ANALYSIS OF RESPONSES TO DRIFTING AND STATIONARY GRATINGS IN V1 OF ALERT MONKEY

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INTRODUCTION

The majority of neurons in monkey primary visual cortex (V1) have overlapping increment and decrement activating regions (ARs) and diverse nonlinear properties ("duplex" cells). However, many of these cells, unlike the "classical complex" cells, exhibit a significant pseudolinear (fundamental, F1) harmonic in the responses to drifting sinusoidal gratings, usually within a limited range of stimulus parameters. At the same time, stationary flashing bars, moving edges and counterphase gratings evoke mostly on-off, or frequency doubled (second harmonic, F2) responses. This mixture of pseudolinear and nonlinear properties suggests that the dynamics of interactions between increment and decrement ARs and powerful surrounds underlies duplex cell behavior.

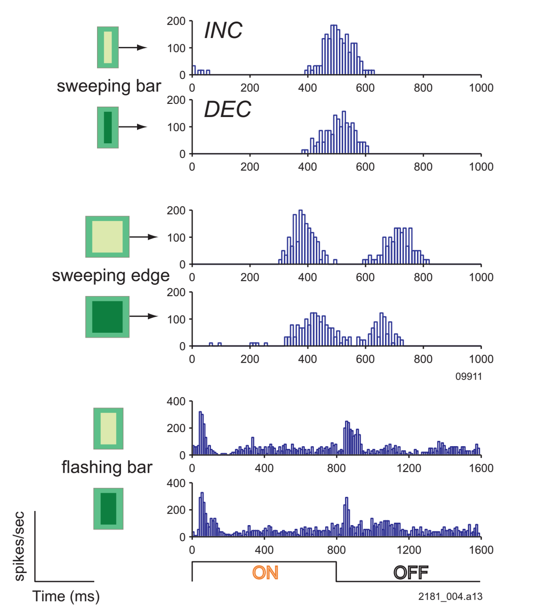
The purpose of this study was to further investigate how the form of the responses to gratings depends on stimulus attributes: temporal frequency, spatial frequency and grating patch width. Such parametric study is needed for understanding duplex cells' receptive field organization and functionality.

METHODS

Extracellular responses of single V1 neurons were recorded while the monkey viewed visual stimuli during a fixation task. Receptive fields' ARs were mapped with sweeping and flashing bars and edges (Fig. 1). Then cells were studied with drifting gratings of systematically varied spatial frequency, temporal frequency and patch width, optimally oriented and centered on the classical receptive field (CRF). The dominant eye position was monitored using scleral search coil and recorded for offline analysis. In most cases, shifts in fixation were compensated online by a feedback loop from the eyetracker to the stimulus generator ("image stabilization"). Since the delay between the shift in the eye position and subsequent correction could be as long as one video frame (6.25 ms), this procedure was not intended to compensate for the fast saccadic eye movements. Therefore, we restricted our analysis to periods of relatively stable fixation (intersaccadic intervals) that were identified using an automated blink- and saccade-detection algorithm (Fig. 2A). The harmonic content of the response was quantified with a fast Fourier transform (FFT).

