TECHNION
VISION RESEARCH LAB

http://www.biomed.technion.ac.il/vision

THE SCHEPENS EYE RESEARCH INSTITUTE

# IN V1 DUPLEX CELLS, THE FORM OF RESPONSES TO GRATINGS DEPENDS ON TEMPORAL AND SPATIAL FREQUENCY

Igor Kagan[1], Moshe Gur[1,2], D. Max Snodderly[2,3]

[1] Dept. of Biomedical Engineering, Technion, Haifa, Israel;
[2] Schepens Eye Research Institute and [3] Dept. of Ophthalmology and Program in Neuroscience, Harvard Medical School, Boston, MA

# Introduction

The majority of neurons in visual cortical area V1 in monkey have overlapping increment and decrement activating regions (ARs) and diverse nonlinear properties ("duplex" cells). However, we have recently shown that many of them exhibit a significant quasi-linear (fundamental, F1) harmonic in the responses to drifting sinusoidal luminance gratings. At the same time, flashing bars, moving edges and counterphase gratings evoke mostly on-off, or frequency doubled (second harmonic, F2) responses. This mixture of quasi-linear and nonlinear properties suggests that the temporal dynamics of interactions between increment and decrement ARs and surround play an important role in shaping the responses of duplex cells.

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

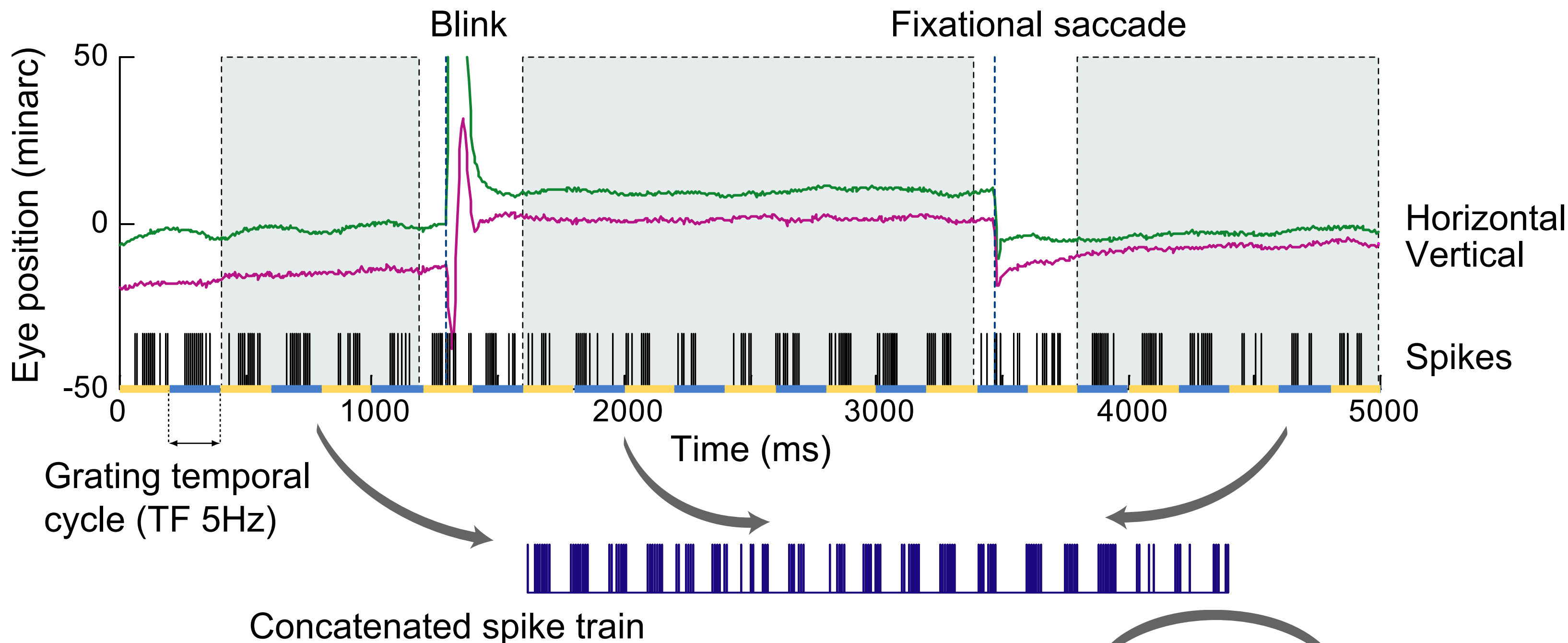
# Methods

Extracellular responses of V1 neurons were recorded while the monkey viewed visual stimuli during a fixation task. Stimuli were grating patches of different spatial and temporal frequency and width, optimally oriented and centered on the receptive