456.1 DIVERSITY OF RESPONSES TO GRATINGS IN V1 OF ALERT MONKEY

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INTRODUCTION

The majority of neurons in monkey primary visual cortex (V1) are complex cells with overlapping increment and decrement activating regions (ARs). However, we recently reported that unlike the "classical" (energy-model) complex cells, they exhibit a diverse mixture of pseudolinear and nonlinear properties, depending on stimulus attributes. Most complex cells respond with significant first harmonic (F1, fundamental) to drifting sinusoidal gratings, but usually within a limited range of parameters. At the same time, stationary flashing bars, moving edges and counterphase gratings evoke mostly on-off, or frequency doubled (second harmonic, F2) responses. These findings show that behavior of complex cells can not be predicted from classical receptive fields' (CRF) spatial maps, and suggest a revised view of underlying mechanisms.

The purpose of this study was to investigate further how the responses to gratings depend on stimulus attributes: temporal frequency, spatial frequency and grating patch width. Such parametric study is needed for understanding complex cells' receptive field organization and functionality.

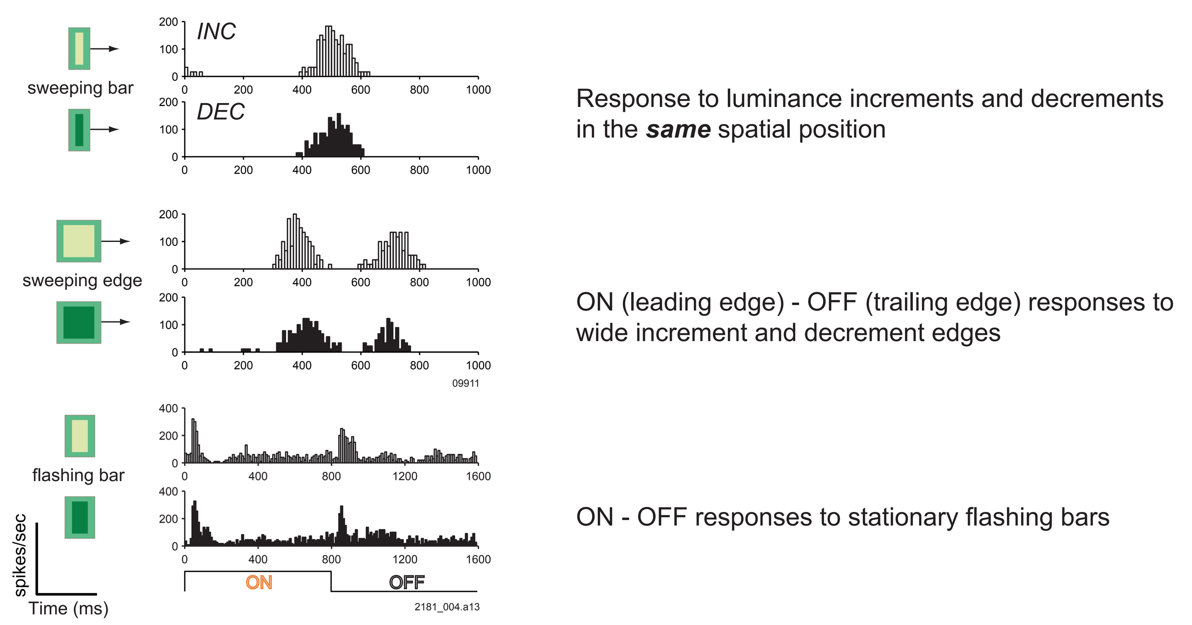
METHODS

Extracellular responses of single V1 neurons were recorded while monkeys viewed visual stimuli during a fixation task. The dominant eye position was monitored using double Purkinje tracker or scleral search coil. In most cases, gaze shifts during fixational eye movements were compensated using online feedback from eyetracker to stimulus generator ("image stabilization"). Because of delays between shifts in eye position and subsequent correction, this procedure was not intended to compensate for the *fast* saccadic movements. Therefore, we restricted our analysis to periods of relatively stable fixation (intersaccadic intervals, or drifts) that were identified using an automated blink- and saccade-detection algorithm.

