

Representation of Surface Luminance and Contrast in Primary Visual Cortex

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In visual perception, object identification requires both the ability to define regions of uniform luminance and zones of luminance contrast. Neural processes underlying contrast detection have been well studied, while those defining luminance remain poorly understood and controversial. Partially because stimuli comprised of uniform luminance are relatively ineffective in driving responses of cortical neurons, little effort has been made to systematically compare responses of individual neurons to both uniform luminance and contrast. Using large static uniform luminance and contrast stimuli, modulated temporally in luminance or contrast, we found a continuum of responses ranging from a few cells modulated only by luminance (luminance-only), to many cells modulated by both luminance and contrast (luminance-contrast), and to many others modulated only by contrast (contrast-only) in primary visual cortex. Moreover, luminance-contrast cells had broader orientation tuning, larger receptive field (RF) and lower spatial frequency Preference, on average, than contrast-only cells. Contrast-only cells had contrast responses more linearly correlated to the spatial structure of their RFs than luminance-contrast cells. Taken together these results suggest that luminance and contrast are represented, to some degree, by independent mechanisms that may be shaped by different classes of subcortical and/or cortical inputs.

Keywords: object identification, physiology, single unit, striate cortex, vision

Introduction

Luminance and contrast are 2 fundamental properties that describe the visual characteristics of objects. Luminance is the amount of light intensity emanating from a luminous source or reflected from an object. Contrast is the magnitude of luminance variation on an object surface relative to the mean luminance (Shapley and Enroth-Cugell 1984). The neuronal mechanisms for processing contrast have been extensively studied. It is well known that, over a restricted range of contrasts, most cells in the primary visual cortex (V1) increase their responses monotonically, then saturate at higher contrasts. Visual adaptation to a contrast level shifts the sensitivity range of V1 cells (contrast gain control), permitting cells to enhance their sensitivity to contrasts above and below the prevailing level (e.g., Movshon and Lennie 1979; Dean 1981; Albrecht and Hamilton 1982; Ohzawa et al. 1982; Sclar et al. 1989; Bonds 1991; Allison et al. 1993; Carandini and Ferster 1997; Gardner et al. 2005; for reviews, see Shapley and Lam 1993; Boynton 2005; Ibbotson 2005; Kohn 2007). The mechanisms responsible for generating responses to luminance contrast are well understood and well accepted models proposed (Priebe and Ferster 2008). Neuronal mechanisms to explain the perception for luminance, particularly for large

uniform luminance, however, are not well understood. In fact, there are relatively few studies that have investigated this property partially because it has been difficult to excite V1 cells with uniform luminance. Instead, reports suggest that uniform luminance evokes intracortical suppression in V1 in comparison with luminance contrast (Tucker and Fitzpatrick 2006; Kumbhani et al. 2007).

Nevertheless, a few studies over the years have continued to report that a portion of V1 neurons in both cats and primates are sensitive to diffuse illumination (Bartlett and Doty 1974; Kayama et al. 1979; DeYoe and Bartlett 1980) or to uniform luminance stimuli (Maguire and Baizer 1982; Squatrito et al. 1990; Komatsu et al. 1996; MacEvoy et al. 1998; Kinoshita and Komatsu 2001; Friedman et al. 2003; Huang and Paradiso 2008). These studies report that V1 neurons show monotonic increases or decreases in response or show V-shape responses to large uniform luminance stimuli (Kinoshita and Komatsu 2001). In response to slowly sinusoidally oscillated luminance, V1 neurons can signal continuous luminance change in a large uniform field and some neurons have their peak responses to intermediate luminance values (Peng and Van Essen 2005). A few studies have considered the neuronal mechanisms underlying the perception of the brightness of uniform surfaces. By modulating the luminance in the regions outside of the classical RF, some studies revealed that activity of neurons in V1 reflect not only the physical luminance but also the induced brightness of uniform surface stimuli (Rossi et al. 1996; Rossi and Paradiso 1999; Kinoshita and Komatsu 2001; Roe et al. 2005; Hung et al. 2007). The local contrast around the border between object and background has been thought to play an important role in the perceived brightness of the object (Shapley and Perry 1986; Reid and Shapley 1988). Furthermore, it has been hypothesized that responses to a uniform luminance stimulus are generated first from responses to the contrast border and then signal the uniform luminance representation (Komatsu et al. 2000; Hung et al. 2007; Huang and Paradiso 2008). How responses of V1 neurons to uniform luminance are generated, however, remains largely unknown.

To address the issue, we directly compared responses of V1 neurons to uniform luminance with responses to contrast using 2 types of stimuli that varied either only in luminance or only in contrast. To measure the luminance response function, we used a stimulus in which the luminance of a circular uniform field was modulated sinusoidally at a low temporal frequency (TF) (Peng and Van Essen 2005). The modulated luminance enhanced neuronal responses and the large stimulus size minimized the contribution of contrast at the edge of the stimulus to responses to luminance. To measure the contrast response function, we used a new type of contrast stimulus by dividing the circular luminance stimulus into 2 semicircles which were statically modulated in luminance in counterphase.

We designed the stimulus in an effort to isolate the contrast component without accompanying motion and spatial frequency (SF) components. This method minimized the differences between our contrast and luminance stimuli. Thus, the low SF property of our contrast stimulus was comparable to that of the uniform luminance stimulus of the large circle, allowing for a more direct comparison between neuronal responses to luminance and contrast. We also compared these response properties with other RF properties in neurons of cat area V1 so as to better understand the mechanisms underlying luminance responses.

Materials and Methods

Physiological Preparation

Twenty-nine normal adult cats (1.5–3 kg) were prepared for extracellular recording using the procedures described in detail elsewhere (Wang et al. 1995, 2007). Briefly, following injection of dexamethasone and atropine (intramuscular, i.m.), anesthesia was induced by ketamine (20–30 mg/kg, i.m.), then an endotracheal tube and a vein catheter were inserted. The animal was anesthetized deeply with a rapid infusion of sufentanil and propofol and was artificially respired. The animal was placed in a stereotaxic apparatus. Next an approximate 2.5 × 2.5 mm craniotomy centered at Horsley-Clarke coordinates P 2.5 mm and L 2.5 mm was made to access cells representing the central visual field in the primary visual cortex (area 17, V1). During recording, anesthesia was maintained with an infusion of sufentanil (0.15–0.22 μg/kg/h, intravenous, i.v.) and propofol (1.8–2.2 mg/kg/h, i.v.) (Victor et al. 2006; Ringach and Malone 2007; Zheng et al. 2007) in a Ringers solution containing 5% glucose. Paralysis was maintained with gallamine triethiodide (10 mg/kg/h, i.v.). The rectal temperature was maintained at 37 °C. The pupils were dilated by local application of homatropine and the nictitating membranes were retracted with phenylephrine hydrochloride. Contact lenses with sufficient power and 3 mm artificial pupils were put on the corneas to focus the eyes on a CRT monitor 57 cm away. During recording, anesthetic depth of the animal was evaluated by continuously monitoring end-tidal CO₂, electrocardiogram, electroencephalography, and by regular testing for responses of the animal to toe or ear pinch while monitoring heart rate changes. Anesthetic level was adjusted accordingly.

Extracellular action potentials were recorded from neurons using a glass-coated tungsten electrodes (1–3 MΩ) and a TDT amplifier and data acquisition system (TDT, Inc., Florida) at a sample rate of 12 kHz. Individual units were further identified off line with TDT OpenSorter. All animal care and experimental procedures conformed to the guidelines of the National Institutes of Health (USA) and were approved by Institutional Animal Care and Usage Committee (IACUC) of Institutes of Biophysics Chinese Academy of Sciences.

