Spike count distributions, factorability, and contextual effects in area V1

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How do neurons in primary visual cortex combine color information from inside and outside the classical receptive field? Recent statistical analysis demonstrates that spike count distributions in monkey data can be factorized into a component selectively determined by the center stimulus, and a component selectively determined by the surround (Movellan et al., 2002). We examine models with significantly fewer parameters that adhere to or approximate this form of factorability. We characterize the goodness of fit of the models to the monkey spike count distributions. This serves a basis for further testing neural factorabilty, and poses theoretical questions about neural coding.

Introduction

A challenging issue in computational sensory processing is understanding information integration across multiple stimulus attributes. We specifically focus on visual spatial integration of color in primary visual cortex (area V1). A neuron is experimentally presented with a center stimulus inside its so-called classical receptive field; and a surround stimulus in an annular region surrounding the classical receptive field. It has been widely documented that the response of a neuron to the optimal center stimulus can be nonlinearly modulated by a surround stimulus that by itself exerts no response in the neuron (e.g., [4, 11]). However, the computational nature of this interaction for a range of center and surround stimuli (i.e., not only center optimal) is not well understood.

Neural responses are often analyzed according to the mean firing rate. But when a neuron is presented with multiple stimulus repeats, one can characterize a full spike count distribution. Indeed, Movellan et al. [9] have recently demonstrated that examination of the spike count distribution can provide insight into how center and surround color information are combined in V1 neurons. Specifically, they showed that the probability of spiking given a center and surround, could be well fit by a model that factorizes into a component selectively determined by the center, and a component selectively determined by the surround. This model (denoted Morton-style factorial) stems from earlier work by Morton and Massaro on information integration in a range of psychophysical experiments [6, 7].

The Morton-style factorial model constitutes a general statistical framework with a large number of free parameters; each spike count is fit with a separate parameter. Here we explore simplified models, with significantly fewer parameters. The reduced models either adhere to or might approximate a Morton-style factorial coding. We test the goodness of fit for the different models.

Methods

Animal methods and preparation are described in detail in Wachtler et al. [11]. Data were collected from awake fixating monkeys. Stimuli were homogenous isoluminant color squares centered on and at least twice the size of the estimated receptive field of the neuron. Eight center stimuli and two surround stimuli were chosen at random, and presented for 500 milliseconds. Spike histograms (0 to 9 spikes) were computed for spike times starting at 50 milliseconds after onset and lasting for 100 milliseconds. Out of 94 units were recorded, 20 were chosen with strongest background effect and a minimum of 16 trials per condition.

The Morton-style factorial model is described in detail in Movellan et al. [8]. In addition, we examine models with a reduced number of parameters, in which a Gaussian distribution is passed through a Sigmoidal nonlinearity. In the simplest case, the mean of the Gaussian distribution is given by the sum of a term that depends on the center and a term that depends on the surround (Additive mean model) . This model is guaranteed to adhere to Morton-style factorability due to the exponential term of the Gaussian. We also examine a model in which the mean is multiplicatively determined by a center and surround parameter (Multiplicative mean model). Note that this model is not guaranteed to adhere to factorability. We have tested through simulation that the model still very closely approximates factorability, at least in the parameter regime of our fits. The multiplicative mean model might bear some similarity to divisive normalization models that have been proposed in area V1 (e.g., [5]).

There are overall 144 data points, 81 free parameters in the Morton-style factorial model, and only 13 free parameters in the Additive and Multiplicative mean models (including the Gaussian variance, Sigmoidal function threshold and gain, and 10 parameters corresponding to center and surround conditions).

Results

The Sigmoidal function provides a nonlinear distortion of the initial Gaussian distribution. For example, when a Gaussian distribution is passed through a Sigmoidal nonlinearity, low values of the distribution are pushed towards zero, resulting in higher kurtosis. This aspect is often observed in the data and well captured by the models.

We fit each of the 20 V1 neurons with the above models. In the Morton-style factorial model, only 2 neurons show significant deviations (chi-square test, 63 degrees of freedom, $p < 0.05$). In the Subtractive mean model, 7 neurons show significant deviations (chi-square test, 131 degrees of freedom, $p < 0.05$). In the Multiplicative mean model, 4 neurons show significant deviations (chi-square test, 131 degrees of freedom).

The chi-square test sets a critical value, but it is also of interest to examine the spread of values obtained with each model. Although the Morton-style factorial model performs best, the chi-square values for the different models are typically correlated.

Discussion

We have examined the concept of Morton-style factorial coding of color stimuli in monkey area V1. The general Morton-style factorial model performs extremely well, suggesting that the brain might compute or approximate a factorial code. It is important to note that we have also tested models with an equivalent number of parameters that severely do not fit the data; as well as simulated data in which Morton-style factorial models perform poorly (see [9]).

Here we have tested models with significantly fewer free parameters, that either adhere to or appear to approximate Morton-style factorability. A nice aspect of these reduced-parameter models is that they provide a smoother fit to the data than the general Morton-style factorable model. The Additive mean model is Morton-style factorable, but does not perform as well as the multiplicative model. We are exploring other model variations, that might adhere to factorability and perform better.

We are also investigating in greater detail those cases in which there are significant deviations in the models. Larger deviations in the model might correspond to cases in which the classical receptive field was underestimated experimentally. We are also exploring model behavior for different spike time windows in the data.

The models discussed here do not describe a specific neural implementation, but are a step forward towards this direction. Future research will be aimed at constructing more realistic neural circuitry. Morton-style factorial codes are often described as feedforward, but more recent work has demonstrated that feedback implementations can in fact be consistent with this form of factorability [8].

This framework for thinking about spike count distributions and factorability can be applied to a number of future directions. Experimentally, factorable models can be tested across other stimulus attributes and neural areas. Theoretically, it has been suggested that a role of early sensory processing might be to increase independence between neuronal responses, when exposed to natural stimuli (e.g., [1, 2, 3, 10]). The line of work presented here and in [9] suggests an alternative (but not mutually exclusive) notion of efficiency: that when conditioning on the number of spikes, external aspects of stimuli in the world are independent. These ideas can be explored through statistical analysis of natural scenes.

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