Presented at: 2004 CSH meeting on Computational and Systems Neuroscience (COSYNE), March 24 - 28, 2004

Modeling V1 complex cells in alert monkeys

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Abstract. Cortical complex cells are usually described as nonlinear energy operators that sum squared outputs of quadrature pairs of linear subunits, responding to drifting sinusoidal gratings with unmodulated elevation of firing rate (F0 harmonic). However, several lines of evidence suggest that the view of complex cells as a uniform class is over-simplified, since energy models do not capture many complex cell behaviors. In alert monkeys complex cells with strongly overlapping increment and decrement regions exhibit a considerable F1 modulation, and a subset of these cells have a *relative modulation* (RM=F1/F0) >1. We have also found that most complex cells show profound dependence of *the response form* (harmonic content), and not only the amplitude, on grating parameters such as spatial and temporal frequency and size, displaying a variety of behaviors ranging from nonlinear unmodulated firing (F0) and frequency doubling (F2) to pseudolinear modulation (F1).

One of the parsimonious explanations could be that at least some of these behaviors, e.g. F1 modulation, result from the imbalance of increment and decrement mechanisms such as incomplete spatial overlap and/or difference in amplitudes of the two regions. We tested this hypothesis using a model that approximates an *apparent* structure of complex receptive fields in our data by pooling two linear (increment and decrement) inputs with Gaussian spatial profile and same biphasic temporal response function. Model cells with various overlaps and amplitude ratios were stimulated with drifting gratings of different spatial frequencies. To quantify the measure of spatial (im)balance we computed a product of overlap index and amplitude ratio. In the model, maximal modulation increased with spatial imbalance, and the correlation for the two measures was high ($r=-0.86$, $p<0.01$). However, the model consistently yielded *lower* RM values than those in the data. Moreover, weak insignificant correlation between RM and spatial imbalance in the data for complex cells ($r=-0.15$, $p>0.01$) was inconsistent with model predictions. Thus, a static spatial imbalance of increment and decrement mechanisms cannot fully predict the presence of strong F1 harmonic in responses of complex cells.

These results and effects of temporal frequency suggest that temporal properties of input channels and possibly the dynamics of interaction between them play an important role in shaping the responses of complex cells. To account for the response diversity exhibited by complex cells, we are developing more realistic models that also include influences of the surround.

1. Introduction

There is a renewed interest in definition, characterization and function of V1 simple and complex cells The source of input to complex cells and organization of their

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receptive fields is a subject of ongoing debate. All extant models aim to explain well-documented (in *anaesthetized* cats and monkeys) nonlinear features of complex cells such as sign-of-contrast (polarity) and spatial phase invariance and nonlinear spatial summation. Feedforward models, mostly variants of the basic energy model (Adelson and Bergen 1985), involve pooling LGN or simple-cell inputs followed by threshold nonlinearities (Caywood et al. 2000; Heeger 1991, 1992a,b; Garcia-Perez 1999; Pollen and Ronner 1982, 1983; Sakai and Tanaka 2000; Spitzer and Hochstein 1985). Recurrent models postulate weak feedforward LGN input and strong intracortical connections (Chance et al. 1999; Tao et al. 2001).

There is a renewed interest in definition, characterization and function of V1 simple and complex cells (Abbott and Chance 2002; Kagan et al. 2002; Mechler and Ringach 2002, Shams and von der Malsburg 2002). The source of input to complex cells and organization of their receptive fields is a subject of ongoing debate. Feedforward models, mostly variants of the basic energy model (Adelson and Bergen 1985), involve pooling LGN or simple-cell inputs followed by threshold nonlinearities (Caywood et al. 2000; Heeger 1991, 1992a,b; Garcia-Perez 1999; Pollen and Ronner 1982, 1983; Sakai and Tanaka 2000; Spitzer and Hochstein 1985). Recurrent models postulate weak feedforward LGN input and strong intracortical connections (Chance et al. 1999; Tao et al. 2001). All extant models, feed-forward and recurrent, explain well-documented (in *anaesthetized* cats and monkeys) nonlinear features of complex cells such as sign-of-contrast (polarity) and spatial-phase invariance and nonlinear spatial summation. However, many nonlinear neurons in alert monkeys show more diverse and elaborate behaviors deviating from traditional notion of complex cells (Kagan et al. 2002, Kagan et al., in preparation; see also Mechler et al. 2002: response variations with the spatial phase). Prevalence of nonlinear complex cells in monkey V1 underlines their importance in visual processing and necessitates their careful analysis.

