Information processing with spiking neurons

in a cortical architecture framework under the

control of an oscillatory signal

Tobias Rodemann ¹ and Edgar Körner

Future Technology Research

Honda R&D Europe (Deutschland)

Carl-Legien-Strasse 30

63073 Offenbach (Main) / Germany

Abstract

In this work we analyze information processing in spiking neurons in the visual

cortex by investigating how short (10 ms) pulse packets of spikes are processed

in cortical neurons. These signals are compliant with constraints of rapid feedfor-

ward recognition in the visual cortex. We add an oscillatory membrane potential

modulation that simulates the effect of 40 Hz (gamma) oscillations. We find that

depending on the oscillation signal the neuron's output depends on different aspects

of the pulse packet: Number and coincidence of spikes and additionally mean spike

latency relative to the oscillation signal.

Key words: Latency Coding, Spiking Neurons, Gamma Oscillation

1 Introduction

Spiking neurons in a realistic cortical environment show a remarkably complex input-output mapping. A number of different functions like integrator (spike count) or coincidence detector have been proposed. However, the actual processing operation surely depends on the type of neuron, the structure of the input and the network environment. In this work we will analyze the input-output relation for a neuronal element in a feedforward processing module of the ventral pathway of the mammalian visual cortex. This brain area has been studied extensively and many biologically inspired models for visual object recognition follow its basic architecture, e.g. [2,7]. Experiments by Simon Thorpe and co-workers on ultra-fast image recognition in monkeys and humans have brought up some serious temporal constraints [9]. The extremely fast recognition of complex stimuli in about 200 ms leaves an upper limit of just 10-20 ms for information transfer between two neurons. Taking into account that cortical neurons fire with rates $\ll 100 \text{ Hz}$ a maximum of one spike per neuron must suffice to transmit information. This prohibits the classic single neuron rate coding approach (and seriously limits recurrent processing). It was therefore proposed [6,9] that the first, fast categorization of inputs is purely feedforward, based on one spike per neuron only and makes use of a temporal coding scheme. Another omnipresent feature of cortical structures is oscillatory activity. Oscillations come in a variety of frequency ranges, with the

Corresponding author. EMail: Tobias.Rodemann@hre-ftr.f.rd.honda.co.jp

gamma range (≈ 40 Hz, cycle length 25 ms) being the most prominent [8]. The highly synchronous activity of a large number of neurons will surely influence information processing in all neurons that are targeted by oscillating neuron populations. In [6] it was proposed that this oscillation signal is used as a reference and control signal for a latency coding scheme that is able to transmit information with single spikes within the time limit of 10 ms. In this work we will analyze how information is decoded and encoded in a cortical processing element subjected to an oscillatory background signal. As potential carriers of information we focus on the number of spikes a neuron receives (roughly corresponding to an ensemble firing rate), their temporal dispersion/variance (a measure of coincidence) and their latencies.

2 Network set-up

As the basic element of our circuit (Fig. 1) we employ a spiking neuron, simulated within the spike response model (SRM) [5] framework, which is closely related to the Integrate & Fire model. The neuron's status variable is its membrane potential. Due to the one spike per neuron limit we focus on the generation of the first output spike only and will neglect all refractory effects from previous spikes. As every synapse receives at most one spike during the integration time window we also neglect synaptic adaptation. Incoming spikes trigger excitatory post-synaptic potentials of the form (α function):

$$\eta_i(t) = w_i \frac{(t - t_i) \cdot e}{\tau} \cdot \exp\left(-\frac{t - t_i}{\tau}\right) \quad (t > t_i) \quad ,$$
(1)

with τ as the EPSP's rise time, w_i as the connection weight, and t_i being the arrival time of the triggering spike from source neuron i. Contributions from different synapses are summed up linearly. For simplification we assume that all connection weights w_i are identical. In addition to these spikes, corresponding to inputs from the previous stage in the processing hierarchy, neurons are also subjected to an external oscillatory signal (see also [3]). This oscillation signal is modeled as:

$$O(t) = \frac{A}{2} \left(1 + \sin \left(\omega t - \frac{\pi}{2} - \phi \right) \right) \quad , \tag{2}$$

with $\omega = 2\pi f$ and f being the frequency of the oscillation. The oscillation can be described by amplitude A, frequency f, and phase ϕ . This signal is added to the membrane potential. If the sum of EPSPs and oscillation exceeds the neuron's threshold Θ , a spike is generated. The simulation is stopped at this point and the time (= latency) of the spike is recorded. We will describe spike input by a low-dimensionally parameterized distribution. We use the model of Gaussian pulse packets [1] for which spike arrival times follow a normaldistribution G(t):

$$G(t) = N \cdot \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(t - t_L)^2}{2\sigma^2}\right) \quad . \tag{3}$$

The three distribution parameters correspond to the total number of spikes N to arrive at the neuron within the 10 ms time frame (= the number of source neurons that generated a spike), the average arrival time t_L (mean input latency), and the width of the distribution σ (standard deviation of the input latencies, a measure of spike coincidence). We note that the neuron takes three input variables (N, t_L, σ) and maps these to a single output spike. Neuronal parameters are taken as fixed and not modified. We changed oscillation parameters to see the effect on the mapping between input variables and output characteristics. We used the following parameter settings: $\tau = 2$ ms, $\Theta = 10 mV$, $w_i = 0.1 mV$, f = 40 Hz, A = (-18) - (+9) mV.