Visual Stimuli

Stimuli were displayed on a CRT monitor (Iiyama HM204DT A, 800 × 600 pixel resolution, 100 Hz refresh rate) subtending 40 × 30° in visual angle in a dark room (0.1 cd/m² measured using ColorCAL colorimeter [CRS, Ltd.]). The animal and the space between the animal and the visual display were covered or surrounded with black boards to allow the animal to only view the display and to avoid scatter effects from other light sources and reflections. Units were isolated on a microelectrode using TDT OpenEX. Once the action potentials of a single neuron were isolated, the size and location of its dominant eye RF were mapped with an oriented short bar controlled by a computer mouse, and the other eye was covered. After preliminary tests, the preferred orientation, motion speed, and SF of the cell were estimated with a patch (approximate RF size) of drifting sinusoidal gratings. The classical RFs of the neurons were mapped quantitatively with the reverse correlation technique (Conway and Livingstone 2003; Liu et al. 2007) and the orientation, direction, and SF selectivities were quantitatively measured with drifting sinusoidal gratings of 100% contrast.

For achromatic luminance and contrast experiments, the visual stimuli were circular patches in area at least 5 times the size of the classical RF of the cell. The luminance stimulus was a uniform patch (Fig. 1A) as described originally by Peng and Van Essen (2005) and the contrast stimulus was formed by dividing the circular patch into 2 semicircles (Fig. 1B). For the luminance stimulus, the luminance of the patch was modulated sinusoidally as L_1 of equation (1) or L_2 of equation (2). The phase at onset was either 0° (initially increasing) or 180° (initially decreasing). L_0 denotes the mean luminance; A is the modulated amplitude of luminance; f is the TF of the modulation; and t is time. The curve below Figure 1A shows the temporal profile of luminance modulation run at $f=0.4$ Hz for 5 s (2 cycles) in one trial. For the contrast stimulus, the luminance of the 2 halves was modulated sinusoidally in counterphase, one in equation (1) and the other in equation (2). Thus, contrast would be generated along the edge between the 2 semicircles and changed continuously as indicated by equation (3). This stimulus is analogous to that used by Tolhurst and Dean (1987) in which 2 static bars located in ON and OFF subregions of a V1 RF were simultaneously modulated sinusoidally in opposite directions of luminance change, but the 2 bars were separated in space. Because contrast is a positive value, we took the absolute value of equation (3) as the contrast value. The curve below Figure 1B shows the temporal profile of contrast variation when luminance is modulated at $f=0.4$ Hz for 5 s (2 cycles), in which the solid line and dashed line represent the opposite polarities (or 180° difference in phase) of the contrast stimulus. The contrast stimulus was presented initially in either polarity, that is, 0° phase (luminance initially decreasing from the mean luminance at the left and simultaneously increasing at the right side of the contrast edge) or 180° phase (the opposite case as indicated by the lowest 2 insets of Fig. 1B). Note that both the luminance and the contrast stimuli were generated by the luminance components that were modulated sinusoidally within the same luminance range and at the same TF.

$$L_1=L_0+A\cdot\sin(2\pi ft) \quad (1)$$

$$L_2=L_0-A\cdot\sin(2\pi ft) \quad (2)$$

$$C=|(L_1-L_2)/(L_1+L_2)|=A/L_0\cdot|\sin(2\pi ft)| \quad (3)$$

To address the issue of contrast at the border between the stimulus patches and background, a checkerboard background was used (Peng and Van Essen 2005). The stimuli were surrounded by a static “checkerboard” texture background, composed of small squares 1/8 the diameter of the stimulus patch. The individual background squares had different levels of the luminance (steps) which linearly covered the full luminance range (0 to $(A+L_0)$). Their luminance levels were randomized in spatial position and redistributed on the background for each trial, and the luminance of individual background squares was selected randomly from a uniform distribution across the full luminance range. This background provided a wide range of local contrast and luminance values at the border between the stimulus patch and texture background, thereby averaging and minimizing effects of the border contrast between the stimulus patches and background.

For each experiment, a set of patch/background stimuli were generated, covering a range of luminance and of contrast levels. For each cell, each stimulus in the set was presented at least 10 times. During each trial, the average luminance of the background, the initial luminance of the luminance patch, and the average luminance of the contrast patch were the same ($=L_0$), and a stimulus was pseudorandomly selected from the set of luminance and contrast stimuli. Each stimulus was exhibited for 5 s with an interstimulus interval of 1 s presenting only the checkerboard background (mean luminance = L_0) between trials. The oriented edge of contrast stimulus was presented along the preferred orientation of the neuron.

All neurons were tested in the 0–100 cd/m² luminance range. The stimulus parameters for this range were $L_0=50$ cd/m², $A=50$ cd/m², $f=0.4$ Hz (2 cycles/5 s). Therefore, the luminance stimulus was modulated between 0 and 100 cd/m² and the contrast stimulus (also modulated between 0 and 100 cd/m²) was varied between 0% and 100% (eq. 3). The luminance of 0–100 cd/m² thus was the luminance component of the 2 stimuli. In addition, a small number of neurons

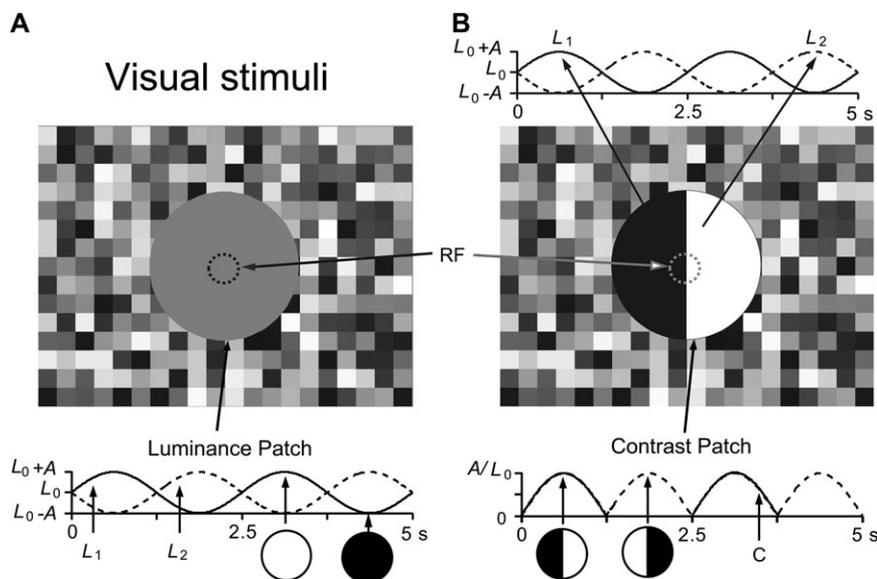


Figure 1. Uniform luminance and contrast stimuli. The visual stimuli are circular patches in area at least 5 times larger than the size of the classical RF (the small dotted line circles inside the patches) of a cell. (A) The spatial configuration of the uniform luminance stimulus. Luminance in the patch varies sinusoidally at 0.4 Hz for 2 cycles of 5 s duration in each stimulus presentation. Sinusoidal curves below the stimulus icon indicate luminance changing initially in the rising (L_1 , solid curve) or falling direction (L_2 , dashed curve), 2 opposite phases, respectively. Open and filled circles indicate the highest and lowest luminances. L_0 is the mean luminance of the stimulus and A is the magnitude of luminance modulating sinusoidally from L_0 . (B) The spatial configuration of the contrast stimulus. Contrast is generated by different luminance changes in 2 semicircular patches. Luminance in the 2 semicircles varies sinusoidally in the opposite directions described by the sinusoidal curves above the stimulus icon with the same parameters as in (A). The resulting contrast change is delineated by the sinusoidal curves and insets below the icon. The solid and dashed curves represent contrast changes in 2 opposite polarities (phases) as indicated by 2 insets consisted of white and black semicircles, respectively. In this case, L_1 , L_2 , L_0 , and A are the same as in (A). C: Contrast ($=A/L_0 \cdot |\sin(2\pi ft)|$, see Materials and Methods).

were tested under $f = 0.8$ Hz (2 cycles/2.5 s). We found no significant differences in responses to the 2 temporal frequencies ($f = 0.4$ Hz, duration = 5 s vs. $f = 0.8$ Hz, duration = 2.5 s; e.g., Fig. 2A-C, Supplemental Fig. S1A-D), and so the data from the 2 conditions were combined.