1. Receptive field mapping

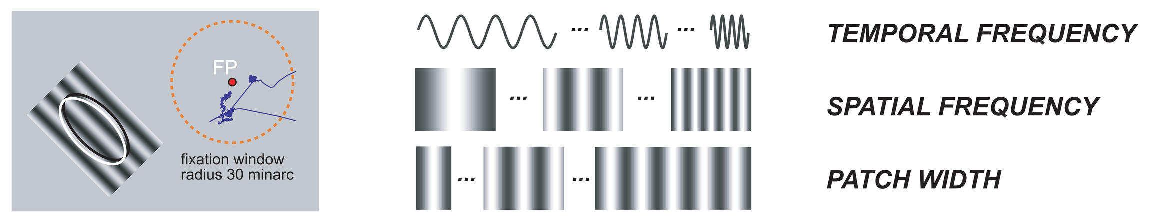
(1.1) Receptive fields were mapped with sweeping and flashing bars and edges and classified as simple or complex based on the measure of overlap of increment and decrements ARs (*Overlap Index*, see *Appendix*).

Typical complex cell responses

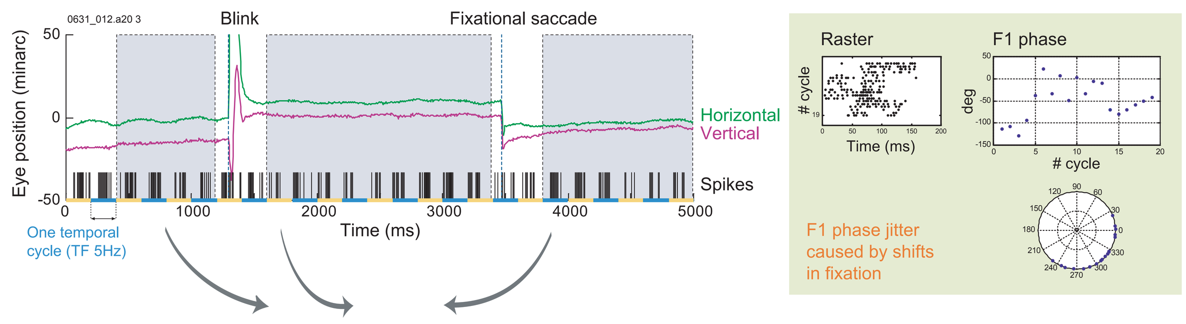


2. Data collection and analysis

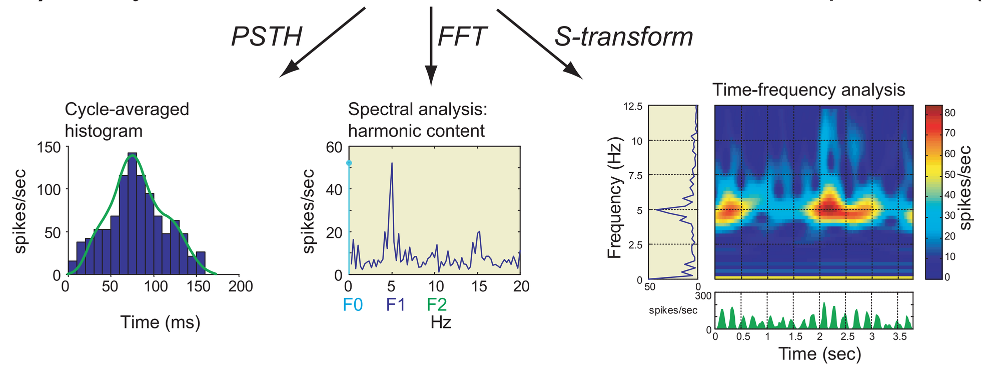
(2.1) Presenting drifting and counterphase (contrast-reversal) gratings, optimally oriented and centered on the classical receptive field (CRF):



(2.2) Selecting "stable fixation" data segments (*example:* one behavioral trial 5 s):



