequency is lost due to filtering. This does not rule out overcomplete representations. Since under this condition the filter bank representations (*e.g.*, the wavelet and Gabor) are invertible in their own right, the signal can be recovered loss-free from the multidimensional time sequence. Figures (2) and (4) depict the case where the filter bank is realized using wavelets. In the language of information theory, the Wavelet Time Encoding subsystem might represent the encoder (transmitter side) whereas Wavelet Time Decoding subsystem might represent the decoder (receiver side) of a communication system.

The output of each filter on the transmitter side is encoded with a TEM modelling the operation of an integrate-and-fire neuron. The TEM consists of a bias, an integrator and a thresholding device (see Figure 3). Its basic operation is very simple. The bounded signal $|x^m(t)| \leq c < b$, $m = 1, 2, ..., M$, is biased by a constant amount b before being applied to the integrator. This bias guarantees that the integrator's output $y^m(t)$ is an increasing function of time. When the output of the integrator reaches a (time dependent) threshold value $\delta^m(t_k^m)$, a spike is triggered at time t_k^m at the output of the m'th device. Immediately thereafter the system is reset to an initial state, assumed here to be 0. Therefore, a spike is triggered when the output of the integrator reaches the triggering mark $\delta^m(t_k^m)$ (called a quanta). Using a *signal-dependent* sampling mechanism, the TEM maps the amplitude information of $(x^m(t))$, $t \in \mathbb{R}$, into timing information (t_k^m), $k \in \mathbb{Z}$ and $m = 1, 2, ..., M$. Recovery is only possibly if the threshold function $\delta(t)$ is known at least at the trigger times (t_k^m), $k \in \mathbb{Z}$ and $m = 1, 2, ..., M$.

Filter bank representations of bandlimited signals have been extensively studied in the literature (see, *e.g.*, [2] and the references therein). However, the sampling of the output of the filter bank is achieved by traditional amplitude sampling and, therefore, the data set for representing stimulus information is substantially different from ours. Note that, as in the case of the single TEM, the values of the time sequence $(t_k^m)_{k\in\mathbb{Z}}$ can be represented using N bits. If the threshold function is known, only these values need to be transmitted to the receiver. This represents an enormous reduction of transmission capacity when compared to the scheme provided by [**?**]. The latter operates with clock based sampling and generates an exponentially higher bit rate (N as opposed to $logN$)!

3 Perfect Stimulus Recovery

In what follows we shall show that under certain conditions the Canonical Model allows for perfect stimulus recovery. We shall investigate the structure of the analysis part of the Canonical Model in section 3.1. The synthesis part is presented in section 3.2.

Throughout this paper f will denote the stimulus and h the mother wavelet. s denotes the dilation factor. Both f and h have finite energy, that is $f,\ h \in L^2(\mathbb{R})$. We shall define the following three operators:

- Dilation Operator

$$(D_s h)(u) = |s|^{1/2} h(su) \tag{1}$$

- Translation Operator
$$(\tau_t h)(u) = h(u-t) \tag{2}$$

- Involution Operator
$$\tilde{h}(u) = \bar{h}(-u) \tag{3}$$

where the bar stands for complex conjugate.

3.1 Analysis

As already mentioned we shall consider the filter bank to have a wavelet representation. The mathematical formalism that we are using, however, it it not limited to such a construction. Gabor filter bank constructions will not be explicitly described due to space limitations. However, our methodology covers these constructs as well.

3.1.1 Wavelet Representation

The continuous wavelet transform (CWT) is given by:

$$\begin{aligned}(W_h f)(t,s) &=< f, \tau_t D_s h >= |s|^{1/2} \int_{\mathbb{R}} f(u)\bar{h}(s(u-t))du \\ &= |s|^{1/2} \int_{\mathbb{R}} f(u)\tilde{h}(s(t-u))du = (f * D_s \tilde{h})(t).\end{aligned} \tag{4}$$

In order to deal with practical implementations, there is a need to sample the time-scale plane. A class of sampling sets that facilitates a simple filter bank implementation is given by:

$$\Gamma = \{t, s_m\}_{m=1,2,\ldots,M} \tag{5}$$

and the analysis filter bank is specified by:

$$(W_h f)(t, s_m) =< f, \tau_t D_{s_m} h >= (f * D_{s_m} \tilde{h})(t) = x^m(t). \tag{6}$$

The mother wavelet h, the number of filters M, and the scales $\{s_m\}$ determine the frequency ranges over which the analysis filter bank operates.