field. Eye position was monitored using scleral search coil and recorded to file. We restricted our analysis to periods of relatively stable fixation (intersaccadic intervals) that were identified using an automated saccade-detection algorithm (**Fig. 1A**). The harmonic content of the response was estimated using a fast Fourier transform (FFT) of the concatenated spike train (**Fig. 1B**).

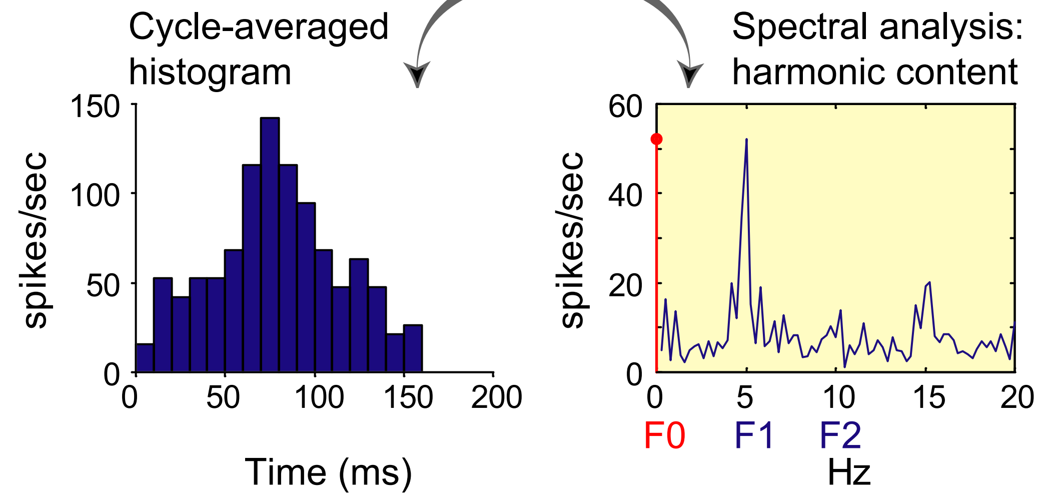
# Data selection and analysis

Fig. 1

## A: Selecting data segments from one behavioral trial




## B: Analysis of concatenated spike train



# Results

Some cells that responded with F1 modulation to high temporal frequency gratings gave frequency doubled (F2, **Fig. 2A**) or mixed (F1, F2, F3, **Fig. 2B**) responses at low temporal frequencies. In other cells, little or no effect of temporal frequency on the responses harmonic content was found (**Fig. 2C**).

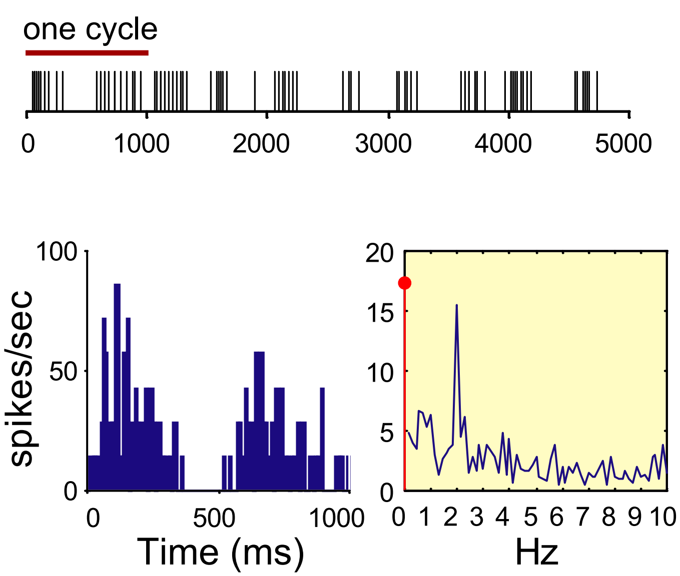
Most cells showed strong dependence of the response form on the grating spatial frequency and width. The three main patterns were: 1) F2 responses to gratings of very low spatial frequency and/or small patch width (**Fig. 3A, B**). This behavior can be explained by time variations of the absolute flux in the receptive field (**Fig. 4**). 2) Decrease of the F2 and increase of the F1 component with increase of spatial frequency and/or width (**Fig. 5**). 3) Decrease of the F1 component and appearance of a "subF1" (i.e. less than F1) modulation with further increase of spatial frequency (**Fig. 6**).

