



Computing with inter-spike interval codes in networks of integrate and fire neurons

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Abstract

Information encoding in spikes and computations performed by spiking neurons are two sides of the same coin and should be consistent with each other. This study uses this consistency requirement to derive some new results for inter-spike interval (ISI) coding in networks of integrate and fire (IF) neurons. Our analysis shows that such a model can carry out useful computations and that it does also account for variability in spike timing as observed in cortical neurons. Our general result is that IF type neurons, though highly non-linear, perform a simple linear weighted sum operation of ISI coded quantities. Further, we derive bounds on the variation of ISIs that occur in the model although the neurons are deterministic. We also derive useful estimates of the maximum processing speed in a hierarchical network.

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1. Introduction

It is well known that neurons communicate using spikes. But how is information encoded in the spikes that travel from one neuron to another? Since outputs of

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neurons are fed to other neurons for further processing, a generic information encoding scheme will need to have the same encoding mechanism at the input to a neuron as at the output. Given such an encoding scheme, neurons of the same type can be organized in multiple layers to perform useful computations [2]. A computational model for a neuron should, therefore, perform computations on its input spike trains and produce the result of the computation at its output with the same encoding as at its inputs. Thus, information encoding, computation and neuron models are part of the same problem and should be consistent with each other.

As an example, consider the Poisson rate coding hypothesis where the spike trains are modelled as Poisson processes, with the rate of the process carrying the relevant information [4]. Softky and Koch showed that the rate coding hypothesis is inconsistent with integrate and fire neuron models [6]. A neuron model which is consistent with the rate coding hypothesis would require a random number generator inside the neuron so that the outputs are Poisson as well. This example illustrates that it is important to consider neuron models together with an information encoding and processing mechanism.

What is a consistent kind of coding mechanism for the widely used integrate and fire (IF) neurons? What computation do IF neurons perform with its inputs and its outputs coded in that fashion? In this paper, we show that inter-spike interval (ISI) coding is a viable coding mechanism that can produce useful computations in networks of IF neurons while being consistent with the above requirements. In addition, we show that the ISI coding and computation mechanisms as suggested here could account for spike timing variability as observed in cortical spike trains.

The rest of this paper is organized as follows. Section 2 establishes the general relationship between ISI coding and IF neurons. Section 3 describes the nature of computations performed on ISI coded streams by IF neurons. This section also describes the source of variability arising from these computations. Section 4 compares these results with previous work and suggests topics for further investigation.

2. ISI coding and IF neurons

One way to encode a stream of non-negative numbers s_1, s_2, \dots, s_N based on ISIs is to use these values to control the time elapsed between successive spikes as given by

$$t_{n+1} - t_n = f(s_{n+1}), \quad (1)$$

where t_n 's are the spike instants and f is a positive valued function. Consider an IF neuron without leak driven by a constant input current I . Such a neuron would produce output spikes at regular intervals T_{out} given by

$$T_{\text{out}} = V_{\theta} C / I, \quad (2)$$

where V_{θ} is the threshold of firing and C is the capacitance of the neuron. We assume that after firing, the membrane potential is reset to zero. The corresponding

expression for a leaky integrate and fire neuron (LIF) with leakage resistance R is given by [7]

$$T_{\text{out}} = RC \ln\left(\frac{1}{1 - (V_{\theta}/IR)}\right). \quad (3)$$

Eqs. (2) and (3) satisfy the general form of ISI encoding given in Eq. (1) with the $f(s) = V_{\theta}C/s$ for Eq. (2) and $f(s) = RC \ln(1/[1 - (V_{\theta}/sR)])$ for Eq. (3). In both cases, T_{out} decreases with increasing I , i.e., f is a decreasing function of the input magnitude.

Inputs to cortical neurons are spikes rather than constant currents. Moreover, any given neuron will have many input synapses carrying different spike streams. Therefore, it is important to know how the output spike intervals of a neuron is related to the input spike intervals on its synapses. In the next section we derive this relationship for an IF neuron with two synaptic inputs.