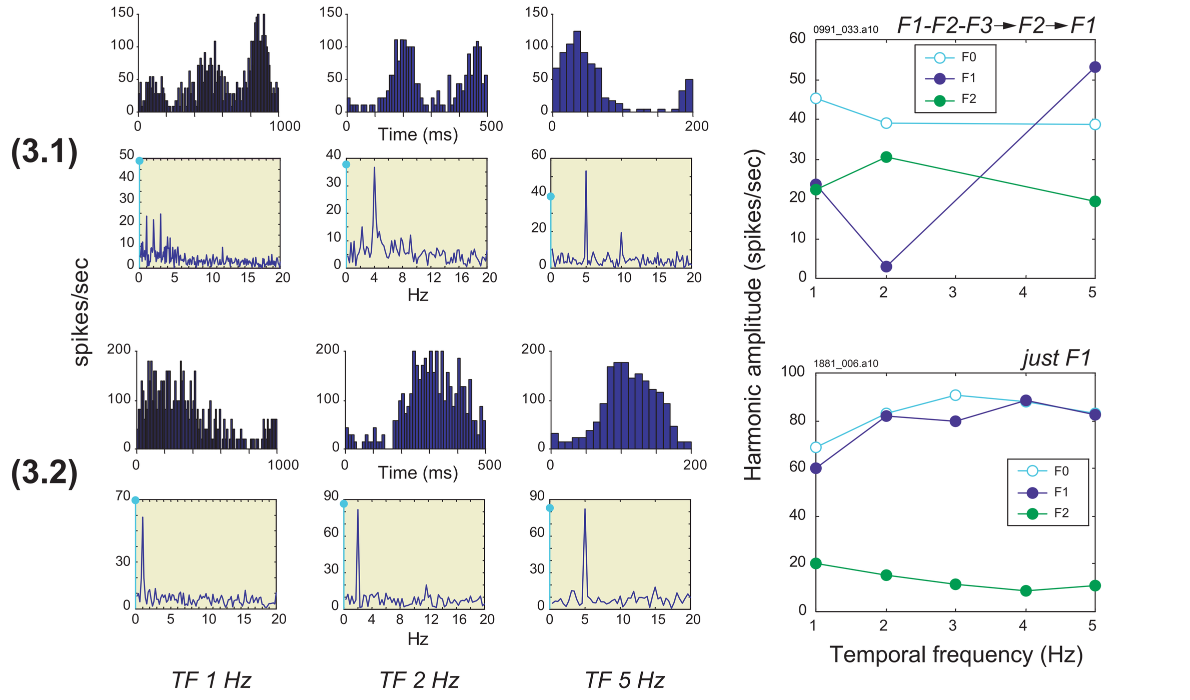
(2.3) Analysis of concatenated spike train (*Appendix*):



RESULTS

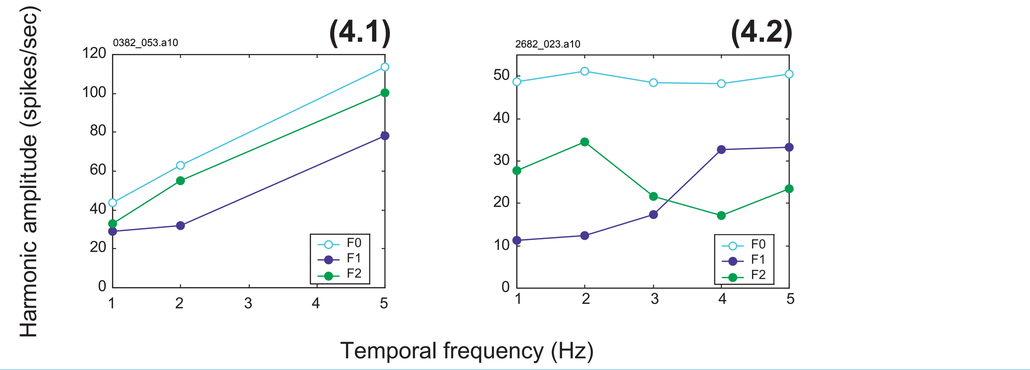
3. Temporal frequency effects - drifting gratings

Most complex cells respond with *significant F1 modulation* to drifting gratings of mid-to-high (3 - 7 Hz) temporal frequency (see *Appendix*). But some of them show frequency doubled (F2) or mixed (F1, F2, F3) responses at low (1 - 2 Hz) temporal frequency (**3.1**). In other cells, little or no effect of temporal frequency on the response harmonics is found (**3.2**).



