

A single spike model of predictive coding

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Abstract

Current models of cortical computation are based on analog quantities instead of single spikes. This paper extends the predictive coding model (8) to the level of neural signaling. Neurons in our model use a mixed strategy to transmit information. Spikes are not only messages of computation, but also carriers of information with analog quantities encoded in their phases. Computation is shared among cells both in time and in space, such that information is signaled probabilistically in a distributed synchronous fashion. Contrary to “noise other than signal” interpretation of irregularity of neural signaling, our model proposes a computational role of such variability.

Key words: Distributed synchrony; predictive coding; probabilistic firing; sparse coding; minimum description length (MDL)

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1 Introduction

Current models of cortical computation are based on analog quantities instead of single spikes. To allow theory to effectively guide experiments, a complete model of the cortex which makes use of single spikes is necessary. Such an extension to signaling level is difficult, as how neurons encode information is still an unresolved mystery. Proposals like rate coding and temporal coding all suffer from the fact that neurons fire highly irregularly. A typical interpretation of the variability is “noise other than signal”, which not only has difficulty to account for the speed, accuracy, efficiency and complexity of biological systems, but is also contradicted by recent studies that show both spike generation (5) and transmission (2) are highly reliable. Instead of treating this randomness as induced by noise, we ask whether it is associated with computation. In particular, we propose in our distributed synchrony model (10) that neurons communicate stochastically by way of probabilistic firing, with firing probabilities encode information such that randomness is directly related to computation.

In this paper, we extend the predictive coding model (8) to make use of single spikes. Contrary to the conventional view of neurons as analog devices communicating digitally with single spikes, we model neurons as digital devices communicate with analog signals which are reflected in the phases of spikes. Supported by voluminous data showing oscillatory pattern of neural activities,

we propose a clock hypothesis, that cortical computation and communication are regulated by clocks. Such clocks are not easily detectable as neurons not only signal probabilistically, but also in a distributed fashion. Evidences of gamma band oscillations (9) suggest a possible frequency such clocks may run on.

2 The Algorithm

The system we choose to illustrate our distributed synchrony model with is the recurrent network connecting lateral geniculate nucleus (LGN) and V1. A particular advantage of modeling LGN-V1 circuitry is the wealth of data of these cortical areas. In particular, there is data showing synchronous timing of LGN cell spikes and V1 simple cell spikes as well as data on phasic responses (1; 3), which directly support coding with synchronous spikes and predictive nature of the computation.

As depicted in figure 1, the predictive coding algorithm is implemented with a network of 72 model LGN neurons and 128 model V1 neurons. In this network, feedback connections from V1 to LGN carry prediction signals, and feedforward connections from LGN to V1 carry signals of mismatch. Contrary to the conventional view of neurons as analog devices communicating digitally, we propose a dual role of spikes, such that they are not only messages, but also carriers. Suppose messages are encoded as probabilities P_m . With P_s stands

for probability of spiking, and with P_p denotes the analog quantity encoded in the phase of spike, we have $P_m = P_s \times P_p$. Therefore, instead of coding with real numbers as in (8; 6) assuming pure rate code, information is transmitted as probabilities P_m as such products - $P_s \times P_p$. P_s when set to be 1 would achieve the most accurate signaling but would also predict unrealistic uniform spiking. P_p when set to be 1, is the usual binary interpretation of spikes as in rate code, but it would suffer from precision problem. As it is clear that the choice of P_s and P_p is a tradeoff between rate coding observation and representation precision, we simply pick them to be of equal value such that $P_s = P_p = \sqrt{P_m}$. Note that such a choice is not the only solution to reflect the above tradeoff. In detail, the mapping from real numbers to probabilities P_m are done via sigmoidal transfer functions 4 and 5, then transmitted with neurons spike with probability $\sqrt{P_m}$, along with $\sqrt{P_m}$ encoded in the phase of such spikes. Decoding is done with estimation of the firing probabilities from spike counts, along with read out of such phase encoded messages. This combined use of spike counts and spike phases is motivated by oscillatory patterns of cortical activities, that the brain may use clocks to regulate signal transmission and estimation. A possible candidate of the value of clock interval is 20 milliseconds, as suggested by experimental evidences of 40-90 Hertz range synchronous oscillations (9). However, as signaling is probabilistic and distributed, clocks are rather difficult to detect.