Data Analyses

To determine whether the modulation of responses was significant, we compared the mean firing rate during the 250 ms centered at the peak response with the spontaneous firing rate during the 250 ms prior to stimulus onset (checkerboard background, mean luminance = L_0 , see above; t -test, $P < 0.05$). To measure responses to luminance (RI) and contrast (RC), we collapsed peristimulus time histograms (PSTHs) from different cycles and different trials into a single 2.5 s cycle, after compensating for the typical 40 ms latency of V1 neurons (Peng and Van Essen 2005) and shifting for the initial stimulus polarity (0° or 180° phase). Histograms were smoothed with a Savitzky-Golay filter (Press et al. 1988; Rossi and Paradiso 1999) with a time constant of 5 data points with each point corresponding to a 50 ms bin. We defined RI and RC as the peak response of the collapsed 2.5 s cycle under the luminance and contrast conditions, respectively. The luminance value that corresponded to this time point was defined as the peak luminance of the neuron (Peng and Van Essen 2005).

Contrast-Luminance Response Index

To quantitatively compare luminance responses and contrast responses, the relative response strength of a neuron to contrast and luminance was evaluated by a contrast-luminance response index (CLRI) defined as

$$\text{CLRI} = \frac{R_c - R_l}{R_c + R_l} \quad (4)$$

R_c denoted to contrast responses and R_l to luminance responses. A value of 0.5 CLRI indicates that contrast responses are 3 times as large as luminance responses, 0 indicates no response biased to either contrast or luminance, and -0.5 indicates that luminance responses are 3 times as large as contrast responses.

Contrast Polarity Selectivity

The contrast stimulus consisted of 2 opposite polarities (see the lowest 2 insets of Fig. 1B). The selectivity of a neuron for this contrast polarity was quantified by a polarity selectivity index (PSI) defined as

$$\text{PSI} = \frac{\sum R(p1) - \sum R(p2)}{\sum R(p1) + \sum R(p2)} \quad (5)$$

where $\sum R(p1)$ and $\sum R(p2)$ were the sum of responses to the 2 polarities over each half (1.25 s) of a stimulus cycle (2.5 s), respectively, to evaluate the overall contrast responses in the 2 opposite polarities. PSI varies from 0 to 1, where 1 indicates that responses of a cell are biased completely to one contrast polarity and 0 indicates no bias to either polarity. A value of 0.33 indicates that responses in preferred polarity direction are twice as large as those in the nonpreferred polarity.

Receptive Field

The spatiotemporal structure of RF was mapped using the reverse correlation method with single optimal bright and dark bars (width = 0.25 – 0.5° , length = 10 – 15°) vertical to the x -axis of an RF (Conway and Livingstone 2003; Liu et al. 2007). To classify cells as simple or complex, RF subregions representing the ON and OFF responses to the bright and dark bars were quantitatively analyzed. The response peak was defined as the time when the spatial profile of responses along RF x -dimension (orthogonal to preferred orientation) yielded the maximal variance after stimulus onset (the optimal time delay, T_{peak}). The spatial profile at the response peak and the temporal profile at the peak spatial position for each of ON and OFF subregions were determined; each profile was fitted by a Gaussian function. The size of each ON and OFF subregion was determined by taking the 25% height of the fitted spatial and temporal curves. These widths were used to calculate the overlap index (OI) of ON and OFF subregions, respectively, in either space map or time map. This was defined as

$$\text{OI} = \frac{(W_{\text{ON}} + W_{\text{OFF}})/2 - \text{Sep}}{(W_{\text{ON}} + W_{\text{OFF}})/2 + \text{Sep}} \quad (6)$$

where W_{ON} and W_{OFF} were the width of ON and OFF subregions, Sep were the separation between the centers of ON and OFF subregions

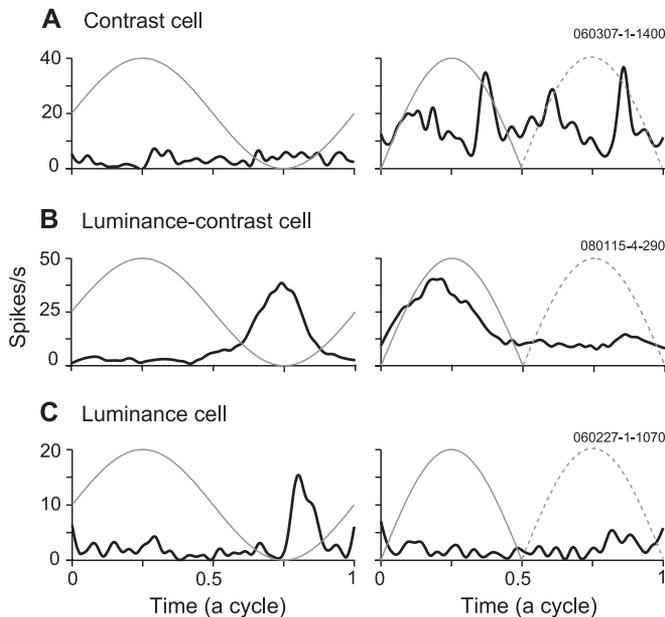


Figure 2. Different responses of 3 types of neurons to uniform luminance and contrast stimuli. The left and right columns are responses of example cells to luminance and contrast stimuli, respectively. Dark lines: response curves; Gray lines: the temporal profiles of luminance or contrast changes in the stimuli (a circle: 2.5 s, 0.4 Hz in (A) and (C); 1.25 s, 0.8 Hz in (B)); Dashed gray lines: the temporal profile of contrast change in the opposite polarity of the stimulus. (A) A contrast cell that did not significantly respond to luminance but responded strongly to contrast. The cells had PSI = 0.00 and CLRI = 0.56. (B) A luminance-contrast cell that responded significantly to both luminance and contrast. The cells had PSI = 0.37 and CLRI = 0.03. (C) A luminance cell that responded significantly to luminance but not to contrast. The cells had CLRI = -0.51.

(Schiller et al. 1976; Kagan et al. 2002; Mata and Ringach 2005). W_{ON} , W_{OFF} , and Sep all were in degrees in space or in ms in time. $(W_{ON} + W_{OFF})/2 + Sep$ was the overall RF width and $(W_{ON} + W_{OFF})/2 - Sep$ is the overlap zone between the 2 subregions. Thus, OI is the ratio of the overlap zone to the total RF width. OI ranges from a negative value to 1: a value of OI = 1 indicates complete overlap of ON and OFF subregions; OI = 0 indicates 2 subregions abutted without overlap; OI < 0 indicates that there is a gap between the 2 subregions. OI was calculated separately in the spatial dimension and the temporal dimension of the spatiotemporal RF map and are referred to as OIS and OIT, respectively. Note that OIS and OIT could not be calculated for the cells that have only a single ON or OFF subregion in both the spatial and the temporal dimensions of their RF maps, namely monocontrast cells.

The RF size was defined as at 25% of the height of the x -dimension spatial profile of the entire RF including both ON and OFF subregions.

