DIVERSITY OF COMPLEX CELL RESPONSES IN V1 OF ALERT MONKEYS

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Short title: Complex cells in macaque V1

262 words in Abstract, 33 Text pages (including 7 pages of References), 12 Figures, 2 Tables.

Keywords: primary visual cortex, alert behaving monkey, simple and complex cells, receptive fields, fixational eye movements, relative modulation, nonlinearity, gratings

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ABSTRACT

We have previously shown that most cells in the alert monkey V1 are complex cells with overlapping increment and decrement activating regions and nonlinear response properties. Diverse responses of these cells to drifting gratings differ from the unmodulated firing usually ascribed to complex cells, and cannot be predicted from receptive field spatial maps. We recorded extracellular responses in V1 of macaques performing a fixation task, while systematically varying spatial and temporal frequency and width of the grating patch. The distribution of relative modulation (F1/F0) was not bimodal. Some cells responded with pseudolinear (F1) modulation to mid-to-high temporal frequency gratings, but showed frequency doubled (F2) or mixed (F1, F2, F3 harmonics) responses at low temporal frequencies. Grating spatial frequency and width profoundly influenced the modulation in most cells. The main patterns were: F2 responses to gratings of very low spatial frequency and/or small width; decrease of F2 and increase of F1 with increase of spatial frequency and/or width; decrease of F1 and appearance of "subharmonic" modulation around 3 Hz with further increase of spatial frequency; increase of relative F1 component with grating width. Finally, the responses of many cells to stationary gratings of mid-to-high spatial frequency unexpectedly exhibited robust low frequency modulation in the range similar to the "subharmonic" modulation elicited by drifting gratings. Thus, the form of the response, not only the amplitude, depended on stimulus parameters. The existing models of cortical cells do not account for the response diversity exhibited by complex cells. These results suggest an alternative complex cell model based on dynamic interactions between increment and decrement ARs and surround.
INTRODUCTION

Since the introduction of linear systems methods to analysis of visual responses, simple and complex receptive fields (RF) in V1 have been extensively studied with sinusoidal gratings. Numerous studies have established that simple cells, characterized by the separation of the RF to increment- and decrement-responsive regions and a linear spatial summation within the RF, respond predominantly with the fundamental (first, F1) harmonic to drifting and counterphase gratings (Carandini et al. 1997). Complex cells with overlapping increment and decrement regions, on the other hand, exhibit profound nonlinearities, and their response to gratings is often dominated by nonlinear harmonics, in particular DC, or F0 (Movshon et al. 1978). Those findings have led to a generally accepted classification of simple and complex cells based on the bimodal distribution of relative modulation (RM, the ratio of F1/F0), which was proposed to be >1 for simple cells and <1 for complex cells (De Valois et al. 1982; Skottun et al. 1991). The result of this practice was that complex cells, with the unmodulated elevation of their firing rate considered as their "principal" response, were assumed to generalize over phase, position and contrast polarity and to perform functions such as gain control, normalization, and cross-orientation inhibition (Carandini et al. 1997; Heeger 1992a; Mel et al. 1998; Pollen et al. 1985).

Several lines of evidence, however, suggest that the view of complex cells as a uniform, basically phase-insensitive class is over-simplified. First, modulated responses of complex cells have been reported by many authors (Dean and Tolhurst 1983; Foster et al. 1985; Glezer et al. 1980; Glezer et al. 1982; Hammond et al. 1989; Holub and Morton-Gibson 1981; Kulikowski and Bishop 1982; Pollen et al. 1978; Pollen and Ronner 1982), and published distributions of RM show many cells in the range of 0.5-1 (De Valois et al. 1982; Mechler et al. 2002; O’Keefe et al. 1998; Skottun et al. 1991). Second, both experimental (Carandini and Ferster 2000) and theoretical (Mechler and Ringach 2002) work demonstrated that the bimodality of the extracellular relative modulation can be a consequence of a threshold nonlinearity, and the underlying distribution of intracellular membrane potential could be
unimodal (ref. to Priebe et al. when accepted). Third, spatial phase-sensitive responses have been
found in complex cells (Mechler et al. 2002; Pollen et al. 1988; Spitzer and Hochstein 1985a; Victor
and Purpura 1998). Finally, we have shown that in the alert monkey many complex cells with
overlapping increment and decrement regions exhibit a considerable F1 modulation, and a subset of
these cells have RM >1 (Kagan et al. 2002a).

These considerations and the dominance of complex cells in macaque V1 prompted us to
systematically study the diversity of complex cells responses to drifting and counterphase gratings. We
found that, depending on stimulus parameters such as spatial and temporal frequency and grating size,
complex cells display a variety of behaviors ranging from nonlinear unmodulated firing (F0) and
frequency doubling (F2) to pseudolinear modulation (F1). A subset of neurons also exhibited a robust
"subharmonic" modulation in response to drifting and stationary gratings. Interestingly, the
distribution of RM for a total sample was not bimodal. Our results demonstrate that complex cells'
receptive fields have intricate nonlinear properties, whose interaction can yield pseudolinear responses
within a limited range of parameters. Current models of complex cells (in particular, energy model) do
not account for these findings, suggesting a more elaborate role of complex cells in visual processing.

Parts of this work have been presented in abstract form (Kagan et al. 2002b,c).
METHODS

Four adult female monkeys (3 *Macaca mulatta*, M42, M45 and M46, and one *Macaca fascicularis*, F42) were used as subjects. Most of the data for this study (a total 203 cells) were from two monkeys, M45 (n=89) and M46 (n=94), and 20 cells were from two other monkeys. Monkeys were trained to fixate on a light-emitting diode (LED) for a water reward. Once the monkey learned the task, a head-holding implant and a recording well were surgically attached to the skull under deep anesthesia. All procedures complied with NIH guidelines and were approved by the Animal Care and Use Committee of the Schepens Eye Research Institute.

*Nerve spike and eye movement recordings*

Fiber electrodes made from quartz-insulated platinum-tungsten alloy (Eckhorn and Thomas 1993) with bare tip lengths of ≤5 µm and impedance at 1 kHz of 3-6 MΩ were most frequently used for extracellular recording. In some experiments glass-insulated platinum-iridium electrodes (Snodderly 1973) with a tip diameter of 1-1.5 µm, and bare tip length of 5-7 µm, were used. In many experiments, we chronically implanted electrodes for several days (up to 2 weeks). During the recording, the electrode could be moved along the vertical axis by the microdrive; at the end of the day the electrode was firmly locked in place. In most cases, single-unit activity was recorded; when multi-unit activity was encountered, cells were sorted online using feature space clustering (BrainWare, TDT) and verified/re-sorted offline using a PCA and fuzzy k-means clustering (Abeles and Goldstein 1977; Gur et al. 1999). Cells were assigned to cortical layers based on histological and/or physiological criteria as previously described (Snodderly and Gur 1995, Gur et al., submitted).