Our network is initialized to be of random connection weights. Neurons learn

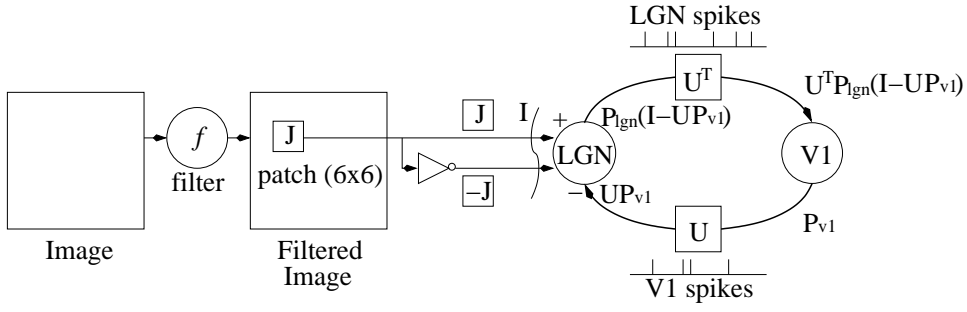


Fig. 1. Algorithm. See text for details.

structures of natural images following the minimum description length (MDL) principle as reflected in the objective function 1, which specifies the overall cost E to be minimized as the weighted sum of three terms: the sum of squares of coding error $\|I - UP_{v1}\|^2$, the total cost of coding $\sum C(P_{v1})$, and the total cost of the circuitry making the prediction $\sum C(U)$, with α and β specifying the relative weights of the later two terms:

$$E = \|I - UP_{v1}\|^2 + \alpha \sum C(P_{v1}) + \beta \sum C(U). \quad (1)$$

In detail, I is a vector of the retinal inputs, U is a matrix denoting weights of feedback synaptic connections from V1 to LGN, P_{v1} refers to message signaled by V1 coding cells in probabilities. Function C specifies cost of coding and cost of circuitry, the particular choice of which is very important in that it determines the kind of representation the coding cells could learn. Olshausen and Field have suggested that sparse coding might be a strategy used by V1 simple cells (6). We use Cauchy distribution as priors of our model parameters P_{v1} and U for its high kurtosis as required by sparse coding.

For training, six 256×256 images of natural scenes are used. To simulate the filtering effect of retinal ganglion cells, the images are pre-processed with a whitening/lowpass filter similar to what used by Olshausen and Field (6), only with a lower cutoff frequency of 50 cycles/picture. Instead of feeding a whole filtered image to the network, training is done with random image patches of size 6×6 taken from the filtered images. To be consistent with the observed ON-center and OFF-center receptive field properties of retinal ganglion cells, an input patch is coupled with a negated version of itself as retinal inputs, essentially allowing signaling of negative numbers.

Synaptic weights of feedforward and feedback connections are denoted as matrices U^T and U as shown in figure 1. Note that weights of feedforward connections and feedback connections happen to be exact matrix transposes of each other. It has been shown by Rao (7) that this property will emerge after training. The synaptic matrix U is initialized to small random numbers and is updated with the average \dot{U} of every 100 training image patches'. The update for the synapses \dot{U} for each patch is calculated by doing a gradient descent on the cost function 1, with the goal to minimize the overall cost E . This is shown in equation 3, in which \hat{P}_{v1} denotes the estimated signal that is decoded from spike counts and phase read outs.

$$\begin{aligned}\dot{U} &= -\frac{k_2}{2} \frac{\partial E}{\partial U} \\ &= k_2((I - U P_{v1}) P_{v1}^T - \frac{\beta}{2} C'(U))\end{aligned}\tag{2}$$

$$= k_2((I - U\hat{P}_{v1})\hat{P}_{v1}^T - \frac{\beta}{2}C'(U)). \quad (3)$$

Cells in the network encode information into probabilities. The mapping from membrane potentials to probabilities are specified by sigmoidal functions 5 and 4, where equation 4 is for LGN cells, and 5 is for V1 cells.

$$P_{lgn}(x) = \begin{cases} \frac{2}{1+e^{-bx}} - 1 & \text{if } x \geq 0 \\ 0 & \text{o.w.} \end{cases} \quad (4)$$

$$P_{v1}(x) = \frac{1}{1 + e^{-cx}} \quad (5)$$

Membrane potentials of V1 cells (x) are calculated by doing a gradient descent on the cost function 1. The update equation of V1 cells' membrane potentials is shown below. In which \hat{P}_{lgn} and \hat{P}_{v1} are estimations of messages signaled by LGN and V1 cells, respecting the fact that recipient cells would need to decode messages from pre-synaptic cells from their spikes. Note that because prediction error $I - U\hat{P}_{v1}$ is transmitted by LGN cells as firing probabilities $P_{lgn}(I - U\hat{P}_{v1})$ according to equation 4, the actual update of x is done with $P_{lgn}(I - U\hat{P}_{v1})$, multiplied with a constant s .