1. Receptive field mapping

Typical duplex cell responses



Response to luminance increments and decrements in the same spatial position

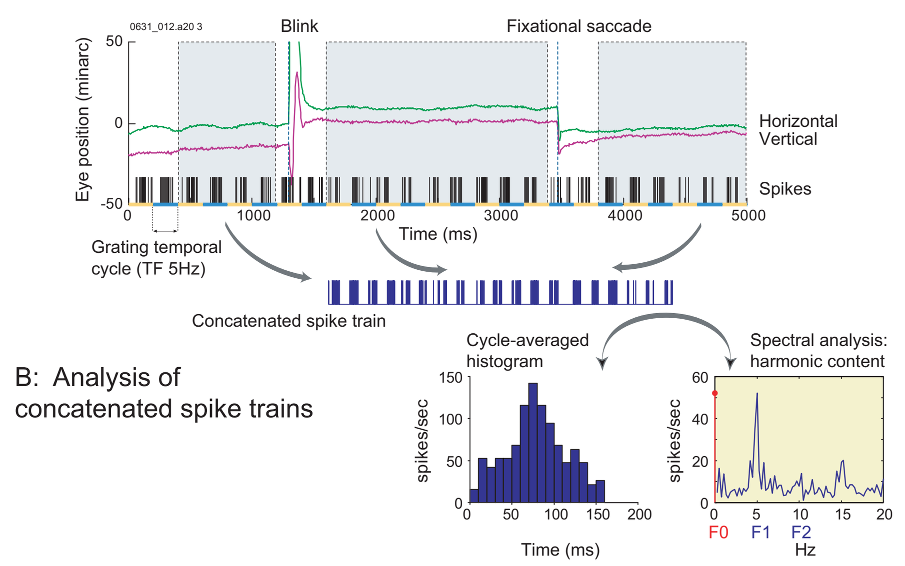
On (leading edge) - off (trailing edge) responses to wide increment and decrement edges

On-off responses to stationary flashing bars

2. Data selection and analysis

A: Selecting stable fixation data segments from one behavioral trial (5 s)

B: Analysis of concatenated spike trains



RESULTS

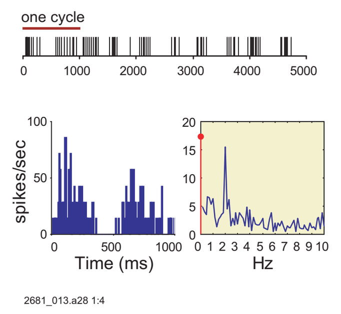
Some cells that responded with F1 modulation to mid-to-high temporal frequency gratings showed frequency doubled (F2, Fig. 3A) or mixed (F1, F2, F3, Fig. 3B) responses at low temporal frequencies. In other cells, little or no effect of temporal frequency on the response harmonics was found (Fig. 3C).

Grating spatial frequency and width profoundly influenced the responses of most duplex cells. The general patterns were: 1) F2 responses to gratings of very low spatial frequency and/or small patch width (Fig. 4). This behavior can be explained by time variations of the absolute flux in the receptive field (Fig. 5). 2) Decrease of the F2 and increase of the F1 component with increase of spatial frequency and/or width (Fig. 6). 3) Decrease of the F1 component and appearance of "subF1" (<F1) modulation with further increase of spatial frequency (Fig. 7).

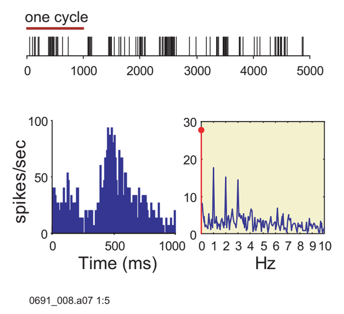
Least expected, the responses of many cells to stationary gratings of mid-to-high spatial frequency exhibited robust low frequency modulation in the range similar to the "subF1" modulation elicited by drifting gratings (Fig. 8). Although our current analysis does not confirm the direct contribution of eye movements to this outcome, further investigation is needed to answer whether it is anintrinsic neuronal property, a network effect, or an interaction of the above with eye movements.

3. Temporal frequency effects

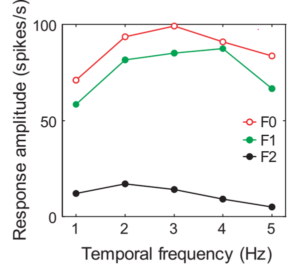
A: Frequency doubling (F2 harmonic) in response to 1 Hz drifting grating, but quasi-linear (F1 harmonic) response to 5 Hz grating (not shown).



B: Mixed F1,F2,F3 harmonics in response to 1 Hz drifting grating, but only strong F1 component to 5 Hz grating (not shown).