The position of the dominant eye was monitored by a double Purkinje image eye tracker (2-3 minarc resolution; 100 Hz sampling rate) or a magnetic field search coil (Robinson 1963; Judge et al. 1980; 1-2 minarc resolution, low-pass filtered at 100 Hz before sampling at 200 Hz) and recorded in a
computer file, together with spike arrival times (0.1 ms time resolution) and spike shapes collected at 20-25 kHz (Gur et al. 1999). The coils were made of Teflon-coated stainless steel AS 634 Cooner wire. During initial experiments we found that the coil may slip during blinks or saccades, yielding inconsistent estimates of eye position from trial to trial. Therefore, we sutured the coil to the sclera in subsequent experiments.

The trial started when the monkey correctly pressed the lever in response to the LED and continued for 5 seconds provided that the gaze remained within a fixation window (±0.5° to ±1°).

Stimulus presentation

Stimuli were displayed on a Barco 7351 monitor at a 60 Hz frame rate, with a Truevision ATVista video graphics adapter, or more recently on a Sony 500 PS monitor at a 160 Hz frame rate, driven by a Cambridge Research Systems VSG2/3F graphic card. Bars were optimized for orientation, length, velocity, and color (white, green or red), 0.9- or 1-log units brighter or darker than the background of 1 or 5 cd/m². Chromatic stimuli were generated by activation of the monitor individual guns. Monochrome sine gratings of 50% or 100% luminance contrast, optimal orientation, length, and color were presented on the same background as the bars and had the same mean luminance as the background.

After the ocular dominance was established, stimuli were viewed binocularly, unless responses during monocular viewing were substantially stronger. The eye position signal for the dominant eye was added to the stimulus position signal at the beginning of each or each second video frame, to compensate for changes in eye position during the intersaccadic intervals (“image stabilization”, Gur and Snodderly 1987, 1997; Snodderly and Gur 1995). Note that the maximum delay between shifts in the eye position and subsequent corrections could be as long as 28 ms for bars and 44 ms for gratings in the old system, and 10 ms in the new system; thus this procedure was not intended to compensate for the fast saccadic movements. Epochs affected by saccades were automatically detected and excluded.
during offline data analysis using a velocity threshold of 10 °/s (Snodderly et al. 2001).

**Receptive field mapping**

The width and location of receptive field activating regions (AR) was estimated with narrow increment and decrement bars swept back and forth at 1.5-7°/s across the receptive field in a direction orthogonal to the optimal orientation axis. The operational term “activating region” is used to distinguish regions that respond to direct stimulation from other (covert) zones that may modify the directly evoked response (e.g. side inhibition or facilitation from subthreshold regions). We will refer to the total region of space occupied by the activating regions as the classical receptive field (CRF).

To increase the precision of measurement and minimize possible effects of response latency, we calculated AR widths using the lowest velocity in the data set that elicited a strong response. Using online image stabilization and offline rejection of data segments containing fixational saccades, we were able to obtain reliable measures of AR widths and locations in spite of inevitable variations in fixation (Gur et al. 1997; Kagan et al. 2002a). Least square Gaussian profiles were fitted to increment and decrement response histograms, and all AR parameters were extracted from the fits. Four standard deviations were taken as AR width \((W)\), encompassing 95% of the response. An overlap index (OI) was calculated as (Schiller et al. 1976):

\[
OI = \frac{0.5 \cdot (W_{INC} + W_{DEC}) - sep}{0.5 \cdot (W_{INC} + W_{DEC}) + sep}
\]

where \(W_{INC}\) and \(W_{DEC}\) denote the width of increment and decrement AR and \(sep\) denotes the separation between AR centers. The OI ranges from negative values for spatially separated ARs to 1 for complete and symmetric overlap. Except for the special case when one AR is completely within the other, OI is the ratio of the overlap zone to the total receptive field width. We have recently shown (Kagan et al. 2002a) that the distribution of the overlap index in alert monkey is bimodal but very uneven; few cells with nonoverlapping ARs \((OI \leq 0.3)\) corresponded to simple cells (Hubel and Wiesel 1962, 1968), and
most cells with overlapping ARs (OI ≥0.5) to complex cells. Current sample did not have a clear-cut border between simple and complex cells, and 5 cells that fell into the range between 0.3 and 0.5 could not be classified unequivocally (Fig. 1A). Based on the notch in the OI distribution at [0.4-0.5] bin we assigned 4 cells (OI 0.32, 0.39, 0.40, 0.40) to the simple class and one (OI 0.49) to the complex. Altogether, the dataset included 23 simple cells (OI mean±SD: 0.08±0.14) and 180 complex cells (OI mean±SD 0.82±0.13).

Since the overlap index ignores relative strength of increment and decrement responses, we also calculated a increment-decrement relative amplitude ratio (RAR), ranging from 1 for equal responses to near zero for very different responses: $RAR = \frac{\min(A_{INC},A_{DEC})}{\max(A_{INC},A_{DEC})}$, where $A$ is the amplitude of the Gaussian fit (Fig. 1B). The scatter plot for RAR vs. OI shows that while simple cells exhibit a wide range of amplitude ratios, most complex cells have approximately balanced increment and decrement mechanisms (Fig. 1C). Finally, we obtained a combined measure of spatial (im)balance (I) that takes into account both the degree of overlap of increment and decrement ARs and their relative strength: $I = OI \cdot RAR$.

Grating experiments

Sinusoidal gratings were restricted in space by a rectangular window of optimal length, same as the mapping bars, oriented parallel to the grating bars and centered on the CRF. Three other parameters – window width in the direction perpendicular to the orientation axis, spatial frequency, and temporal frequency – were systematically varied. The width varied from a fraction of the CRF to a size much wider than the CRF (98 cells). Spatial frequency varied from 0.1 to 11 cycles per degree (cpd), most frequently from 0.5 to 5 cpd (179 cells). Temporal frequency varied from 0.5 to 8 Hz, most frequently from 1 to 5 Hz (56 cells). Even when we did not collect data for the full range of each stimulus parameter, every effort was made to use near-optimal spatial and temporal stimulus conditions, as defined during preliminary tests. Two types of gratings – drifting and counterphase
(contrast-reversal) – were used. For directional cells, drift was always in the preferred direction. Counterphase gratings were temporally modulated by a square or sine wave, and in most cells more than one spatial phase was tested.

The fast Fourier transform (FFT) was used to compute the discrete Fourier transform (DFT) of neuronal responses, using as input either the raw concatenated spike train (sequence of 1s and 0s, where each 1 represents a spike in a spike train re-sampled at 1 kHz), or a cumulative histogram of spike arrival times averaged over one stimulus cycle. The two methods yielded very similar results for the frequency range of interest. The magnitude (spikes/s) of the response harmonics was extracted as

\[ F_k = \frac{2}{N} |DFT_k|, \quad k = 1\ldots N, \]

where \( N \) is the length of the DFT vector. The relative modulation (RM) of the response to a drifting grating was calculated as (De Valois et al. 1982):

\[ RM = \frac{F_1}{F_0}, \]

where \( F_1 \) is the magnitude of the first (fundamental) harmonic and \( F_0 \) is the mean firing rate (DC). We did not subtract the mean ongoing (spontaneous) firing rate with a uniform field from the \( F_0 \), since we often observed the suppression of the ongoing firing during or immediately following the stimulus-evoked response.