3. Computations with ISI encoded input streams

Consider ISI streams encoding static values s_1 and s_2 applied as inputs to an IF neuron with synaptic weights w_1 and w_2 . We assume that streams s_1 and s_2 were produced by IF neurons with the same threshold and capacitance. Initially we consider neurons with no leakage. We then know that values s_1 and s_2 correspond to input interspike intervals T_1 and T_2 where $T_1 = V_{\theta}C/s_1$ and $T_2 = V_{\theta}C/s_2$. Let T_{out} be an output ISI for these inputs. We assume that the firing threshold is such that $T_{\text{out}} > 2 \max\{T_1, T_2\}$. Then during the interval T_{out} , synapse 1 received approximately T_{out}/T_1 spikes and synapse 2 received approximately T_{out}/T_2 spikes. These input spikes increment the membrane potential of the neuron eventually making it reach the threshold and fire T_{out} units after its previous firing. If each spike causes an increment V_{δ} in the membrane potential, on an average, the neuron fires when the following condition is met

$$w_1(T_{\text{out}}/T_1) + w_2(T_{\text{out}}/T_2) = V_{\theta}/V_{\delta}. \quad (4)$$

Thus, using Eq. (2), the quantity s_{out} encoded by the output ISI T_{out} can be derived as

$$s_{\text{out}} = (V_{\delta}/C) \left(\frac{w_1}{T_1} + \frac{w_2}{T_2} \right) = (V_{\delta}/V_{\theta})(w_1s_1 + w_2s_2). \quad (5)$$

If we assume the ratio V_{δ}/V_{θ} to be the same for all neurons producing the input spike streams, a general approximate input–output relationship holds for a neuron with multiple inputs: $s_{\text{out}} = \Sigma_i w_i s_i$, where i runs over all synapses of this neuron. Thus, even though the IF neuron is highly non-linear, the input–output relation between the spike intervals remains a linear function.

The above derivations of output ISIs are only approximate since we did not consider the cases where two simultaneous input spikes fire an output spike. The

maximum output ISI T_{\max} will occur subsequent to a spike that was fired by two coincident spikes on the input streams. The next firing, which terminates the ISI corresponding to T_{\max} would then occur synchronously with spikes on either of the synapses. Without loss of generality, we assume that this happens synchronously at synapse 1. Then $T_{\max} = n_1 T_1$, where n_1 is the number of spikes received at synapse 1. Further, the number of spikes received on synapse 2 during this interval is given by $n_2 = \lfloor T_{\max}/T_2 \rfloor$. Equating the weighted number of spikes to the firing threshold we get an upper bound on the maximum output ISI T_{\max} . Similarly, a lower bound for the minimum ISI T_{\min} can be derived. The two bounds are as given below by

$$T_{\max} \leq \frac{(V_\theta/V_\delta) + \max\{w_1, w_2\}}{(w_1/T_1) + (w_2/T_2)}, \quad T_{\min} \geq \frac{(V_\theta/V_\delta) - \max\{w_1, w_2\}}{(w_1/T_1) + (w_2/T_2)}, \quad (6)$$

where V_θ is the firing threshold and V_δ is the increment in membrane potential caused by an incoming spike.

Although the exact probability density of the ISI variation was not derived, from symmetry arguments we conclude that the average output ISI is the one given by Eq. (4). This implies a new way of interpreting the output of an IF neuron with static ISI coded inputs. The output ISIs, on an average, represent the weighted sum of the quantities represented by the input ISIs. The output ISIs vary about this average and the variance depends on the relative magnitude of the voltage increments caused by an input spike. This jitter could account for part of the variability of cortical spike trains.