3.1.2 Time Encoding and Representation

To simplify the notation in this section with will drop the upper index m of $x^m(t)$. We shall assume that $x = x(t), t \in \mathbb{R}$, with $|x(t)| \leq c < b$, is a finite energy signal on $\mathbb{R}$ bandlimited to $[-\Omega, \Omega]$. Note that the bandwidth of each filter depends on the bandwidth of the mother wavelet and the dilation factor.

The integrator constant κ, the upper bound of neuron threshold δ, the bias b in Figure 3 are strictly positive real numbers and $x = x(t)$ is a Lebesgues measurable

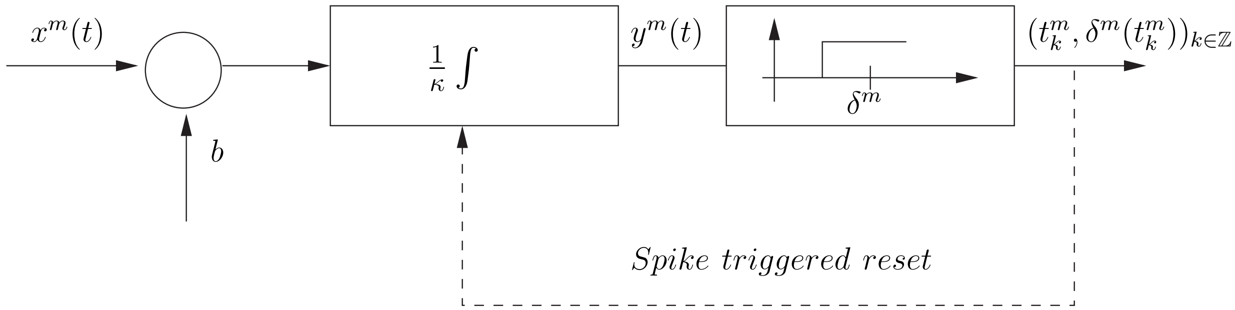

Figure 3: Time Encoding with the Integrate-and-Fire Neuron.

function that models the input signal to the TEM for all $t,\ t \in \mathbb{R}$. The output of the integrator in a small neighborhood of t_0, $t > t_0$ is given by:

$$y(t) = y(t_0) + \frac{1}{\kappa}\int_{t_0}^{t}[x(u) + b]du. \tag{7}$$

Note that, due to the bias b, $y = y(t)$ is a continuously increasing function.

Remark 1 Informally, the information of the input $(x(t))_{t\in\mathbb{R}}$ is carried by the signal amplitude whereas the information of the output signal is carried by the trigger times t_k and threshold values $\delta(t_k)$, for all $k,\ k \in \mathbb{Z}$. A fundamental question, therefore, is whether the Time Encoding Machine encodes information loss-free. Loss-free encoding means that $x(t)$ can be perfectly recovered from $(t_k, \delta(t_k))_{k\in\mathbb{Z}}$.

Lemma 1 (t-Transform) *For all input signals $x = x(t),\ t \in \mathbb{R}$, with $|x(t)| \leq c < b$, and threshold functions $\delta(t)$, $t \in \mathbb{R}$, with $0 < \delta(t) \leq \delta$, the output is a strictly increasing set of trigger times (t_k), $k \in \mathbb{Z}$, obtained from the recursive equation*

$$\int_{t_k}^{t_{k+1}} x(u)du = -b(t_{k+1} - t_k) + \kappa\delta(t_{k+1}). \tag{8}$$

for all $k,\ k \in \mathbb{Z}$.