The phase (in degrees) of response harmonics was calculated as

\[ \text{phase} = (\text{angle}(DFT) + \pi/2) \cdot 180/\pi, \]

where \( \text{angle}(DFT) = \text{imag}(\log(DFT)) \) is the phase of the elements in a complex DFT vector. To eliminate discontinuities (jumps) due to phase wrapping, a simple "unwrapping" algorithm was applied. The algorithm minimized the standard deviation of a set by adding \( 2\pi \) to each phase (one at a time), re-calculating it, and then choosing the minimal standard deviation.

**Compensation of the effects of eye movements on grating responses**

All data presented in this paper were selected from raw trial records by discarding segments
contaminated by saccades ("no saccades" mode, Kagan et al. 2002a). However, even during the intersaccadic (drift) intervals, slower movements, noise in the eyetracker signal, small calibration errors, and minor deviations from linearity could cause position errors of a few minutes of arc that are difficult to eliminate. These residual position errors result in a shift of the retinal image of sinusoidal stimuli and corresponding jitter of the phases of the neuronal responses, thus underestimating the modulation in the "no saccades" mode. To correct for the phase jitter, an additional measure of the relative modulation was calculated by dividing the "no saccades" data into segments corresponding to one temporal cycle of the grating and averaging the RMs of individual segments (cf. Bridge and Cumming, 2001; Cumming et al. 1999). This procedure is equivalent to phase alignment in the frequency domain ("aligned" mode). However, the RM values derived from analysis of the "aligned" segments may be overestimates if there are significant phase shifts in the neuronal responses due to other factors, such as cycle-to-cycle variability or intrinsic temporal properties of the neurons (Garcia-Perez 1999). Therefore, we present the summary RM data based on both modes of analysis.

Time-frequency analysis

To visualize changes in the harmonic content of the response to gratings of different parameters, we used the S transform (ST, Stockwell et al. 1996), which is an extension of the short time Fourier transform (STFT) and the Wavelet transform (WT). ST reveals frequency variations over time by localizing a signal with frequency-adapted Gaussian scaling windows:

\[
S(f, \tau) = \frac{|f|}{\sqrt{2\pi}} \int_{-\infty}^{\infty} h(t) e^{-(r-t)^2/2} e^{-2\pi i f \tau} dt ,
\]

where \( f \) is frequency, \( \tau \) - time, and \( h(t) \) is the time signal. The details of the transform calculation for the discrete case are given in Stockwell et al. (1996).

Prior to applying ST, the neuronal firing rate signal was obtained by convolution of the PSTH (10 ms bin width) with a Gaussian window (\( \sigma=15 \) ms). The use of the ST is illustrated in the Results.
Statistical analysis

Individual cells’ PSTHs were plotted with a 10 ms bin width, smoothed with a Gaussian window ($\sigma=15$ ms). Correlations between variables were calculated using the Spearman r or the Pearson r. Values reported for individual parameters are means±SD. All analyses were done with custom software written in MATLAB (MathWorks).
RESULTS

A total of 203 V1 neurons, mostly at 2-6° eccentricity, and 11 cells at the periphery (>10° eccentricity, recorded from buried cortex) were studied. Recording sites included a broad sample of all laminar locations. All cells were tested with sweeping bars and drifting sinusoidal gratings, and 89 cells were tested with counterphase gratings. Cells were classified as simple (n=23) and complex (n=180, Fig. 1A), based on the spatial overlap of the increment and decrement zones (see Methods; Kagan et al. 2002a). In this paper, we mainly focus on complex cells, and simple cells are included for comparison.

We describe first the population distributions of relative modulation in responses to drifting gratings and its relationship to spatial organization of receptive fields. Next we consider the diversity and the dependence of grating responses on stimulus parameters – spatial and temporal frequency and window width.

Distributions of relative modulation to drifting gratings

A presumed estimator of "linearity", the relative modulation (RM, De Valois et al. 1982; Skottun et al. 1991, see Methods) of the response to a "near-optimal" drifting grating, is commonly used to distinguish simple and complex cells in anesthetized monkeys and cats. This procedure is based on the bimodality of the RM distribution: simple cells with RM >1 modulate at the temporal frequency of the grating, while complex cells with RM <1 show very little or no such modulation, their principle response being an elevation of the mean firing rate.

However, we have previously shown that in alert monkey the relative modulation distribution does not show a dichotomy, and that the degree of modulation does not correlate with classification based on spatial mapping (Kagan et al. 2002a). Here we confirm those results with a new data set from another monkey (94 neurons). The distribution of the relative modulation for the stimulus condition
eliciting a maximal harmonic (F0, F1 or F2) over the entire set of stimulus parameters is shown in Fig. 2A,B for the two analysis modes, "no saccades" and F1 phase "aligned" (see Methods). The distributions are not bimodal, and many cells have RM in the range of 0.5-1. In the "aligned" mode, the distribution is shifted to more modulated values, and the percentage of cells with RM >1 increases from 21% to 37%, roughly similar to values reported in anesthetized monkeys (Mechler et al. 2002; Ringach et al. 2002; Skottun et al. 1991), suggesting that the "alignment" indeed compensated for eye movement effects. However, even in the "aligned" mode there is no trough around 1, as found in the anesthetized preparation.

We were interested in the full range of modulation behaviors, partly because the response modulation may be a more important means of transmitting information than the maximal response, F0 in particular (Reich et al. 2001; Mechler et al. 2002), and partly because it can provide better understanding of RF mechanisms. Therefore we have also analyzed responses to stimulus condition producing the maximal RM (and at least 10 spikes/s maximal harmonic). In 99 cells, the stimulus parameters resulting in the maximal harmonic (usually termed "optimal" condition) coincided with the condition that elicited maximal RM. In 104 cells these conditions differed by spatial frequency (80 cells), grating window width (7 cells), or both (17 cells). The difference between the amplitude of the maximal harmonic in the two conditions was 27±19 spikes/s, or 35±17%, but RM increased by 57±24%. In can be seen that most cells exhibited at least some degree of F1 modulation, and 36% to 59% had maximal RM >1, depending on the mode of correction for eye movements (Fig. 2C, D).

Relative modulation and spatial organization

Next we asked how the degree of relative modulation to drifting gratings corresponds to spatial organization of RFs. On average, complex cells were less modulated than simple cells (Table 1, Fig. 2). However, the RM was not a good predictor of the spatial organization: although simple cells, as a
rule, had high RM, complex cells exhibited a wide range of RM, and a subset of complex cells (14% to 53%) had RM >1.

