Signal Processing With Spikes

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Abstract

In the past, notable advances in the understanding of neural processing have been made when sensory systems were investigated from the viewpoint of adaptation to the statistical structure of its input space. Here, we point out that emphasis on the input structure has happened at cost of the biological plausibility of the corresponding neuron models which process the natural stimuli. Hence, we propose a spiking neuron model to process natural stimuli for which we derive here a learning rule to estimate its parameters.

1 Introduction

Science is about exploring structure and function of incompletely understood systems or phenomena. What concerns the system "brain" or the phenomena of "learning" or, say, "vision", great advances have been made since the debates in the early 20th century whether individual neurons are the basic elements of the nervous system or not (keyword neuron doctrine). Since then, much emphasis has been on *structure*, i.e. on individual neurons or on how distinct classes of neurons are connected with each other. However, the *functional* aspect of these networks of neurons cannot be fully understood by its structure alone: How are the interconnected neurons marshaled to give rise to behavior? Why are the neurons as they are? Why are they connected they way they are?

2 Background

These kind of questions were mostly addressed from the second half of the 20th century onwards. The brain was considered as a information processing system, and principles of signal processing and information theory were used to understand the *function* of some parts of the brain (redundancy reduction hypothesis) [2]. As information theory requires knowledge about the statistical structure of the information source, this approach triggered research into properties of the sensory environment, especially with respect to vision [4, 6, 14, 16], and its link to neural processing [1, 3, 5, 15, 17]. What regards vision, in addition to the principles of information theory, other principles were used to explain its function in the form of "The early visual system might be optimized for . . . ", including energy expenditure [18], minimal wiring among neurons [8], or minimal number of active neurons [12]. The early visual system comprises the retina, thalamus and the primary visual cortex. But higher visual areas have also been investigated in this manner, making interesting predictions on yet undiscovered cell types [9, 10].

3 Research question

What regards the early visual system in the retina, multiple "principles of operation" for its function have thus been formulated. Which is the right one? We think that this question is ill posed since it is unlikely that the forces of evolution can be reduced to a single optimization scheme. But it is worth remembering that the above theories for the retina use the following assumptions which we might summarize as linear rate-coding assumption.

- Information is conveyed using a firing rate code.
- Retinal processing is described by a linear filter.
- The statistics of the natural scenes is described by the power spectrum.

Although these assumptions are of course well justified as a first approximation to reality, we feel it is

time to re-consider some of them. Motivation comes from the finding that the linear rate-coding assumption becomes a limiting factor for the deeper understanding of the retina – as explained above, actually different optimization schemes give the same results under that assumption – and for the link to experimental results. First, single spikes were found to be information carrier in the early visual system of for example the fly [13], second, significant redundancy was found between retinal ganglion cells (also for cells with non-overlapping receptive fields) [11]. Hence, in the following, we re-address the neural processing of the retina. Specifically, we make the modification that neurons are modeled as integrate and fire elements, so that the research question becomes
Which properties of the neural system "retina" can be explained with the function-*hypothesis that neurons in the retina encode the input with spikes such that it can be linearly reconstructed from the spike times with a minimal reconstruction error.*

4 Processing natural stimuli with spikes

Here, we present a learning rule for the minimization of the reconstruction error. The learned filters and their relation to the early visual system will be discussed elsewhere. Further, we limit ourselves to a single neuron. In Section 4.1, we present the model, in Section 4.2 we derive a learning rule for the minimization of the reconstruction error, and in Section 4.3, we discuss the obtained learning rule.

4.1 Model

A neuron is modeled with the SMR_0-model [7]

$$u(t) = \eta(t) + \int_0^t \kappa(t-s) I(s) \mathrm{d}s, \tag{1}$$

where

$$\eta(t) = \sum_{f: t^f < t} \eta_0 \exp\left(-\frac{t - t^f}{\tau_r}\right) \tag{2}$$

$$I(s) = \int_0^s w(s-v) Y(v) \mathrm{d}v. \tag{3}$$

The spike times $\{t^f; f = 1, 2, \dots\}$ are defined by the instant of time where u reaches the threshold θ. Each spike triggers the reset of u from θ to $\theta - \eta_0$, and the neuron enters a time of reduces excitability modeled with an exponential kernel with refractory time constant τ_r. The neuron is driven by external input I, which is obtained through linear filtering of the natural stimulus Y with the encoding filter w. The kernel κ models the soma impulse response function with an exponential kernel with time constant τ_m.

From the obtained spike times $\{t^f\}$, we linearly reconstruct the stimulus Y via

$$\hat{Y}(t) = \sum_{f: t^f < t + T_d} \Phi(t - t^f), \tag{4}$$

with the decoding filter Φ and estimation time delay T_d.

Both the encoding filter w and the decoding filter Φ are unknown, and have to be found in order to minimize the average reconstruction error J

$$J = \left\langle \frac{1}{2} \int_0^{T_t} e(t)^2 \mathrm{d}t \right\rangle \tag{5}$$

$$\text{where } e(t) = \hat{Y}(t) - Y(t), \tag{6}$$

and <> denotes the sample average over the database of natural stimuli Ω_Y.

4.2 Learning rule to minimize the reconstruction error

Above, we have silently assumed that we know the spike timings $\{t^f\}$ exactly. However, both in experiments as well as in computer simulations, spikes can only be tracked to a maximal temporal precision Δ. This implies that the integration in Eq. (1) has to be replaced by a summation, and all variables take values in bins of size $h \geq \Delta$. This means that only finitely many parameters $w[1], \dots, w[N]$ and $\Phi[-Nd], \dots, \Phi[Nt-1]$ with $N = Nd + Nt = (T_d + T_t)/h$ have to be learned.

For a steepest descent learning algorithm, direct calculation shows that the gradient for the encoding filter is given by

$$\frac{\partial J}{\partial w[n] h} = \left\langle \sum_{k=1}^{Nt} h e[k] \Psi_n[k] \right\rangle \tag{7}$$

$$\Psi_n[k] = \sum_{k^f \in T(n, k+Nd)} \Phi[k - k^f] c_n^f \tag{8}$$

$$c_n^f = \frac{1}{\alpha(u[k^f] - u[k^f - 1])} \Bigg(\bar{Y}[k^f - n] + \sum_{p^m \in T(n, k^f)} c_n^m \eta_0 \exp\left[-\frac{(k^f - 1 - p^m) h}{\tau_r} \right] \Bigg), \tag{9}$$

where $n = 1, \ldots, N$. The term $T(x, y)$ denotes the set of spike times k^f satisfying $x \leq k^f < y$, and the constant α is a real number slightly less than 1. $\bar{Y}$ is the natural stimulus Y input after filtering with the soma response kernel κ.

Similarly, for $n = -Nd, \ldots, Nt - 1$ the gradient for the decoding filter is given by

$$\frac{\partial J}{\partial \Phi[n]h} = \left\langle \sum_{k^f \in T_n} e[k^f + n] \right\rangle \quad (10)$$

$$\text{for } T_n = T(\max(1, 1 + n) - n, Nt - n). \quad (11)$$

4.3 Interpretation

We discuss the obtained formulae for the gradients for the decoding and encoding filters.

4.3.1 Decoding filter

From Eq. (4), we see that the reconstruction kernel $\Phi[n]$ bears a a different interpretation for $n > 0$ and $n < 0$. That is why we obtain slightly different formulae for the gradient of the decoding filter Φ.

For $n = k - k^f < 0$, the spike k^f happens after the time step k for which we try to *reconstruct* Y. Thus, by $\Phi[n]$ we try to estimate the stimulus which precedes the spike at k^f by n units. Here, T_n becomes

$$T_n = T(1 + |n|, Nt + |n|), \quad (12)$$

so that for, say, $n = -Nd$, we consider spikes happening from $Nd + 1$ till the end $N = Nd + Nt$, and the gradient is given by the sum of errors which were made Nd time steps before the spike event.

For $n = k - k^f > 0$, however, the spike k^f happens before the stimulus $Y[k]$ which we try to approximate with $\Phi[n]$. Thus $\Phi[n]$ is used to *predict* from the spike time k^f the stimulus which happens n time units afterwards. Here, T_n becomes

$$T_n = T(1, Nt - n), \quad (13)$$

so that for, say, $n = 1$, we consider spikes happening from time step 1 till $Nt - 1$, and the gradient is given by sum of errors made one time step after the spike event.

4.3.2 Encoding filter

The gradient of the encoding filter w is given by the inner product between the reconstruction error e and the function Ψ_n. From the formulae, we see that this function is a superposition of shifted, weighted decoding filters. The weighting coefficient c_n^f is determined by the input $\bar{Y}[k^f - n]$ and the prior coefficients $c_n^1 \ldots c_n^{f-1}$ as well as the slope with which the membrane voltage u crosses the threshold θ. The influence of the prior coefficients decays exponentially with the distance between the the spike times. Since η_0 is a constant less than zero, the influence of the prior coefficients is subtractive for spike times which are close together.

5 Summary

In the ongoing search for understanding of the early visual system great advances have been made through investigations in the statistical properties of natural stimuli. We pointed out that the corresponding neuron models, which process the natural stimuli, tend to be however too simple and might be a limiting factor for further advances. Here, we made the step to biologically more plausible models and considered processing of natural stimuli by means of spiking neurons. Requiring linear reconstructability of the input from the spike train, we derived a learning rule for both encoding and decoding filter, showing thus how parameters of a spiking neuron model can be learned from natural stimuli.

Acknowledgments

This study is partially supported by Grant-in-Aid No. 17022012 for Scientific Research on Priority Areas System study on higher-order brain functions from the Ministry of Education, Culture, Sports, Science and Technology of Japan. MG is further supported by MEXT grant No. 040680.

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