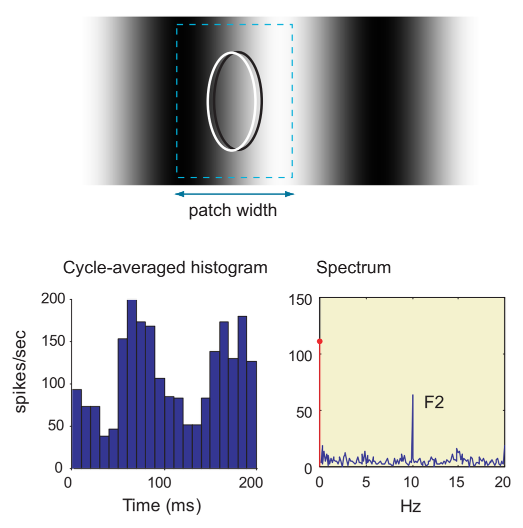


C: No effect - relative amplitude of harmonics remains constant across temporal frequencies.



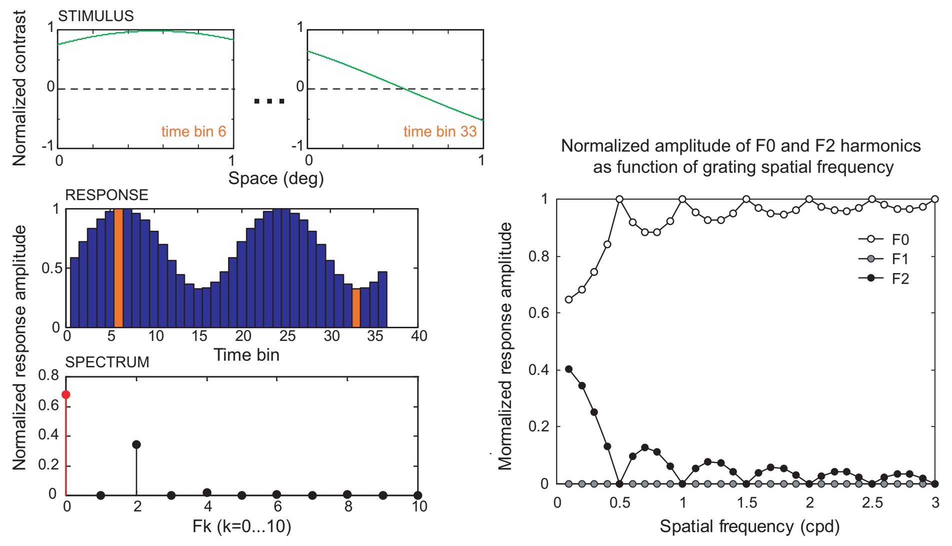
4. Spatial frequency-dependent doubling (I)

Duplex cell (overlapping increment and decrement ARs) F2 response to grating of low spatial frequency



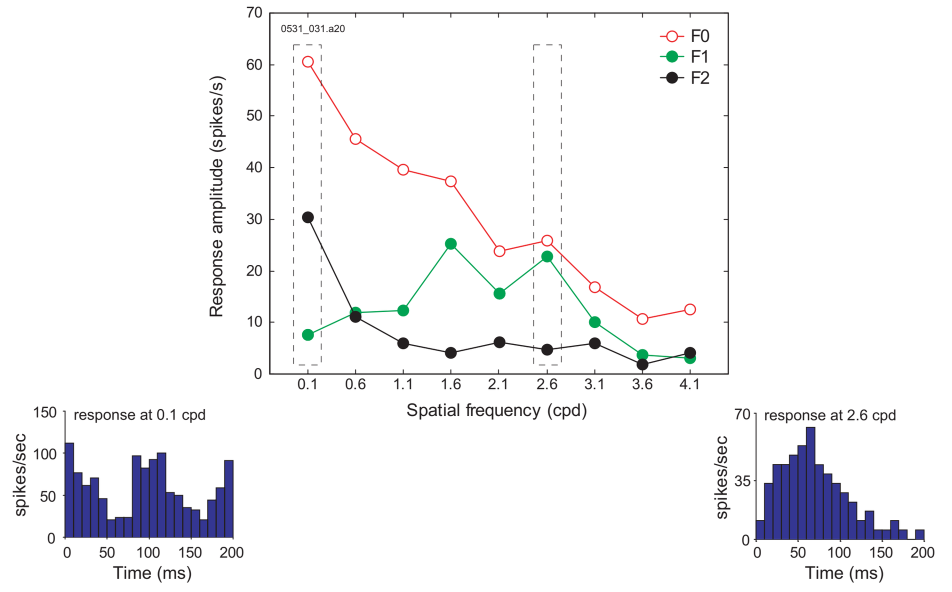
5. Spatial frequency-dependent doubling (II)

