Cartesian and non-Cartesian responses in LGN, V1, and V2 cells

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(Received October 25, 2000; Accepted November 16, 2001)

Abstract

Cell responses to drifting Cartesian (parallel) and non-Cartesian (concentric, radial, and hyperbolic) stimuli were recorded in and beyond the classical receptive field (CRF) in the lateral geniculate nucleus (LGN), V1, and V2 of anesthetized monkeys. Many cells were equally responsive to Cartesian and non-Cartesian, especially concentric, gratings. Around 15% of cells in each area were significantly more responsive to concentric compared to parallel gratings; however, cells significantly more responsive to parallel compared to concentric gratings were more numerous in the cortex. While many cells responded to hyperbolic and radial gratings, few were most responsive to these gratings. Cell selectivity decreased for Cartesian and increased for non-Cartesian gratings from V1 to V2 and the relative response varied as a function of stimulus extent with respect to the CRF. Complex, nonoriented, nondirectional cells with a low aspect ratio responded best to non-Cartesian gratings. These results cannot be fully explained using Gabor linear/energy models of simple and complex receptive fields (RFs) although such models predict some cells to respond equally to Cartesian and non-Cartesian gratings. Cells significantly more responsive to non-Cartesian gratings can be accounted for by CRF selectivity influenced by modulation from the nonclassical receptive field (nCRF). The present study shows that Cartesian/non-Cartesian selectivity is not an emergent property of V4 cells but is present at all levels of early visual processing being subserved by a subset of cells with specific tuning properties.

Keywords: Cartesian gratings, Non-Cartesian gratings, Lateral geniculate nucleus, Visual cortex, Receptive field

Introduction

Form and pattern discrimination of objects in complex scenes is instantaneous, and in most cases requires little conscious effort. Ample evidence suggests that the spatial and temporal information available at the retina is successively transformed by the LGN, striate and extrastriate cortex to extract the salient image features and to facilitate object recognition (Wilson et al., 1990); the most plausible model of form perception involving massive parallel processing where at each successive hierarchical level more global aspects of the image are analyzed. While initial cortical processing filters the spatial extent, color, speed of movement, direction, orientation, luminance, etc. of the visual image (De Valois & De Valois, 1988; Levitt et al., 1994; Gegenfurtner et al., 1996) higher cortical regions beyond V4 appear to match identified objects with stored descriptions and information (Felleman & Van Essen, 1991; Van Essen et al., 1992).

Many initial studies of V1 processing measured cell responses to one-dimensional (1D) stimuli and led to the idea that the visual system performs a local two-dimensional (2D) Fourier analysis (De Valois & De Valois, 1988) because 1D sinusoidal gratings of various orientations, spatial frequency (SF), and phase can form a complete representation of any 2D pattern (Weisstein & Harris, 1980). However, more complex, often feature-based, patterns have been found to be more relevant stimuli at higher levels of cortical processing (Kobatake & Tanaka, 1994). Therefore, 2D non-feature-based stimuli may be useful in understanding the connection between filter-based early analysis and feature-based higher analysis. The Cartesian and non-Cartesian periodic gratings used in this study give three distinct stimulus classes based upon spatial derivative operators and are defined by sets of axes along which the modulation functions form a linear orthogonal basis.

Although Cartesian and non-Cartesian patterns are not present in isolation in the natural world, such 2D stimuli may be more appropriate to use than 1D patterns since the retinal image and the visual system must be performing a 2D analysis of light variations across space. Furthermore, these gratings are abstractly related to common environmental and ecological aspects of motion and form in complex images and have properties that permit quantitative analysis of responsivity along well-defined stimulus dimensions (Hoffman, 1966; Gallant et al., 1996). Such stimuli are also similar to the structure of large optical flow patterns associated with expansion, contraction, rotation, shear and translational movement.
used to examine motion selectivity in area MST (Duffy & Wurtz, 1997) and to patterns previously used to study form in V2 and V4 (Gallant et al., 1996; Hegde & Van Essen, 2000).

The inferotemporal pathway (IT) processes information about form and color. Many properties of higher areas in this pathway (Hegde & Van Essen, 2000) are also present to some degree, in lower areas, including V1 (De Valois & De Valois, 1988; Levitt et al., 1994; Gegenfurtner et al., 1996). The responsivity and selectivity of V4 cells to Cartesian and non-Cartesian gratings in their CRF (Gallant et al., 1996) suggests that V4 cells encompass a more complex, global type of form analysis compared to V1. This analysis is intermediate to the highly complex form analysis in the IT cortex.