The responses of many cells to stationary gratings of middle to high spatial frequency unexpectedly exhibited robust modulation similar to the "subF1" modulation elicited by drifting gratings (**Fig. 7**).

# Temporal frequency effects

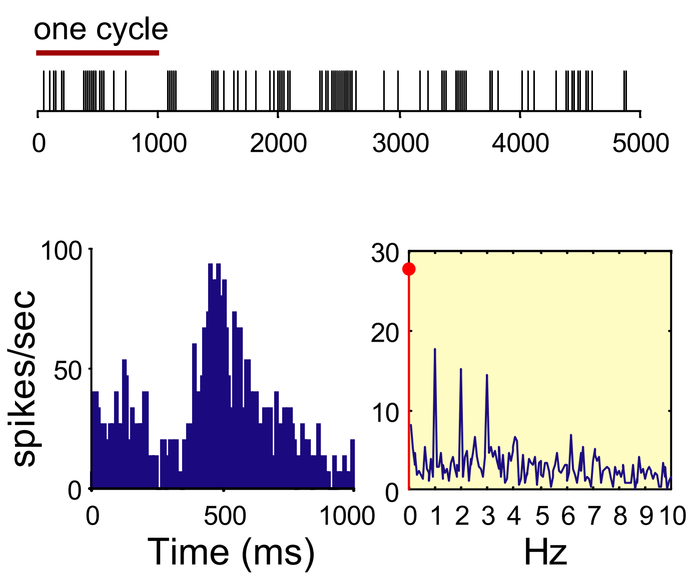
Fig. 2

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



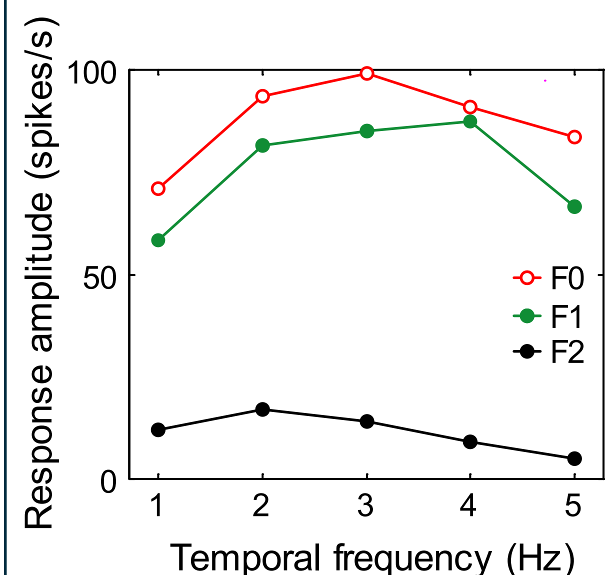

2681_013.a281:4

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




0691_008.a07 1:5

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

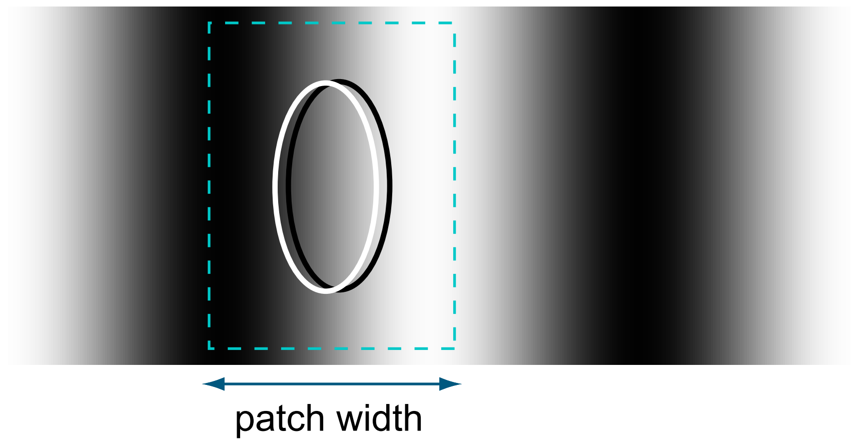


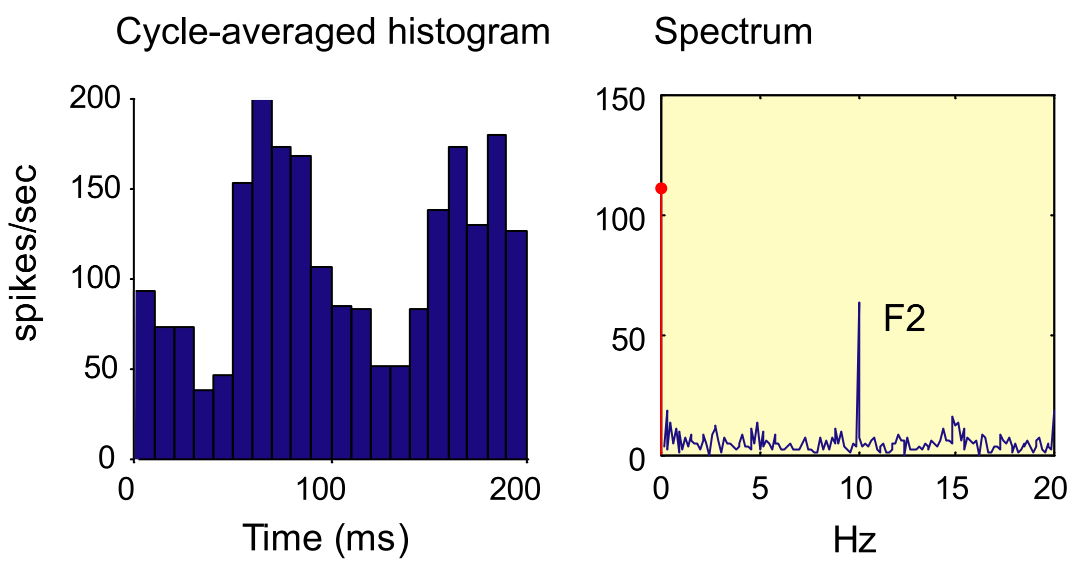

1881_006.a10

# Spatial frequency-dependent doubling

Fig. 3

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



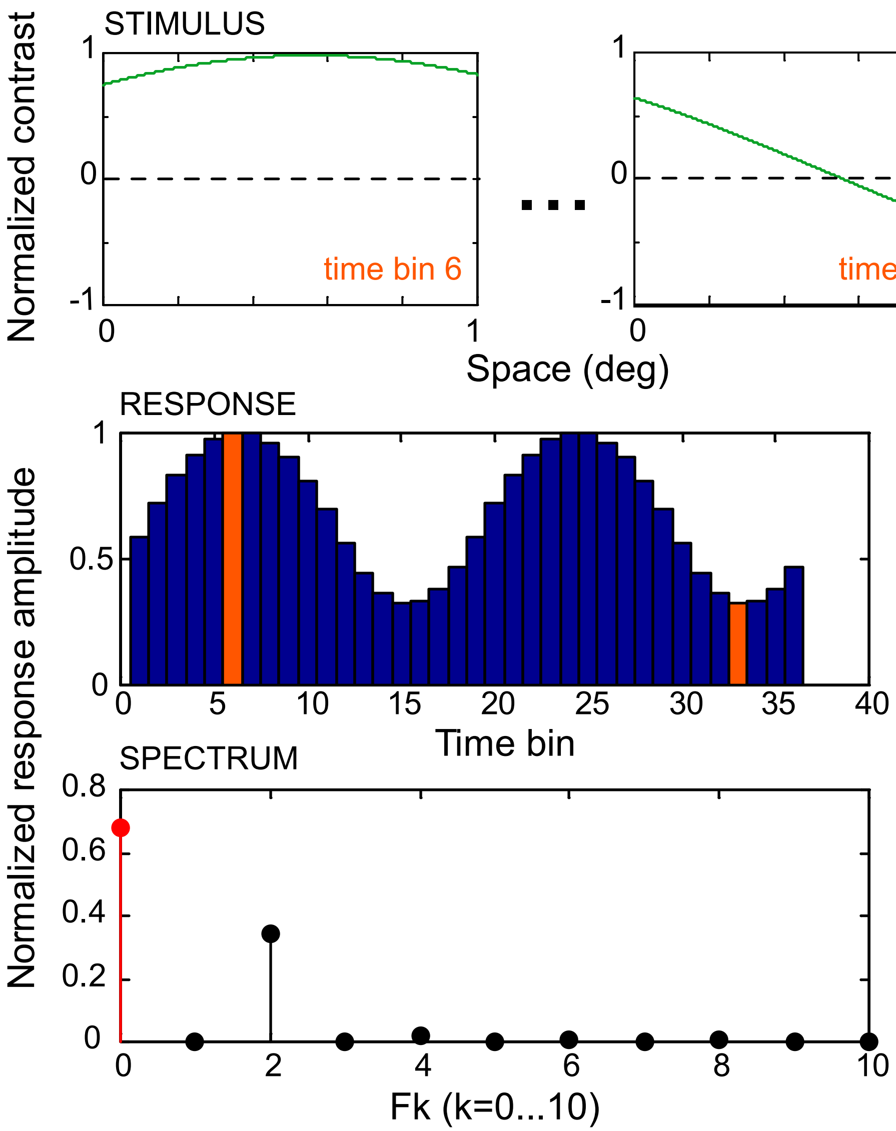




2181_005.a10 9 10

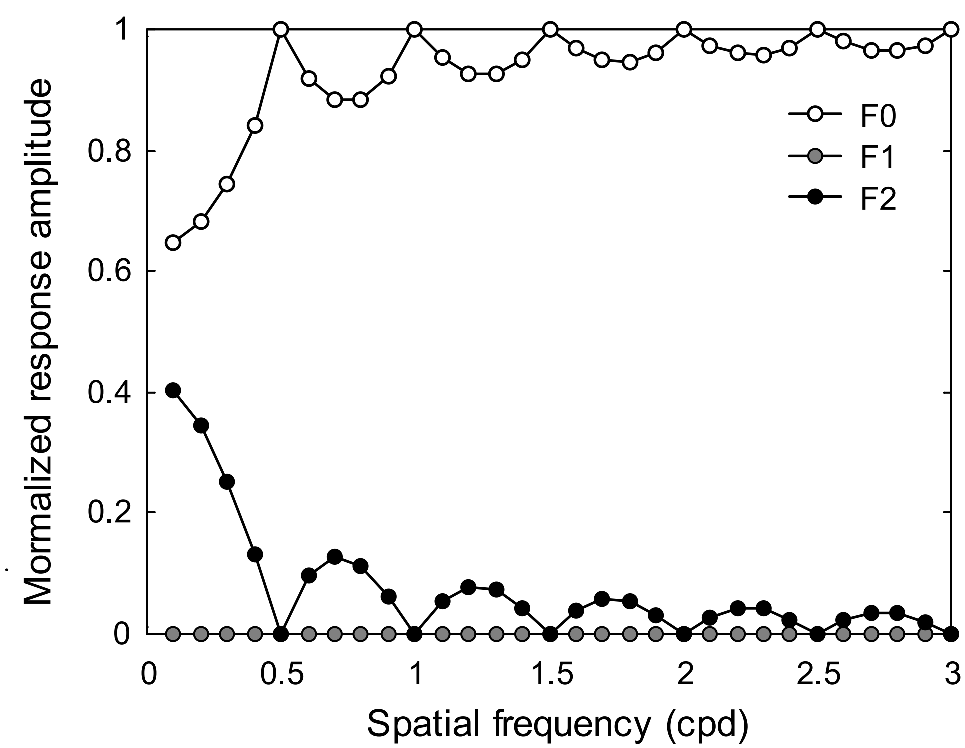
# Spatial frequency-dependent doubling

Fig. 4

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



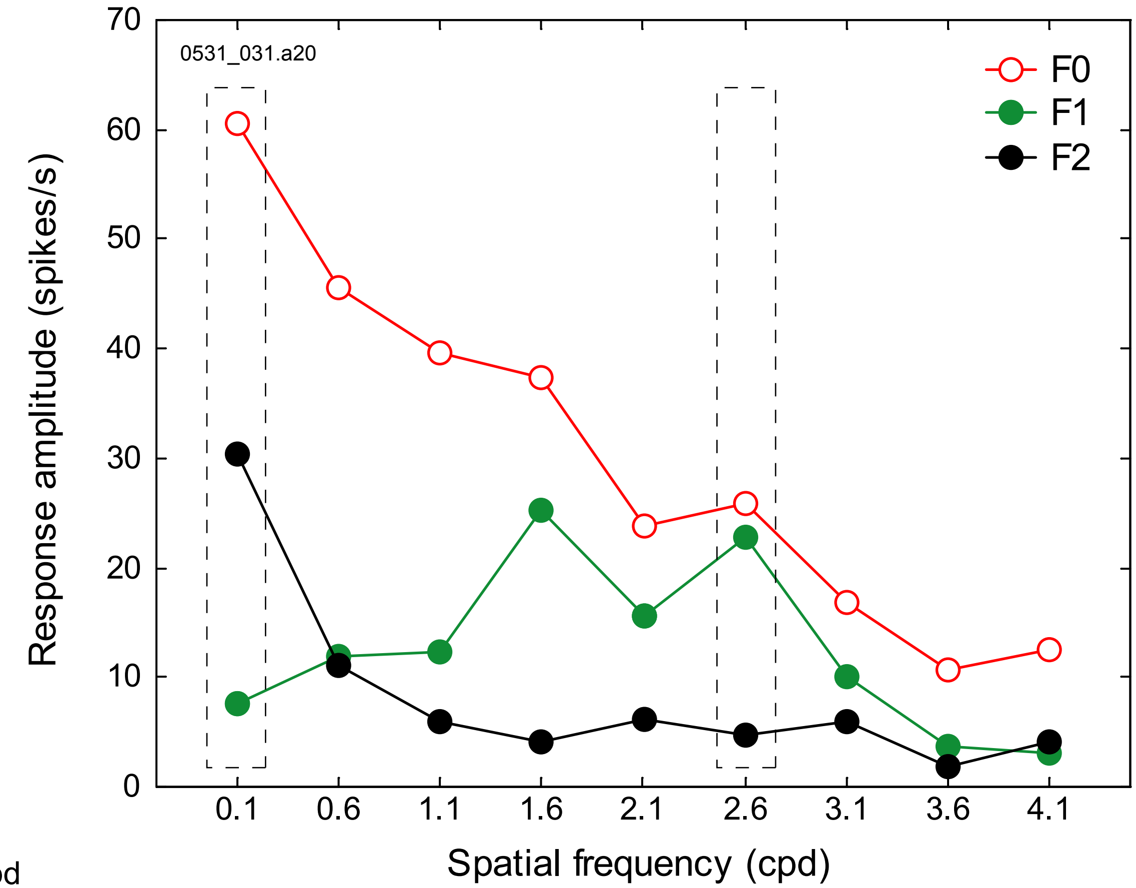

Normalized amplitude of F0 and F2 harmonics as function of grating spatial frequency