The goals of the present (ongoing) study are:
(1) To characterize spatial and temporal properties of complex cells in various conditions.
(2) To evaluate existing models against experimental results.
(3) To develop more realistic models compatible with a wide range of complex cell behaviors.

2. Methods

2.1. Neurophysiology

Extracellular responses of single V1 neurons were recorded while alert monkeys performed a fixation task. Classical receptive fields (CRF) were mapped with sweeping and flashing bars and edges and classified as simple or complex based on the spatial overlap of increment and decrement activating regions (ARs). Least-square Gaussian profiles were fitted to bar response histograms in order to estimate CRF spatial parameters (Fig. 1):

$$w_{INC,DEC} = 4\sigma \tag{1}$$

$$OI = \frac{0.5(w_{INC} + w_{DEC}) - sep}{0.5(w_{INC} + w_{DEC}) + sep} \tag{2}$$

$$RAR = min(A_{INC}, A_{DEC})/max(A_{INC}, A_{DEC}) \tag{3}$$

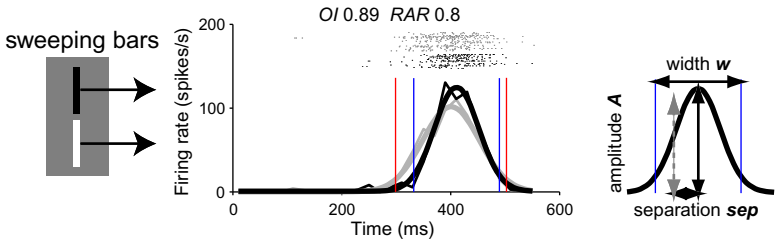

Figure 1.

Then neurons were studied with drifting and counterphase (contrast-reversal) gratings of systematically varied spatial frequency (SF), temporal frequency (TF) and patch width (W), optimally oriented and centered on the CRF. Responses were Fourier-analyzed and relative modulation (RM=F1/F0, the ratio of 1st and 0th harmonics) was calculated for all stimulus conditions.

2.2. Modeling

The receptive fields (RFs) of model subunits (afferent inputs) are simulated as linear spatiotemporal filters. For simplicity we consider only spatial dimension that is perpendicular to the neuron's preferred orientation. Each subunit is characterized by a spatial RF $\psi(x)$ (Gaussian, DoG or Gabor function) and a temporal impulse response (TIR) $h(t)$. Formally, for Gabor function:

$$\psi(x) = \frac{1}{\sqrt{2\pi}\sigma} exp\left[-\frac{x^2}{2\sigma^2}\right] cos(2\pi\rho x + \phi) \tag{4}$$

where ρ is the tuning spatial frequency, σ is the space constant, and ϕ is the spatial phase.

The subunit's TIR is described by a difference between $(m+1)-$ and $(n+1)-$ stage lowpass filters:

$$h(t) = H(t)\left[\gamma\frac{\alpha(\alpha t)^m exp[-\alpha t]}{m!} - \delta\frac{\beta(\beta t)^n exp[-\beta t]}{n!}\right] \tag{5}$$

where H is Heaviside's unit step function and all parameters are positive. The TIR is monophasic when δ=0, and monophasic, biphasic or triphasic otherwise. TIR in temporal quadrature is obtained by convolving a given TIR with $q(t) = -1/(\pi t)$ (Hilbert transform).

