Inter-spike Interval Coding and Computation with Integrate and Fire Neurons

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1 Background

It is well known that neurons communicate using spikes. However, it is not known how information is encoded in the spikes that travel from one neuron to another. Any information encoding mechanism using spikes should also consider computations done by the neurons. This paper to introduces Inter-spike Interval (ISI) coding as a viable coding and computational mechanism in neural networks with Integrate and Fire neurons. Moreover, the ISI coding and computation as suggested by this paper could account for part of the observed variability of cortical spike trains.

Traditionally, the spike train outputs from a neuron is modelled as a Poisson process, with the rate of the Poisson process carrying the relevant information. For rate coding to work, we need either large number of independent neurons to encode the same information or long time scales. Consider an integrate and fire neuron with synapses of weights w_1 and w_2 respectively. It can be shown that the output rate will be a monotic function of $s_1 * w_1 + s_2 * w_2$ where s_1 and s_2 are the rates of the inputs.

This study shows that similar computations can be done using Inter-spike Interval coding and Integrate and Fire neurons.

2 ISI Coding

In ISI coding, the information is encoded in the time interval between spikes. Consider encoding a stream of non-negative numbers $m_1, m_2, \cdot m_n$. Then, following equation denotes a way to encode the information in inter-spike intervals.

$$t_{n+1} = t_n + M/(m_{n+1} + 1) + d \qquad (1)$$

where t_n denotes the spike instants, d is the minimum separation between spikes and M is the maximum amplitude that can be encoded. With this sort of encoding, large amplitudes correspond to small inter-spike intervals and vice versa.

3 Integrate and Fire Neurons and ISI Coding

For an integrate and fire neuron without leak excited by a constant current I, the output inter-spike interval T_{out} will be a constant given by

$$T_{out} = V_\theta * C/I \tag{2}$$

. 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 an integrate and fire neuron with leakage resistance R is given by,

$$T_{out} = R * C/ln(1 - (V_\theta/I * R)) \tag{3}$$

The above two equations relate how the amplitude of the current I gets encoded as the ISI T_out. As it can be seen from the equations, a large I corresponds to small inter-spike intervals and vice versa.

3.1 Computations on ISI streams using an Integrate And Fire Neuron

Consider integrate and fire-neurons with ISI coded spike streams as their input. We show that the output inter-spike intervals approximately represent a sum-of-products like operation on the input inter-spike intervals.

3.1.1 Computation on Static Streams

Consider ISI streams encoding static values s_1 and s_2. Apply this as input to an integrate and fire-neuron with weights w_1 and w_2. The Inter-spike interval of the output will correspond to the value $w_2 \times s_1 + w_2 \times s_2$ (with scaling and possibly non-linearity).

To see this, assume that V_θ is the firing threshold of the neuron and C its capacitance. Also assume that streams s_1 and s_2 were produced by Integrate and Fire neurons of the same threshold and capacitance. Initially we consider only neruons with no leakage current. 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 $T_2 - V_\theta * T_2/s_2$. Let T_{out} be an output inter-spike interval for these inputs. We assume that the firing threshold is such that $T_{out} > 2 * max\{T_1, T_2\}$. 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. If each spike causes an increment V_δ in the membrane potential, the firing condition can be written (approximately) as

$$w_1 * (T_{out}/T_1) + w_2 * (T_{out}/T_2) = V_\theta/V_\delta \tag{4}$$

Then the quantity s_{out} encoded by the output ISI T_{out} is given by

$$\begin{aligned} s_{out} &= V_\theta * C/T_out \\ &= (V_\delta/C) * (\frac{w_1}{T_1} + \frac{w_2}{T_2}) \\ &= (V_\delta/V_\theta) * (w_1 * s_1 + w_2 * s_2) \end{aligned}$$

If we assume that the ratio V_δ/V_θ is the same for all neurons, then the output ISI consistently encodes the sum of product function.

Next, we show that this result holds good also for integrate-and fire neurons with a leakage resistance R. With a leakage resistance R and a capacitance C, the membrane voltage leaks exponentially with a time constant $\tau = R*C$. With this, we know that an input current I gets encoded in the output ISI T as

$$I = \frac{V_\theta}{R * (1 - e^{-T/\tau})} \tag{5}$$

As considered in the previous case, let T_{out} be the output ISI corresponding to inputss_1 and s_2. Then the approximate condition for firing of the neuron is given by

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

By comparing with equation blah, the output quantity s_{out} encoded by the output ISI T_{out} can be found as

$$\begin{aligned} s_{out} &= \frac{V_\theta}{R * (1 - e^{-T_{out}/\tau})} \\ &= (V_\delta/R) * (\frac{w_1}{e^{-T_1/\tau} - 1} + \frac{w_2}{e^{-T_2/\tau} - 1}) \\ &= (V_\delta/V_\theta) * (w_1 * s_1 + w_2 * s_2) \end{aligned}$$

3.1.2 Time Varying Inputs

Consider a step change on one of the input streams. Since the integrate and fire neuron loses all the history of inputs after firing, the maximum time take for the output ISI of the integrate and fire neuron to reflect this change would be given by

$$t <= 2 * T_{out}^{max} \tag{6}$$

where T_{out}^{max} is the maximum ISI of the output spike stream. Let $T_{out}^{max} = KT_{in}^{max}$where T_{in}^{max} is the maximum ISI at the input and $K >= 2$ 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 continuous current, then by sampling theorem, $T_{in}^{max} <= 1/(2f_{max})$, where f_{max} is the maximum input frequency . Then $T_{out}^{max} <= (K/2) * f_{max}$. This means that the maximum frequency that can be represented by the spike trains drop by a factor of K for every stage of integrate and fire neuron.

3.2 Inter-spike interval variability

The above derivations of output ISIs were only approximate. Even when the input ISIs are static, the output inter-spike intervals can vary. Here we derive bounds on this variation.

3.2.1 Inter-spike Interval Bounds

Consider an integrate and fire neurons with two static ISI coded input streams and no leak. Let T_1 and T_2 be the inter-spike intervals of streams 1 and 2. And let w_1 and w_2 be the synaptic weights. The maximum ISI at the output will follow when the neruon was fired by two coincident spikes on the input streams.

Let T_{max} be the maximum ISI and consider the time interval after the neuron has fired the first spike of this ISI. The next firing will happen syncrhonous with either spikes on synapse one or two. Without loss of generality, assume that this happens synchronously with synapse1. Then $T_{max} = n_1 T_1$, where n_1 is the number of spikes received on synapse 1. Then 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 upperbound on the maximum output inter-spike interval as

$$T_{max} \leq \frac{V_\theta + max\{w_1, w_2\} * V_\delta}{(w_1/T_1) + (w_2/T_2)} \tag{7}$$

Similarly, the minimum ISI can be show to be lowerbounded by

$$T_{min} >= \frac{V_\theta - max\{w_1, w_2\} * V_\delta}{(w_1/T_1) + (w_2/T_2)} \tag{8}$$

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

4 Comparison with Rate Coding

ISI coding is indeed an instantaneous rate coding. However now more information is carried in the inter-spike intervals. The spike trains are now not Poisson processes. Also, multiple neurons are not required to encode the rate.

5 Rank Order Coding Vs ISI

Simon Thorpe showed that computations can be performed using Rank Order Coding (ROC). But ROC restricts the neurons to spike only once. It requires syncrhonization of all the inputs. These requirements seem artificial. Whereas, ISI coding is the natural form of coding done by Integrate and Fire neurons.

6 Example Application to Associative Memory

ISI Coded streams can be stored in a Correlation Matrix Memory made up of Integrate and Fire neurons. This has been (roughly) verified using a simulation.

7 Discussion

Nuerons in a neural network perform all their functions using a sum of product operation followed by a thresholding. How to implement such a computation in biological neurons using spikes has been a subject of constant debate. This paper proposes a computational mechanism using inter-spike-interval coding and this could potentially explain some of the variability seen in cortical spike trains.