The two factors that could contribute to the presence of modulation in complex cells are incomplete overlap of increment and decrement ARs (OI) and/or difference in their respective amplitudes (relative amplitude ratio, RAR). There was no significant correlation between overlap index and relative modulation within the complex cell class, but the overall increment-decrement (im)balance measure (I, product of OI and RAR) was weakly correlated with the modulation (Fig. 3). However, the observed correlation was much weaker and corresponding levels of the RM much higher than would be predicted from a model that sums rectified responses of increment and decrement Gaussian ARs with similar ranges of spatial overlaps and relative amplitude ratios (Fig. 3; Kagan et al., in preparation). These results suggest that factors other than a static spatial imbalance of increment and decrement mechanisms exert a strong influence on the modulation behavior of these neurons.

Spatial frequency tuning

We constructed spatial frequency selectivity curves for the maximal harmonic, and estimated low and high frequency cutoffs at $1/\sqrt{2}$ (71%) of the peak response. In 48 cells where both cutoffs were reached, the full bandwidth (defined as the difference between these cutoffs) was 2.1±1.1 cpd (or 1.8±0.9 octaves, median 1.68 octaves), ranging from 0.5 to 5 cpd. The bandwidth of band-pass simple cells was narrower than in complex cells (1.3±0.5 octaves, 1.9±0.9 octaves). Sixty-seven cells had a high frequency cutoff (low-pass), and in 28 cells a low frequency cutoff was reached. Thirty-six cells were not tuned to spatial frequency in the range tested (usually 0.1-5 cpd), and in 24 cells data were collected at only one or two frequencies.

The two remarkable characteristics of the spatial frequency selectivity in our data are the broad tuning of many complex cells and the preference for low frequencies. Distributions of optimal frequencies for the maximal harmonic and maximal RM stimulus conditions are shown in Fig. 4.
Simple and complex cells shared a similar distribution pattern, with a mode at 1 cpd. Means for maximal harmonic and maximal RM conditions were $1.8\pm1.2$ and $1.9\pm1.4$ cpd for simple cells and $1.5\pm1.1$ and $1.2\pm0.9$ for complex cells respectively, slightly lower than the values reported for anesthetized monkeys at comparable eccentricities (cf. 2.2 cpd in Foster et al. 1985; 2.2 – 3.2 cpd in De Valois et al. 1982). In 49/97 cells where spatial frequencies in maximal RM and maximal harmonic condition were different, the spatial frequency producing maximal RM was outside one or two of the 71% cutoffs.

One way to look at the spatial frequency selectivity in a sample with a wide range of CRF sizes is to calculate the number of grating cycles within the CRF (complexity index, CI, Glezer et al. 1980). Distributions of CI for the maximal harmonic and maximal RM conditions are shown in Fig. 5. The initial idea behind the complexity index was to reveal a presence of RF "subunits". We did not find evidence for multiple subunits in many complex cells, unlike complex cells described in earlier papers in cat (Glezer et al. 1980; Pollen and Ronner 1983; Movshon et al. 1978) and anesthetized monkey (Foster et al. 1985), where complex cells had larger CIs than simple cells and most cells had CI >1. The distribution for the maximal harmonic condition was

In the maximal RM condition, 45% of cells had a CI around 0.5, so that about half grating cycle filled the CRF; and about 62% had a CI ≤1 (Fig. 5B).

Effects of spatial frequency on response modulation

While the effects of the grating spatial frequency on response amplitude (maximal harmonic) have been extensively studied, there was no systematic study of the relationship between the spatial frequency and the harmonic content of the response. In this section we focus on this relationship in responses to drifting gratings. Most complex cells tested with wide enough range of frequencies exhibited a profound dependence of the response modulation on the stimulus frequency. Forms of this
dependence were very diverse, but four general patterns could be extracted: 1) Frequency doubling (F2 modulation) at the lowest spatial frequencies; 2) Decrease of F2 and increase of F1 with increase of spatial frequency; 3) F1 modulation at low spatial frequencies and prevalence of F0 component at higher frequencies; 4) Decrease of F1 harmonic and appearance of sub-harmonic (subF1) modulation at mid-to-high spatial frequencies. These and other behaviors are summarized in Table 2 and Figure 6.

A simple nonlinear behavior such as F0-dominated unmodulated firing is expected in complex cells with largely overlapping increment and decrement activating regions. Similarly, an even harmonic frequency doubling can readily be explained for a sign-of-contrast invariant receptive field. We have recently suggested that the F2 modulation at low spatial frequencies and/or small grating windows (see below) reflects the time course of the overall luminance flux into the field during one temporal cycle, each of two response peaks corresponding to a passage of a bright or a dark lobe of the grating (Kagan et al. 2002a).

The presence of a pseudolinear F1 component in complex cells' responses is harder to explain. In the companion paper (in preparation) we discuss possible complex cell models that would generate F1 harmonic in response to drifting gratings. Here we were interested in examining the conditions under which this behavior occurs in complex cells. In the subset of 141 complex cells with a maximal RM >0.5, the mean number of grating cycles per CRF was only 0.66±0.83 (median 0.45). In 54/141 cells the spatial frequency producing the maximal RM was lower than the one producing the maximal harmonic, by 1.7±0.9 octaves, while only 16/141 cells showed the reverse relationship – the spatial frequency in the maximal RM condition was higher than in the maximal harmonic condition by 1.9±1.1 octaves. In 71/141 cells where the spatial frequency was the same for both conditions (1.16±0.74 cpd), the mean number of cycles per CRF was 0.58±0.34 (median 0.48). Thus, it appears that low (but not too low) spatial frequency is an important factor behind F1 modulation in most complex cells. It is worth noting, however, that even when this frequency was not the most effective frequency in sense of
maximal harmonic, only in 24/54 cells the maximal RM spatial frequency was outside the 71% bandwidth. Thus, many complex cells can modulate at the drift temporal frequency without a significant drop in firing rate.

Another striking feature of complex cell responses was a sub-harmonic (subF1) modulation, usually occurring at mid-to-high (2.5-5 cpd) spatial frequencies (Fig. 7). We observed this modulation in 41 complex and 2 simple cells. Since the subF1 modulation is not synchronized to the drift temporal frequency, the cycle-averaged PSTH would not show it (Fig. 7B). However, a raster comprising multiple temporal cycles would reveal a series of prolonged bursts followed by silent periods (Fig. 7A). This firing pattern corresponds to a clear peak in the spectrum of the concatenated spike train (Fig. 7C). The range of modulation was 2-4 Hz (mean 2.9±0.4 Hz). In individual neurons, it can vary with the spatial frequency or the width of the grating. Most neurons that exhibited this kind of modulation also had a significant F1 harmonic at lower spatial frequencies (Table 2). However, the frequency of sub-harmonic modulation seems to be independent of the drift temporal frequency. In fact, modulation in a similar frequency range was also found in response to stationary gratings (see next section).