Visual stimuli are presented as spatiotemporal functions $S(x,t)$. For each subunit i we first perform integration over space:

$$g_i(t) = \int_{-\infty}^{\infty} S(x,t)\psi(x)dx \tag{6}$$

and then we convolve the resulting function $g_i(t)$ with a subunit's TIR $h_i(t)$:

$$V_i(t) = h_i(t) * g_i(t) \tag{7}$$

Then subunits are half-wave rectified and summed, and the resulting model response V_m represents an idealization of extracellular firing rate:

$$V_m(t) = \sum_{i=1}^{n} \lfloor V_i(t) \rfloor \tag{8}$$

All simulations are performed using custom software written in MATLAB. (Fig. 2).

3. Results

3.1. Spatial organization of V1 receptive fields

Most complex cells have strongly overlapping and approximately balanced increment and decrement ARs (Fig. 3).

3.2. Relative modulation and spatial (im)balance

Still, many complex cells exhibit strong F1 modulation to drifting gratings. We tested whether incomplete spatial overlap or amplitude difference between increment and decrement ARs could account for F1 responses of complex cell, in the model that sums rectified responses of two ARs. For similar ranges of OIs and RARs, the correlation between RM and overall spatial (im)balance ($I = OI \times RAR$) is much weaker and corresponding levels of RM much higher in the data than in the model ($r_{complex} = -0.17, r_{model} = -0.88$). Thus, high F1 cannot be fully explained by a static spatial imbalance of increment and decrement ARs (Fig. 4).

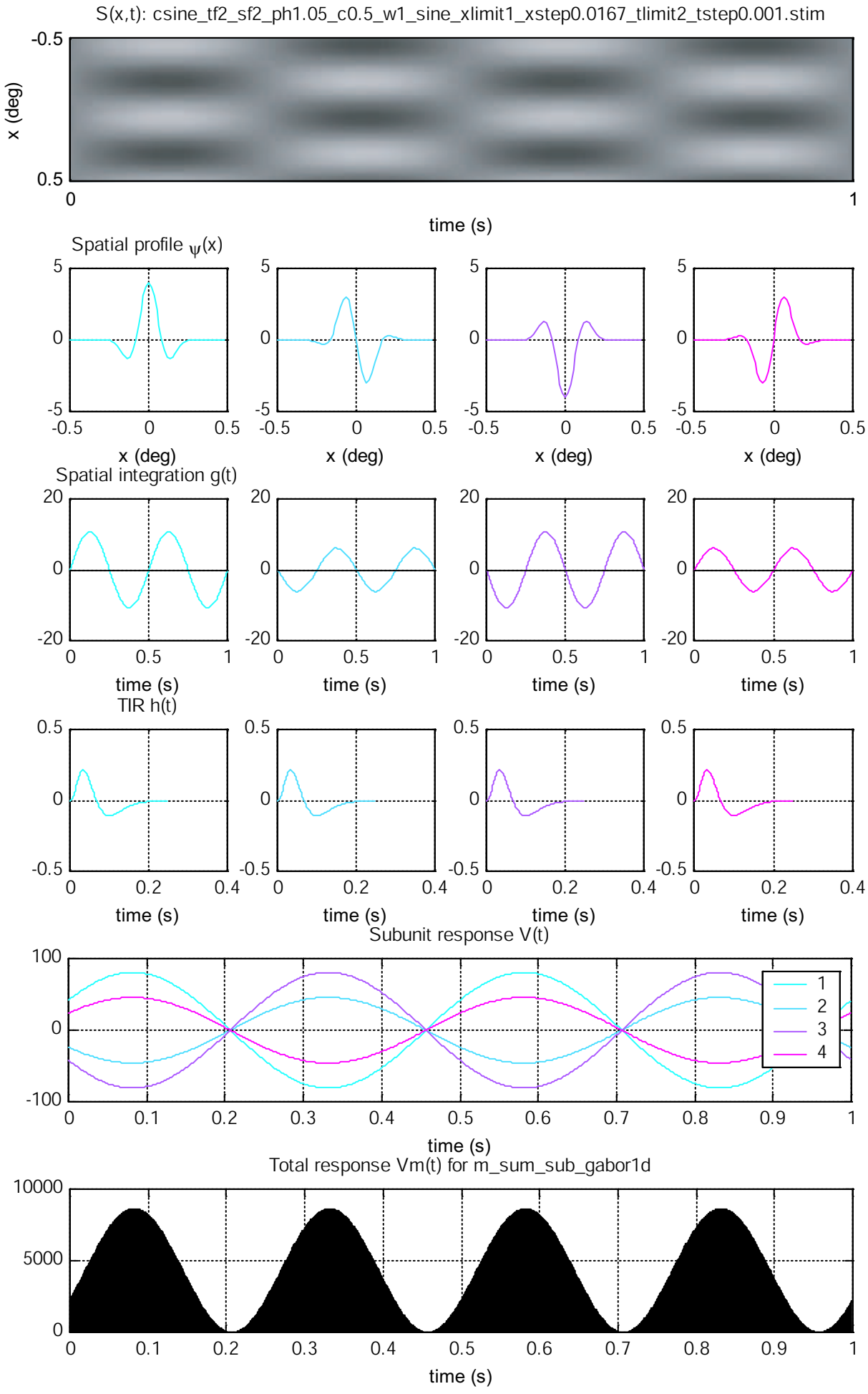
S(x,t): csine_tf2_sf2_ph1.05_c0.5_w1_sine_xlimit1_xstep0.0167_tlimit2_tstep0.001.stim
x (deg)
-0.5
0.5
0
1
time (s)
Spatial profile ψ(x)
x (deg)
Spatial integration g(t)
time (s)
TIR h(t)
time (s)
Subunit response V(t)
1
2
3
4
time (s)
Total response Vm(t) for m_sum_sub_gabor1d
time (s)