4. Temporal frequency effects - counterphase gratings

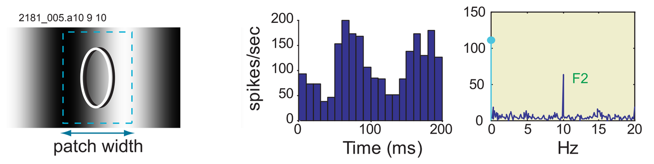
Similarly, responses to counterphase gratings, although predominantly *frequency doubled* (**4.1**), sometimes show strong F1 harmonic at high temporal frequencies, especially when modulated by sine-wave temporal function (**4.2**).



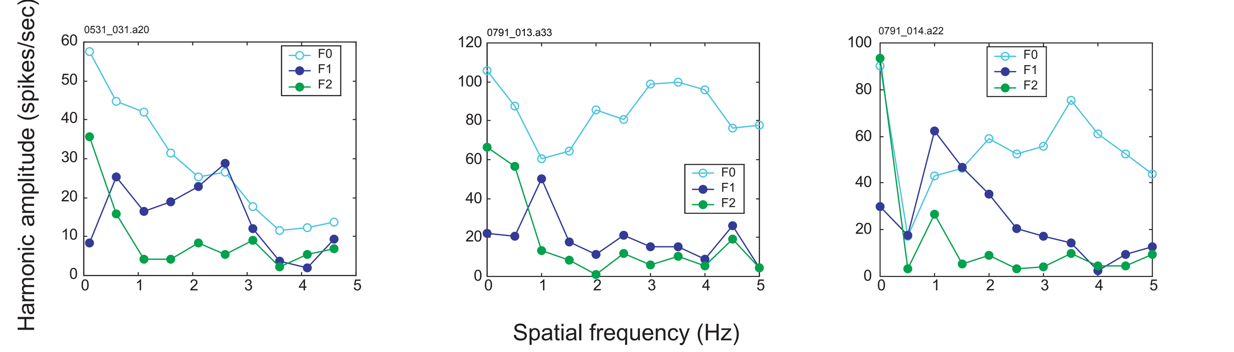
5. Spatial frequency effects - drifting gratings

Spatial frequency strongly influences the response form of most complex cells. The three most general patterns are:

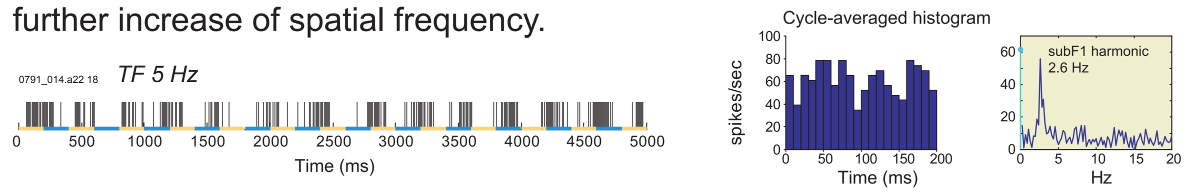
(5.1) F2 responses to gratings of very low spatial frequency (and/or small width). This behavior can be explained by the time course of the absolute flux in the receptive field (see *Appendix*).