Proof: The Time Encoding Machine is described in a small neighborhood of t_0, $t > t_0$, by:

$$\frac{1}{\kappa}\int_{t_0}^{t}[x(u) + b]du = \delta(t). \tag{9}$$

Since the left hand side is a continuously increasig function and the threshold function is bounded $0 < \delta(t) \leq \delta$ and continuous, there exists a time $t = t_1$, $t_0 < t_1$, such that the equation above holds. Thus, the (output) sequence of times $(t_k)_{k\in\mathbb{Z}}$, is strictly increasing for all $k,\ k \in \mathbb{Z}$, and the recursion (8) follows.

Corollary 1 (Upper and Lower Bounds for Trigger Times) *For all input signals $x = x(t),\ t \in \mathbb{R}$, with $|x(t)| \le c < b$, the distance between consecutive trigger times t_k and t_{k+1} is given by:*

$$0 < t_{k+1} - t_k \le \frac{\kappa\delta}{b-c}, \tag{10}$$

for all $k,\ k \in \mathbb{Z}$.

Proof: Since $|x(t)| \le c$, it is easy to see that

$$-c(t_{k+1} - t_k) \le \int_{t_k}^{t_{k+1}} x(u)du \le c(t_{k+1} - t_k). \tag{11}$$

By replacing the integral in the inequality above with its value given by equation (8) and solving for $t_{k+1} - t_k$ we obtain the desired result. The upper bound is achieved for a constant input $x(t) = c$ and $\delta(t) = \delta$, for all $t,\ t \in \mathbb{R}$, respectively.

Remark 2 If $x(t)$ is a continuous function, by the mean value theorem there exists a $\xi_k \in [t_k, t_{k+1}]$, $k \in \mathbb{Z}$, such that:

$$x(\xi_k)(t_{k+1} - t_k) = -b(t_{k+1} - t_k) + \kappa\delta(t_{k+1}), \tag{12}$$

i.e., the sample $x(\xi_k)$ can be explicitly recovered from information contained in the time difference $t_k - t_{k+1}$, and $\delta(t_{k+1})$, $k \in \mathbb{Z}$. Intuitively, therefore, any class of input signals that can be recovered from its samples can also be recovered from $(t_k, \delta(t_k))_{k\in\mathbb{Z}}$.

Remark 3 The output of each neuron operates at an average rate that is proportional to the effective bandwidth of each of the filtered signals, respectively. Thus, by choosing the bandwidth of each filter appropriately, the processing capacity on each branch of the transmitter and receiver can be controlled.

3.2 Synthesis

A simple algorithm for the recovery of a bandlimited signal f from the sequence of trigger times $(t_k^m, \delta^m(t_k^m))$, $k \in \mathbb{Z}$ and $m = 1, 2, ..., M$ can be implemented in two phases:

- Resolving Time - recovering the continuous filtered waveform $(x^m(t))_{t\in\mathbb{R}}$ from the $(t_k^m, \delta^m(t_k^m))_{k\in\mathbb{Z}}$'s.
- Resolving Scale - recovering the original bandlimited signal $f(t)$ by combining the continuous filtered waveforms $x^m(t)$, $m = 1, 2, ..., M$.