Figure 2.

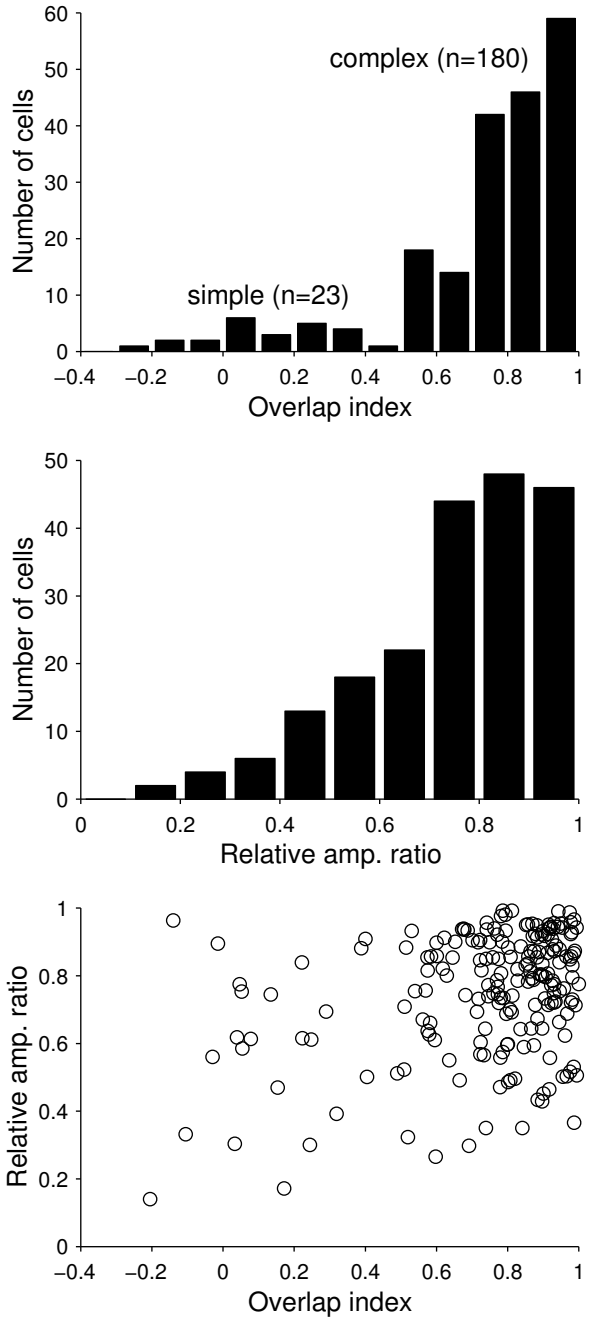
complex (n=180)
simple (n=23)
Number of cells
Overlap index
Number of cells
Relative amp. ratio
Relative amp. ratio
Overlap index