Responses to stationary gratings

In the anesthetized preparation the response to a stationary grating presented for a long time would decline rapidly after an initial transient (e.g. Muller et al. 2001). The situation is very different in the alert monkey, where even during fixation the stimulus is actually never "stationary" because of fixational eye movements. Therefore, depending on the RF spatiotemporal properties, V1 neurons are activated during the presentation of a stationary stimulus in response to the motion and position changes imposed by saccades, slower eye movements and drifts (Snodderly et al. 2001). The typical eye movement-related activity is bursts or gaps following the saccades and incoherent firing in response to slower shifts and smooth drifts of eye position.
Unexpectedly, we have also encountered a different type of activation during presentation of stationary gratings. The responses of 18 complex and 2 simple cells to stationary gratings of mid-to-high spatial frequency exhibited a robust modulation in the range of 2.9±0.4 Hz, similar to the sub-harmonic modulation elicited by drifting gratings in these cells (Fig. 8A). The modulation frequencies were similar in both stationary and drifting cases (r=0.54, p<0.05). The coincidence of sub-harmonic and stationary grating-evoked modulation in the same cells and the lack of temporal frequency dependence imply that both behaviors may reflect the same phenomenon.

It is unlikely that the observed modulation is a direct consequence of stimulus motion generated by eye movements. The mean velocity of the eye position drift (multiplied by the spatial frequency of a grating to obtain temporal frequency) and the eye movement spectra (Fig. 8C) did not correspond to the ~3 Hz response modulation frequency range (Fig. 8B). Also, the modulation occurred with and without “image stabilization”. However, eye movements may trigger this modulation by activating an otherwise subthreshold mechanism. 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 eye movements.

One additional piece of data fits these observations. In many cells, including those that displayed the subharmonic modulation, responses to flashing bars of a long enough duration (≥400 ms) followed a peculiar pattern (Fig. 9): a regular ON response was followed by a silent period and then additional burst occurred before the bar has been turned off. The time course of this pattern roughly fits the ~3 Hz modulation, suggesting that this bursting behavior may be a characteristic of the response to various "stationary" stimuli.

**Effects of grating window width**

It is a well-established fact that neurons in V1 receive signals from regions far beyond the extent of CRF (e.g. Allman et al. 1985; Blakemore and Tobin 1972; Cavanaugh et al. 2002; DeAngelis
et al. 1994; Sceniak et al. 2001; Freeman et al. 2001). Typically a suppressive effect on the response amplitude (maximal harmonic in the case of gratings) is found when the surround is stimulated by the same stimulus as the center. Indeed, 50/98 cells tested with different grating patch widths showed reduction of the maximal harmonic to at least 71% (1/√2) of the maximum response when the grating was extended beyond the CRF (side inhibition), while 11 cells showed some augmentation of the response. For all 203 cells the most effective windows (51±31 minarc) were 1.5±1.0 times larger than the CRF. On average, side-inhibited cells were suppressed by 47±21% by extended stimuli. For these cells, the optimal window was 1.4±0.8 times the CRF width, and the inhibitory window was 3.2±2.2 times the CRF width. In another 8 cells, 6 of which were had very large CRFs (3.3±1.3 degrees), suppression occurred already within the CRF borders. 25/98 cells showed essentially no dependence of the response amplitude on the grating width, and 4 cells where we did not extend the grating beyond the CRF showed spatial summation within the CRF area.

There is no particular reason to believe, however, that the non-classical surround equally influences all the harmonic components of the response. In 30/98 cells, 29 complex and 1 simple, we found a strong differential effect of the grating width on the response harmonics. The extension of the grating most frequently resulted in an enhancement of the RM (by 65±20%, 23 cells), along with a decrease of the F2 harmonic in those cells that exhibited frequency doubling at smaller windows at the same spatial frequency (13/23 cells, Fig. 10A). Maximal RM was achieved with windows 3.5±2 times the CRF width. In 10/23 cells F1 exceeded F0 at larger windows. In 13/23 cells the increase of RM with window width was accompanied by a suppression of the maximal harmonic by 48±15% (Fig. 10B). In the remaining 10/23 cells, an increase of the window width did not bring about a significant decrease of the maximal harmonic, and the higher RM reflected only an increase of F1 component (Fig. 10C).
The opposite pattern, the decrease of F1 and a shift to F2, subF1, or an unmodulated firing with an increase of window width was observed in 7 cells (Fig. 10D). Taken together, these results suggest very specific influences of the surround on the responses of cortical cells.

**Effects of temporal frequency on response modulation**

The maximal harmonic of most cells was only broadly tuned to temporal frequency, in agreement with previous studies (Foster et al. 1985; Hawken et al. 1996). In some cases, however, the temporal frequency of a drift could have a strong effect on the response form. In particular, in 22/56 cells where data for a range of temporal frequencies were recorded, a slow frequency (1-2 Hz) led to frequency doubled or mixed (F1, F2, F3 of almost equal amplitude) responses, while a faster drift (3-5 Hz) resulted in the prevalence of F1 harmonic (Fig. 11A,B). This dependence can probably be attributed to the timing of stimulation of increment and decrement parts of the RF. For example, one can speculate that if a grating spatial frequency is low enough to cover the whole RF with a half cycle of either polarity at a time, and if increment and decrement mechanisms exert a mutual suppression with a certain time constant, then during a slow drift there is enough time to recover from the inhibitory influence and the cell is responsive to both polarities, while at a faster rate only one (the more dominant) mechanism is active. Alternatively, during faster drift both increment and decrement responses could be present, but a relative difference in latency/duration may result in shifting their temporal phases toward a less uniform firing. We have also observed an analogous transition from F1 to F2 modulation in responses to counterphase gratings.

**Responses to counterphase gratings**

In a previous study we have found that responses of complex cells to counterphase gratings were predominantly frequency doubled (Kagan et al. 2002a). However, we have used only a 2 Hz square wave temporal function to modulate the gratings. Here we have also used a sine wave function
and in 28 cells we tested a range of temporal frequencies. Altogether 89 cells, 83 complex and 6 simple, were tested with counterphase gratings. The responses of simple cells were predominately F1 harmonic, and only one cell responded with F2 modulation. The form of the response in complex cells, however, depended in some cases on the spatial and temporal frequency of the stimulus, and sometimes the response to sine and square temporal modulation differed even if all other parameters were identical. Deviations from a typical frequency doubled behavior included: 1) F1 response at higher temporal frequencies (4-5 Hz), but F2 response at lower temporal frequencies (1-2 Hz); 2) F2 response at mid-high spatial frequencies (2-5 cpd), but F1 response at low spatial frequency (0.5-1 cpd); 3) Square wave temporal modulation resulted in F2 response while sine wave yielded F1 response. These patterns are illustrated in Fig. 12. Similar to the drifting grating case, low spatial frequency and/or high temporal frequency tended to transform the nonlinear even harmonic response to a pseudolinear F1 modulation. The difference between square (abrupt) and sine (gradual) transition reveals the importance of temporal dynamics in shaping complex cells' response.

DISCUSSION

In this paper we show that in complex cells the form of the response to gratings, and not just the response amplitude, exhibits a profound and systematic dependence on the stimulus spatial and temporal parameters. The primary finding is that complex cells show a variety of modulation behaviors, deviating from a traditional energy mechanism. The most novel finding is that the harmonic content of the response, and in particular the relative modulation, could be influenced by the spatial extent of a grating patch.