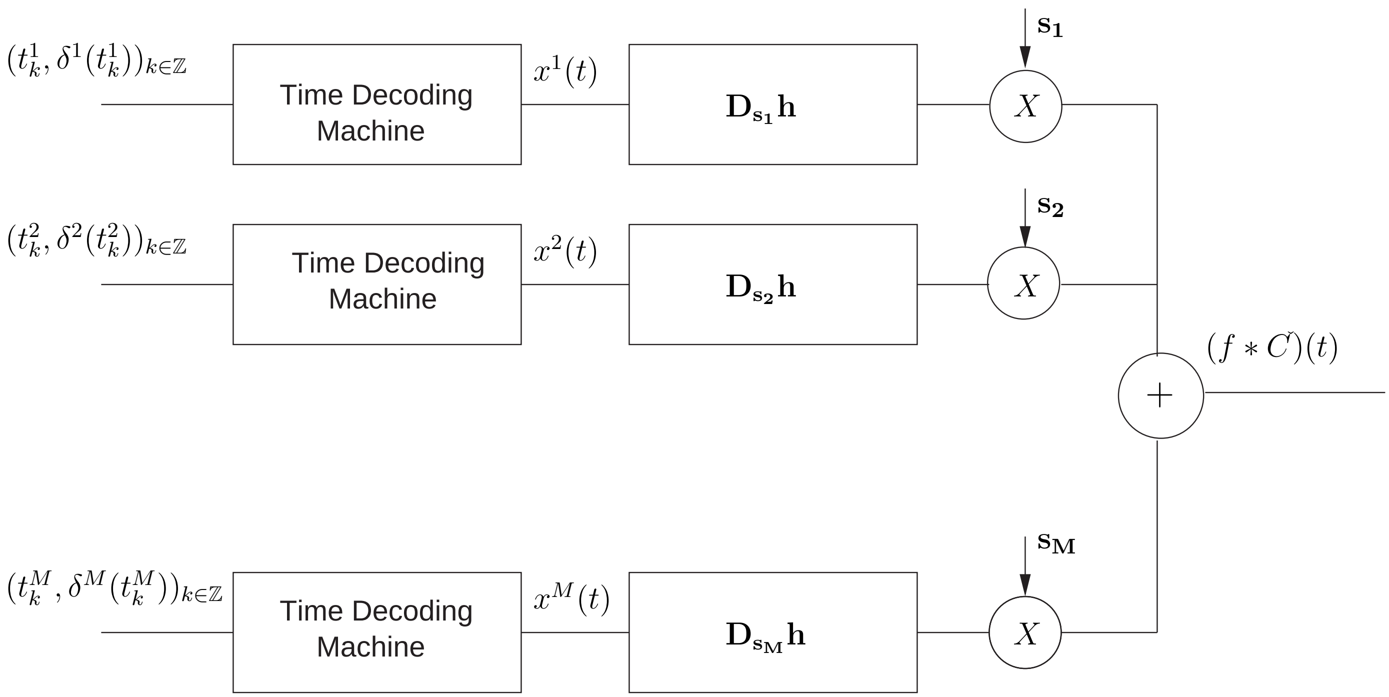

Figure 4: Wavelet Time Decoding.

3.2.1 Time Decoding and Recovery

Again, to simplify the notation in this section we will drop the upper index m of $x^m(t)$. We shall assume that $x = x(t), t \in \mathbb{R}$, with $|x(t)| \leq c < b$, is a finite energy signal on $\mathbb{R}$ bandlimited to $[-\Omega, \Omega]$. Note that the bandwidth of each filter depends on the bandwidth of the mother wavelet and the dilation factor.

Lemma 2 *Let the operator $\mathcal{A}$ be given by:*

$$\mathcal{A}x = \sum_{k\in\mathbb{Z}} \int_{t_k}^{t_{k+1}} x(u)du \; g(t - s_k), \tag{13}$$

where $g(t) = sin(\Omega t)/\pi t$ and $s_k = (t_{k+1} + t_k)/2$. We have:

$$\| \; I - \mathcal{A} \; \| \leq r \tag{14}$$

where I is the identity operator and $r = \frac{\kappa\delta}{b-c}\frac{\Omega}{\pi}$.

Proof: See Theorem 7 of [4].

The construct of the operator $\mathcal{A}$ above is highly intuitive and utilizes an integrated version of $x(t)$ on the interval $[t_k, t_{k+1}]$. Dirac-delta pulses are generated at times s_k with weight $\int_{t_k}^{t_{k+1}} x(u)du$ and then passed through an ideal low pass filter with unity gain for

$\omega \in [-\Omega, \Omega]$ and zero otherwise. The values of $\int_{t_k}^{t_{k+1}} x(u)du$ are available at the TDM through equation (8).