Figure 3.

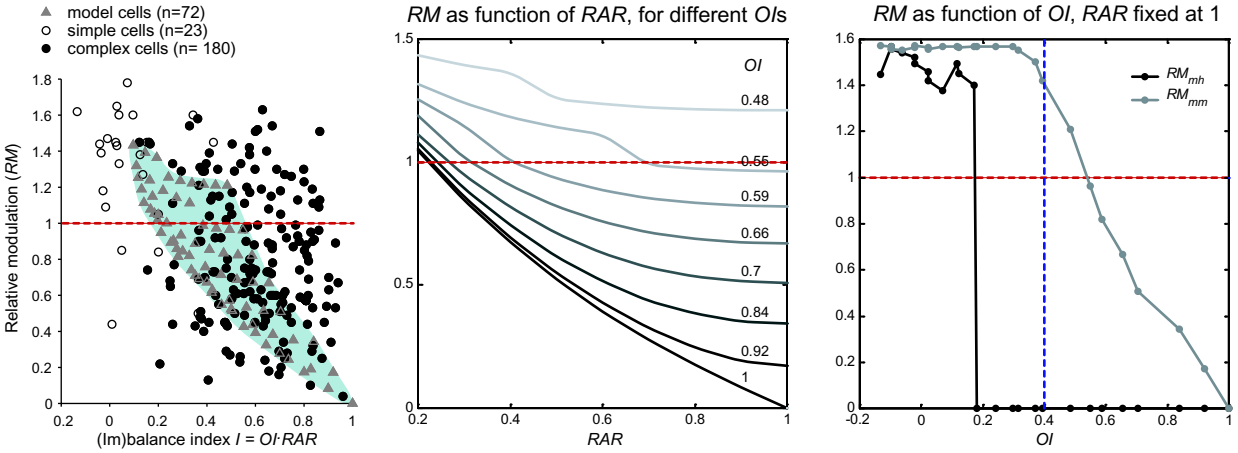

Figure 4.

3.3. Modulation patterns depend on stimulus parameters

While complex cells show a variety of responses both within a cell and across cells, several principle systematic patterns are discernible: 1) Drifting gratings of very low spatial frequency cause frequency-doubling (F2). 2) Drifting gratings of low-to-mid spatial frequency cause pseudo-linear F1 modulation. 3) Further increase of spatial frequency removes F1 harmonic and yields F0 or "subF1" firing. 4) Low drift temporal frequency (1-2 Hz) tends to evoke F2 or mixed (F1-F2-F3) response, while higher (4-5 Hz) temporal frequency yields F1 harmonic. 5) Increase of grating patch width often cancels F2 harmonic and increases RM. 6) Responses to counterphase gratings are typically frequency-doubled; deviations from a typical F2 response: low spatial frequency and/or high temporal frequency transforms even-harmonic to F1 modulation, similarly to drifting case.

3.4. Shortcomings of energy models

Clearly, the energy model cannot generate F1 responses to drifting gratings. Moreover, when we unbalance increment and decrement components by perturbing location or amplitude of input subunits, the resulting dependence of modulation on grating spatial frequency does not follow experimental trends described in 3.3, except for frequency-doubling at very low SF (Fig. 5). Similar results were obtained using models that sum multiple even-Gabor subunit pairs.