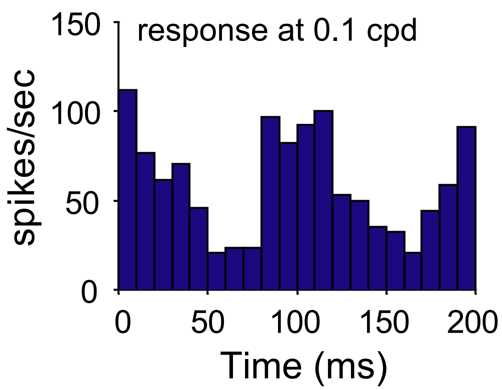


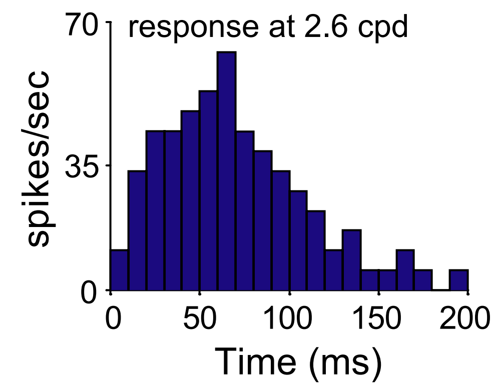
# Spatial frequency effect

Fig. 5

Increase of F1 and decrease of F0 with spatial frequency



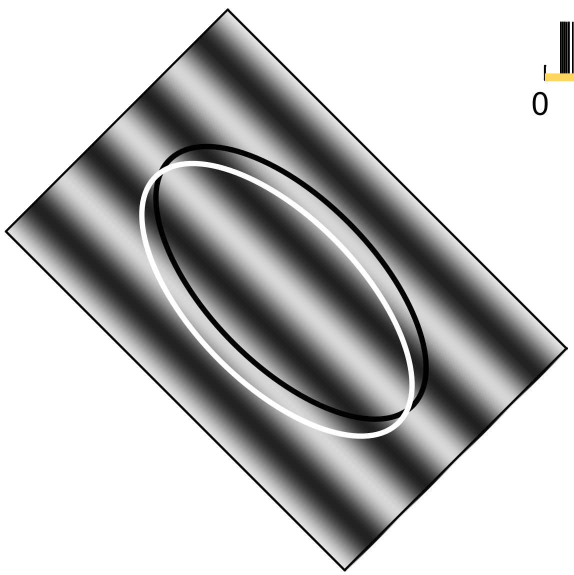



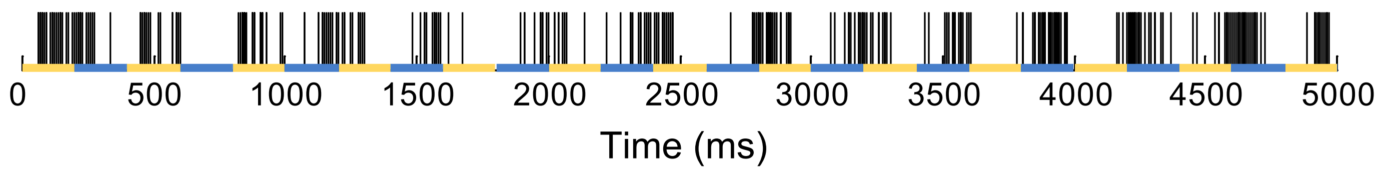
# Spatial frequency effect

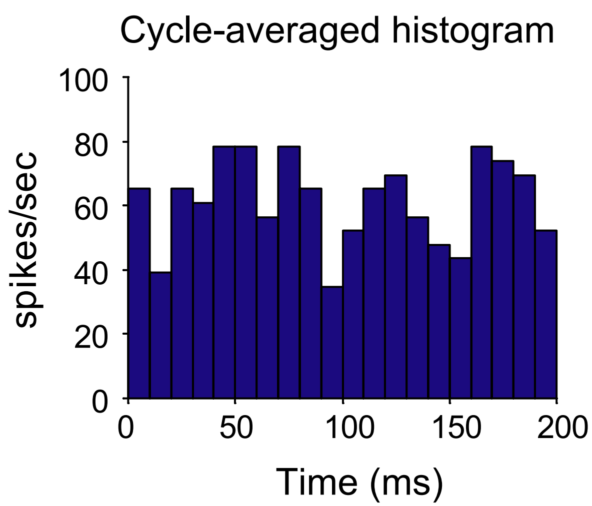
Fig. 6

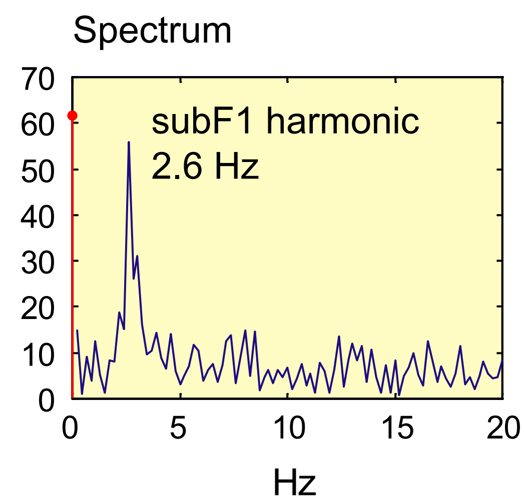
"SubF1" modulation to drifting grating of high spatial frequency

