

1 Introduction

While progresses in experimental neuroscience and computational neuroscience have contributed tremendously to brain study, a general theory of cortical computation remains elusive. In particular, a gap is missing between the two areas of study. Experimental measurements and data analysis that follows have been focusing on interpreting neuronal signals without or with very little guidance of high level computation. One reason of that is current cortical computation models abstract away individual spikes but use analog numbers, resulting it difficult to relate to experimental data. Even though such abstractions are helpful and necessary to simplify modeling, a complete model of the cortex would have to relate to basic neuronal signaling to understand how information is processed in the brain.

The focus of this paper is to show that abstract computations of current models can be carried out in a more biological-realistic fashion. In particular, we extend predictive coding model [RB99] 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. In our model, neurons communicate at discrete times - run on a clock, and the signals are analog quantities encoded in the phases of single spikes with respect to the clock. Evidences of gamma band oscillations [TBB99] suggest a possible frequency the clock may run on.

It is well known that cortical cells fire irregularly. Instead of treating this randomness as induced by noises, we suggest that cells communicate probabilistically. The idea of stochastic firing not only fits well with observed randomness in neural data, but also improve robustness of computation. It also explains why it is difficult to recover the clock if computations are clock-based.

2 The Algorithm

In our specific model circuit that uses predictive coding, we chose the LGN-V1 connections because of the wealth of data that exists for that circuit.

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 prediction error. Instead of coding with real numbers as in [RB99, OF97], information

being computed and transmitted are neurons' firing probabilities. For example, instead of sending prediction and error of prediction by way of firing rates directly, cells in the network fire probabilistically via sigmoidal transfer functions 4 and 5. The quantities to be signaled, i.e., the firing probabilities of neurons, are encoded in the phases of spikes. Spikes alone are merely carriers of information, encoding and decoding are done with respect to clock cycles. A possible candidate of the value of clock interval is 20 milliseconds, as suggested by experimental evidences of 40-90 Hertz range synchronous oscillations. Note that the exact frequency does not affect computation in our current model for there is no explicit time interval setup but rather clock ticks. However, having a rather long clock interval that is on the order of tens of milliseconds allows several computational processes to be multiplexed as long as they are out of phase.

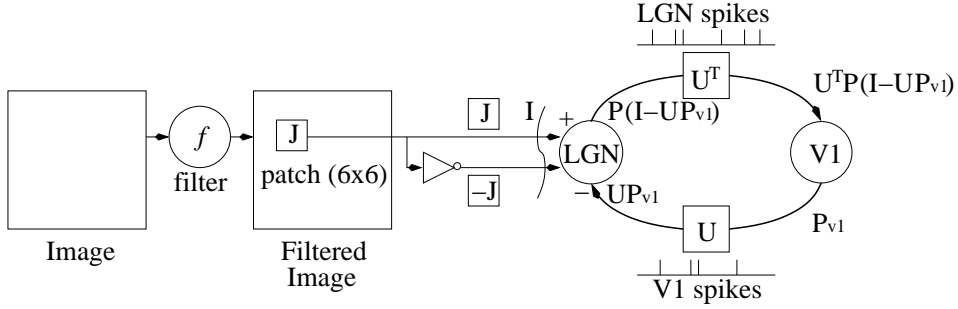


Figure 1: **Algorithm**

The Minimum Description Length formulation interprets cortical receptive fields as resulting from the interaction of two effects: 1) the error in prediction and 2) the cost of the circuitry making the prediction. In our formulation the latter cost is measured in terms of the firing probabilities of the neurons and their synapses. The exact firing probabilities and synapses are estimated as to minimize the overall cost defined in equation 1.

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

In detail, as shown in the above equation, E denotes the overall energy which is the quantity to be minimized, $\|I - UP_{v1}\|^2$ is the sum of squares of prediction errors, where 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 the probabilities of firing of V1 coding cells. $\alpha \sum C(P_{v1}) + \beta \sum C(U)$ refers to weighted sum of expected cost of coding. The particular choice of function C 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 [OF97]. We use Cauchy distribution as priors of our model parameters P_{v1} and U for it has high kurtosis as required by sparse coding. The corresponding function for computing cost of coding given Cauchy prior is shown in equation 2 below.

$$C(x) = \log(1 + ax^2) \quad (2)$$

For training, six images of natural scenes are used. Each of size in pixels 256×256 . 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 [OF97], 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, note that consecutive input patches can be of different images. To be consistent with the observed ON-center and OFF-center receptive field properties of retinal ganglion cell, an input patch is coupled with a negated version of itself as retinal inputs.

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 [RB97] 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 . In detail, \dot{U} is computed according to equation 3.

$$\begin{aligned} \dot{U} &= -\frac{k_2}{2} \frac{\partial E}{\partial U} \\ &= k_2((I - UP_{v1})P_{v1}^T - \frac{\beta}{2}C'(U)) \end{aligned} \quad (3)$$

Cells in the network encode information into probabilities of firing. 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 are calculated by doing a gradient descent on the cost function 1. The update equation of V1 cells' membrane potentials 6 is shown below. \hat{P}_{lgn} and \hat{P}_{v1} in equations are estimations of firing probabilities of LGN and V1 cells, simply respect the fact that recipient cells would need to decode probabilities of firing of pre-synaptic cells from 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 .

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

3 Results

The receptive fields after training are shown in Figure 2. These are readily seen to be oriented, localized, and bandpass.

