

## Abstract

Many investigators now characterize visual cortical neurons with rapid presentation of stationary gratings. Typically, stimulus phase is randomized, and responses are averaged across phase. Here, we examine V1 neural responses to such stimuli, but focus on phase-specific aspects of the response. We recorded extracellular action potentials of single cells with tetrodes in area 17 of anesthetized, paralyzed cats. To explore the spatial phase dynamics, we presented a balanced pseudo-random sequence of stationary gratings (optimal orientation and spatial frequency) at four spatial phases and blanks, and calculated the response kernels by correlating the spike responses with presentations of individual phases and phase pairs. V1 neurons were characterized with drifting gratings with  $F1/F0 > 1$  implying simple cells and complex otherwise. As expected from a filter-and-rectify model, first- and second-order kernels for most (but not all) simple cells were phase sensitive. For some simple cells, the preferred phase depended on the time since stimulus presentation. However, first-order kernels for most (but not all) complex cells were also phase sensitive, whereas second-order kernels were generally sensitive to phase difference but not absolute phase. The temporal profile for second-order kernels were likewise insensitive: presentation of a particular phase pair could show nonlinear facilitation in adjacent time intervals but nonlinear suppression at longer time intervals. These studies reveal unexpected aspects of the dynamics of complex cells: they may display spatial phase preference in their first-order responses, and sensitivity to phase pairs may be time-dependent.

## Introduction

The receptive fields of many V1 neurons, as assessed with traditional steady-state drifting gratings, are direction selective<sup>1</sup>. The generation of direction selectivity in V1 neurons has been attributed to a phase-time inseparable receptive field structure—the locations of ON and OFF receptive field sub-regions shift over the course of the neuronal response (as shown by reverse-correlation with white-noise stimulus checkerboards)<sup>2</sup>. In addition, research has shown that nonlinear mechanisms (e.g., spatial quadrature) are used by V1 neurons to accentuate steady-state direction selectivity<sup>3</sup>. Moreover, V1 neurons can be segregated into simple and complex cell classes based on the phase-dependent modulation of their spike responses (i.e., the  $F1/F0$  ratio) to steady-state drifting gratings<sup>4</sup>. Simple cells are characterized by phase-sensitive responses ( $F1/F0 > 1$ ), while complex cells are phase-insensitive ( $F1/F0 < 1$ ). Nevertheless, both simple and complex cells can be direction selective, suggesting that steady-state direction selectivity is not solely determined by phase-dependence. Therefore, we examined how the linear and nonlinear dynamics of spatial phase tuning in V1 neurons—as characterized by a rapid presentation of stationary gratings—is related to direction selectivity and phase-dependent spike rate modulation (i.e.,  $F1/F0$ ) for steady-state drifting gratings.

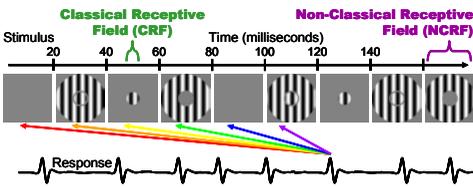
## Methods

We used drifting gratings to characterize the spike responses of V1 neurons. Individual neurons were classified as simple when  $F1/F0 > 1$  and complex otherwise. A direction selectivity index ( $DSI$ ) was calculated from the average spike responses at the preferred ( $r_{pref}$ ) and anti-preferred ( $r_{anti}$ ) orientations (see Equation 1).  $DSI = 1$  if there is no response to the anti-preferred orientation, and  $DSI = 0$  if the responses to the preferred and anti-preferred orientations are equal.

$$DSI = \frac{(r_{pref} - r_{anti})}{(r_{pref} + r_{anti})}$$

Equation 1. Direction Selectivity Index.

We also presented a rapid (20 ms per frame), pseudo-random sequence of stationary gratings (optimal orientation and spatial frequency) at four spatial phases (0°, 90°, 180°, 270°), and blanks (mean luminance), as depicted below. The sequence was dictated by a non-binary m-sequence, and orthogonal sequences were shown simultaneously in the classical and non-classical receptive fields of V1 neurons. Reverse-correlation of the spike response with individual stimulus elements at several stimulus-response delays (i.e., [20, 40, 60, 80, 100, 120] ms) provided estimates of the linear dynamics of spatial phase tuning (i.e., first-order kernels). Reverse-correlation of the spike response with pairs of stimulus elements at several pairs of stimulus-response delays within or between receptive field regions provided estimates of the nonlinear dynamics of spatial phase tuning (i.e., second-order kernels). Here we focus on interactions within the **classical receptive field**.