Previous works examined the influence of various stimulus attributes on the response maximal harmonic, or focussed on specific combinations of stimulus parameters optimized for "best" response in the sense of maximal firing rate. While this approach led to many important results, it is clear that a
neuron's response is not characterized solely by the maximal harmonic, or rate code (Victor and Purpura 1998). One important aspect is the fine temporal coding of visual features (Mechler et al. 1998; Reich et al. 2001); another aspect is the "coarser" modulation, expressed in the frequency domain as other than F0 significant harmonics. Surprisingly, the quantitative relationship of harmonic content to stimulus parameters remained largely unexplored, although several studies described the dependence of F1 modulation on spatial or temporal frequency of the grating (Holub and Morton-Gibson 1981; Kulikowski and Bishop 1982; Movshon et al. 1978; Pollen et al. 1978).

**F1 modulation in simple and complex cells**

Our results are consistent with the view of simple cells as quasilinear half-wave rectified operators, responding to virtually all effective drifting and counterphase gratings with a dominant F1 harmonic. Although we do not have sufficient data on simple cells to make a strong statement, it seems that their relative harmonic content is rather invariant to changes in grating parameters.

It is usually assumed that the principal response of complex cells to drifting gratings is a steady elevation of their firing rate, although many studies in anesthetized animals noted a weak modulation at the grating temporal frequency when stimulated with the "optimal" spatial frequency, with RM about 0.2-0.5, and some cells with RM between 0.5 and 1. Complex cells in our sample were, on average, even more modulated (Fig. 3, Table 1). Similarly to simple cells, they frequently had a robust F1 harmonic in their response, but its occurrence and relative strength usually depended on grating attributes. Moreover, most complex cells, even those showing a strong pseudolinear F1 component in response to some stimulus configurations, would exhibit nonlinear responses to other stimulus conditions. In addition, complex cell responses to moving and flashing bars and edges were intensively nonlinear. Therefore, complex cells clearly violate the superposition principle and thus their limited pseudolinear behavior is different from the type of linearity found in simple cells.
Mechanistically, the modulation of simple and complex cells forms a continuum - unlike the data in anaesthetized monkeys and cats, the RM distribution in our sample was not bimodal. Differences in network properties, in a balance between inhibitory and excitatory mechanisms, and in the resting/threshold potential may account for this outcome. Interestingly, the RM based on the intracellular membrane potential in anesthetized cats is also unimodal (Carandini and Ferster 2000; ref. to Priebe et al. when accepted), and Mechler and Ringach (2002) showed that a nonlinear threshold transformation from the intracellular potential could yield the bimodality observed in the RM based on extracellular firing. The lack of bimodality in the alert state could be attributed to a lower threshold that would cause the firing rate to follow more linearly the membrane potential, but a considerable F1 modulation observed in complex cells contradicts with this idea, because the intracellular RM in anesthetized cats is strongly skewed towards low values (ref. to Priebe et al. when accepted). Alternatively, a stronger inhibition in the alert state could suppress the unmodulated component of the synaptic input, leading to a more modulated membrane potential, and the threshold transformation could be more linear.

Response diversity in complex cells

The goal of this study was to determine how the harmonic content of the response depends on stimulus conditions. Many cells that were weakly or not modulated in the optimal (for the maximal harmonic) condition gave robustly modulated responses to another combination(s) of grating parameters. A difference between conditions within a cell dataset can be very strong – the response can vary between F2, F1, F0 or subF1 modulation along the stimulus parameters space.

Several authors have noted that complex cells could respond to a low spatial frequency with a significant F1 modulation (Movshon et al. 1978; Skottun et al. 1991; Mechler et al. 2002). We have confirmed and quantified this behavior in a large portion of our sample. It should be noted, however, that many such cells also exhibited a frequency-doubled modulation in response to even lower spatial
frequencies. Moreover, in contrast to previous studies, for many complex cells the low spatial
frequency leading to F1 response was also the "optimal", or almost as effective as the "optimal",
frequency.

Besides spatial frequency, temporal frequency and the width of grating patch also proved to have
an effect on the diversity of behaviors seen in complex cells. The appearance of frequency doubling in
some cells at low temporal frequency differs from the pseudolinear modulation described by Pollen et
al. (1978) and Kulikowski and Bishop (1982) in "periodic" complex cells in the cat, but reminds the
doubling at some specific (not just low) temporal frequencies observed in the anaesthetized monkey
(Hawken et al. 1996).

The effect of extending the grating width beyond the CRF on the response harmonic content
should be interpreted with caution. We defined the CRF as a minimal response field with narrow
sweeping bars, but results from several labs suggest that such mapping underestimates the CRF extent
relative to the area summation tests (Cavanaugh et al. 2002; Jones et al. 2001). However, in many
cases we are confident that it was a differential influence of the non-classical surround that led to the
variation of modulation with grating width.

Spatial phase selectivity

The traditional notion of simple and complex cells might lead to the view that in simple cells all
stimulus attributes are represented in a phase-dependent manner, whereas in complex cells – in a
phase-independent manner (e.g. De Valois et al. 1982; Pollen and Ronner 1983). However, it has been
demonstrated that simple and complex cells show both phase-dependent and phase-independent
behavior (Mechler et al. 2002; Pollen et al. 1988; Spitzer and Hochstein 1985a,b; Victor and Purpura
1998). Studies of complex cells with compound drifting gratings indicate that even harmonics
(especially F0 and F2) but also odd harmonics, including the fundamental, contribute strongly to the
response (Mechler et al. 2002; Pollen et al. 1988). Similar to simple cells, a systematic dependence of
response harmonics on the relative phase of the component gratings was found in complex cells (Mechler et al. 2002).

Spatial phase is essential in extracting image features, especially in the framework of local Fourier analysis (Victor and Purpura 1998). However, absolute phase information may not be of great importance in spatial pattern recognition, since the relative phase offset between response components, together with their amplitude, are sufficient to uniquely specify the pattern (Pollen et al. 1982; 1985).

The dependence of complex cell responses on the absolute spatial phase is a subject for further research. Even if complex cells are mostly invariant to the phase of a stationary pattern, many of them convey information about the temporal frequency of the phase (or polarity of contrast) change in the F1 component of their response. In a drifting grating, these parameters are confounded – the spatial phase varies with the time course determined by the temporal frequency. The fact that changes in eye position lead to jitter of the response phase implies at least some phase dependence, but in this case the effect could be contaminated by the response to the actual stimulus motion resulted from the eye movement. In few cases where we used non-stabilized drifting gratings, we saw a consistent dependence of the F1 phase on the eye position. A direct test of the phase-dependence for drifting gratings will require systematically varying the initial spatial phase of the grating, together with precise control of eye position.