The stated results can be extended to time varying input streams by imposing appropriate constraints on the maximum rate of change of the input streams. Since an IF neuron loses all the history of inputs after firing, a step change at any of the input streams is reflected at the output within a time $t \leq 2T_{\text{out}}^{\max}$ where T_{out}^{\max} is the maximum ISI of the output spike stream. Let $T_{\text{out}}^{\max} = KT_{\text{in}}^{\max}$ where T_{in}^{\max} is the maximum ISI at the input and $K \geq 2$ is a constant that depends on the time constant of the neuron and its synaptic strengths. If we assume that the input spike trains are faithful samples of a bandlimited input current, then by the sampling theorem, $T_{\text{in}}^{\max} \leq 1/(2f_{\max})$, where f_{\max} is the maximum frequency component of the input current. Then $T_{\text{out}}^{\max} \leq (K/2)f_{\max}$. This means that the maximum frequency that can be represented by the spike trains drops by a factor of $K \geq 2$ for every layer of IF neurons in a layered architecture. If this condition is violated for any layer, the output spike stream can no longer be interpreted as ISI coded as described in this paper. Knowing the minimum rate at which neurons at the highest level of the hierarchy should respond would give us an upper bound on the input frequencies that can be faithfully represented and processed using the ISI coding scheme described here.

The result that the basic type of computation is of the sort $s_{\text{out}} = w_1 s_1 + w_2 s_2$ is not only valid for IF neurons, but also holds for LIF neurons. For a LIF neuron with leakage resistance R and capacitance C , the membrane voltage decays exponentially with a time constant $\tau = RC$ as given in Eq. (3). Therefore, on an average, the neuron fires when the following

condition is met:

$$\begin{aligned} & w_1(1 + e^{-T_1/\tau} + e^{-2T_1/\tau} + \dots + e^{-((T_{\text{out}}/T_1)-1)T_1/\tau}) \\ & + w_2(1 + e^{-T_2/\tau} + e^{-2T_2/\tau} + \dots + e^{-((T_{\text{out}}/T_2)-1)T_2/\tau}) \\ & = (e^{-T_{\text{out}}/\tau} - 1) \left(\frac{w_1}{e^{-T_1/\tau} - 1} + \frac{w_2}{e^{-T_2/\tau} - 1} \right) = V_\theta / V_\delta. \end{aligned}$$

By comparing this with Eq. (3), the quantity s_{out} encoded by the output ISI T_{out} becomes

$$s_{\text{out}} = (V_\delta / R) \left(\frac{w_1}{e^{-T_1/\tau} - 1} + \frac{w_2}{e^{-T_2/\tau} - 1} \right) = (V_\delta / V_\theta)(w_1 s_1 + w_2 s_2). \quad (7)$$

4. Discussion

The question of how spike timing is used for computations has been under debate for a long time [1–3]. The challenge lies in finding coding and computational mechanisms that are consistent with neuron models. Rate coding with Poisson distributed spikes has been suggested as one mechanism for encoding information in spikes [4]. But the traditional view of Poisson spikes cannot be implemented with IF neurons [6]. The ISI coding mechanism we suggested for IF neurons can be interpreted as an instantaneous rate code. However, in our scheme the spikes are more precisely timed and hence can carry information at a higher rate compared to Poisson rate coding [5]. Rank order coding (ROC) [2] is another spike-timing-based computation suggested in the literature. However, ROC has the disadvantage that a slight delay in the onset of one of the inputs can disrupt the entire chain. Poisson rate coding and ROC can be considered to be at the opposite extremes of a continuum of spike coding mechanisms. The ISI coding we suggested here can be positioned somewhere between these extremes, thus giving a tradeoff between information rate and synchronicity requirements. Since ISI codes are nothing but rate codes with precise timing, all the results we derived in Section 3 are valid in general for all rate codes.

There has been extensive discussion about the nature of variability of spike trains in cortex [6,4]. Suggested mechanisms for this variability include random firing thresholds and stochastic synapses. The ISI coding mechanisms we suggested here demonstrate that the variability of the spike trains could, at least in part, arise as a natural consequence of computations based on ISI coded spike stream inputs, even in entirely deterministic IF neurons. More studies are required to verify what percentage of the observed cortical variability of spike trains can be explained using this approach.

We know that neurons in the lower levels of a cortical hierarchy need to respond faster compared to neurons higher up in the hierarchy. Our model predicts a drop in the maximum frequency as more computational layers are stacked like in a hierarchical architecture. Clearly, there is a tradeoff between speed of processing and

accuracy of representation at each stage. Further studies are required to quantify this tradeoff. Also, the question of how learning could occur in ISI coded networks is left as a topic for further study.

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