Orientation Tuning

The mean spike rates, r_k , of a neuron in response to orientation angles, θ_k , of a drifting sinusoidal grating were measured. The stimulus angles, θ_k , ranged from 0° to 180° in equal steps of 22.5° and were presented randomly. The strength of orientation tuning was quantified by circular variance (CV) which was defined as $CV=1-|R|$. R is the result calculated from r_k with

$$R = \frac{\sum_k r_k e^{i2\theta_k}}{\sum_k r_k} \quad (7)$$

the angles expressed in radians (Ringach et al. 2002; Alitto and Usrey 2004). CV ranges from 0 to 1. A CV near 0 indicates strong orientation selectivity, while CV near 1 indicates a total absence of orientation selectivity.

Direction Tuning

A direction selectivity index (DSI) was defined as

$$DSI = 1 - NP/P \quad (8)$$

where P and NP denoted responses to a stimulus moving in the preferred (P) direction compared with the stimulus moving in the null or nonpreferred (NP) direction, respectively. A DSI = 0 indicates no direction selectivity and a DSI = 1 indicates selectivity for only one of the 2 directions.

Spatial Frequency Tuning

Responses of cells were measured with drifting gratings of spatial frequencies ranging from 0.1 to 2.0 cycles/degree (c/d). The SF tuning curve was first fit by a difference of Gaussian (DOG) functions:

$$R(sf) = R_0 + P_e e^{-((sf - \mu_e)/2\sigma_e)^2} - P_i e^{-((sf - \mu_i)/2\sigma_i)^2} \quad (9)$$

where R_0 , P_e , P_i , μ_e , μ_i , σ_e , and σ_i were optimized to provide the least squared error fit to the data (Sceniak et al. 2002). Then the optimal SF and bandwidth were extracted from the fitted curves. The SF evoking the maximal response was taken as the optimal SF, and the bandwidth was estimated as the width at the half height of the fitted curve.

Results

We recorded 259 cells that responded significantly above baseline to the luminance stimulus or contrast stimulus or to both ($P < 0.05$, t -test for all data hereafter except as noted) that were modulated sinusoidally from the 0 to 100 cd/m² luminance range at 0.4 Hz in a large field (Fig. 1). These 259 cells were recorded from the region representing the lower quadrant of the contralateral central visual field (eccentricity $\sim 5^\circ$) across all cortical layers of area 17 (V1). To examine whether neuronal responses to luminance and/or contrast are related to other RF properties, precise RF maps were obtained for 160 cells using the reverse correlation method and orientation, direction, and SF tuning data were obtained for 119 cells using sinusoidal gratings in the second half of the study. RF sizes of the 160 cells at 25% of the height of RF profile along x -dimension were between 0.75° and 7.08° with a mean of $2.61 \pm 1.18^\circ$ (mean \pm standard deviation, here and for all data presented hereafter). Our large patches of luminance and contrast stimuli were 10 – 16° in diameter size depending on the RF size of the cell tested. The sizes of these stimuli ensured that the RFs of the studied cells were located completely inside the stimuli and were at least 4° from the border of the stimulus. Of the 119 cells tested with 100% contrast drifting gratings, 13% of the cells (15/119) were simple cells with modulation indices (MIs, ratio of F_1/F_0) > 1 and 87% (104/119) were complex cells with MI < 1. In the following sections, we first address the neuronal response properties to large uniform luminance and contrast stimuli and then compare the relationships of luminance and contrast responses of these cells with other RF properties.

Luminance and Contrast Responses

In the main experiments, luminance was modulated from 0 to 100 cd/m² ($L_0 = 50$ cd/m², $A = 50$ cd/m²) and the resulting contrast stimulus varied between 0% and 100% (eq. 3). Within the confines of our stimulus design, the cells responded differently to the large uniform luminance and contrast stimuli. Figure 2A shows a cell that modulated its responses significantly to contrast ($P < 0.05$, right panel of Fig. 2A) and not to luminance (left panel of Fig. 2A, $P > 0.05$). The cell in Figures 2B responded significantly to both luminance and contrast. Another example cell (Fig. 2C) modulated its responses significantly to luminance ($P < 0.05$) but not to contrast

($P > 0.05$). All 3 kinds of cells were observed in all layers of cortex.

Figure 3A shows the scatter plot of contrast responses of all 259 cells against their luminance responses. As can be appreciated from the data, there were clearly stronger responses to contrast than to luminance in this population of cells. To compare luminance responses and contrast responses, we calculated an index for contrast responses and luminance responses using CLRI described in Materials and Methods. The CLRI distribution of the cells appeared to fall on a continuum with contrast-only and luminance-only responses at the 2 ends (Fig. 3B) and with a bias toward contrast response. In our design, cells having a CLRI > 0.5 (contrast responses 2 times larger than luminance responses; e.g., CLRI = 0.56 for the cell in Fig. 2A) were termed contrast cells, those with CLRI < -0.5 (luminance responses twice larger than contrast responses; CLRI = -0.51 for the cell in Fig. 2C) were termed luminance cells and those with $-0.5 < \text{CLRI} < 0.5$ (responded well to both luminance and contrast; CLRI = 0.03 for the cell in Fig. 2B) were termed luminance-contrast cells. Note that those contrast cells with the CLRI much larger than 0.5 (rightmost of Fig. 3B) had no response to the large uniform luminance stimulus. Out of our population, 55% (142/259, Fig. 2A) were contrast cells, 2% (6/259, Fig. 2C) were luminance cells, and the remaining 43% (111/259, Fig. 2B) were luminance-contrast cells. Overall, there were more cells that responded to contrast (98%, 253/259) than to luminance (45%, 117/259). It is possible that we underestimated the number of luminance-only cells given that CLRI < -0.5 is a strict criterion for luminance-only cells and that responses were strongly biased to contrast (Fig. 3). Therefore, we also analyzed the data using a more liberal criterion in which we classified cell types based on whether responses were significant relative to their spontaneous firing rate (see Materials and Methods) without referring to CLRI. Using this criterion, 47% of cells (122/259) responded only to contrast ($P < 0.05$, t -test; Fig. 3A,B), 49% of cells (127/259) responded to

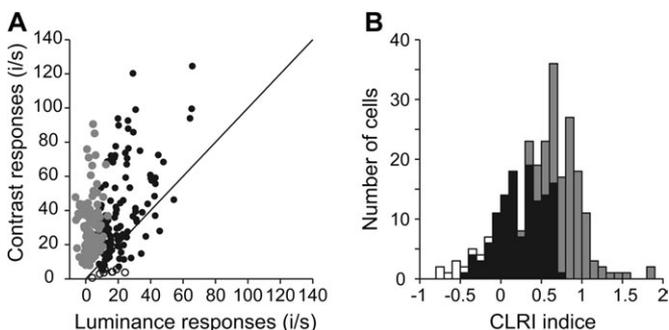


Figure 3. Luminance responses and contrast responses in population. (A) Contrast responses were plotted against luminance responses in a population of 259 cells. The responses (i/s: spikes/s) were the net firing rates after subtracted the spontaneous firing rate. Each dot represents one cell. The solid line is the diagonal line. (B) Distribution of CLRIs of the population of 259 cells. A negative value of CLRI means that luminance responses of a cell were larger than its contrast responses and a positive one means that contrast responses were larger than its luminance responses. The example contrast cell, luminance-contrast cell, and luminance cell in Figure 2A–C had CLRI = 0.56, CLRI = 0.03, and CLRI = -0.51 , respectively. The gray, dark, open dots in (A) and the corresponding gray, dark, open bars in (B) denote to the contrast-only cells, luminance-contrast cells, luminance-only cells that were classified based on t -test criterion in comparison with the classifications based on CLRI criterion. Note that those cells at the leftmost of the abscissa in (A) had luminance responses < 0 and at the rightmost of the abscissa in (B) had a value > 1 because their luminance responses were lower than the spontaneous firing rate.

both luminance and contrast ($P < 0.05$), and 4% (10/259) responded only to luminance ($P < 0.05$). Thus, when we used this more liberal criterion, we obtained approximately twice the number of luminance-only cells.