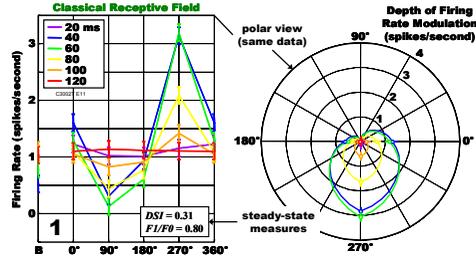


A preferred spatial phase exists in any first-order kernel if the response to one phase is significantly greater than the response to any other phase. A V1 neuron whose preferred spatial phase changes in time has *multimodal* phase-time dynamics (and may be phase-time inseparable). Other V1 neurons have *unimodal* phase-time dynamics (and are phase-time separable). We also derive a measure of the first-order phase-sensitivity ( $PS$ ) based on the circular variance of the  $N=4$  kernel values  $k^{(i)}$  at the phase angle  $\theta_i \in \{0, \pi/2, \pi, 3\pi/2\}$  (see Equation 2).  $PS = 1$  if three of the kernel values are equal and a fourth is greater than the others, and  $PS = 0$  if all four kernel values are equal.

Equation 2. First-Order Phase Sensitivity.

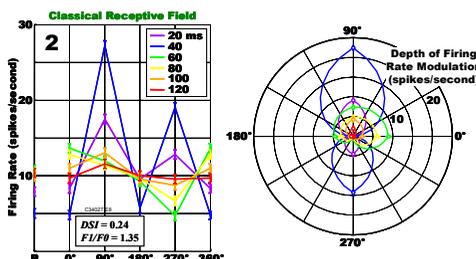
## First-Order Dynamics

- Unimodal, separable phase-time dynamics
- First-order phase sensitive ( $PS=0.67$ )



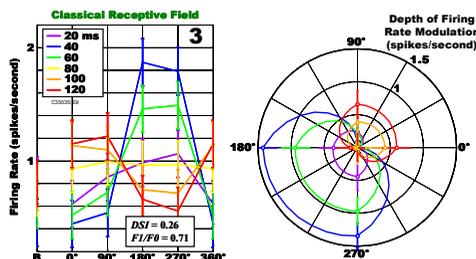
- Non-direction selective complex cell

- Multimodal, inseparable phase-time dynamics
- First-order phase insensitive ( $PS=0.22$ )



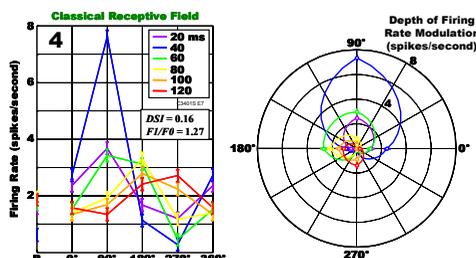
- Non-direction selective simple cell

- Multimodal, but separable phase-time inversion
- First-order phase sensitive ( $PS=0.66$ )



- Non-direction selective complex cell

- Multimodal, inseparable phase-time shift
- First-order phase sensitive ( $PS=0.71$ )



- Non-direction selective simple cell

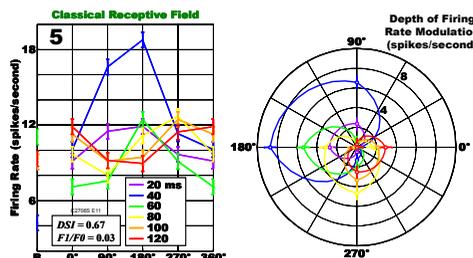
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# Linear and Nonlinear Spatial Phase Dynamics in Cat Primary Visual Cortex

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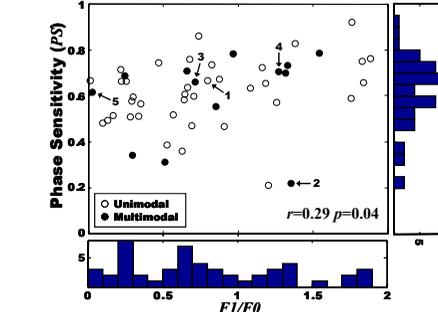
Society for Neuroscience, Thirty-Fourth Annual Meeting  
Motion and Optic Flow — Monday PM, October 25, 2004