3.5. Alternative model: separate increment and decrement channels, mutual suppression

- - No "push-pull" mode.
- - Perfectly balanced increment and decrement channels.
- - Each channel contains transient and sustained subunits.
- - Mutual inhibition between channels with fixed time constant of 100 ms.
- - When two polarities are present in the input, only one (first) channel is firing.

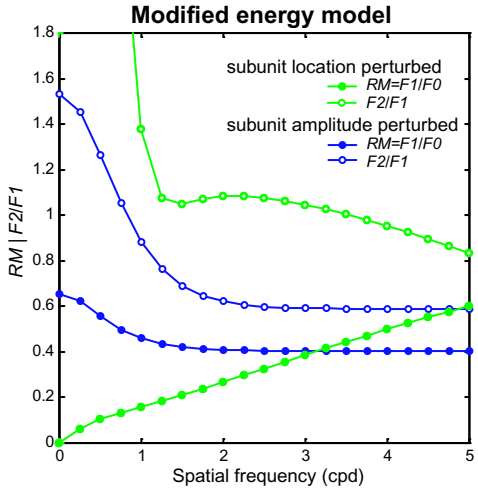
Modified energy model
subunit location perturbed
RM=F1/F0
F2/F1
subunit amplitude perturbed
RM=F1/F0
F2/F1
RM | F2/F1
Spatial frequency (cpd)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
0
1
2
3
4
5

Figure 5.

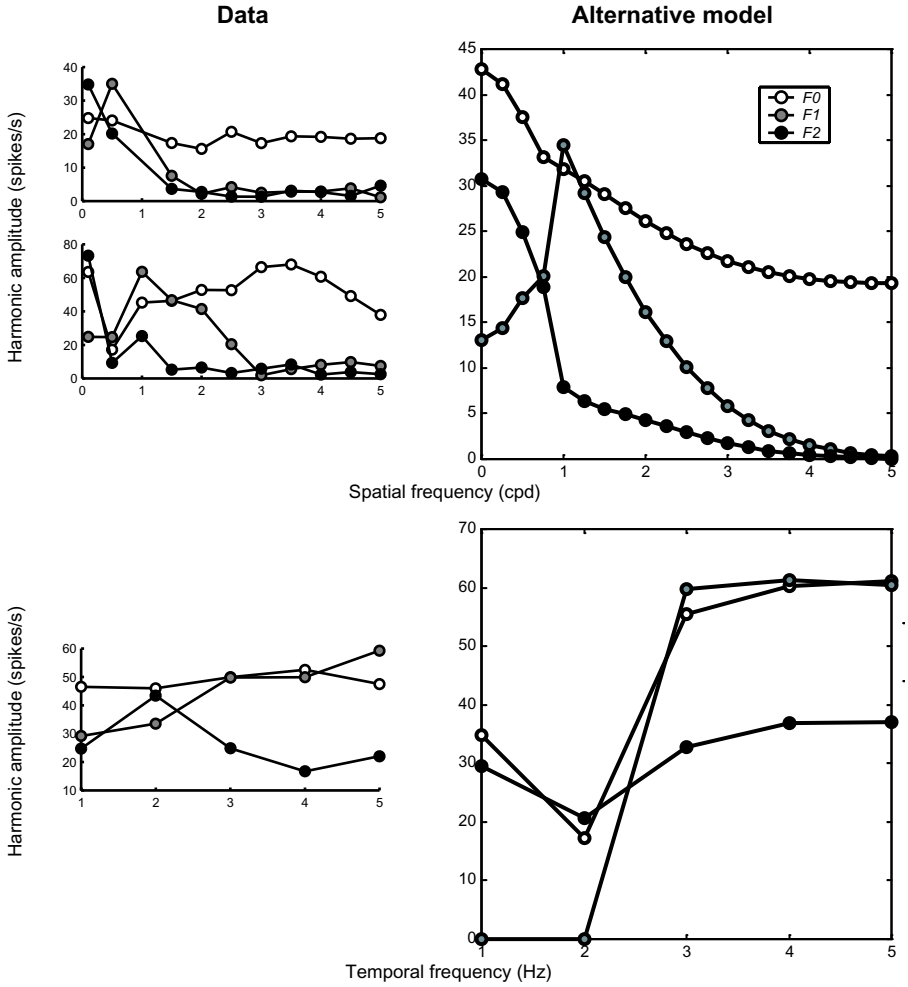

Figure 6.