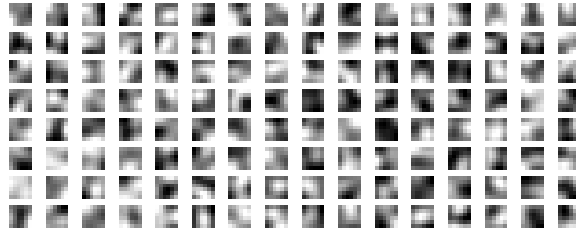


Fig. 2. Receptive fields of 128 model neurons of size 6x6. They are localized and oriented that are consistent with simple cell observations.

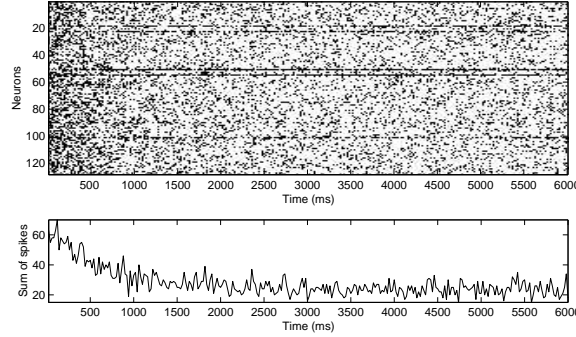


Fig. 3. Top: raster plot of 128 neurons' response to one stimulus presented for 6 seconds. A couple of Cells fire with almost unity probability. Bottom: PSTH (over cells, instead of over trials) show phasic response, which is due to the predictive nature of the computation.

$$\begin{aligned}
\dot{x} &= -\frac{k_1}{2} \frac{\partial E}{\partial x} = -\frac{k_1}{2} \frac{\partial E}{\partial P_{v1}} \frac{\partial P_{v1}}{\partial x} \\
&= k_1 [U^T (I - U \hat{P}_{v1}) - \frac{\alpha}{2} C'(P_{v1})] \otimes P'_{v1} \\
&\doteq k_1 [U^T s \hat{P}_{lgn} - \frac{\alpha}{2} C'(P_{v1})] \otimes P'_{v1}.
\end{aligned} \tag{6}$$

The receptive fields after training are shown in Figure 2. These are readily seen to be oriented and localized, consistent with data of V1 simple cells.

Even though computation are clock-based, cells fire irregularly as shown in figure 3. By summing over spike trains, the population response appear phasic due to the predictive nature of the computation.

Using fMRI to study neural activities in monkey cortex, Logothetis and col-

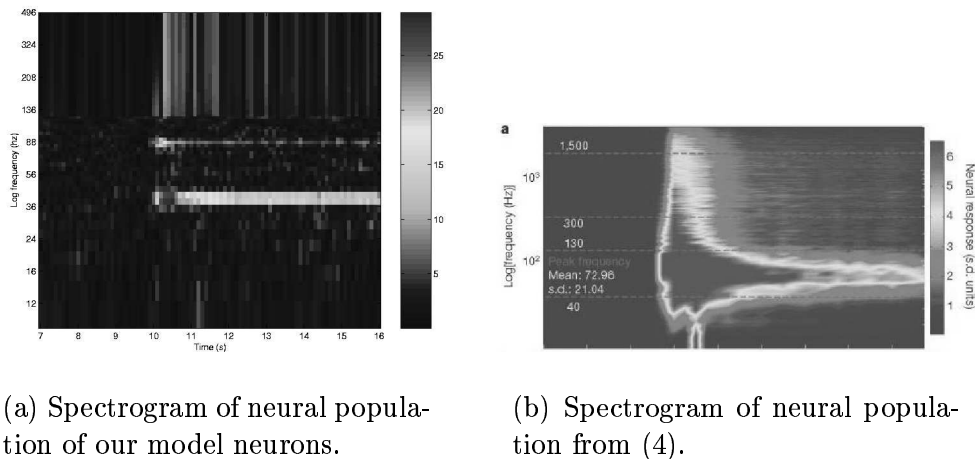


Fig. 4. Oscillatory patterns suggest the use of clocks in cortical computation. Note that in both figures, magnitudes of oscillations are in units of the standard deviation of the pre-stimulus period.

leagues (4) have reported gamma band oscillations (figure 4(b)). We have done a similar analysis on our simulated spike train data and find comparable patterns. Such a comparison is shown in figure 4.

3 conclusions

In this paper we extend predictive coding (8) to the level of neural signaling, such that information is encoded as probabilities, and it is transmitted with a mixed strategy using spike counts and spike timing. Coding by spike counts is essentially the rate coding hypothesis. It is supported by data showing the association of spike counts with stimulus values. Coding by phases enables more accurate representation and is supported by data showing oscillatory neural activities. Besides reconciling rate coding with temporal coding, our model also suggests the computation role of irregular firing, as information is

encoded as probabilities, and signaled by populations of neurons distributively. Through learning to represent inputs, model V1 neurons in our model LGN-V1 circuitry developed receptive fields resembling those of V1 simple cells, as driven by a minimum description length principle.

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