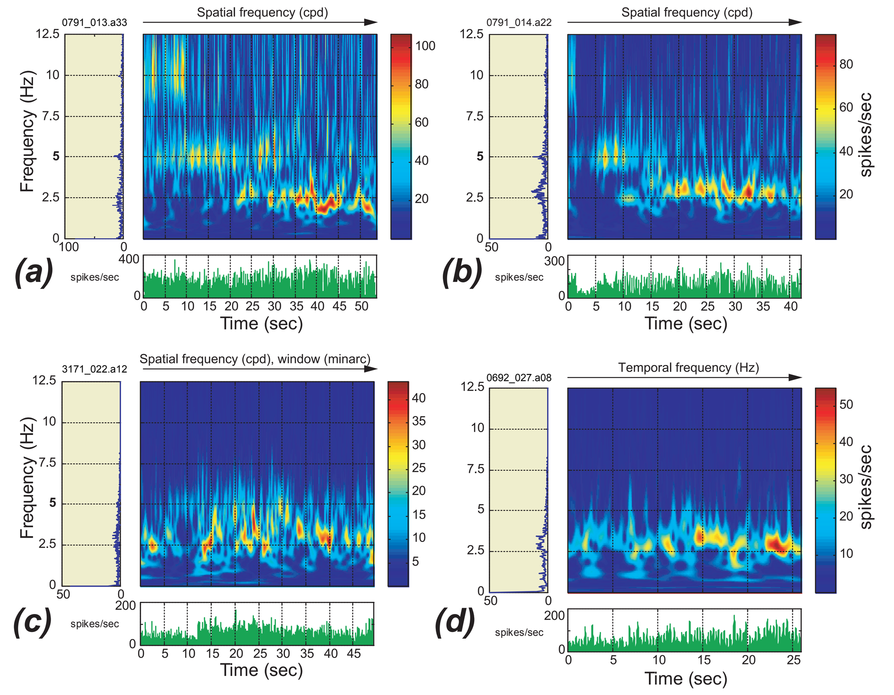
(5.2) Decrease of the F2 and increase of the F1 component with increase of spatial frequency.



(5.3) Decrease of the F1 component and appearance of **"subF1"** modulation with further increase of spatial frequency.