4. Summary

4.1. Conclusions

Complex cells exhibit behaviors incompatible with current models, particularly variants of the energy model. Static spatial imbalance of increment and decrement ARs is not strong enough to yield observed levels of F1 modulation, and cannot account for dependence of the harmonic content on stimulus spatial and temporal frequency. We could not find a simple amendment to any of existing models that would render it compatible with complex mutually-inconsistent behaviors (which is probably not surprising...). Our results suggests that the timing of suppressive interactions and other temporal effects are crucial, but the exact mechanism has yet to be elucidated. A simple "**First-Takes-All**" model was able to reproduce effects of spatial and temporal frequency consistent with data (Fig. 6).

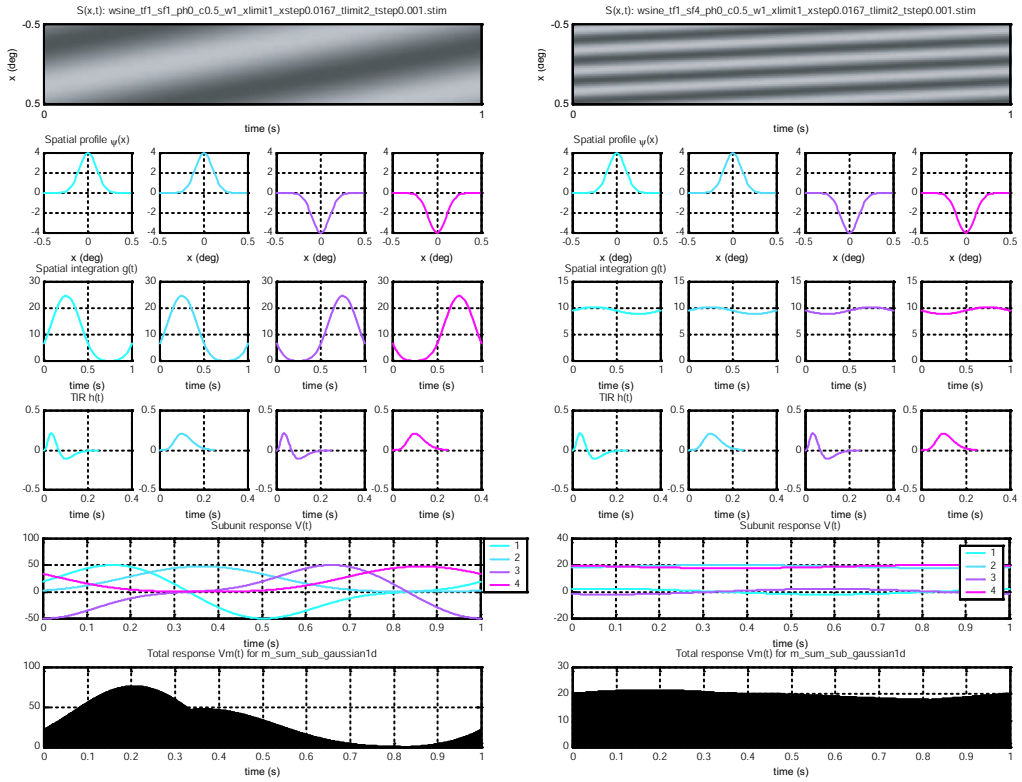

Figure 7.

4.2. Future work

1) Incorporate effects of overlapping surrounds.
2) Incorporate recurrent connections and synaptic depression.
3) Cell-by-cell parameter estimation and comparison of data with model performance.

5. Acknowledgements

We thank Bilgin Ersoy, Michele Rucci and Alan Saul for useful discussions. Supported by NIH EY12243.

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