When the luminance of the static uniform stimulus was modulated sinusoidally in the range of 0–100 cd/m^2 at the low TF of 0.4 Hz, luminance-contrast cells and luminance cells (45%, 117/259, Fig. 4) responded significantly to a certain range of luminance values (e.g., left panels of Fig. 2B,C). Within the 0–100 cd/m^2 luminance range, we determined the luminance value that produced the peak response of a cell (see Materials and Methods). Most cells (79%, 92/117, Fig. 4) had a peak response in the low luminance range ($< 25 \text{ cd}/\text{m}^2$), a few (9%, 11/117) were in the high luminance range ($> 75 \text{ cd}/\text{m}^2$, Fig. 4), and the remaining cells (12%, 14/117) were in the mid luminance range (25–75 cd/m^2). The dashed curve in Figure 4 shows the expected distribution of the probability of luminance samples contained in the sinusoidal stimulus. The stimulus probability distribution can account for the small peak in the cell distribution at the high luminance of 90–100 cd/m^2 , but it is obvious that the distribution cannot completely account for the high percentage of cells in the low luminance range of 0–10 cd/m^2 .

Independent Luminance and Contrast Responses

From Figures 2 and 3, it is clear that responses of many contrast cells at the right end of the CLRI distribution (Fig. 3B) were well modulated by the contrast stimulus but poorly by the luminance stimulus, even for the same range of luminance modulation contained in the contrast stimulus (e.g., Fig. 2A), while a few luminance cells at the left end were largely modulated by the luminance stimulus but failed to respond to the contrast stimulus in the same luminance range (e.g., Fig. 2C). Importantly, these results show that the contrast

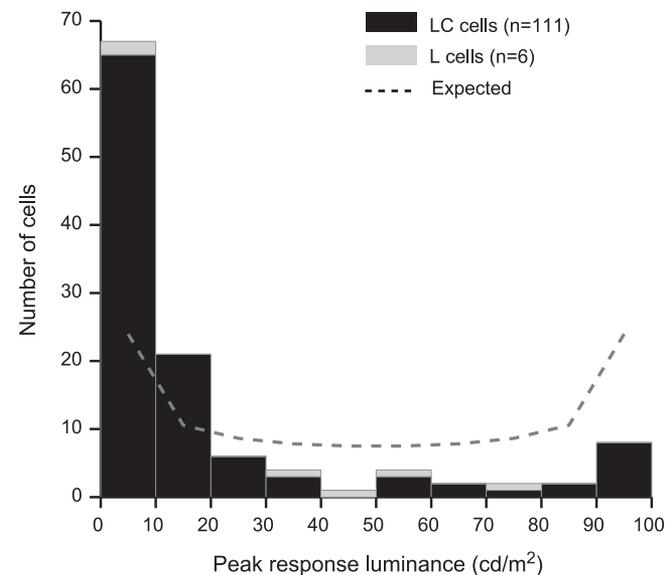


Figure 4. Most of luminance-sensitive neurons respond to low luminance. The abscissa is the luminance to which a cell showed the peak response when luminance modulated at a slow TF of 0.4 Hz, $n = 117$, including 111 luminance-contrast cells (LC, filled bars) and 6 luminance cells (L, open bars). The dashed curve is the expected distribution of the probability of stimulus samples in the sinusoidal luminance change. Note that contrast cells were excluded from the analysis because they had no significant ($P > 0.05$) response to uniform luminance.

responses of the contrast cells were independent of luminance and the luminance responses of the luminance cells were independent of contrast. Further study showed that the luminance responses and contrast responses of luminance-contrast cells were independent as well (see Supplementary Material).

If contrast responses are independent of luminance information, as suggested above, the same range of contrast that is generated by different ranges of luminance should yield similar contrast responses. We examined the responses of contrast cells to the same contrast (0–100%) but to different luminance ranges, namely either 0–100 or 0–50 cd/m^2 (eq. 3; $L_0 = 50 \text{ cd/m}^2$ and $A = 50 \text{ cd/m}^2$ or $L_0 = 25 \text{ cd/m}^2$ and $A = 25 \text{ cd/m}^2$). A subset of contrast cells ($n = 55$) were tested with both luminance ranges. The example cell in Figure 5A exhibited almost identical response profiles to the 2 contrast stimuli (dark and gray lines in Fig. 5A) even though they had a difference of 50 cd/m^2 in luminance level. Figure 5B shows the scatter plot for the magnitudes of contrast responses for a population of 55 contrast cells. The 2 responses were highly correlated ($r = 0.96$, $P < 0.01$, slope = 0.99), distributed along the main diagonal (solid line in Fig. 5B). The mean responses to these 2 luminance ranges were not significantly different (41.14 ± 25.97 and 40.00 ± 26.58 spikes/s, $n = 55$; $P > 0.05$). Therefore, contrast responses were not dependent on luminance ranges of stimuli.

Relationships of Luminance-Contrast Cells and Contrast Cells with Other RF Properties

Do the different luminance and contrast responses relate to other RF properties of these cells? To address the issue, we measured RF maps of 160 cells, the orientation and direction tunings of 119 cells, and SF tunings of 118 cells recorded in the second half of the study. We analyzed the relationships between the overall distribution of CLRI and these RF parameters but did not observe strong correlations. Based on the categories of luminance-contrast cells and contrast cells described above, however, we did observe certain differences in RF properties between the luminance-contrast cells and contrast cells. The types of cells classified based on

a t -test criterion also showed similar results. In the following sections, we describe the results using the CLRI criterion. For RF properties of luminance cells, see examples in the Supplementary Material.

Orientation and Direction Selectivity of Luminance-Contrast Cells and Contrast Cells

We have shown that contrast cells only responded to contrast and luminance-contrast cells responded to both luminance and contrast (Figs 2A,B and 3B). The modulated contrast responses of these cells to the contrast edge stimulus depended on the orientation of the stimulus as expected (data not shown). One could also ask whether there is any difference in orientation tuning between the 2 groups of cells. We examined the orientation responses of 118 cells that were tested using drifting gratings. To describe the degree of selectivity, the strength of orientation tuning was evaluated by CV (Batschelet 1981; Swindale 1998) which ranges from 0 (high) to 1 (low selectivity) (see Materials and Methods). CV is thought to be quite robust against variability in the data due to noise (Shou and Leventhal 1989; Ringach et al. 2002; Alitto and Urey 2004). A $CV < 0.5$ indicates an obvious degree of selectivity (Shou and Leventhal 1989; Ringach et al. 2002). The average CV of contrast cells (0.50 ± 0.17 , $n = 71$, Fig. 6A) was significantly lower than that of luminance-contrast cells (0.60 ± 0.17 , $n = 47$, $P < 0.01$, Fig. 6B). The contrast cell population also contained a higher percentage of cells strongly selective for orientation ($CV < 0.5$; 48%, 34/71) than the luminance-contrast cell population (23%, 11/47; $P < 0.05$, t -test).

We also compared the degree of direction selectivity of contrast cells and luminance-contrast cells again tested using drifting gratings. There was no obvious difference between the 2 groups of cells in their DSI (0.44 ± 0.23 , $n = 71$ and 0.39 ± 0.27 , $n = 47$; $P > 0.05$).

