Category: 2.1 Spiking neuron (of session 2: Neural network models and algorithms)
Distributed Synchrony - Understanding the Brain at the Single Cell Level

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Abstract

How does the brain process information? Can it be understood at the single cell level? This paper proposes a predictive coding model based on the use of distributed synchronous spikes. We test the hypothesis that information is encoded in neurons’ probability of firing, which are updated spatial-temporally at precise moments. Therefore, synchronous spikes are distributed across groups of cells in a time-varying fashion. The dynamic nature of synchronous oscillation may account for the relative difficulty of detecting precisely timed spikes in experiments as well as the irregular firing patterns of single neurons. Through the use of distributed synchronous spikes, we show that a sparse, overcomplete representation of information can be learned under the governance of a predictive coding principle. Neurons in this network develop localized and oriented receptive fields, and their spike trains appear random.

1 Introduction

The brain is a complex adaptive system which evolves under the driving force of learning. To understand and model the brain, we need to know how information is represented in the brain and what learning principles govern its organization.

Addressing the question of neural coding, there are two main classes of models – rate coding and temporal coding. Rate coding, which states that information is encoded in the frequency of firing, has been widely used in both experimental and theoretical study. One serious problem with conventional rate coding is its slowness. Human can recognize a complex novel visual scene in under 150 milliseconds (ms). Given that there are 10 or more processing stages and considerable conduction delays, participating neurons need to fire within 10 ms [13]. To slow down computation even more, from the fact that neurons often have irregular firing patterns [3, 11], a large window is needed for getting a robust estimation of firing rate. Hence, neurons need to fire at frequencies much higher than the typical 10 - 100 Hz firing rates of cortical neurons. In addition, rate coding limits the amount of information can be transmitted because it ignores all the information might be contained in the temporal structures of spike trains.

In contrast to rate coding, which simply treats irregular firing patterns as caused by noises, temporal coding explores the possibility that spike timing may contain information. One class of temporal coding models is that of synchronous firing models, which state that precise timing of spikes contains information. With synchronous firing, computation is distributed across cells and is bound together with the timing of spikes. In this model, no slow temporal averaging is needed to propagate signals, instead, signals are transmitted with multiple neurons spiking together. With the use of multi-cell recording techniques such as micro-electrode arrays, synchronous firing patterns have been found within the retina [7], within LGN [1, 14, 4], within cortex [4], between retina, LGN and cortex [4] and even within the cerebellum [17]. Besides supporting fast computation, synchronous firing allows multiplexing – multiple computational processes going through the same cell as long as there is no interference caused by overlapping phases. Multiplexing may contribute to the amazing computation power of the brain because it allows cells to be utilized in a more efficient manner. Also, with synchronous firing, “binding” becomes obvious, different parts of computation are bound together in a “firing together, belonging together” way. However, it is generally hard to discover precise spike timing patterns and reproduce some of the experimental results. Critics have argued that observed synchrony might be an artifact of data sampling and analyzing techniques, or may emerge purely by chance [3].

To fill the gap between the synchronous firing model and experimental data, we propose here that there might exist dynamic groupings of neuronal populations in the brain. In other words, synchronous spikes might ac-
usually get distributed over groups of neurons in a time varying fashion. Because the set of neurons participating in a computational process may vary over time, it would be of no surprise that synchronous firing patterns are so hard to capture. In our model, this dynamic grouping is made possible through the development of an overcomplete representation. The receptive fields of our model neurons overlap so that cells with similar receptive fields are capable of taking over each other’s task. Furthermore, by modeling neurons as firing probabilistically, the cells that get “picked” each time to send spikes are different so that synchronous spikes are distributed. In addition to relating synchronous firing with experimental findings, benefits of this distributed synchrony hypothesis include, alleviated cell load and reliable transmission in case of cell death or connection problems.

What kind of learning rules could govern the operation of the brain? Following Rao and Ballard’s work on predictive coding [9], we extend their model, which is based on the firing rate hypothesis, to use distributed synchronous spikes as coding primitives. Predictive coding models the brain as a predictor of its input. It makes use of the vast amount of feedback connections in the brain to carry top-down predictions from higher levels of processing. Working towards making good predictions, cells signaling the residual errors “reward” themselves with less firing, which in turn, save them on metabolic cost. In essence, predictive coding works by allowing cells to evolve under the governance of an economical coding scheme. Consistent with observed receptive fields properties of simple cells, and the fact that our input data are natural images with sparse structures, our predictive model develops a sparse, overcomplete representation. This is accomplished by borrowing ideas from Olshausen and Field’s work on sparse coding [8] and in addition, by utilizing a spatial weighted averaging technique for the development of overlapping receptive fields. Simulation results show that single cells’ spike trains appear random, consistent with experimental findings, also our model neurons develop properties comparable to simple cells.