The apparently phase-independent (frequency doubled) responses of many complex cells to counterphase gratings, equivalent to ON-OFF responses to flashes, are hard to reconcile with the F1 modulated responses to drifting gratings, unless there is a substantial difference between responses to transient (square counterphase) and steady-state (drifting) stimuli (cf. Mechler et al. 1998). In this respect it is remarkable that responses to counterphase gratings modulated by a square temporal function often tended to show doubling even when sine wave counterphase gratings led to F1 responses. Still, some complex cells had F2 dominated responses to both sine and square modulated
counterphase gratings, but F1 response to drifting gratings. Hawken et al. (1996) also observed striking differences between the temporal-frequency tuning to drifting and counterphase gratings.

**Functional implications**

There is a renewed interest in definition and function of simple and complex cells (Abbott and Chance 2002; Kagan et al. 2002a; ref. to Mata and Ringach when accepted; Mechler and Ringach 2002; ref. to Priebe et al. when accepted). It has become increasingly clear that complex cells behave more diversely and elaborately than has been previously thought. The energy model (Adelson and Bergen 1985; Heeger 1991, 1992a,b; Pollen and Ronner 1982, 1983, 1988) falls short of accounting for these behaviors: the effects of varying the stimulus configuration on the response modulation, pseudolinear F1 responses, and response variations with the spatial phase (Mechler et al. 2002). Our preliminary simulations indicate that complex cells response patterns cannot be entirely explained by an incomplete overlap or a simple imbalance between increment and decrement input mechanisms – some nonlinear interactions should be introduced as well.

The question may arise why should we bother describing V1 responses to simple gratings in the alert monkey while these stimuli may not be very applicable to an ultimate understanding of natural vision, for which transient responses to abruptly presented stimuli (Mechler et al. 1998; Muller et al. 2001; Snodderly et al. 2001) and feature extraction (Mechler et al. 2002) are far more relevant. We suggest that rigorous spatial mapping and the investigation of RF dynamics with simple stimuli still has merit, and should be combined with studies of natural sequences and model-oriented dynamic broadband "noise" stimuli (Touryan et al. 2002; Vinje and Gallant 2002).

Until recently, most studies on functional processing in primary visual cortex dealt with simple cells (e.g. Artun et al. 1998; Carandini et al. 1997, Carandini and Heeger 1994; Chance et al. 1998; Heeger 1993; Heeger et al. 1996; Reich et al. 2001; Troyer et al. 1998; Wielaaard et al. 2001). But, given that complex cells dominate primate’s V1, and that their functional significance is probably
proportional to their number, the importance of thorough characterization of complex cells cannot be overestimated. Our conjecture that properties of complex cells such as contrast polarity invariance and absolute phase insensitivity may be advantageous for object and scene perception in a constantly changing environment (Kagan et al. 2002a) has been recently reinforced by a theoretical study that demonstrated a robust representation by the classical model complex cell population (Shams and von der Malsburg 2002). We hope that these results and our new findings indicating great heterogeneity and diversity in complex cells will help to correct a bias towards simple cells in thinking about primate V1.
ACKNOWLEDGEMENTS

Supported by NIH EY12243 and the Fund for the Promotion of Research at the Technion. We thank Dario Ringach for useful discussions.
REFERENCES


TABLES

Table 1. Mean±SD of RM for stimuli producing the maximal harmonic or the maximal RM*

<table>
<thead>
<tr>
<th>Response criterion for choice of stimulus parameters</th>
<th>RM, &quot;no saccades&quot;</th>
<th>RM, &quot;aligned&quot; F1 phase</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>simple (23)</td>
<td>complex (180)</td>
</tr>
<tr>
<td></td>
<td>complex (180)</td>
<td>simple (23)</td>
</tr>
<tr>
<td>maximal F0 or F1</td>
<td>1.20 ± 0.38</td>
<td>0.54 ± 0.39</td>
</tr>
<tr>
<td></td>
<td>1.48 ± 0.28</td>
<td>0.81 ± 0.37</td>
</tr>
<tr>
<td>maximal RM</td>
<td>1.29 ± 0.36</td>
<td>0.80 ± 0.37</td>
</tr>
<tr>
<td></td>
<td>1.56 ± 0.23</td>
<td>1.04 ± 0.34</td>
</tr>
</tbody>
</table>

*Numbers of cells are in parentheses.
### Table 2. Effects of grating spatial frequency on harmonic content of the response*

<table>
<thead>
<tr>
<th>Response pattern</th>
<th>Simple cells</th>
<th>Complex cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frequency doubling at low frequencies (F2 - ...)</td>
<td>--</td>
<td>41</td>
</tr>
<tr>
<td>F2 – F1; F2 – F1 – F0</td>
<td>--</td>
<td>11/16</td>
</tr>
<tr>
<td>F2 – F0; F2 – F0 – F1</td>
<td>--</td>
<td>7/1</td>
</tr>
<tr>
<td>F1 – F0</td>
<td>--</td>
<td>49</td>
</tr>
<tr>
<td>F0 – F1; F0 – F1 – F0</td>
<td>--</td>
<td>8</td>
</tr>
<tr>
<td>F1 – subF1; F1 – F0/subF1; F1 – F0 – subF1</td>
<td>--</td>
<td>23/4/2</td>
</tr>
<tr>
<td>F2 – F1 – subF1; F0 – F1 – subF1; F0 – subF1</td>
<td>--</td>
<td>6/2/3</td>
</tr>
<tr>
<td>Frequency doubling at all frequencies</td>
<td>--</td>
<td>2</td>
</tr>
<tr>
<td>Unmodulated firing at all frequencies</td>
<td>--</td>
<td>4</td>
</tr>
<tr>
<td>Strong F1 harmonic at all frequencies</td>
<td>16</td>
<td>19</td>
</tr>
<tr>
<td>SubF1 modulation at all frequencies</td>
<td>--</td>
<td>2</td>
</tr>
<tr>
<td>No differential effect on harmonic content</td>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>Not tested with enough range</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>23</strong></td>
<td><strong>180</strong></td>
</tr>
</tbody>
</table>

*Note that a particular complex cell could be present in more than one category, therefore sum of the numbers across rows exceeds a total number of complex cells.
FIGURE LEGENDS

Fig. 1. Spatial organization of receptive fields.

A: Distribution of the overlap index (OI) for the sample of 203 cells. See Methods for details of OI calculation. Most cells in our sample are complex cells with overlapping increment and decrement activating regions (AR). B: Distribution of the relative amplitude ratio (RAR) for the same sample. C: Scatter plot of RAR vs. OI.

Fig. 2. Relative modulation distributions for different stimulus conditions and analysis modes, for simple and complex cells.

Complex cells (n=180) are represented by dark bars, simple cells (n=23) by light bars. Left column: “no saccades” analysis mode. Right column: “aligned” analysis mode. Top row: RM distributions for stimulus conditions eliciting the maximal harmonic F0 or F1. Bottom row: RM distributions for stimulus conditions producing maximal RM. See Table 1 for means of the distributions.

Fig. 3. Spatial organization and relative modulation.