LGN cells have RFs that should respond optimally to non-Cartesian concentric gratings and the shape and response properties of V1 and V2 RFs would predict some response to these gratings. Modulation from the nCRF for V1 and V2 cells should also influence the relative cell responsivity to 1D versus 2D gratings. Evidence for V1 cell selectivity to other 2D patterns also suggests that such cells may respond to non-Cartesian gratings and threshold perception of similar patterns can be predicted based on 2D SF analysis (Kelly & Magnuski, 1975).

Because information from V1 to V2 forms the major input to both MT/MST and V4, we investigated responses in LGN, V1, and V2 cells using Cartesian and non-Cartesian stimuli. The specific question in this study is whether selective responsivity to non-Cartesian gratings is an emergent cell property in regions beyond V1 and V2 or whether robust responses can be found at all levels of initial visual processing. If responses are found in V1 and V2, this leads to the question of whether a specific subset of cells at each level encodes responses to these gratings. Therefore, this paper also analyzes whether non-Cartesian responses in V1 and V2 can be predicted from responses to 1D gratings or from the CRF characteristics of these cells.

Methods

Cartesian (parallel) gratings \((R_p)\) are produced by eqn. (1).

\[
R_p(x, y) = A \cos(2\pi f_p[(x \cos \phi) - (y \sin \phi)] + \theta),
\]

where \(A\) is the luminance amplitude, \(f_p\) is the parallel grating SF, \(\theta\) is the phase, and \(\phi\) is the orientation.

Concentric \((R_c)\), radial \((R_r)\), and hyperbolic \((R_h)\) gratings are produced by eqns. (2–4).

\[
R_c(x, y) = A \cos(2\pi f_c[\sqrt{x^2 + y^2}] + \theta),
\]

\[
R_r(x, y) = A \cos(2\pi f_r[\arctan(x/y)] + \theta),
\]

\[
R_h(x, y) = A \cos(2\pi f_h \sqrt{[(x \cos \phi) - (y \sin \phi)]}
\]

\[
\times [(x \sin \phi) + (y \cos \phi)] + \theta),
\]

where \(f_c\) is the concentric SF, \(f_r\) is the radial spoke number/360 deg, and \(f_h\) is the hyperbolic SF. Stimuli were drifted across the RF at a constant temporal frequency between 2–4 Hz. Parallel gratings translated in either direction perpendicular to the grating’s orientation. Concentric and hyperbolic gratings contracted or expanded, while radial gratings rotated, with respect to the center point. Spatial frequency was specified in cycles/degree visual angle.

Stimuli in any experimental run were presented in random order in a circular, hard-edged aperture matched to the RF size determined using reverse correlation receptive-field mapping. They were presented monocularly to the best responding eye for 4 s; no cells required binocular stimulation to elicit the best response. The interstimulus delay ensured that the cell did not remain in an adapted state due to overstimulation by the previous pattern.

Cells were recorded from 12 monkeys (Macaca fascicularis and Macaca mulatta). The surgical and recording techniques have been detailed elsewhere (De Valois et al., 2000), all procedures being in accord with NIH guidelines and approved by the local Animal Care and Use Committee. The majority of V1 and V2 cells were recorded at locations near the V1/V2 border; however, some V1 cells were recorded from probes located further posterior towards the occipital pole resulting in a more foveal receptive-field location. All cortical RFs were within the central 8 deg of the contralateral lower visual field with respect to the recording hemisphere. The LGN receptive fields were within the central 10 deg of the visual field.

A computer program which presented bars of light at different orientations, sizes, and bar/background color combinations was used to search for a cell. When a cell was isolated, the RF location and borders were subjectively determined using various sized wands and computer-generated bar-shaped stimuli moved in and around the RF on the blank monitor background. It is important to establish the center of the RF before obtaining responses to non-Cartesian stimuli because, unlike parallel gratings, non-Cartesian gratings are symmetrical about a central origin. Therefore, 2D reverse correlation RF mapping was carried out using discrete stimulus patches (Cottaris & DeValois, 1998) that were much smaller than the size of the RF, at the cell’s optimal orientation and color or luminance preference to confirm the center and size of the RF. If a well-defined RF profile was not obtained using 2D reverse correlation, a profile was obtained, at each of two orthogonal orientations, using 1D reverse correlation and discrete overlapping bars. The stability of the RF location was remeasured at the end of all experiments on the cell. If the RF had moved by more than one quarter of its original size from the original central location, measurements were repeated at the new position. In this study, the CRF of the cell was defined as the area of the visual field in which a single stimulus elicited an excitatory neuronal response. The aperture of all the stimuli (except those used to study the nCRF) were between 1–1.5 times the size of the CRF. Therefore, the stimulus was never smaller than the CRF and in many cases was slightly greater than the CRF in order to be confident that it encompassed the less responsive RF subregions not defined by reverse correlation RF mapping.

Once the RF was positioned in the center of the monitor, SF and orientation tuning were measured, using parallel gratings with apertures matched to the size of the RF, using the appropriate fixed set of SFs (low, middle, or high range depending on the cell’s tuning; SFs varied between full field to 14 cycles/deg). Spatial-frequency tuning for concentric, radial, and hyperbolic gratings was also measured using the same range of SFs as used for sinusoidal SF tuning. Orientation tuning was measured using parallel gratings at 30-deg angles. Tuning for these dimensions were repeated until the optimal SF and orientation were determined based on the consistency and magnitude of the cell responses. Any one cell needed to be held for at least an hour to obtain a full set of data.

Responses were obtained from the recorded spike discharge during each stimulus presentation where the data from each cycle
of the grating produced an average firing rate as a function of time during one cycle; a peri-stimulus-time-histogram (PSTH). The PSTH was then Fourier analyzed to obtain the mean firing rate and the amplitude and phase of the first harmonic of the response to each stimulus. LGN cells and striate cortex simple cells have a modulated discharge to a drifting grating, and thus a larger first harmonic than mean response. Complex cells, on the other hand, have a larger mean than first harmonic response. The response measure was the first harmonic for LGN and simple cells, and the mean firing rate for complex cells.

The effect of stimulus size on the Cartesian/non-Cartesian cell responsiveness was examined by presenting gratings within a single experiment at four different aperture sizes (two larger and two smaller than the optimal stimulus aperture; increasing or decreasing by a logarithmic progression). Confirmation of the centration of the stimulus was tested by presenting gratings at four different positions (right, up, left, and down with respect to the RF center).

The purpose of the position experiment was to show that movement of the stimulus by equal amounts in any direction away from the centered position reduced the cell response equally therefore indicating, within a single experimental run, that the stimulus was centered correctly. The four offcenter positions differed equally in any run and were between half and one full width of the stimulus aperture.

Results

This analysis presents results obtained from 41 LGN, 48 V1, and 66 V2 cells. All cells were responsive to at least one of the parallel, concentric, radial, or hyperbolic gratings. However, not every cell was responsive to all gratings. In general, all cells were responsive, to some degree, to both parallel and concentric gratings. About half the cells were responsive to radial or hyperbolic gratings but only a very small percentage were significantly more responsive to these than to parallel or concentric gratings.

Spatial-frequency tuning can be quantified by determining the cell’s bandwidth (Fig. 1 shows examples of comparative tuning in cortical cells for concentric and parallel gratings). This was calculated by fitting a Gaussian function to each cell’s spatial-frequency tuning curve (Geisler & Albrecht, 1997). There was less low spatial-frequency attenuation for LGN cells than for cells in V1 and V2. If the response of the cell at the lowest spatial frequency did not drop to half the response at the peak spatial frequency, the cell was classified as lowpass. Using this criterion, more than 70% of LGN cells were lowpass while only 17% of V1 cells and 6% of V2 cells were lowpass, the mean bandwidth for V1 and V2 cells being 1.7 octaves.

The relative cell response to parallel versus concentric, radial, or hyperbolic gratings is given by the concentric (CI), radial (RI), or hyperbolic (HI) index, respectively [eqn. (5)].

\[
\text{Response index} = \frac{R_{\text{non-Cartesian}}}{(R_{\text{Cartesian}} + R_{\text{non-Cartesian}})}. \quad (5)
\]

An index of 1 indicates a cell that responds to concentric, radial, or hyperbolic gratings only; an index of 0 indicates a cell responsive to parallel gratings only; and an index of 0.5 indicates a cell that is equally responsive to both Cartesian and non-Cartesian gratings.

Fig. 2A indicates a unimodal CI distribution centered around 0.5 for cells in each visual area. A Gaussian distribution fitted to each histogram provided an estimate of the sample mean and standard deviation. The sample means were 0.54 for LGN cells, 0.50 for V1 cells, and 0.51 for V2 cells which were not significantly different using two-tailed independent t-tests. The main difference between the CI distributions was that the range for LGN cells was considerably narrower than that for cortical cells consistent with other properties that have a narrower distribution and less variability in the LGN compared to V1 (Derrington et al., 1984; Lennie et al., 1990). The LGN distribution was also skewed towards a CI > 0.5.

However, quantile-quantile analysis [a descriptive statistical method (Rice, 1988) for comparing the quantiles, or percentiles, of two different distributions where the distribution numbers do not have to be equal] indicated qualitative systematic deviations between the shapes of the LGN and both the V1 and V2 CI distributions where the V1 distribution <0.5 broadened compared to LGN cells. Therefore, V1 cells more responsive to parallel gratings had, on average, a lower CI (0.38) than equivalently distributed LGN cells (0.44) consistent with the decrease in sample mean between the LGN and V1 cell populations. The distribution did not broaden for cells with a CI > 0.5, indicating that the CI of such cells was more similar in LGN and V1.

This result suggests that parallel gratings are a more effective stimulus for V1 and V2 cells while concentric gratings are relatively less effective in the cortex compared to the LGN. There was no systematic deviation between the V1 and V2 CI distribution, indicating no difference in the effectiveness of parallel versus concentric gratings for such cells. Cells with a CI > 0.67 are twice as responsive to concentric gratings, while cells with a CI < 0.33 are twice as responsive to parallel gratings. Using these criteria, 12% of LGN cells were more than twice as responsive to one or the other grating. In fact, these cells were all more responsive to concentric stimuli (CI > 0.67). On the other hand, 34% of V1 cells (19% CI < 0.33; 15% CI > 0.67) and 30% of V2 cells (11% CI < 0.33; 19% CI > 0.67) were twice as responsive to one stimulus class over the other.

Many cells were responsive but had lowpass tuning for radial gratings and were given a non-Cartesian index value of zero. Furthermore, most of the tuned cells were more responsive to parallel gratings (Fig. 2B). In fact, only 52% of LGN cells responded better to any radial grating compared to a full-field stimulus; the median RI, including lowpass cells, for the LGN distribution being 0.02. Similarly, many V1 and V2 cells had lowpass tuning. However, the median RI was higher for both V1 (0.34) and V2 cells (0.31) than it was for LGN cells (0.02). This indicates that more cortical cells were tuned and more responsive to radial gratings compared to the full-field (zero SF) stimulus (75% V1; 62% V2) although the majority of these cells were less responsive overall to radial than to parallel gratings.

For cells selectively tuned for radial gratings (excluding lowpass cells), the distributions were clearly unimodal (Fig. 2B) and the mean RI was similar (0.43 LGN; 0.42 V1; 0.47 V2). However, the spread of the distribution for the cortical samples broadened indicating there to be more cells with bandpass tuning having a high RI. Such cells, therefore, give some evidence for increased selectivity for radial gratings in the cortex, where 5% of V1 cells and 8% of V2 cells were more than twice as responsive (RI > 0.67) to these gratings. There were no LGN cells twice as responsive to radial gratings. Interestingly, no V1 cells and only two V2 cells responded better to radial than to any other Cartesian or non-Cartesian grating indicating that radial gratings are not a good stimulus for LGN cells, and, while a few cells in the cortex showed significant responses to such gratings, responsivity is clearly skewed towards parallel gratings.
Similar to the sample of cells responsive to radial gratings there was a large number of LGN cells (34%) that were responsive to hyperbolic gratings but had lowpass SF tuning ($HI = 0$). However, there were no such V1 and V2 cells. The median $HI$ (including lowpass cells) for the LGN distribution (Fig. 2C) was 0.41, which indicates that, although there was a substantial number of lowpass cells, there was a significant number of cells responsive to hyperbolic gratings other than the full-field stimulus. This was in

Fig. 1. Spatial-frequency tuning curves for cortical cells more responsive to parallel than concentric gratings ($CI = 0.17$), equally responsive to both gratings ($CI = 0.51$), and more responsive to concentric than parallel gratings ($CI = 0.74$).
contrast to the results for the LGN RI distribution where the median RI was 0.02.

The mean HI for LGN cells tuned for hyperbolic gratings (excluding lowpass cells) was 0.52. In V1 the mean HI was 0.42. However, cells with a HI > 0.5 were in almost every case more responsive to some other non-Cartesian grating. Only one V1 cell was more responsive to hyperbolic gratings than to any other stimulus. The mean V2 HI was 0.48, with only one cell giving its best response to hyperbolic compared to all other Cartesian and non-Cartesian gratings.

Compared to the distribution of LGN responses for concentric and radial gratings, the distribution for hyperbolic gratings was broader with 14% of LGN cells more than twice as responsive to hyperbolic than to parallel gratings and 7% of cells twice as responsive to parallel than to hyperbolic gratings. Furthermore, in the LGN HI distribution, 66% of cells were responsive to hyperbolic gratings other than zero SF. In comparison, 52% of cells were responsive to radial gratings other than zero SF and all LGN cells were responsive to concentric gratings other than zero SF.

In summary, while responses to radial and hyperbolic gratings were found in some cells, especially in the cortex, the amplitude of their tuning function responses was not sufficient to suggest that these gratings were the most significant stimuli for these cells. Concentric gratings, however, were a significant stimulus for most LGN cells and also for a large number of V1 and V2 cells, often producing equal or greater cell responses than the equivalent SF parallel grating. In many instances, cells responded best to concentric gratings compared to all other Cartesian and non-Cartesian stimuli.

Orientation selectivity was analyzed as a function of the CI for V1 and V2 cells. There was a significant difference in orientation selectivity for V1 cells responsive to parallel versus concentric gratings (t-value 2.6; P 0.02). The CI for orientation-selective cells increased as the orientation bandwidth increased. Specifically, the average CI for cells narrowly tuned for orientation (half-bandwidths <20 deg) was 0.39, indicating that the majority of these cells preferred parallel gratings. The average CI was 0.51 for cells with moderate orientation tuning (half-bandwidths 20 to 60 deg). Finally, the average CI was 0.60 for nonoriented cells.

The SF bandwidth (octaves) was analyzed as a function of the CI for V1 and V2 cells; however, there was no significant difference in the mean SF bandwidth for cells with a CI < 0.33 or >0.67 indicating that SF tuning did not vary consistently as a function of the CI and that orientation rather than SF selectivity is more predictive of a cell’s non-Cartesian responsivity, especially for concentric gratings.

The aspect ratio (AR) provides a measure of the cell’s relative orientation and SF tuning characteristics [eqn. 6].

$$AR = \frac{(2^{2w} - 1)/(2^{2w} + 1) \ast 1/\sin(\Delta O_{1/2})}{\Delta w}, \quad (6)$$

where $\Delta w$ is the spatial-frequency full bandwidth in octaves and $\Delta O_{1/2}$ is the orientation half-bandwidth in degrees (Webster &
De Valois, 1985). For both V1 and V2 cells, the AR increased as a function of the CI. Cells more responsive to concentric gratings were relatively more broadly tuned for orientation than for SF. These differences were statistically significant for both V1 (t-value 2.04; P 0.05) and V2 (t-value 2.6; P 0.02).

The direction index (DI) was analyzed as a function of the CI for V1 and V2 cells [eqn. (7)].

\[
DI = 1 - \left( \frac{\text{Response}_{\text{nonpreferred direction}}}{\text{Response}_{\text{preferred direction}}} \right)
\]

Few directional cells (DI > 0.7) in either V1 (7%) or V2 (11%) responded better to concentric than to parallel gratings; the majority of these cells being more responsive to parallel gratings. There was a significant difference in the average DI for V1 cells with a CI < 0.33 and V1 cells with a CI > 0.67 (t-value 2.62; P 0.02) indicating that cells more responsive to concentric gratings are less directional than cells more responsive to parallel gratings. This is consistent with the fact that concentric gratings drift in opposite directions from their central origin providing a suboptimal stimulus for directional cells compared to a parallel grating drifting in the preferred direction.

Parallel gratings of optimal SF and orientation but of different aperture sizes were presented to 39 cortical cells. Similarly, responses to different-sized optimal SF concentric gratings were measured for 35 cortical cells. This experiment was also performed on 30 LGN cells. LGN cells were size invariant for these gratings and there was no difference in the CI to either smaller or larger concentric or parallel gratings as a function of the stimulus size (Fig. 3). For cortical cells, the average response to concentric gratings larger than optimum decreased 9% relative to the optimal sized grating, compared to a 22% decrease relative to the optimal-sized grating for concentric gratings smaller than optimum. On the other hand, for parallel gratings the average response to larger gratings decreased 23% compared to <2% decrease for smaller gratings. These results suggest that the CI for cortical cells varies as a function of the stimulus size.

Because non-Cartesian gratings are radially symmetrical about an origin, it is important that they be centered on the CRF. Partial stimulation of the CRF by non-Cartesian gratings could result in response amplitudes for non-Cartesian stimuli that appear similar to responses elicited by parallel gratings. The average cell response to the centered stimuli across all cells was significantly greater than the average cell response to stimuli at any noncentral position for both cortical and LGN cells (Fig. 4). There was no significant difference in the responsivity at any of the noncentral positions, which indicates that there was an equal decrease in the average cell response as the stimulus moved off the RF in any direction. This confirms that the stimuli were centered with respect to the RF and that the results were not due to stimulus misalignment. Noncentral positions did not give zero responses as the noncentral positions, although equally displaced in any single run, varied for different runs between one half and one full diameter from the center of the receptive field. Runs from many cells were averaged in these plots and indicate that all noncentral position responses decreased equally. Furthermore, Fig. 4 indicates that V1 and V2 cells were not position invariant with respect to Cartesian and non-Cartesian gratings. In this respect, they differ from V4 cells which were shown to be position invariant to similar Cartesian and non-Cartesian gratings (Gallant et al., 1996).

Discussion

While visual processing of parallel gratings has been studied extensively since the 1970s, the use of circular gratings in vision...
LGN, V1, and V2 cell Cartesian and non-Cartesian responses

Studies have been more sporadic. The Fourier transformation of a concentric grating is an annulus indicating power at every orientation of the fundamental SF. The spectrum for an equivalent SF parallel grating consists of two points 180 deg apart on this annulus. The power of the Fourier fundamental decreases with increasing concentric SF but remains constant across all SFs for parallel gratings (Kelly & Magnuski, 1975). Therefore, only at relatively low SFs will the magnitude of the Fourier fundamental for concentric gratings be similar to that for the equivalent SF parallel grating and therefore, the responsiveness of cells will converge when each grating contains a small number of cycles covering the CRF.

The population responses of cells presented in this paper were consistent with the amplitude spectra of the Fourier transformations of concentric and parallel gratings as predicted by Kelly and Magnuski, 1975 (specifically, Kelly & Magnuski showed that contrast-sensitivity functions for parallel sinusoidal gratings and concentric gratings crossed at a spatial frequency of just below 1 cycle/deg: the contrast-response function being bandpass for parallel gratings and lowpass for concentric gratings). In this study, for cortical cells the average concentric index decreases as a function of the optimum peak spatial frequency of the cell. Furthermore, the average concentric index is >0.5 at spatial frequencies below 1.2 cycles/deg, indicating that at low spatial frequencies cells are, on average, more responsive to concentric gratings. At higher peak spatial frequencies (>1.2 cycles/deg), the mean concentric index is <0.5, indicating that these cells are, on average, slightly more responsive to parallel compared to concentric gratings. Interestingly, for LGN cells the average CI does not change as a function of peak SF confirming that parallel gratings are not as significant a stimulus for LGN cells as they are for cortical cells. Finally, in the population results the parallel or concentric grating that elicited the best response for cells with a CI < 0.33 had a larger number of cycles/stimulus field than the parallel or concentric grating that elicited the best response for cells with a CI > 0.67.

The most relevant physiological study with which to compare the present results used parallel, concentric, radial, and hyperbolic gratings to examine V4 cell responses of the anesthetized monkey (Gallant et al., 1996); no previous studies have comprehensively examined responses to these gratings in V1 and V2 of anesthetized monkey. It was found that about 20% of V4 cells were more responsive, by a factor of two, to one of the non-Cartesian compared to Cartesian stimuli with a significant bias of responsivity to concentric gratings for stimuli within the CRF; there were no cells significantly more responsive to Cartesian gratings (Gallant et al., 1996). In the present study, 19% of V2 cells were more responsive, by a factor of two, to concentric than to parallel gratings, 8% more responsive to radial than to parallel gratings, and 8% more responsive to hyperbolic than to parallel gratings. In Vi, a similar number of cells were twice as responsive to non-Cartesian as to Cartesian gratings (15% concentric; 5% radial; 8% hyperbolic).

One of the most obvious differences between the results of this study and that of V4 cells is the lack of cells responsive to parallel gratings in V4 (Gallant et al., 1996) compared to V1 and V2 (Mahon & De Valois, 1999). In the present study, 19% of V1 cells compared to 11% of V2 cells were more than twice as responsive to parallel as to concentric gratings; 20% of V1 cells compared to 15% of V2 cells were more than twice as responsive to parallel as to radial gratings; and 24% of V1 cells compared to 16% of V2 cells were more than twice as responsive to parallel as to hyperbolic gratings. For all three non-Cartesian comparisons, Cartesian selectivity decreases from V1 to V2. This trend, and the earlier data set (Gallant et al., 1996), suggests a shift in selectivity towards non-Cartesian gratings at higher levels of visual processing (Mahon & De Valois, 1999) rather than the emergence of responses to these gratings in V4. Furthermore, selectivity for non-Cartesian gratings in V1 and V2 is more moderate than that reported in V4 and higher visual areas.

The present study showed that orientation tuning was predictive of the cell’s responsivity to concentric gratings. As the CI increased, the median orientation bandwidth increased. In general, V1 and V2 cells that responded well to concentric gratings had considerably broader orientation bandwidths than cells that preferentially responded to parallel gratings. However, there was no systematic relationship between a cell’s CI and its SF bandwidth and no directional cells that responded strongly to concentric gratings. Therefore, the orientation tuning of a cell appeared to be the better predictor of a cell’s non-Cartesian responsivity. This relationship between the cell orientation-tuning characteristics and Cartesian/non-Cartesian responsivity was confirmed by the cell’s AR where V1 and V2 cells relatively more broadly tuned for orientation and relatively more narrowly tuned for SF were more likely to prefer concentric gratings. The AR was a significant predictor of a cell’s non-Cartesian responsivity for both V1 and V2 cells. No such analysis has been reported for V4 cells.

V4 cells are broadly tuned for orientation and in general have low peak SF values and broad SF bandwidths (Desimone & Schein, 1987). Therefore, it would be predicted that V4 cells showing significant non-Cartesian responsivity might have properties similar to the V1 and V2 cells responsive to non-Cartesian gratings found in this study. Interestingly, 13% of V4 cells responded poorly or not at all to sine-wave gratings although these cells were not systematically tested to see whether they were significantly responsive to any other type of stimulus (Desimone & Schein, 1987).

The results of the present study indicate that the relative responses of cells to Cartesian and non-Cartesian gratings fall along a continuum rather than into distinct and separate physiological cell classes. Furthermore, selectivity systematically increases for non-Cartesian and decreases for Cartesian gratings from V1 to V2 consistent with the decrease in orientation selectivity with successive processing levels suggesting that one role of a cortical pathway involving nonoriented cells might involve encoding simple aspects of nonoriented 2D structure. Finally, the present study showed that V1 and V2 cells were not invariant with respect to their responses to parallel and concentric gratings and that the relative responsivity of cells to parallel and concentric gratings varied as a function of stimulus size. This effect was not seen in the LGN. These results add to the number of more complex analyses performed by cells at the earliest level of visual processing when both the CRF and its modulation by surrounding regions are considered.

The strength and area of the center and surround regions of LGN cells determine their SF tuning characteristics. The LGN RF profile is two-dimensional, with the sensitivity of the center and surround regions decreasing in every direction relative to the RF center. Cartesian gratings have constant luminance along one dimension and only change contrast along the orthogonal direction, and therefore do not optimally stimulate the circular surround region of LGN RFs. However, an optimal SF concentric grating has a luminance profile that modulates equivalently in all directions. Therefore, concentric gratings would not only optimally stimulate the RF center (as indeed the parallel grating does) but
would also optimally stimulate the surround (which the parallel grating does not). When the surround is extremely weak, nonoptimal and optimal gratings would produce much the same result; the response amplitude, in effect, determined by the center region alone, which is optimally stimulated by both gratings. However, the total strength of the center or surround is determined by both the RF area and the strength per unit area and therefore the tuning properties of LGN cells are dependent upon both these parameters.

LGN cells have a range of relative strengths between center and surround regions (Croner & Kaplan, 1995) where cells that have strong surrounds exhibit greater low SF attenuation and bandpass tuning. The average CI for bandpass LGN cells, which have a stronger surround than do cells with lowpass tuning, was 0.59 indicating greater responsivity to concentric than to parallel gratings.

Using a model LGN RF, based upon the difference of two Gaussians, model CI values increase as a function of the relative strength of the center and surround; the CI being >0.5 only for cells that have strong surrounds. As the strength of the surround decreases, the CI decreases and becomes <0.5, indicating stronger responses to parallel gratings in model LGN cells only with very weak surrounds.

Varying the extent of the RF surround in model cells has a smaller but systematic effect on the relative response of LGN cells to parallel versus concentric gratings. The CI range obtained from model cells due to variation in the relative strength and extent of the center and surround could account for the CI range found in this study.

The RFs of striate cells are well modeled by a Gabor function (Marcelja, 1980; Hawkin & Parker, 1987). The output of simple cells in the striate cortex is commonly modeled by the half-wave-rectified linear operation of these cells. The most widely accepted model for complex cells is that they contain linear subunits and that the complex cell response is the combined rectified output of these subunits (Heeger, 1992). However, a Gabor model of simple cells or an energy model of complex cells does not account for all of the data in this study because the elongated shapes of the postulated subunits cannot account for the selective responsivity seen for circularly symmetrical non-Cartesian gratings.

One factor that might account for cortical cell responsivity to non-Cartesian gratings is the nCRI, an area outside the CRF that modulates the response of many cells (Hubel & Wiesel, 1965; Allman et al., 1985; Knierim & Van Essen, 1992; Silitto & Jones, 1996). Many response properties of the CRF are matched by antagonistic mechanisms in the immediate surrounding field of many cells causing maximum modulation (usually suppression) if extended stimuli match the properties of both the center and surround RF regions.

Effects from these otherwise silent regions have been shown to be present in many cells at all levels of cortical processing (Allman et al., 1985).

In this study, the modulatory effects from the immediate area surrounding LGN RFs did not influence the responsivity for parallel and concentric gratings of different extents. However, for cortical cells there was less response suppression when concentric gratings were extended beyond the CRF than when parallel gratings were similarly extended into the nCRI. Orientation-specific inhibitory modulation from completely extensive nonclassical surrounds, as well as SF and orientation-specific divisive normalization from the influence of surrounding cells, could explain this result and suggests a mechanism for producing significant responses to concentric gratings in simple and complex cells.

If the surrounding region of the CRF had similar SF and orientation tuning as the CRF, an optimally oriented parallel grating would match the orientation of the nCRI at every location. If the nCRI were suppressive, this would reduce the cell’s response to a large patch of an optimally oriented parallel grating compared to a smaller patch of a parallel grating. On the other hand, a concentric grating has multiple orientation axes that are orthogonal along any two perpendicular meridians. Such an extended grating would only cause optimal suppression in the nCRI at the half the number of positions that the extended parallel grating would. The response would therefore be greater than it would to the equivalent parallel grating because stimulation of the nCRI would cause less suppression of the overall response. For concentric gratings, a similar outcome should occur for cells with a complete nCRI as well as for end-stopped RFs. However, side-stopped cells, that only had suppression from the flanks, might not give larger responses to concentric than to parallel gratings.

Therefore, to a first approximation, the CI range found for cortical cells in this study can be accounted for by a model whereby nonoriented or broadly oriented cells are modulated by orientation-specific cells in the nCRI surround. This model would account for cells that respond significantly better to concentric than to parallel gratings and for the finding that the relative cell response increases for concentric gratings and decreases for parallel gratings as the stimulus extends within the regions of the nCRI surround. The results are also in accord with the notion that stimulation of the nCRI increases the degree of sparse coding in the cortex and therefore increases the selectivity of neural filters in their efficient representation of more natural images (Vinje & Gallant, 2000).

Acknowledgments

This research was supported by National Institutes of Health Grant EY-00014. L.E. Mahon was supported by an Ezell Fellowship from the American Optometric Foundation. He also wishes to acknowledge the support of Nicolas Cottaris, Tony Wilson, and Sylvia Elfar during the lengthy data-recording sessions.

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