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

Odelia Schwartz[1], Javier R. Movellan[2], Thomas Wachtler[3],

Thomas D. Albright[1], and Terrence J. Sejnowski[1,2]

[1]*Howard Hughes Medical Institute, The Salk Institute for Biological Sciences*

[2]*Institute for Neural Computation, University of California, San Diego*

[3]*Neurobiology & Biophysics, University of Freiburg, Germany*

Abstract

Neural models of contextual integration typically incorporate a mean firing rate representation. We examine representation of the full spike count distribution, and its usefulness in explaining contextual integration of color stimuli in primary visual cortex. Specifically, we demonstrate that a factorizable model conditioned on the number of spikes can account for both the onset and sustained portions of the response. We also consider a simplified factorizable model, that parametrizes the mean of a Gaussian distribution and incorporates a logistic nonlinearity. The model can account for the sustained response but does not fair as well in accounting for onset nonlinearities. We discuss implications for neural coding.

Keywords: Spike count distribution; Factorizability; Integration; Contextual; Color; V1

Sensory neurons exhibit striking nonlinear behaviors in the integration of contextual information. For example, it has been widely documented that the response of a neuron to an optimal center stimulus inside the classical receptive field can be nonlinearly modulated by a surround stimulus that by itself exerts no response in the neuron (e.g., [1, 2]). However, the computational nature of this interaction for a range of center and surround stimuli is not well understood. Here we focus on contextual integration of color in primary visual cortex (area V1) [3].

Neural responses are often analyzed and modeled according to the mean firing rate. But when a neuron is presented with multiple stimulus repeats, one can also characterize the fluctuations around the mean firing rate, and more generally, a spike count distribution. Specifically, we examine a neural model that is factorizable in the spike count domain: conditioned on each spike count (say 0 spikes, 1 spike, and so on) the probability of response can be factorized into a component selectively determined by the center, and a component selectively determined by the surround. Similar models have been developed by Morton and Massaro to explain a wide range of information integration data in the psychophysical realm [4, 5], and hence have been called *Morton Massaro* [6, 7].

We demonstrate the ability of the Morton Massaro model to account for color contextual effects in V1 neurons, in comparison to a control model. The control is chosen to exemplify that there exists a model with the same number of free parameters as Morton

Massaro, that cannot account for the data. This illustrates that the Morton Massaro model can explain the data not merely due to flexibility in its number of free parameters. An earlier version of this work is described in Movellan et al. [7]. We also consider a parametric spike count distribution model, the *Gaussian logistic* model, that conforms to Morton Massaro factorizable coding, but contains significantly fewer parameters. Both factorizable models account well for the sustained response, including suppression when the center matches the surround color; Morton Massaro fairs better in characterizing the onset of the response, including suppression when the center matches the surround color, and excitation when the center is opposite the surround color.

Methods

Animal experimental methods and preparation are described in detail in Wachtler et al. [3]. Data were collected from awake fixating rhesus monkeys. Stimuli were homogenous isoluminant color squares centered on and at least twice the size of the estimated receptive field of the neuron. A background stimulus surrounding the center was either color or neutral gray. The color surround was typically chosen from the colors to which the neuron showed a clear response. For each trial, one of eight center stimuli and one of the two surround stimuli were presented for 500 milliseconds. A total of 94 units were recorded, and 20 units were chosen with strongest background effect and a minimum of 16 trials per condition. Spike histograms were computed for spike times at the onset (a window at 50-100 milliseconds following stimulus presentation) and the sustained response (100-200 milliseconds).

Typical nonlinearities observed in the mean firing of V1 neurons for a neutral gray versus color surround are described in [3]. The color surround often induces most suppression when the center is matched to the surround color. In addition, excitation for the color surround condition is sometimes observed when the center is the opposite color of the surround. We find that such excitation is particularly prominent during the early stages (onset) of the response, albeit that the color surround alone does not elicit a response. The combination of excitation and suppression cannot be explained by a multiplicative (factorizable) model in the mean firing rate domain (data not shown here).

Alternatively, we consider models of the spike count distribution. For each center and surround stimulus, a spike count distribution is computed by counting in a given time window the number of stimulus repeats that lead to 0 spikes, 1 spike, 2 spikes and so on.

The Morton Massaro model is defined as follows:

$$\mathcal{P}\left(r|c,s\right) = \frac{C(c,r)S(s,r)}{\sum_k C(c,k)S(s,k)} \tag{1}$$

where $\mathcal{P}\left(r|c,s\right)$ is the probability of r spikes for center c and surround s, $C(c,r)$ represents the support of the center component, and $S(s,r)$ the support of the surround component. That is, conditioned on the number of spikes r, the response probability can be factorized into a component dependent on the center, and a component dependent on the surround. This form of model can be understood in the context of a Bayesian system: $\mathcal{P}\left(r|c,s\right) = \frac{\mathcal{P}(c,s|r)\mathcal{P}(r)}{\sum_k \mathcal{P}(c,s|k)}$. We assume conditional independence of center and surround given the response: $\mathcal{P}\left(c,s|r\right) = \mathcal{P}\left(c|r\right)\mathcal{P}\left(s|r\right)$; and transform the conditional probabilities $\mathcal{P}\left(c|r\right)\mathcal{P}\left(s|r\right)$ into joint probabilities $\mathcal{P}\left(c,r\right)\mathcal{P}\left(s,r\right)$ and prior $\mathcal{P}\left(r\right)$ (equivalently for the denominator). This effectively yields equation (1), with the term $C(c,r)S(s,r)$ absorbing both the joint probabilities and prior.

We examine a control model for comparison:

$$\mathcal{P}\left(r|c,s\right) = \frac{C(c,r) + S(s,r)}{\sum_k C(c,k) + S(s,k)} \tag{2}$$

with the same number of parameters as the Morton Massaro model.

We also introduce a parametric model, the Gaussian logistic model, in which the spike count distribution for center c and surround s is given by a Gaussian distribution passed through a logistic nonlinearity:

$$R(s,c) = logistic(X(s) + X(c)) \tag{3}$$

where $X(s) \sim \mathcal{N}(\mu(s);\sigma)$, and $X(c) \sim \mathcal{N}(\mu(c);\sigma)$ are Gaussian distributions with mean μ and standard deviation σ; and $logistic(Y) = 1/(1 + exp(-(Y - \theta) * \alpha))$ includes threshold θ and gain α. Thus, the mean of the input to the logistic function changes with c and s. Also, the logistic function defined for values between 0 and 1, is scaled to go between 0 and the maximal number of spike counts.

Note that this formulation does not include the number of spikes as a free parameter. Therefore, equation (3) is not conditioned on the number of spikes, as are equations (1) and (2). In addition, one can prove from the properties of a Gaussian distribution that this simplified model adheres to Morton Massaro factorizability. Nevertheless, the parametrized model is more constrained and does not necessarily entail the full capabilities of Morton Massaro. For this data set and up to 9 spikes, there are overall 144 data points, 81 free parameters in the Morton Massaro and Control models, and only 13 free parameters in the Gaussian logistic model.

Results

We fit each of the V1 neurons with the Morton Massaro, the control, and the Gaussian logistic model. Figure 1 depicts the V1 spike count distribution and estimated Gaussian logistic model fit for an example neuron. The logistic function provides a nonlinear distortion of the initial Gaussian distribution. For example, when a Gaussian distribution is passed through a logistic nonlinearity, low values of the distribution are pushed towards zero, resulting in higher kurtosis. This property is apparent in the data, and well captured by the Gaussian logistic model (also by the more general Morton Massaro model, see [7]).

Another aspect of interest is whether the models can capture mean firing rate nonlinearities. From the model fits of the spike count distribution, one can compute the mean tuning curves. Figure 2 plots the mean tuning curves and model fits for the example neuron for the sustained and onset response. The tuning curves are plotted in polar coordinates along an isoluminant plane, in which the radius corresponds to the strength of the mean spike rate. Each polar plot compares the response of the neuron for a color surround versus a gray surround. Both factorizable models account for the sustained response, in which there is suppression for center matching the color surround; Morton Massaro also captures the nonlinearity apparent at the onset, including both suppression as before, and excitation for center opposite the color surround. For comparison, the control model with the same number of free parameters as Morton Massaro cannot account for the mean tuning curve data.

We also compare the Chi-square values of the 20 V1 neurons for the different models for the onset and sustained response. Figure 3 shows scatter plots of the normalized (by

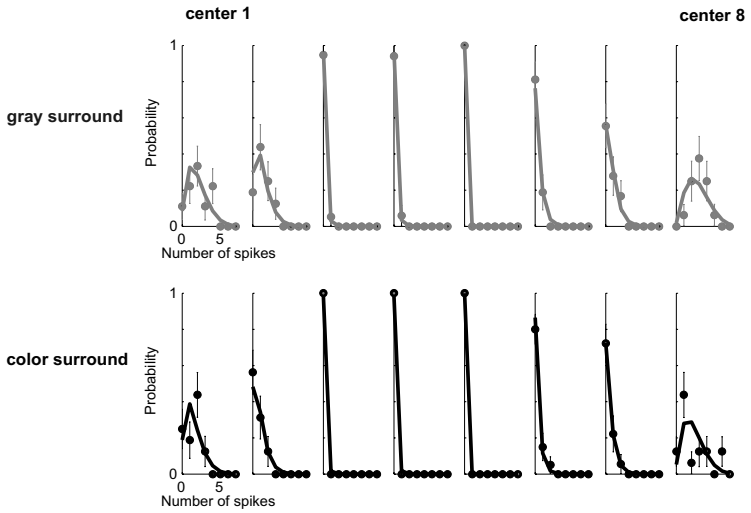

Fig. 1: Spike count distribution representation and Gaussian logistic model fit for example V1 neuron for window 100-200 msec. Each histogram is computed for a given center and surround condition. First row corresponds to 8 color center stimuli on neutral gray surround; second row corresponds to the same stimuli on color surround. Data are given by open symbols and model fits by solid lines. Error bars are obtained from bootstrapping.

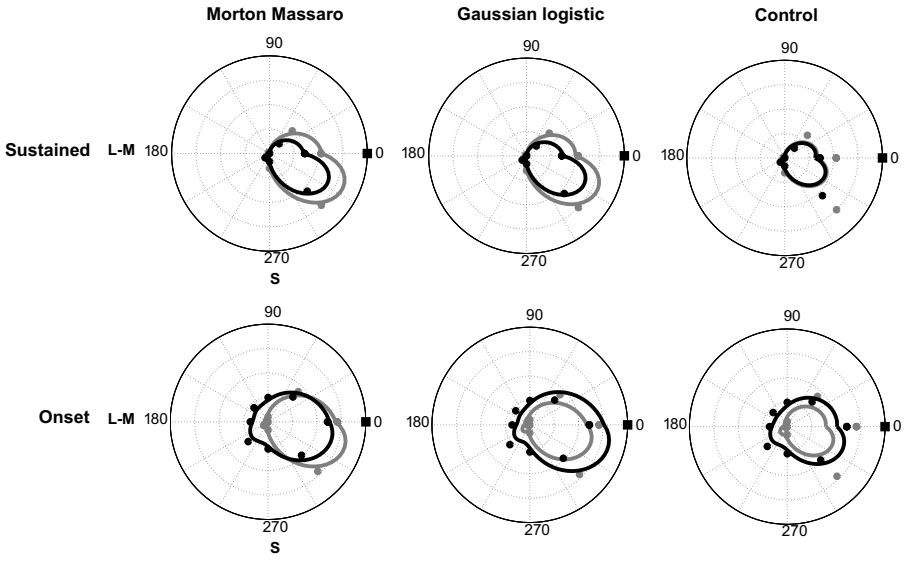

Fig. 2: Mean spike counts of data and model fits of example V1 neuron. Top row: mean tuning curves computed for sustained response (100-200 msec); Bottom row: mean tuning curves computed for onset (50-100 msec). Mean spike counts are calculated from the estimated spike count distributions in Figure 1, and plotted as tuning curves in polar coordinates along the (L-M,S) plane. Data are given by open symbols and model fits by solid lines. Gray corresponds to neutral gray surround, and black to color surround. Black square indicates the background color for the color surround condition. Note that for the control model sustained response, the gray and black lines largely overlap.

the degrees of freedom) Chi-square values for all 20 neurons for the different models. One can set a critical value, signifying significant deviations from the model. During sustained response, 2 neurons show significant deviations to the Morton Massaro model (chi-square

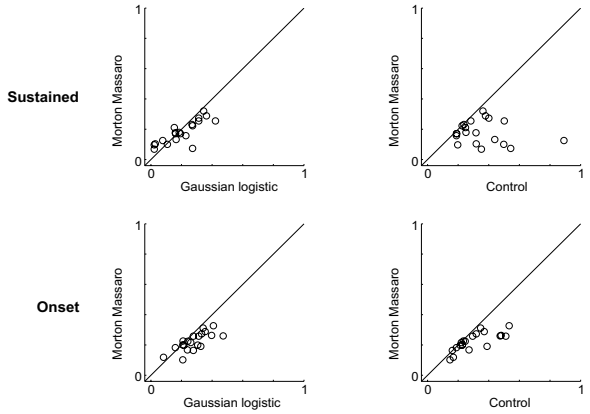

Fig. 3: Scatter plots of normalized Chi-square values for the 20 neurons as a function of the different models. Top: sustained response; bottom: onset. To compare across models, we subtract from each Chi-square value the corresponding degrees of freedom, and normalize the axis between 0 and 1. Y axis always corresponds to normalized Morton Massaro Chi-square; the X axis corresponds to either the Gaussian logistic (left) or Control model (right). Points below unit slope line indicate a lower normalized Chi-square value for the Morton Massaro model.

test, $144 - 81 = 63$ degrees of freedom, $p < 0.05$); 4 to the Gaussian logistic ($144 - 13 = 131$ degrees of freedom, $p < 0.05$); and 12 to the control model ($144 - 81 = 63$ degrees of freedom, $p < 0.05$). At onset, 5 show significant deviations to the Morton Massaro model; 11 to the Gaussian logistic; and 9 to the control model. The Morton Massaro model performs better than the Gaussian logistic and control for both the sustained and onset response, as seen by the number of significant deviations, and by most points falling below the unit slope line in the scatter plots. Both factorizable models perform better than the control model for the sustained response.

Discussion

We have shown that a factorizable operation combining center and surround information per each number of spikes, as in the Morton Massaro model, can account for contextual color nonlinearities in area V1. In contrast, a control model with the same number of parameters as Morton Massaro could not explain the data. These results suggest that the number of spikes might play an important role in neural representations, and that factorizable coding conditioned on the number of spikes might constitute a general principle for cortical processing.

The Gaussian logistic model offers a step forward towards thinking about neural implementations. However, although the Gaussian logistic model conforms to spike count distribution factorizability, it is more constrained in its computation per number of spikes. In practice, it could not account as well for the combination of excitation and suppression often apparent at early stages of the response. We are investigating in greater detail those cases in which there are significant deviations from the model. Deviations from the model might occur if the classical receptive field was underestimated experimentally. We are also examining variations of the parametric model, and how these might relate to divisive normalization models that have been proposed for the mean firing rate (e.g., [1, 8]).

This framework for thinking about spike count distributions and factorizability can be

applied to a number of future directions. In the modeling perspective, it will be pertinent to construct more realistic neural circuitry that can account for the data. Morton Massaro factorizable codes are often described as feedforward, but more recent work has demonstrated that feedback implementations can in fact be consistent with this form of factorizability [6]. Additionally, we have tested the model under two time windows (termed onset and sustained), but a more complete model ought to account dynamically for the response over time. Experimentally, factorizable models should be examined across other stimulus attributes and neural areas, with the goal of understanding the generality of spike count factorizability. We have also found that many experiments either include too few stimulus repeats, or do not explore sufficiently combinations of contextual stimuli–our results emphasize the need to increase both. 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., [9, 10, 11, 12]). The line of work presented here and in [7] 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.

References

[1] J R Cavanaugh, W Bair, and J A Movshon. Nature and interaction of signals in the receptive field surround in macaque V1 neurons. *Journal of Neurophysiology*, 88(5):2530–2556, 2002.

[2] J Allman, F Miezin, and E McGuinness. Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area. *Perception*, 14:105–126, 1985.

[3] T Wachtler, T J Sejnowski, and T D Albright. Representation of color stimuli in awake macaque primary visual cortex. *Neuron*, 37:681–691, 2003.

[4] D W Massaro. *Perceiving talking faces*. MIT Press, Cambridge, MA, 1989.

[5] J Morton. The interaction of information in word recognitiom. *Psychological review*, 76:165–178, 1969.

[6] J R Movellan and J L McClelland. The Morton Massaro law of information integration: implications for models of perception. *Psychological Review*, 108:113–148, 2001.

[7] J R Movellan, T Wachtler, T D Albright, and T J Sejnowski. Morton-style factorial coding of color in primary visual cortex. In *Adv. in Neural Info. Proc. Syst.*, volume 15. MIT Press, 2002.

[8] D J Heeger. Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, 9:181–198, 1992.

[9] F Attneave. Some informational aspects of visual perception. *Psych. Rev.*, 61:183–193, 1954.

[10] H B Barlow. Possible principles underlying the transformation of sensory messages. In W A Rosenblith, editor, *Sensory Communication*, pages 217–234. MIT Press, Cambridge, MA, 1961.

[11] A J Bell and T J Sejnowski. The 'independent components' of natural scenes are edge filters. *Vision Research*, 37(23):3327–3338, 1997.

[12] O Schwartz and E P Simoncelli. Natural signal statistics and sensory gain control. *Nature Neuroscience*, 4(8):819–825, August 2001.