Scatter plot of the maximal relative modulation vs. a measure of increment-decrement spatial (im)balance in the RF (I, the product of OI and RAR). Open circles represent simple cells, close circles – complex cells, and gray triangles – predictions of complex cell model with different combinations of OI and RAR. The correlation between I and maximal RM within complex cell class was very weak (r=−0.17, p>0.01, although there was a more significant relationship between these measures for the whole sample (r =−0.33, p <0.01), since simple cells were over-represented among the strongly modulated cells. Similar but slightly stronger dependencies were found for maximal harmonic RM (r=−0.25, r=−0.41, p<0.01, scatter plots not shown). However, the model predicted much stronger correlation (r=−0.88) between the spatial imbalance and the modulation, and much lower levels of RM as compared to real complex cells (close circle points in the area above model responses).
Fig. 4. Spatial frequency tuning.

Spatial frequency distributions. Bin borders: [0 0.25 0.75 1.5:1:5.5]. Empty parts of the bars – simple cells, filled parts – complex cells. **A:** Maximal harmonic condition. Mean spatial frequency: 1.8±1.2 cpd (simple cells), 1.5±1.1 cpd (complex cells). **B:** Maximal RM condition. Mean spatial frequency: 1.9±1.4 cpd (simple cells), 1.2±1.0 cpd (complex cells).

Fig. 5. Complexity index.

The distribution of the number of grating cycles that can be fitted within the cell’s CRF, calculated as the product of grating spatial frequency and CRF width (CI). Empty parts of the bars – simple cells, filled parts – complex cells. Bin width 0.2 cycle/CRF. **A:** Maximal harmonic condition. Median CI: 0.8±0.7 (simple cells), 1.0±1.5 (complex cells). **B:** Maximal RM condition. Median CI: 0.8±0.9 (simple cells), 0.8±1.7 (complex cells). For both response criteria the modes of the CI distributions are between 0.5 and 1, implying that most cells were tuned for a low spatial frequency. Very high CIs (>3) belong to cells in the peripheral eccentricities with extremely large CRFs, recorded from buried cortex.

Fig. 6. The dependence of response harmonics on grating spatial frequency.

Representative responses of four complex cells to sine wave gratings drifting at 5 Hz. The amplitude of F0, F1 and F2 harmonics is shown as a function of spatial frequency. **A, B:** (1001_013.a23, 0791_014.a22) F2-F1-subF1 pattern: frequency doubling at lowest spatial frequencies, pseudolinear F1 responses at low spatial frequencies, decrease of F1 and appearance of subharmonic (subF1) modulation in about 3 Hz range (not shown, see Fig. 8). **C, D:** (1091_014.a26, 2791_023.a16) F1-F0 pattern: F1-dominated response at low spatial frequencies is replaces by F0 component at higher spatial frequencies.
Fig. 7. Subharmonic modulation.

The same complex cell and the same dataset as in Fig. 7B (0791_014.a22). **A:** Four rasters of 5 s trials are shown. Sine wave profile under rasters represents the time course of the 5 Hz temporal drift. The grating spatial frequency was 3.5 and 4 cpd. The distinct response modulation was not synchronized to the temporal cycle of the grating (200 ms), therefore the cycle-averaged PSTH was essentially flat (B). The spectrum of the bottom raster reveals a peak at 2.6 Hz, but the exact frequency of modulation may drift from 2 to 4 Hz within and between individual trials and cells. **D:** S-transform of the concatenated dataset across the spatial frequency (see Methods). The amplitude of different harmonic components is coded by the intensity of the hue, ranging from 0 (black) to 90 (white) spikes/s. The F2-F1-subF1 "evolution" of the response with the frequency/time is obvious in this plot.

Fig. 8. Typical "bursty" response to stationary grating.

**A:** Responses of a complex cell to a stationary sinusoidal grating of 3 cpd spatial frequency during one behavioral trial of a 5 s duration (1201_005.a05-5). Eye position (thick line - vertical, thin line - horizontal) is plotted along with the spike train raster at the bottom. A robust modulation (bursting), corresponding to a 2.8 Hz peak in the spectrum (B), is seen in the response. The spectra of eye position traces (C) do not have a significant peak at the response modulation frequency. The mean eye velocity in this trial, 0.17 deg/s, would match a 0.5 Hz frequency, and not a 2.8 Hz, at 3 cpd.

Fig. 9. Typical "rebound" response to flashing bar.

The raster plot and PSTH of the response to a bar repeatedly flashing (on and off) in the CRF (complex cell 1991_014.a10). The time course of the stimulus is depicted below the time axis. In addition to strong ON and weak OFF responses, an intermediate burst appeared around 400 ms after the flash onset, but clearly before the stimulus was turned off. This discharge pattern was typical for many complex cells.
Fig. 10. The dependence of response harmonics on grating window width.

Representative responses of four complex cells to sine wave gratings drifting at 5 Hz. The amplitude of F0, F1 and F2 harmonics is shown as a function of the patch width. Vertical dashed lines indicate the size of CRF. **A:** (2791_029.a07) Frequency doubling at a small window and F1 response at larger windows. **B:** (2471_006.a12) Decrease of the F0 component and increase of the RM. **C:** (0991_007.a06) Increase of the F1 component without a significant decrease in the maximal harmonic. **D:** (3171_009.a07) Decrease of the F1 component and appearance of a subF1 modulation (the subharmonic component is not shown).

Fig. 11. The dependence of response harmonics on grating temporal frequency.

Representative responses of three complex cells to drifting sine wave gratings. The amplitude of F0, F1 and F2 harmonics is shown as a function of temporal frequency. **A:** (1332_007.a06) F1/F2/F3-F2-F1 pattern. **B:** (0991_033.a10) F2-F1 pattern. **C:** (1881_006.a10) An example of temporal-frequency invariance: F1 response is present at all temporal frequencies.

Fig. 12. Responses of complex cells to counterphase gratings.

Representative responses of three complex cells to counterphase sine wave gratings. The amplitude of F0, F1 and F2 harmonics is shown as a function of the temporal (A, C) or spatial (B) frequency. **A:** (2682_023.a10) Sine wave temporal function. Frequency doubling at lower temporal frequencies is replaced by an F1-dominated response at higher temporal frequencies. In this cell, a similar behavior was observed in the response to a square wave modulated grating (not shown). **B:** (0513_041.a07) The dependence of the response harmonics on the spatial frequency (sine wave modulated grating). Low spatial frequency yielded F1-dominated responses, while higher spatial frequencies resulted in frequency doubling. **C:** (1091_017.a21/1091_016.a09). The difference between sine and square temporal modulation. In the square wave case (circles), the response was F2-dominated at 1 and 2 Hz.
but changed to F1-dominated at 4 and 5 Hz. In the sine wave case (diamonds), the response was already F1-dominated at 1 and 2 Hz.
Figure 1:
Figure 2:
Figure 3:
Figure 4:
Figure 5:
Figure 6:
Figure 7:
Figure 8:
Figure 9:
Figure 10:
Figure 11:
Figure 12: