

## The Neuronal Computation Time

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### Abstract

In a realistic model of a neuron, a change of the input firing probabilities results in a delayed change of the output firing probability. Such a latency is dependent on the type of computation performed by the neuron (summation or multiplication) and is observed only at the onset of a stimulus. Decreases of input frequencies are immediately transmitted. This onset-offset asymmetry represents a constraint on the design of neural networks based on realistic neurons.

### 1. INTRODUCTION

Time plays a fundamental role in biological neurocomputation. The timing of sensory inputs is not simply additional information exploited, for instance for sound source localization [1] or visual motion detection [2]. The loss of temporal information causes the whole perceptual process to collapse. In the visual system for instance, the receptive field properties can only be measured by using moving or transient stimuli, binocular cells require well timed inputs [3] and static images projected on the retina simply cease to be perceived [4].

As information progresses in the brain, its temporal characteristics are exploited and altered. In higher areas, information is also encoded in the temporal domain. The time of spikes encodes spatial location in hippocampus [5] or the shape of visual patterns [6].

Time also plays an essential role in learning. For instance, in classical conditioning experiments [7] or in the encoding of long term memory [8].

With regards to the importance of timing, it is as important to understand what determines the mean firing frequency of a neuron [9] than the time at which this frequency appears. Our study therefore addresses the following question: How much time does it take for a change in the firing probabilities at the inputs of a neuron to be reflected by a change in the output firing probability ?

To answer that question we have simulated a multilayer network of leaky integrate-and-fire neurons. Such neurons receive and produce spikes. Their characteristics and computational properties are described in detail elsewhere [9].

Traditionally, delays are considered to arise from axonal, synaptic and dendritic transmission. Our results show that there are also computational delays. Summation does not introduce delays in most cases. Multiplication is a typical feature extraction, or decision, operation which implies a delay. In both summation and multiplication modes, the latencies show a dependence on the previous activity of the neuron, a fact that may be exploited in attentional mechanisms. The stronger a new input and the larger the preceding input, the shorter the delay. These findings support the hypothesis that the earliest information is also the most relevant [10,11].

## 2. RESULTS

A three layer pyramidal neural network is simulated. All neurons have 4 inputs. There are 16 input neurons, 4 hidden neurons and 1 output neuron. All inputs fire with the same frequency but with random phases and irregular interspike intervals. The frequency is initially set to  $f_0$ . After 50 ms, the frequency is increased to  $f_1$  for 50 ms.

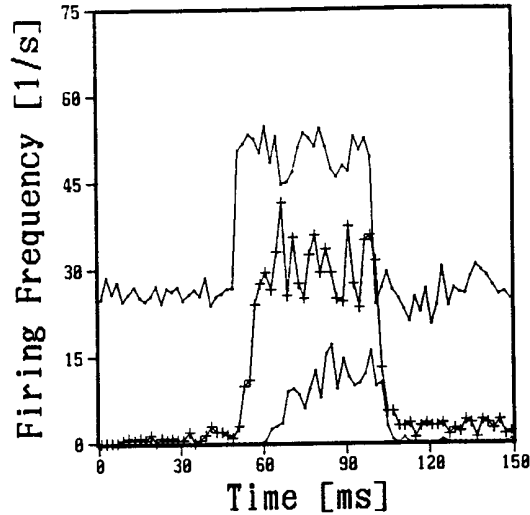


Figure 1. The top curve is the firing probability of each input neuron. At  $t=50$  ms there is a step increase from  $f_0=25$  Hz to  $f_1=50$  Hz. At  $t=100$  ms there is a step decrease from 50 to 25 Hz. The middle curve is the firing probability of a hidden layer neuron. It increases from approximately 1 Hz to 30 Hz with a delay at half height of 5 ms. The 4 hidden neurons feed into the output neuron which fires with an extra delay of 11 ms.

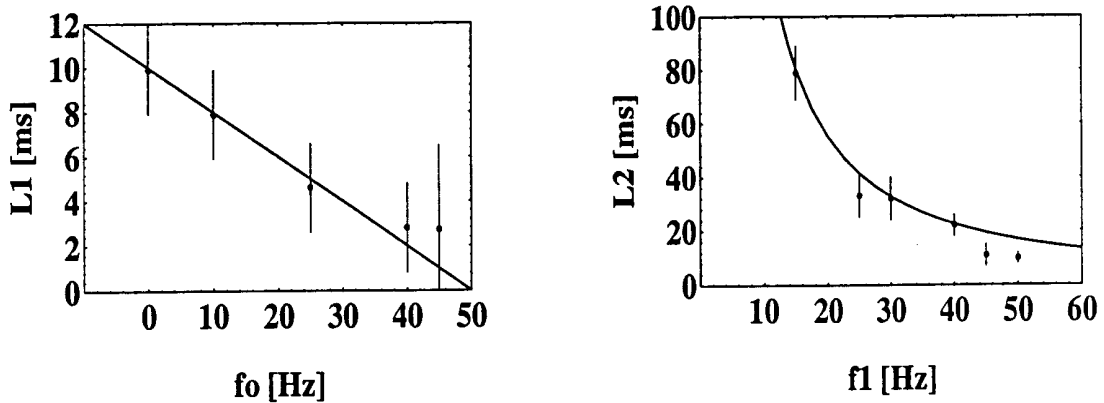


Figure 2. (a) Latencies ( $L_1$ ) versus initial frequency  $f_0$  in the case of a step to  $f_1=50$  Hz. The latency is proportional to the amplitude of the step ( $f_1-f_0$ ). (b) Latencies ( $L_2$ ) versus frequency step  $f_1$  in case of a zero initial input frequency ( $f_0=0$ ). The solid line follows the function  $L_2(f_1) = \text{Exp}[-1.3\ln(f_1)-1]$  adapted from [12]. It does not match the data for large values of  $f_1$ .

An example of the response of the network to such a step change of the input conditions is shown in figure 1 for neurons in the multiplication mode. The firing probability of the hidden nodes rises progressively to the output frequency corresponding to the new input conditions. This transient phase lasts longer for the output neuron which receives an already delayed input. We define the computation time as being the delay

between the time of change in input frequency at the time at which half of the output frequency change has occurred.

Interestingly, the delays are asymmetric, i.e. a decay of input frequency is immediately propagated through the layers.

There is a progressive decrease in frequency level as the information propagates from layer to layer. This phenomena is specific to the multiplication mode [9].

For a fixed value of  $f_1$ , the onset delays decrease linearly with the initial input frequency  $f_0$  (figure 2a). In the case of a zero initial frequency and a variable step, the delays decrease as the step  $f_1$  becomes larger (figure 2b).

In contrast to these results, similar measurements in the summation mode show no latencies when the neuron is in a firing state (not completely at rest) and when the neuron is initially at rest, the latency is inversely proportional to the frequency increase.

### 3. DISCUSSION

The latencies described elsewhere were all related to single continuous inputs [10,12,13]. In our case, the inputs are multiple and made of spikes. Their effects depend strongly on the operation mode of the neuron.

Multiplication is based on the detection of nearly coincident input spikes arriving within a small time window. For that purpose, the RC decay time of the LIFN and the synaptic weights must be set to sufficiently small values to prevent 3 (in our example) nearly coincident inputs inducing firing. They must also be sufficiently large to enable 4 nearly coincident inputs to raise the potential to the threshold. In our model, the weights are the amplitude of the current pulse injected at the synapse following an input spike. The smaller the time window during which a group of spikes arrives, the larger the resulting potential rise but there is also a smaller probability for 4 spikes to realize such a coincidence.

Such a carefully tuned system is very sensitive to the value of the background potential remaining from preceding non-effective input spikes. The larger the background, the larger the allowed time window for "near-coincidences" and the larger the number of spike configurations which can induce firing. Therefore, we expect the increase in firing frequency to be a non-trivial function of the variations of the background potential.

In the summation mode, the neuron operates as a spike-counter, reaching the threshold after a predetermined total number of input spikes have arrived (for instance 4). For that purpose, the time constant RC must be set to a large value, such that there is only a negligible decay of the potential before the neuron fires. The weights are such that each input spike rises the potential by 1/4 of the threshold. As long as the neuron receives inputs, its membrane has always a certain potential between 0 and the firing threshold. Any input spike can be the one that causes the firing. Therefore, as long as the neuron is in a firing state, a change in input frequency can immediately cause a change in output frequency. If the neuron is at rest, then it must wait for the necessary number of input spike to arrive before it can fire.

The onset-offset asymmetry reported here is a new feature. As the membranes potential is continuously decaying, the threshold can only be reached during an input spike. When the input spikes cease to arrive, a neuron immediately ceases to fire, and this is true at any level of a hierarchical network. There would have been an offset delay if we had included the dendritic propagation in our model. But the basic fact that output spikes are locked to one of the input spikes remains. This phenomena implies a very rapid propagation of reductions in input frequencies.

Onset-offset asymmetries are also observed in the visual system. There is a higher sensitivity to decrements of the intensity of a stimulus [14] and, in light adapted bullfrog retinal ganglion cells, the latency of the first spike signaling onset depends on the intensity while the latency of the first spike signaling offset is almost independent [12].

The onset-offset asymmetry also implies that input signals must have a minimum duration in order to propagate through a given number of multiplication neuronal layers. This computational constraint may justify the minimum duration of the response of retinal ganglion cells to brief flashes of light [15].

In the field of artificial neural networks, there is a growing interest in exploiting the temporal dimension of neurocomputing. For, instance, the use of latencies is explored in artificial vision [10]. Leaky integrators are used for storing temporal sequences [16] or for motion detection [17]. A model of the winner-takes-all mechanism using lateral inhibition operates on the basis of spike firing times [11].

#### 4. CONCLUSION

Leaky integrate-and-fire neurons show computation-dependent latencies with an asymmetric onset-offset behaviour. The onset latency must be taken into account when modelling neural networks operating in the temporal domain, especially when multiplication operations are involved, as in feature extraction tasks. The asymmetry imposes then a minimum duration to input signals.

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