Let $x_l = x_l(t)$, $t \in \mathbb{R}$, be a sequence of bandlimited functions defined by the recursion:

$$x_{l+1} = x_l + \mathcal{A}(x - x_l), \tag{15}$$

for all $l,\ l \in \mathbb{Z}$, with the initial condition $x_0 = \mathcal{A}x$.

Proposition 1 (Operator Formulation) *Let $x = x(t)$, $t \in \mathbb{R}$, be a bounded signal $|x(t)| \leq c < b$ bandlimited to $[-\Omega, \Omega]$. Under the conditions mentioned above, the operator $\mathcal{A}$ is invertible and the signal x can be perfectly recovered as*

$$\lim_{l \to \infty} x_l(t) = x(t), \tag{16}$$

and

$$\| x - x_l \| \leq r^{l+1} \| x \| . \tag{17}$$

Proof: Closely follows Theorem 1 in [7].

Let us define $\mathbf{g} = [g(t - s_k)]^T$, $\mathbf{q} = [\int_{t_k}^{t_{k+1}} x(u)\ du]$ and $\mathbf{G} = [\int_{t_l}^{t_{l+1}} g(u - s_k)\ du]$. We have the following

Corollary 2 (Matrix Formulation) *Under the assumptions of Proposition 1 the bandlimited signal x can be perfectly recovered from $(t_k, \delta(t_k))_{k \in \mathbb{Z}}$ as*

$$x(t) = \lim_{l \to \infty} x_l(t) = \mathbf{g}\mathbf{G}^+\mathbf{q}. \tag{18}$$

where $\mathbf{G}^+$ denotes the pseudo-inverse of $\mathbf{G}$. Furthermore,

$$x_l(t) = \mathbf{g}\mathbf{P}_l\mathbf{q}, \tag{19}$$

where $\mathbf{P}_l$ is given by

$$\mathbf{P}_l = \sum_{k=0}^{l} (\mathbf{I} - \mathbf{G})^k. \tag{20}$$

Proof: Formally identical to the proof of Theorem 2 in [7].

3.2.2 Recovery Using Wavelet Frames

With "hat" denoting the Fourier transform we note that

$$(x^m)\hat{}\,(\omega) = (\hat{f} \cdot D_{s_m^{-1}} \bar{\hat{h}})(\omega) \tag{21}$$

By multiplying both sides with $s_m \cdot D_{s_m^{-1}} \hat{h}$ we obtain:

$$\begin{aligned}\sum_{m=1}^{M} s_m \cdot (x^m)\hat{}\,(\omega)(D_{s_m^{-1}}\hat{h})(\omega) &= \sum_{m=1}^{M} s_m \cdot (\hat{f} \cdot D_{s_m^{-1}}\bar{\hat{h}})(\omega)(D_{s_m^{-1}}\hat{h})(\omega) \\ &= \hat{f}(\omega) \sum_{m=1}^{M} s_m \cdot |D_{s_m^{-1}}\hat{h}(\omega)|^2\end{aligned} \tag{22}$$

Let us assume that

$$C = \sum_{m=1}^{M} |\hat{h}(s_m^{-1}\omega)|^2 > 0. \tag{23}$$

for all $\omega \in [-\Omega, \Omega]$. We shall denote by $c(t)$, $t \in \mathbb{R}$, the inverse Fourier transform of $C^{-1}(\omega)$, *i.e.*, $c(t) = (C^{-1})\check{}(t)$ for all $t, t \in \mathbb{R}$. We have the following

Proposition 2 *The stimulus $f(t)$ can be perfectly recovered from $(x^m(t))_{t\in\mathbb{R}}$, $m = 1, 2, ..., M$ and*

$$f(t) = (\sum_{m=1}^{M} s_m \cdot (x^m * D_{s_m} h) * c)(t) \tag{24}$$

provided that

$$C = \sum_{m=1}^{M} |\hat{h}(s_m^{-1}\omega)|^2 > 0. \tag{25}$$

for all $\omega \in [-\Omega, \Omega]$.

4 Conclusions

In this paper we presented a Canonical Model for time encoding and stimulus recovery for sensory systems. The model consists of a filter bank followed by a cascade of integrate-and-fire neurons. The advantage of the model is that it allows to control the average rate of spike generation. Most importantly, the Canonical Model is invertible even though the constituent filters have overlapping frequency bands and the integrate-and-fire neurons operate with different (possibly time dependent) thresholds. In addition to the trigger times, the values of the threshold evaluated at the trigger times are required for recovery. The invertibility property is remarkable particularly because the individual TEMs are non-linear devices.

The Canonical Model helps elucidate some of the key open questions of temporal coding for sensory systems. First, stimuli encoded by a single integrate and fire neuron can be recovered loss-free from the neural spike train. The recovery of the stimulus requires information about the trigger times (spikes) and the (time dependent) thresholds. There is no need to repeat an experiment to obtain additional spike train data about the stimulus. Clearly using spikes for recovering the stimulus from a single running experiment is a defining biological requirement. Second, the Canonical Model shows that the same stimulus can be recovered using different filter transfer functions and integrate-and-fire neuron parameters. The latter result seems to be particularly noteworthy because the choice of bounded thresholding functions leads to different representations of the stimulus without information loss. An algorithm that performs perfect recovery and is insensitive with respect to the value of the threshold appears in [8].

References

[1] Adrian, E.D., *The Basis of Sensation: The Action of the Sense Organs*, Christophers, London, 1928.

[2] Benedetto, J.J. and Teolis, A., *A Wavelet Auditory Model and Data Compression*, Applied and Computational Harmonic Analysis, Vol. 1, pp. 33-28, 1993.

[3] Duffin, R. J. and Schaeffer, A.C., *A Class of Nonharmonic Fourier Series*, Transactions of the American Mathematical Society, Vol. 72, pp. 341-366, 1952.

[4] Feichtinger, H.G. and Gröchenig, K., *Theory and Practice of Irregular Sampling.* In J.J. Benedetto and M.W. Frazier, editors, Wavelets: Mathematics and Applications, pp. 305-363, CRC Press, Boca Raton, FL, 1994.

[5] Hudspeth, A.J. and Konishi, M., *Auditory Neuroscience: Development, Transduction and Integration*, PNAS, Vol. 97, No. 22, pp. 11690-11691, October 2000.

[6] Keat, J., Reinagel, P., Reid, C.R., and Meister, M., *Predicting Every Spike: A Model for the Response of Visual Neurons*, Neuron, Vol. 30, pp. 803-817, June 2001.

[7] Lazar, A.A. and Toth, L.T., *Time Encoding and Perfect Recovery of Bandlimited Signals*, Proceedings of the IEEE International Conference on Acoustics, Speech, and Signal Processing, Vol. VI, pp. 709-712, April 6-10, 2003, Hong Kong.

[8] Lazar, A.A. and Toth, L.T., *Sensitity Analysis of Time Encoded Bandlimited Signals*, Proceedings of the IEEE International Conference on Acoustics, Speech, and Signal Processing, May 17-21, 2004, Montreal, Canada, to appear.

[9] Masland, R.H., *The Fundamental Plan of the Retina*, Nature Neuroscience, Vol. 4, No. 9, September 2001, pp. 877-886.

[10] Meister, M. and Berry, M.J. II, *Neural Code of the Retina*, Neuron, Vol. 22, pp. 435-450, March 1999.

[11] Ng, M., Roorda, R.D., Lima, S. Q., Zemelman, B.V., Morcillo, P. and Miesenbök, G., *Transmission of Olfactory Information between Three Populations of Neurons in the Antennal Lobe of the Fly*, Neuron, Vol. 36, pp. 463-474, 2002.