- Multimodal, inseparable phase-time shift
- First-order phase sensitive ( $PS=0.62$ )

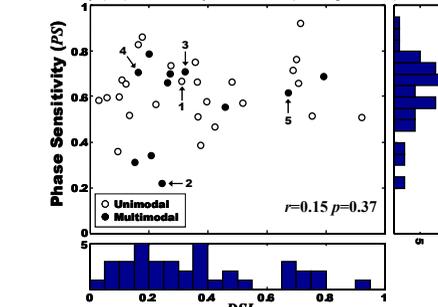


- Direction selective complex cell

- Steady-state phase-dependent spike rate modulation ( $F1/F0$ ) and first-order phase sensitivity ( $PS$ ) are weakly correlated



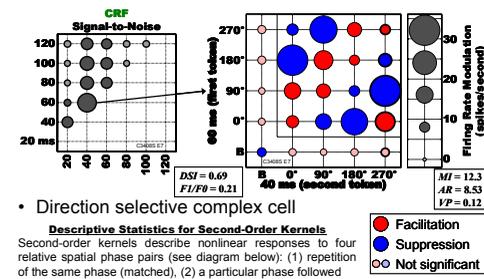
- Steady-state direction selectivity ( $DSI$ ) and first-order phase sensitivity ( $PS$ ) are weakly correlated (not significant)



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## Second-Order Dynamics

- Peak nonlinear response is usually (36/47) found in the [40, 60] ms kernel in the **classical receptive field**



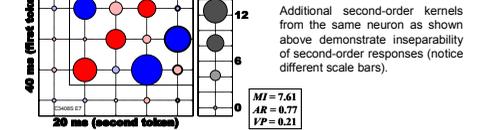
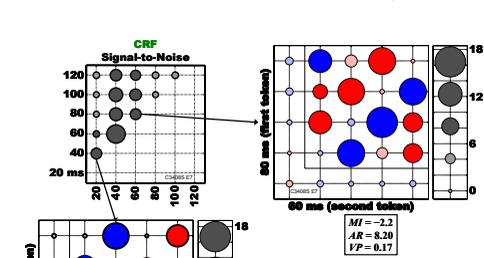
- Direction selective complex cell

**Descriptive Statistics for Second-Order Kernels**  
Second-order kernels describe nonlinear responses to four relative spatial phase pairs (see diagram below): (1) repetition of the same phase (matched), (2) a particular phase followed by its contrast inversion, a flicker interaction (inverted), (3) phase precession in the preferred direction (advanced), and (4) phase precession in the anti-preferred direction (receded). Since the nonlinear responses of our V1 neurons were similarly aligned along these four axes, we calculated two measures (see equations below). Matched-Inverted ( $MI$ ) is the mean difference between second-order kernel values  $k^{(i)}$  along the matched and inverted axes.  $MI > 0$  indicates a relative nonlinear facilitation for phase matching coupled with a relative nonlinear suppression for phase inversion (as shown above). Advanced-Receded ( $AR$ ) is the mean difference between the kernel values along the advanced and receded axes, which quantify spatial quadrature interactions.  $AR > 0$  indicates nonlinear facilitation for phase advancement (apparent motion in the preferred direction) coupled with nonlinear suppression for phase recession (apparent motion in the anti-preferred direction, as shown above). In addition, we derive an index of the second-order phase specificity ( $VP$ ) based on the distribution of variance along these four axes.  $VP = 1$  if three of the  $N=4$  kernel values on each axis are equal and the fourth is greater.  $VP = 0$  if all four kernel values on each axis are equal.

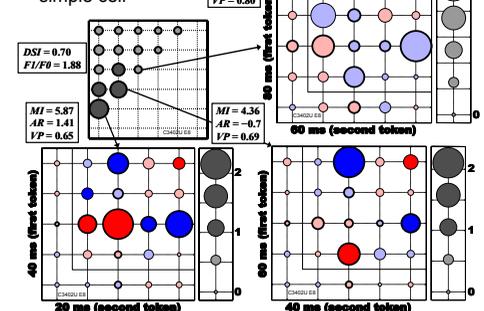
$$MI = \frac{\sum (k_{MI}^{(1)} - k_{MI}^{(2)}) + \sum (k_{MI}^{(3)} - k_{MI}^{(4)})}{N}$$

$$AR = \frac{\sum (k_{AR}^{(1)} - k_{AR}^{(2)}) + \sum (k_{AR}^{(3)} - k_{AR}^{(4)})}{N}$$

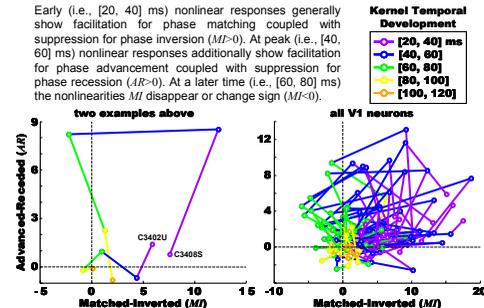
$$VP = \sqrt{\frac{\sum (k_{MI}^{(1)} - k_{MI}^{(2)})^2 + \sum (k_{MI}^{(3)} - k_{MI}^{(4)})^2 + \sum (k_{AR}^{(1)} - k_{AR}^{(2)})^2 + \sum (k_{AR}^{(3)} - k_{AR}^{(4)})^2}{\sum (k_{MI}^{(1)} - k_{MI}^{(2)})^2 + \sum (k_{MI}^{(3)} - k_{MI}^{(4)})^2 + \sum (k_{AR}^{(1)} - k_{AR}^{(2)})^2 + \sum (k_{AR}^{(3)} - k_{AR}^{(4)})^2}}$$



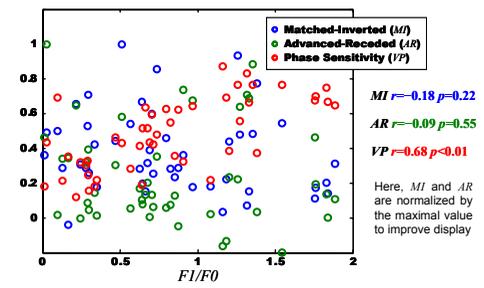
- Direction selective simple cell



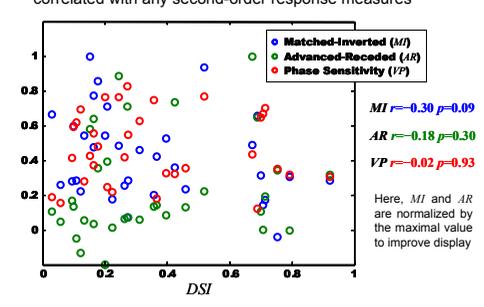
- Nonlinearities are time dependent and relatively consistent across all V1 neurons



- Steady-state phase-dependent spike rate modulation ( $F1/F0$ ) is strongly correlated with second-order phase sensitivity ( $VP$ )



- Steady-state direction selectivity ( $DSI$ ) is not significantly correlated with any second-order response measures



## Conclusions

These studies reveal unexpected aspects of V1 neurons that could not have been predicted from the responses to steady-state drifting gratings.

- Linear Dynamics**
  - Contrary to expectations simple cells can be phase insensitive and complex cells can be phase sensitive (first-order)
  - Direction selective V1 neurons can be phase sensitive or insensitive (first-order)
    - direction selectivity is not solely determined by an inseparable receptive field structure
- Nonlinear Dynamics**
  - There is a strong bias for simple cells to be phase sensitive and complex cells to be phase insensitive (second-order) but both simple and complex cells may exhibit phase sensitive or insensitive nonlinear responses
  - The magnitude of nonlinear responses (i.e., spatial quadrature interactions) does not predict the steady-state direction selectivity in V1 neurons and vice versa
  - Nonlinearities in V1 neurons are strongly time-dependent
    - sensitivity to stimulus constancy and flicker develops early (20-60 ms) in the response
    - sensitivity to spatial quadrature interactions develops later (40-80 ms) in the response

## References

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- Dekolovic, G.C., Chong, L., and Freeman, R.D. (1995) Receptive-field dynamics in the central visual pathways. *Trends in Neurosciences* 18(10): 451-458.
- Rieser, J.J., Soodak, R.E., and Shapley, R.M. (1991) Directional selective and spatial structure of receptive fields of simple cells in cat striate cortex. *Journal of Neurophysiology* 66(2): 505-520.
- Skottun, B.C., De Valois, R.L., Gross, D.H., Movshon, J.A., Albrecht, D.G., and Bonds, A.B. (1987) Classifying simple and complex cells on the basis of response modulation. *Vision Research* 27: 1079-1086.