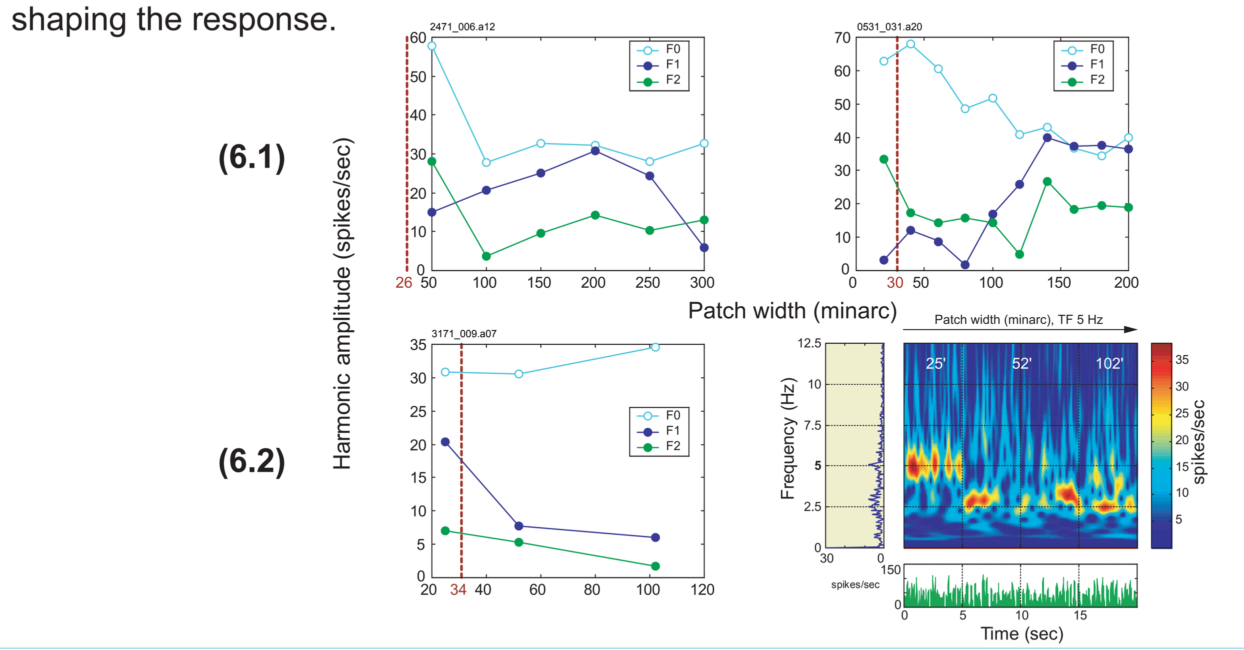


The range of sub-harmonic frequency is 2.8 ± 0.5 Hz. In individual cells, it can vary with the spatial frequency or the width of the grating (**a**, **b**, **c**, *TF 5 Hz*), but it seems independent of the drift temporal frequency (**d**).



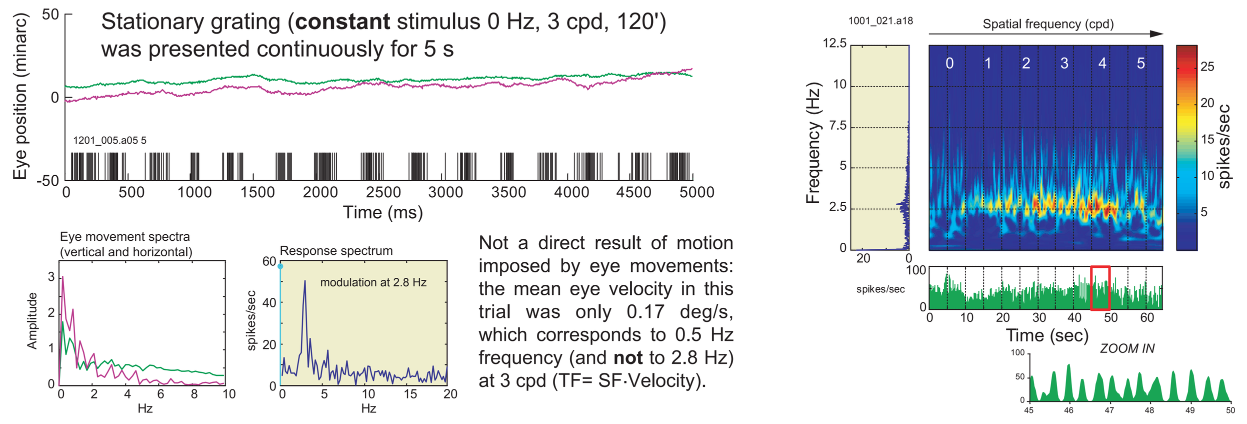
6. Patch width effects - drifting gratings

Changing grating patch width often modifies the form of the response, and not just the response amplitude (*i.e. side-inhibition*). Small (less or equal to CRF) windows lead to F2 (**6.1**) or sometimes to F1 responses, and extending gratings beyond the CRF may result in increase of F1 component (**6.1**) or appearance of sub-harmonic modulation (**6.2**). This suggests that surrounds play an active role in shaping the response.



7. Response to stationary gratings

Least expectedly, the responses of many cells to stationary gratings, usually of mid-to-high (2 - 5 cpd) spatial frequency, exhibited robust low frequency (2.8 ± 0.5 Hz) modulation in the range similar to the "subF1" modulation elicited by drifting gratings. Although our current analysis *does not show* the correlation between this modulation and eye movement spectra, further investigation is needed to answer whether it is an intrinsic neuronal property, a network effect, or an interaction of the above with the ***activation*** caused by small eye movements.



CONCLUSIONS

- In complex cells, the form of the response to gratings (the harmonic content), and not just the response amplitude, exhibits systematic dependence on stimulus attributes (thus violating a "pure" energy model).
- Existing models of V1 receptive fields do not capture the observed diversity of complex cell behaviors.
- These results support the notion of an elaborate spatiotemporal structure of complex cells receptive fields.

http://igoresha.virtualave.net/Work/SfN02