2 Distributed synchrony

The dynamic grouping of synchronous firing neurons has been observed in rat’s cerebellum by Welsh and colleagues [17], and in developing lateral geniculate nucleus (LGN) of ferrets by Weliky [16]. Both groups recorded from a rather large number of cells. Welsh’s group recorded simultaneously from about 30 Purkinje cells of awake and non-anesthetized rat during skilled movement, and reported regrouping of synchronous firing neurons which happened at tens of millisecond speeds. A varying synchronous LGN activity has been reported by Weliky through simultaneously recording from 8 LGN cells of ferrets before eye opening. Further evidences of time-varying population synchrony have been found in monkey motor cortex by Baker and colleagues [2], and also by Grammont and Riehle [5].

A crucial condition of our distributed synchrony model is that, to allow computation be carried out by different cells from one moment to the next, there must exist several “candidate” neurons with similar receptive fields, and those cells need to be in close proximity so that they can share some common input. This is consistent with observations of topographic maps wherein neurons with similar properties are organized into cortical columns. In addition, it has advantages such as increased reliability and alleviated cell metabolic load. To have neighboring neurons developing similar receptive fields, we propose that neurons not only update their estimates of firing probability in a temporal manner - from past history, but also by a spatial averaging of neighboring cells’ estimates. This spatial averaging relates well with firing rate model in that, instead of averaging over time which may delay computation, neurons sample from neighborhood to get an instant estimate of probability of firing. To be specific, this spatial average is done by using a gaussian weighting window centered at the cell itself, so that influence of neighboring cells decrease with increasing distance. By controlling firing probability with this neighborhood constraint, neurons’ receptive field slowly varies and neighboring cells show similar receptive field properties, as shown in figure 4.

3 Predictive coding on the basis of distributed synchronous spikes

In order to relate high level functionality of the brain with its low level coding mechanisms, we extend Rao and Ballard’s predictive coding model [9] which is based on the firing rate hypothesis, to use distributed synchronous spikes. Predictive coding models the brain as a hierarchical network whose parameters are used to predict its inputs. It makes use of the substantial feedback connections in the brain to carry top-down predictions from higher level processing. Therefore, neurons signaling residual errors of predictions fire less and less as computation converges. By having top-down predictions trying to cancel bottom-up input, cells save on metabolic cost because firing is expensive. Stein et al. [15] have reported observations of enhanced gamma frequency corticocortical synchronizations for novel stimuli, which may sug-
gest the use of predictive coding and “cancelling” role of top-down predictions. Additional evidence of this comes from Singer’s lab [4], they have found that oscillation persists in the case of dynamic stimuli, but weakens over time for static stimuli. The observed oscillatory nature of synchrony may be due to the fact that, in order to make the cancellation possible, input from lower level and higher level cells need to arrive at the current level of processing at the same time, therefore, cells need to fire at a fixed interval. This oscillatory nature of synchrony has not only been observed with multi-cell recording [15, 4], but also with EEG [6, 10] and with MEG [12].

In our simulation study, we model only a subset of the cortical circuit - LGN and V1. The network is shown in figure 1, in which LGN cells receive bottom-up input $I$ from retinal ganglion cells and top-down prediction input $UP$ from our model V1 cells. The residual errors $I-UP$ are computed to allow estimation of probability of firing $P$ which is estimated spatial-temporally. Note that computation is carried out at fixed intervals to allow “cancellation”. Synaptic weights of feedforward and feedback connections are denoted by matrices $U^T$ and $U$ respectively. To simulate retinal ganglion cell filtering effects, we preprocess our input images with the same whitening/lowpass filter as in Olshausen and Field [8] only with a lower cutoff frequency. In addition, to simulate ON/OFF center receptive fields effects of LGN cells, we double the filtered input by adding a negated version. The result of the preprocessing is denoted by an image vector $I$ as shown in figure 1.

In the case of learning to represent natural images, Rao and Ballard [9] used a minimum description length principle to trade off cost of coding with residual error. However, their use of a multivariate gaussian prior prevents their model neurons from developing a sparse representation which is essential in coding natural images because of sparse structures of those images. Olshausen and Field [8] have shown the necessity of using a non-gaussian prior for learning a sparse code. Based on those concerns, our cost function is designed as follows,

$$E = ||I-UP||^2 + \alpha \sum_{i=1}^{i=n} S(P_i) + \beta \sum_{i=1}^{i=m} \sum_{j=1}^{j=n} S(U_{ij})$$

(1)

where $I$ is an image vector of size $m \times 1$ preprocessed as mentioned above, $U$ is an matrix of size $m \times n$ representing the synaptic weights of feedback connections, and its transpose denotes those of feedforward connections, $\alpha$ and $\beta$ are constants, $P$ stands for probability of firing of coding neurons, and is of size $n \times 1$, it is defined by the following sigmoid function,

$$P(x) = \frac{1}{1 + e^{-x}}$$

(2)

in which $x$ represents the membrane potential.