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 colleagues [LPA⁺01] have reported gamma band oscillations5(a). We have done a similar analysis on our simulated spike train data and find comparable patterns.

References

- [LPA⁺01] Nikos K. Logothetis, Jon Pauls, Mark Augath, Torsten Trinath, and Axel Oeltermann. Neurophysiological investigation of the basis of the fmri signal. *Nature*, 412:150–157, 2001.

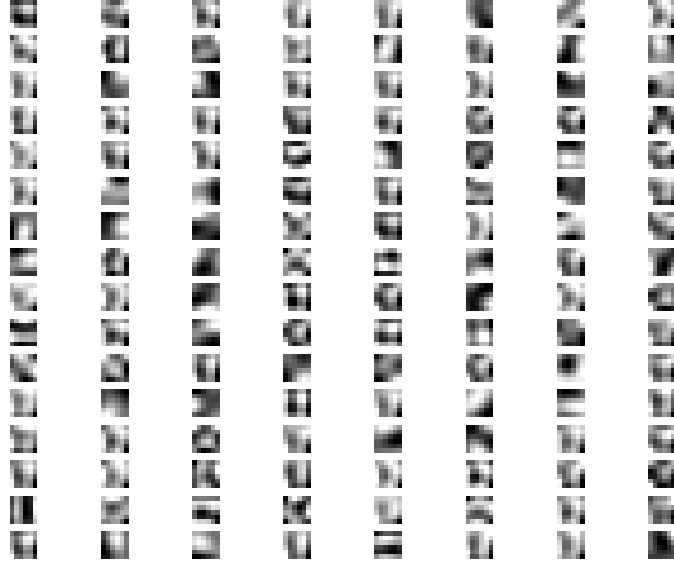


Figure 2: Receptive fields of 128 model neurons of size 6x6. Localized, oriented and bandpass, consistent with simple cell observations.

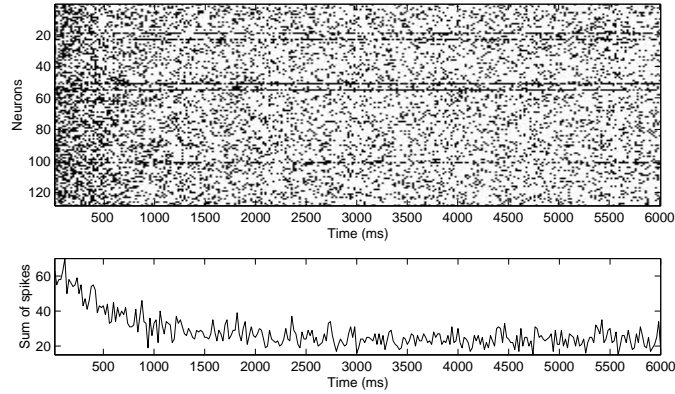
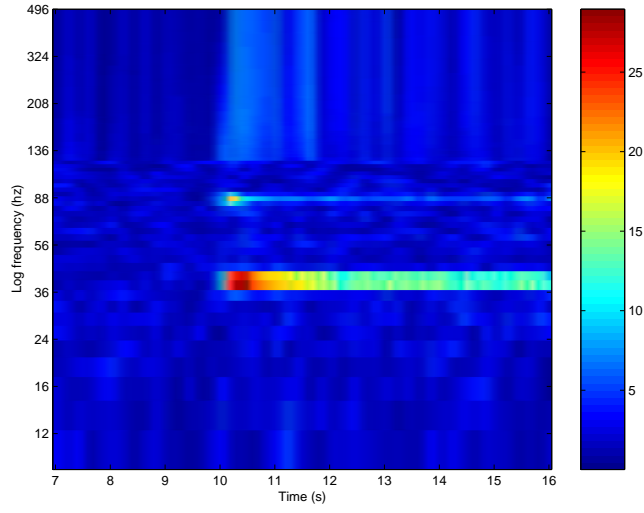
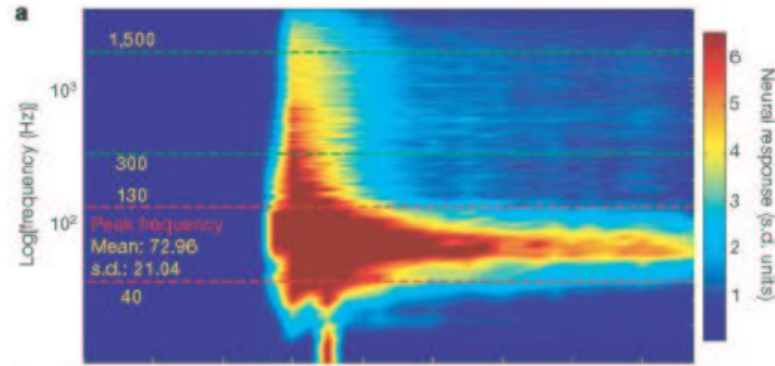


Figure 3: Top: raster plot of 128 neurons' response to one stimulus presented for 6 seconds. A couple of Cells fire with almost unity probability. Bottom: PSTH (over cells, instead of over trials) show phasic response, which is due to the predictive nature of the computation.



(a)

Figure 4: Spectrogram of neural population of our model neurons. Magnitudes of oscillations are in units of the standard deviation of the prestimulus period.



(a)

Figure 5: Spectrogram of neural population from [LPA⁺01].

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- [TBB99] Catherine Tallon-Baudry and Olivier Bertrand. Oscillatory gamma activity in humans and its role in object representation. *TICS*, 3:151–162, 1999.