3 Results

Without the oscillation signal the decision whether the neuron generates a spike or not is independent of the mean input latency t_L . The output latency can be well approximated by the t_L plus a fixed offset. Both N and σ have only a small influence on the output latency, but determine whether the threshold is exceeded or not. For our choice of parameters the number of spikes has a greater influence on the maximum membrane potential than the width of the pulse packet. The number of spikes and the variance of input spike latencies

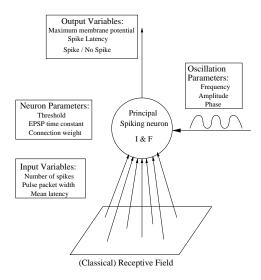


Fig. 1. The network element under investigation. A spiking neuron receives spikes from neurons within its receptive field and is furthermore subjected to a membrane potential oscillation.

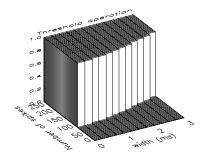


Fig. 2. Two dimensional threshold operation. The oscillation signal is disabled. The neuron spikes (output 1) if the number of spikes is high and the width of the pulse packet low enough. We note that the width of the pulse packet (coincidence) has a lower impact than the number of spikes.

are decoded in the neuron and a two-dimensional "threshold" operation (Fig.

2) determines whether a spike is emitted or not. If a spike is emitted its latency will encode the average latency of incoming spikes.

When adding the oscillation signal the neuron's maximum membrane potential becomes very sensitive to t_L . Therefore the spike generation process is latency dependent. The relative weighting of t_L compared to N and σ can be scaled up and down by increasing or decreasing the absolute value of the oscillation

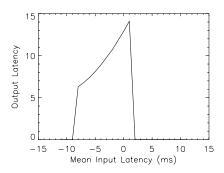


Fig. 3. Output latency as a function of the mean input latency relative to the peak of the oscillation signal. Parameters: $N=200, \ \sigma=1 \ ms, \ A=-18 \ mV$. Values of zero indicate that no spike was generated.

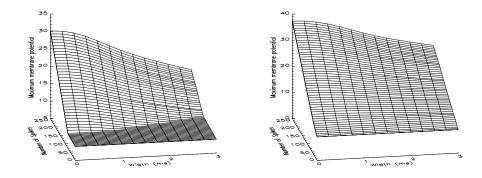


Fig. 4. Maximum membrane potential as a function of N and σ for mean input latencies of -5 ms (left) and +5 ms (right) relative to the minimum of the oscillation. Results are for a positive oscillation with 9 mV amplitude.

amplitude. For a strong oscillation signal (excitatory or inhibitory) both the generation of an output spike and the latency of this spike depend strongly on input latencies (Fig. 3). The neuron can thus decode input latencies. The output latency is still largely controlled by t_L but in a non-linear manner. The maximum membrane potential is determined by all three input variables (see Fig. 4). For large oscillation amplitudes mean input latency dominates but for intermediate values N, t_L and σ all have to be taken into account. A very interesting finding is the very strong dependence of the latency decoding mechanism on the phase relation between the pulse packet and the oscillation.

If the pulse packet arrives in the rising phase of the oscillation, higher input latencies will lead to a higher maximum membrane potential (read: the later the better). If spikes arrive in the decreasing phase of the oscillation, earlier arriving spike will generate a higher membrane potential.

4 Summary and conclusion

We have used short pulse packets of spikes as inputs for biologically feasible spiking neurons in the visual cortex. These pulse packets are short enough to fit temporal constraints put forward by [4,9] for the fast feedforward recognition in mammals. We also added an oscillatory membrane potential modulation that mimics the well known gamma oscillation. Under these conditions the neurons input-output relation does not conform to standard models of neural operation. Instead we find that the neuron's output is highly sensitive to all three input parameters that characterize the pulse packet. Information can be encoded and decoded in all three of these parameters. Probably the most efficient variable to encode information in is mean input spike latency, at least when the oscillation amplitude is high. The neuron can very efficiently encode the mean input latency in its output latency and also make a latency dependent threshold operation. With a high threshold the neuron can act as a latency-based thresholding element while for very low thresholds the neuron just encodes the mean input latency into its output latency. Consequently, spike latencies can play a role analogous to firing rates in classical models. However, latencies are far more efficient in terms of processing time, information capacity per spike and energy consumption.

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