SF Selectivity of Luminance-Contrast Cells and Contrast Cells

Given that luminance-contrast cells not only respond to contrast but also to uniform luminance, one might predict that they would show a low SF preference to the uniform

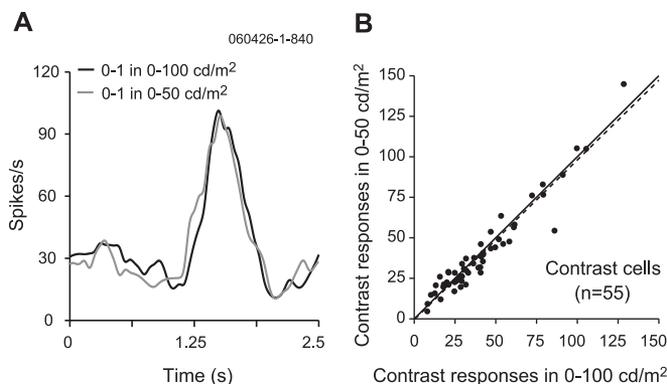


Figure 5. Contrast responses of contrast cells are independent of the luminance ranges that define the contrast stimuli. (A) Response profiles of an example contrast cell to two 0–100% contrast stimuli that were generated by 0–100 cd/m^2 (dark response curve) and by 0–50 cd/m^2 luminance ranges (gray response curve) were almost identical. (B) Scatter plot of the peak response magnitudes of 55 contrast cells to the 2 contrast stimuli. Two responses (spikes/s) were highly correlated ($r = 0.96$, $P < 0.01$, slope = 0.99 (the dashed line), $n = 55$). The solid line is the diagonal line. Note that these cells responded significantly only to contrast.

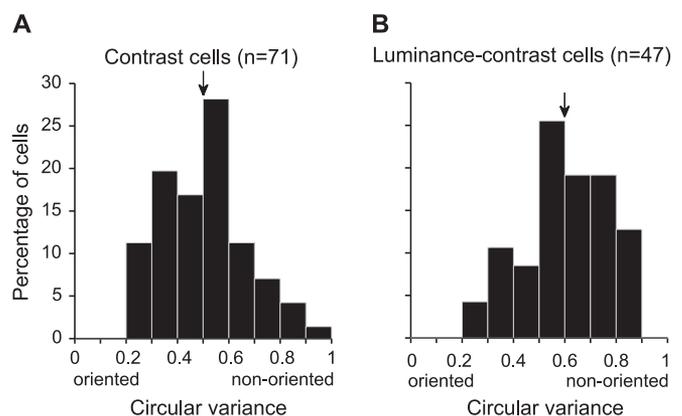


Figure 6. Orientation selectivity of contrast cells is significantly stronger on average than that of luminance-contrast cells. (A) Distribution of orientation tuning strength (CV) for 71 contrast cells. The arrow indicates the mean of $CV 0.50 \pm 0.17$ for the cells. (B) Distribution of orientation tuning strength (CV) for 47 luminance-contrast cells. The arrow indicates the mean of $CV 0.60 \pm 0.17$ for the cells. Oriented: cells having oriented responses; Nonoriented: cells having nonoriented responses.

luminance stimulus. To address this possibility, we compared the SF selectivity of contrast cells and luminance-contrast cells. A set of 117 cells were available for this analysis. They were tested with drifting gratings with SFs ranging from 0.1 to 2.0 c/d, the range of SFs normally seen in cat V1. The 0.1 c/d SF relative to the RF sizes of most V1 cells recorded in the study is comparable in spatial scale with the contrast stimulus generated from the 2 semicircles which were in area at least 5 times larger than the classical RF sizes in the current experiments. The preferred SF of contrast cells (0.59 ± 0.35 c/d, $n = 70$; Fig. 7A) was significantly higher on average than that of luminance-contrast cells (0.40 ± 0.22 c/d, $n = 47$; $P < 0.01$; Fig. 7B). The percentage of contrast cells having an optimal SF < 0.3 c/d (17%, 12/70) was significantly smaller than that of luminance-contrast cells (47%, 22/47; $P < 0.01$). Additionally, the SF tuning bandwidth of the former (0.36 ± 0.17 c/d, $n = 70$) was broader than that of the latter (0.26 ± 0.09 c/d, $n = 47$; $P < 0.01$). The relationship between the preferred SF and SF tuning bandwidth has been shown for cells in monkey V1 (see Fig. 10B of De Valois et al. 1982).

RF Maps of Luminance-Contrast Cells and Contrast Cells

To see whether the distinctions in responses of contrast cells and luminance-contrast cells to large uniform luminance and contrast stimuli are related to their classification as simple and complex cells or RF structure, we analyzed their modulated responses to drifting gratings and the spatiotemporal organization of their RF ON-OFF subregions (see Supplementary Material). Overall, we did not observe large differences in the classification of simple versus complex cells and in RF structure between luminance-contrast cells and contrast cells. The only observable difference was that luminance-contrast cells contained more temporally defined simple cells, namely those that had ON-OFF subregions largely overlapping in the spatial dimension and largely segregating in temporal dimension, than contrast cells (17%, 8/47 vs. 5%, 4/87, $P < 0.05$). The spatiotemporal organization of the RF ON-OFF subregions of most temporal simple cells in the sample (10/12) was separable and the 2 remaining luminance-contrast cells were spatiotemporally inseparable.

Another difference between the contrast cells and luminance-contrast cells was that the percentage of monococontrast cells that had a single ON or OFF subregion in their spa-

tiotemporal map was statistically lower in the contrast cells (11%, 11/98) than in the luminance-contrast cells (23%, 14/61; $P < 0.05$). Additionally the orientation selectivity of the monococontrast cells was relatively weaker (mean CV: 0.67 ± 0.14 , $n = 17$) than that of the simple, complex, and unclassified cells (mean CV: 0.52 ± 0.17 , $n = 101$, $P < 0.01$). It is possible that the cells having one single ON or OFF subregion and those temporal simple cells having segregated ON-OFF subregions in temporal dimension are more capable of carrying information about surface luminance change over time.

Finally, the average size of the RF of contrast cells at 25% height of the x -dimension profile, the region including both ON and OFF subregions ($2.35 \pm 0.99^\circ$, $n = 98$; $P < 0.01$; Fig. 8A), was significantly smaller than that of the luminance-contrast cells ($3.04 \pm 1.41^\circ$, $n = 61$; Fig. 8B). Thus, contrast cells and luminance-contrast cells can be distinguished not only based on their responses to luminance and contrast but also based on correlated differences in RF structure and size.

Contrast Polarity Selectivity of Luminance-Contrast Cells and Contrast Cells

Many contrast cells and luminance-contrast cells were selective for the contrast polarity of the stimulus, that is, their responses were dependent on the contrast polarity or phase (e.g., Fig. 2B, right profile). Thirty-five percent (49/142) of contrast cells and 22% luminance-contrast cells (24/111) showed a strong selectivity for the contrast polarity of the stimulus edge measured with the PSI (see Materials and Methods) > 0.33 , indicating that the responses were more than twice as strong to one contrast polarity compared with the other. Contrast cells were significantly larger in mean PSI than luminance-contrast cells (0.28 ± 0.23 , $n = 142$ vs. 0.21 ± 0.19 , $n = 111$; $P < 0.01$).

We compared PSI with OIS and OIT for 134 cells. For these cells, the PSI was weakly correlated inversely with the OIS ($r = -0.39$, $P < 0.01$) but not with the OIT ($r = 0.01$, $P > 0.05$). This relationship of PSI with OIS was further examined separately in contrast cells and luminance-contrast cells. The inverse correlation between PSI and OIS for contrast cells was significant ($r = -0.57$, $n = 87$, $P < 0.01$; Fig. 9A) but was not significant for the luminance-contrast cells ($r = -0.00$, $n = 47$, $P > 0.05$; Fig. 9B). The results illustrate that contrast responses of contrast cells are related to the spatial organization of RF ON-OFF subregions.