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





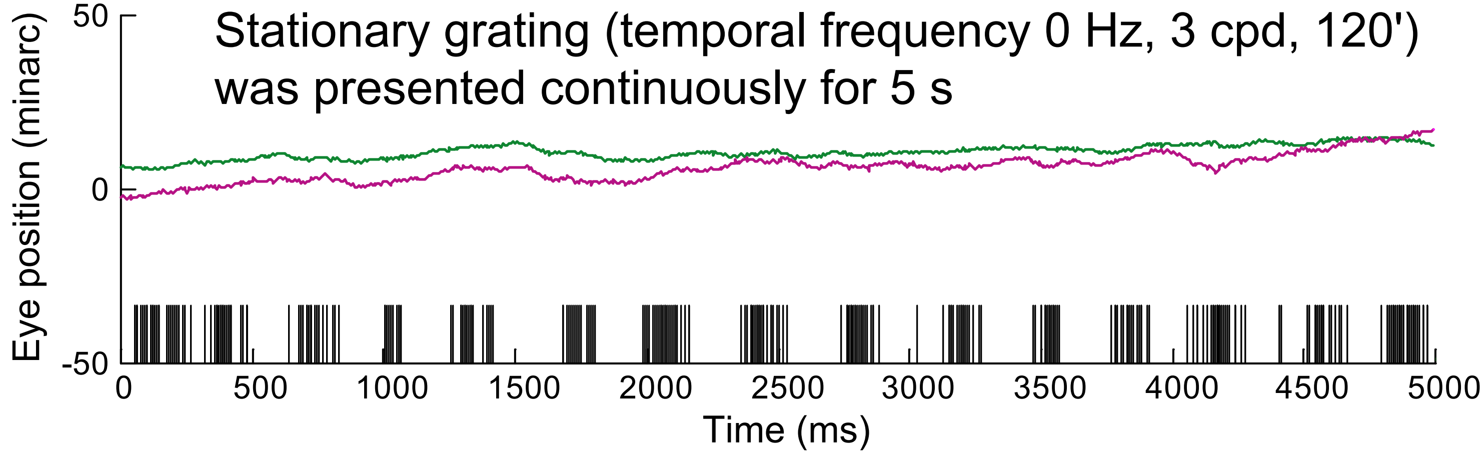




0791_014.a22 18

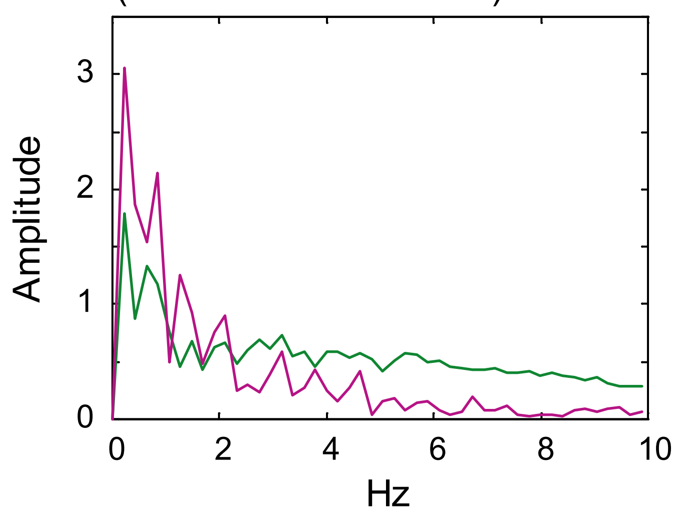
# Response to stationary grating

Fig. 7

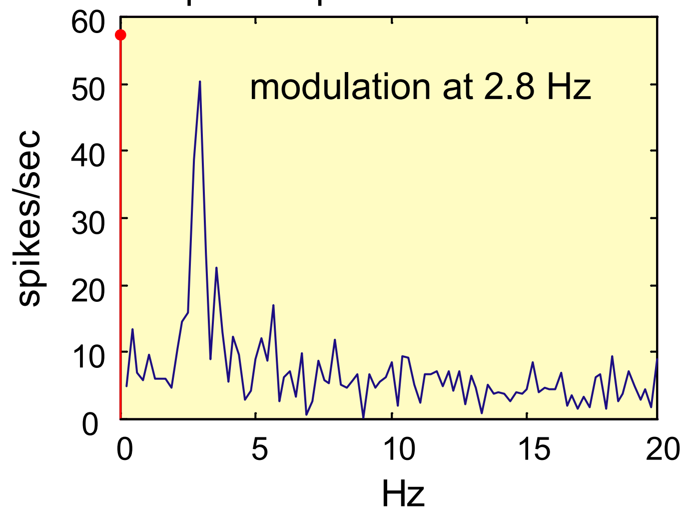
Unexpected modulation in response to the "constant"
- except for the eye movements - stimulus




Eye movement spectra
(vertical and horizontal)




Response spectrum




It's unlikely that the observed modulation is the direct result of motion imposed by the 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)

1201_005.a05 5

# Conclusions

- ✓ In duplex cells, the harmonic content of the grating response depends on stimulus attributes.
- ✓ Current models of V1 receptive fields do not capture the observed diversity of duplex cells' behavior.
- ✓ These results support the notion of an elaborate spatiotemporal structure of duplex cells' receptive fields.