Modeling frequency doubling using linear summation of absolute flux in contrast-invariant receptive field



6. Spatial frequency effects (I)

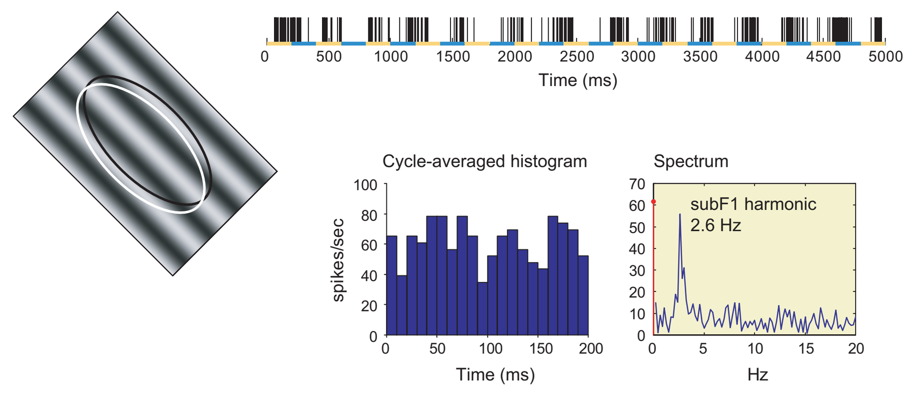
Increase of F1 and decrease of F0 with spatial frequency



7. Spatial frequency effects (II)

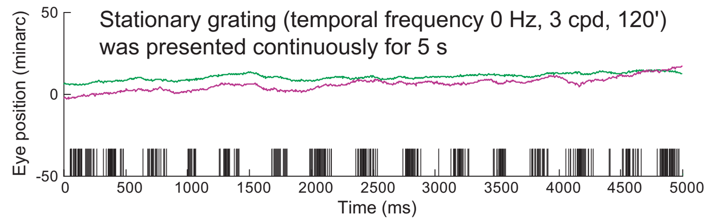
"SubF1" modulation to drifting grating of mid-to-high spatial frequency

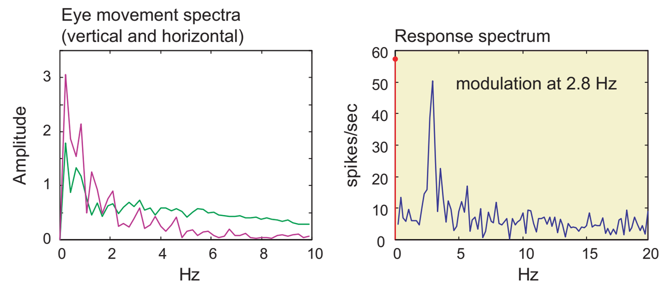
Grating temporal frequency (F1) 5 Hz, spatial frequency 4 cpd



8. Response to stationary grating

Unexpected modulation in response to the "constant" - except for the eye movements - stimulus





It's unlikely that the observed modulation is a direct result of motion imposed by eye movements: the mean eye velocity in this trial was only 0.17 deg/s, which corresponds to 0.5 Hz modulation at 3 cpd SF.

(TF= SF·Velocity)

CONCLUSIONS

- In duplex cells, the form of the response to gratings (the harmonic content), and not only the response amplitude, exhibits systematic dependence on stimulus attributes.
- Existing models of V1 receptive fields do not capture the observed diversity of duplex cell behavior.
- These results support the notion of an elaborate spatiotemporal structure of duplex cells receptive fields.

http://www.bm.technion.ac.il/vision/VSS02