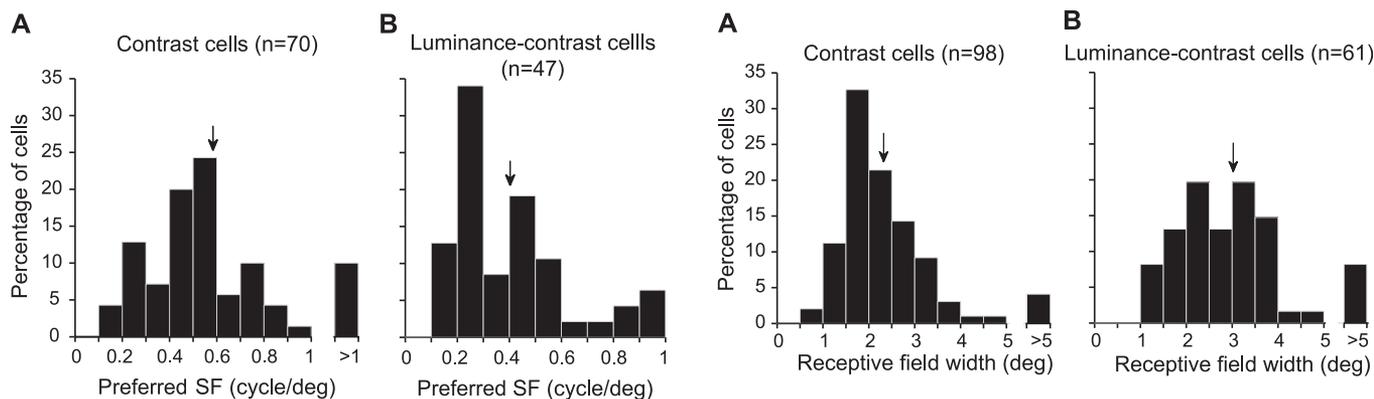


Figure 7. Spatial frequencies of luminance-contrast cells are significantly lower on average than that of contrast cells. (A) Distribution of the preferred SF for 70 contrast cells with the mean of 0.59 ± 0.35 c/d (arrow). (B) Distribution of the preferred SF for 47 luminance-contrast cells with the mean of 0.40 ± 0.22 c/d (arrow).

Figure 8. Luminance-contrast cells have significantly larger RFs on average than contrast cells. (A) Distribution of RF widths for 98 contrast cells with the mean of $2.35 \pm 0.99^\circ$ (arrow). (B) Distribution of RF widths for 61 luminance-contrast cells with the mean of $3.04 \pm 1.41^\circ$ (arrow). Note that the monococontrast cells having a single ON or OFF subregion were included in (A) and (B).

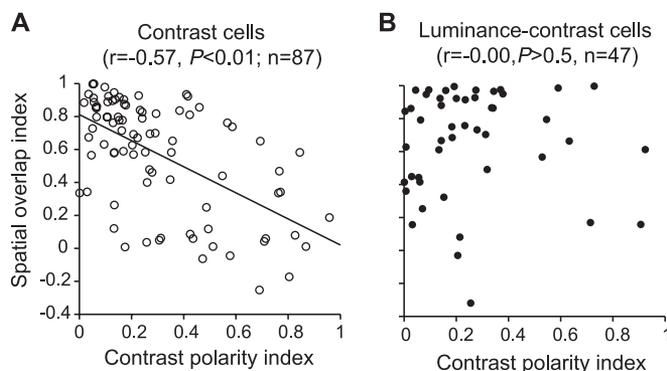


Figure 9. Contrast polarity selectivity of contrast cells is significantly correlated to spatial organization of ON-OFF subregions of their RFs but not for luminance-contrast cells. (A) Overlap indices of ON-OFF subregions in space of contrast cells were plotted against contrast PSIs. Abscissa represents contrast PSIs and ordinate represents spatial overlap indices (OISs) for 87 contrast cells. The correlation between these 2 parameters is significant ($r = -0.57$, $P < 0.01$) and the solid line represents the linear regression line with a slope of -0.79 , illustrating the trend that the more selective for contrast polarity a contrast cell is, the more segregated in spatial map its ON and OFF subregions are. (B) The same scatter plot for 47 luminance-contrast cells shows no correlation between the 2 indices.

Consistently, among monochromatic cells, the average PSI of contrast cells was larger than that of luminance-contrast cells (0.39 ± 0.17 , $n = 11$ vs. 0.11 ± 0.09 , $n = 14$, $P < 0.01$).

Discussion

Summary

This study was designed to explore the neural mechanisms underlying luminance representation in the primary visual cortex. Based on our stimulus design, which employed a large uniform luminance and contrast edge, we found a few cells responding only to luminance (luminance cells), many cells responding only to contrast (contrast cells), and many others responding to both luminance and contrast (luminance-contrast cells). These 3 classes of cells were, however, not trimodally distributed but fell along a continuum at population level. There were many more neurons responsive to the contrast edge than to surface luminance stimuli. We also showed that the luminance and contrast responses in V1 were largely independent not only within the population of luminance cells and of contrast cells but also within the responses of luminance-contrast cells (see Supplementary Material).

Importantly, our results also showed that these cell classes differed in several other respects. Luminance-contrast cells had broader orientation tuning (Fig. 6), lower SF preferences (Fig. 7), and larger RFs than contrast cells (Fig. 8). Contrast responses of contrast cells also were more linearly correlated to the spatial organization of RF ON-OFF subregions than those of luminance-contrast cells (Fig. 9). These distinctions may offer clues as to the different mechanisms used by these different categories of cells to generate their responses to uniform luminance and/or contrast. We consider these issues below in the light of what has been published by others.

Luminance Responses in Comparison with Previous Studies

V1 neurons in both cats and primates have been shown to be sensitive to static uniform luminance (Maguire and Baizer 1982;

Squatrito et al. 1990; Komatsu et al. 1996; MacEvoy et al. 1998; Kinoshita and Komatsu 2001; Friedman et al. 2003; Huang and Paradiso 2008) and to luminance sinusoidally modulated in time in a large uniform field (Rossi et al. 1996; Rossi and Paradiso 1999; Peng and Van Essen 2005; Roe et al. 2005; Hung et al. 2007). Within the confines of the stimulus luminance modulated continuously in a large field, most luminance-sensitive cells (79%, 92/117, Fig. 4) in cat V1 responded mainly to low luminance. The probability of stimulus samples in the sinusoidal change of luminance (dashed curve of Fig. 4) could explain the small peak at the high luminance of 90–100 cd/m^2 of Figure 4 but not fully explain the large peak at the low luminance of 0–10 cd/m^2 . This might be partially due to the fact that the modulation of the luminance relative to the background (50 cd/m^2) is much larger for the low luminance phase (0 cd/m^2) than for the high luminance phase (100 cd/m^2). The phenomenon of preferring dark luminance across a population of cells was also observed in the visual cortex of awake monkeys (Peng and Van Essen 2005). This strong bias in response to dark surface luminance relative to background could be related to the functional organization of ON and OFF signals in V1. It has been reported that OFF-center afferents predominate in the representation of the area centralis in layer 4 of cat V1 and that the number of neurons having predominant OFF signals is also greater in layers 2/3 of monkey V1 (Jin et al. 2008; Yeh et al. 2009). In human V1, functional magnetic resonance imaging signals in responses to decreasing luminance are stronger than to increasing luminance (Olman et al. 2008). This bias toward response to decreasing luminance over increasing luminance could explain the greater sensitivity and faster reaction times, in human, in detecting a decrease over an increase in luminance (Krauskopf 1980; Whittle 1986; Chubb et al. 2004; Badcock et al. 2005).