To charge for the cost of coding and at the same time to encourage a sparse representation, we borrowed from Olshausen and Field’s [8] a cost function for coding units $S(x)$, which is of the following form,

$$S(x) = \log(1 + x^2)$$

(3)

The particular choice of $S(x)$ is not important as long as the distribution it corresponds to is non-gaussian.

Estimation of $x$ and $U$ is accomplished through the use of the EM algorithm and gradient descent. $P$ is computed according to the above sigmoid function with $x$ as input, and then updated spatially using a gaussian weighted window to encourage the formation of overlapping, slowly varying receptive fields. The particular gaussian window for weighting we use is $N(0,3)$. Instead of training on whole images at once, simulation is done with patches of size $8 \times 8$. In detail: 1) $U$ is initialized to small random numbers. 2) upon seeing each patch, $x$ is first initialized to $U^TI$, then is updated using gradient descent. 3) $P$ is computed from $x$ according to equation 2, then recomputed using the normal distributed weighting vector. The estimation of $x$ and $P$ continues until $E$ converges, then a $U$ is computed for this patch. 4) $U$ gets updated by the average $\bar{U}$ of every 100 patches.

Results of training after 100,000 patches are shown in figure 2 - 5. The top portion of figure 2 shows spike trains of the 60 model V1 neurons stimulated by 8 image patches, each stays for 100 ticks, one can see that with dynamic grouping of synchronous firing, single

![Figure 1: Predictive coding model network](image-url)

Figure 1: Predictive coding model network Shows our current two-layer network with LGN as input layer, and with V1 as coding layer. Signaling in this network at done at precise moments with a fixed interval $\Delta t$ in order to make evaluations of predictions possible. Furthermore, input from retinal ganglion cells $I$ (excitatory) arrive repeatedly to allow convergence of top-down prediction $UP$ (inhibitory). With $U^T$ and $U$ denoting synaptic weights of feedforward and feedback connections respectively, residual error signals $I-UP$ carried by the feedforward pathway arrive at V1 cells as $U^T(I-UP)$ to influence their estimates of probability of firing $P$ as in gradient descent method. V1 coding cells signal their predictions according to their probability of firing $P$ and the predictions carried by the feedback pathway arrive at input layer as $UP$ at the same time as the lower level input $I$, residual errors $I-UP$ are then calculated and signaled by LGN cells.
neurons’ spike trains appear random. The bottom part of figure 2 shows a PSTH that is the result of summing over the above 60 neurons, instead of trials as in conventional PSTH. The phasic response shown is due to computation convergence. Figure 3 shows that neighbor cells are capable of taking over computation, therefore, allowing spikes to be distributed in a dynamic manner. It can be seen in this figure that similar reconstructions are signaled by different coding neurons at two different times. In addition, our model neurons have developed localized and oriented receptive fields as shown in figure 4.

Synchronous oscillations have been found by Singer’s group [4] in cat’s cortex. In particular, they found that oscillation pattern varies w.r.t. dynamic and static stimuli. With dynamic stimuli, oscillation persists, whereas with static stimuli, oscillation weakens over time. This difference in oscillation patterning may be caused by phasic response of the network during the course of convergence. To show that, we did a sliding window autocorrelation study on our model neurons under two different types of stimuli - moving bars and static image patches. The results shown in figure 5 appear to be comparable with Singers’ result [4].

4 Conclusions and future work

In this paper we proposed a distributed synchrony hypothesis, in which neurons are modeled as coding information probabilistically, and computation are shared among cells in a spatial-temporal manner. Therefore, even though synchronous oscillations are used for neural signaling, single cells’ spike trains appear random, and synchrony is only observable at population level. To show that such a coding mechanism can support computation, we extend Rao and Ballard’s predictive coding model which is based on the use of firing rates, to use distributed synchronous spikes as coding primitives. By modeling the brain as a predictor of its inputs, through the use of a Minimum Description Length principle, reconstruction errors are traded off with cost of reconstruction units, to avoid the problem of overfitting and to allow generalization. Furthermore, borrowing ideas from Olshausen and Field’s [8], given that natural images appear to have sparse structures, we impose a non-gaussian prior on coding parameters to allow sparse coding. To encourage the formation of “candidate” cells that act as computation back ups of each other, a spatial averaging is used to update estimates of probability of firing, with a gaussian weighting vector. In particular, this spatial averaging can be made possible through lateral interactions of cells. The added redundancy not only allows a overcomplete representation, which has the advantages of robust coding and alleviated cell load, it is also consistent with observation of topographical maps.

The problems associated with our current model are: 1) Currently the probabilities of firing are computed
from estimated membrane potential with the help of a sigmoid function. Ideally, for a model using spikes as coding primitives, the estimation of probability of firing should be computed from individual spikes. Our further work will address this issue; 2) Our network has only two layers, with LGN as the input layer and V1 as the coding layer. To simulate the brain in a larger scale, we need to extend our network to a more complete one - a hierarchical cortical patch network.

References