Moreover, our results also showed that the neurons sensitive to large uniform luminance also responded selectively to the orientation and SF of stimuli. Thus, their sensitivity to large uniform luminance does not negate their ability to respond to other aspects of stimuli. These luminance-sensitive cells could represent multiple features about objects, including surface luminance and contrast edges depending on the context. Their properties would allow them to detect not only surface luminance changes but also potentially changes in texture. In other contexts such as Craik-O'Brien-Cornsweet illusion, for example, the luminance-contrast cells with their RFs oriented along the contrast border of the illusory stimulus could signal the difference in luminance adjacent to the border which would be signaled by their contrast responses. By the mechanism of a border-to-surface shift in the relative timing of responses (Hung et al. 2007; Huang and Paradiso 2008), the correlated activity between these cells and those cells sensitive to luminance and having RFs located in the uniform flanks away from the border could signal the induced luminance change of the 2 flanking regions by their luminance responses.

Our current study suggests that cat V1 contains 2–4% luminance-only cells. Although the exact percentage of luminance-only cells might be affected by the potential misposition of the contrast stimulus relative to RFs of cells (Fig. 1 and Supplementary Fig. S3), we placed the contrast edge inside the most contrast-sensitive region of RFs based on the coordinates (x , y) of RF ON/OFF structure of the cells that were measured using the reverse correlation (see Materials and Methods and Supplementary Material), so that this possibility of

misposition was low for most of the cells we tested. In another related study (unpublished), we also found 4% (9/218) of our cells responded only to a uniform stimulus when we compared responses of cat V1 neurons to uniform surface luminance with those to 100% contrast sinusoidal gratings in a patch at least 5 times larger in area than an RF. Because in the latter study the large stimulus of contrast sine wave gratings completely covered the RF of a cell and contained 8 spatial phases relative to its RF center, there was no problem in mispositioning the contrast stimulus relative to the oriented ON/OFF structure of an RF. The 2 sets of data thus consistently suggest a low number (2–4%) of luminance-only cells in cat V1. A few early studies showed that 40% of V1 cells in squirrel monkeys and 24% V1 cells in macaques were responsive to diffuse continuous light (Bartlett and Doty 1974; Kayama et al. 1979), whereas in cat V1 this percentage was found to be only 2.2% (DeYoe and Bartlett 1980). Bartlett and Doty (1974) further showed that 16% of V1 cells in squirrel monkeys responded only to the diffuse continuous light. Therefore, in spite of differences between experimental designs, our results appear to agree with those of other investigators, showing that, unlike in primates, luminance-only cells are relatively rare in cat V1. It is possible that if electrodes are targeted at the low SF domains of V1 under the guidance of optical imaging of intrinsic signals (Shoham et al. 1997), more luminance-only cells will be found. Regardless of the exact percentage (which may be affected by sampling issue), the important thing is that we demonstrate that the luminance-only cells do exist in cat V1 (10 of 259 cells; Figs 2C and 3B) and are distinct from luminance–contrast cells and contrast-only cells. In principle encoding of luminance would not require a large number of neurons. The small population of luminance-only cells may be adequate to effectively represent uniform luminance. In the study of neural correlates of the perceived brightness, a small number of cells in cat V1 have been thought to substrate the representation of object surface brightness (Rossi et al. 1996; Rossi and Paradiso 1999). Moreover, it is important to keep in mind that luminance information is carried not only by the luminance-only cells but also by luminance–contrast cells which occur in much larger numbers and also are capable to providing information about surface luminance.

Independent Luminance and Contrast Processing

We showed that contrast responses were independent of luminance responses. Several previous results also revealed differences in responses of V1 neurons to luminance and contrast. The effects of stimulus size on cortical neuronal responses to uniform luminance stimulus were rather different from those to contrast grating stimulus and generally could not be predicted reliably from each other when both stimuli were presented statically (MacEvoy et al. 1998). Moreover, responses in monkey V1 to a uniform surface were delayed relative to those to the surface's border (Huang and Paradiso 2008). For stimuli wherein both local luminance and contrast were presented using drifting gratings, it has been shown that responses of neurons in cat V1 were strongly modulated by both the local mean luminance and the contrast but in an approximately separable manner (Geisler et al. 2007). Psychophysical studies in humans have also shown that luminance and contrast signals appear to be processed by separate mechanisms (Badcock et al. 2005; Allard and Faubert 2007). All of these studies support the conclusion that luminance and

contrast processing in the cortex involves independent mechanisms.

In interpreting our results, it may be helpful to distinguish between luminance changes over time and luminance changes across space which can be regarded as temporal contrast and spatial contrast, respectively. Measurements of independent cortical responses for luminance and contrast may require manipulating temporal and spatial contrast separately, as in our current study. Conversely, manipulating both together (e.g., drifting gratings) may lead to the dependence of contrast responses on luminance levels as described by Geisler et al. (2007). Moreover, local luminance and contrast in natural images have been found to be independent (Frazor and Geisler 2006) or dependent depending on spatial factors (Lindgren et al. 2008). With regard to the interaction between luminance and contrast, uniform luminance changes also have been shown to affect contrast processing (Huang and Paradiso 2005; Tucker and Fitzpatrick 2006) and visa versa (Roe et al. 2005; Hung et al. 2007). Taken together, these studies suggest that the independence or dependence of the cortical mechanisms for processing temporal and spatial contrast depends largely on visual context.

What is the benefit to visual perception of having independent machinery for luminance and contrast? Luminance and contrast are fundamental stimulus variables of images encoded by the visual system. Distributions of local luminance and contrast in natural images tend to be statistically independent (Mante et al. 2005; Frazor and Geisler 2006; Geisler 2008). The independence of luminance and contrast coding, we see in the cortex reflects these statistical distributions found in natural images. In the other words, we suggest that the responses of V1 neurons reflect the statistics of the stimuli they represent. Independent responses to luminance and contrast were predicted by the efficient coding hypothesis (Geisler 2008). Using this coding strategy, neurons responsive to both luminance and contrast can still detect contrast across variations in luminance and detect luminance across variations in contrast. Because these variations constantly occur in natural scenes, this strategy may be important in helping an animal navigating through its environment. This would aid perception in the presence of continuous changes in luminance and contrast. In fact, the perception of contrast in humans has been found to be constant across changes in luminance over a wide range of luminance values under natural viewing conditions (Peli et al. 1996). In human, local luminance noise has a greater impact on the detection of luminance than contrast, while local contrast noise has a greater impact on the detection of contrast than luminance (Allard and Faubert 2007).

Possible Mechanisms for Luminance Responses

We know that contrast responses are associated with orientation responses the generation of which is well understood (Priebe and Ferster 2008). Here, a key question is what mechanisms are responsible for generating responses of cortical cells to uniform luminance. At present this remains unclear although there are several likely scenarios.

Previous studies have suggested that the distinction between luminance and contrast processing begins at the retina and lateral geniculate nucleus (LGN) (Shapley and Enroth-Cugell 1984; Shapley and Lam 1993; Mante et al. 2005). Our findings show that luminance–contrast cells in cat V1 have larger RFs and

lower preferred SFs than contrast cells and that the contrast responses of contrast cells are more linearly correlated to RF spatial organization than luminance-contrast cells. Additionally, we have preliminary evidence (unpublished) showing that the preferred speeds of luminance-contrast cells are significantly higher than those of contrast cells (21.25 ± 15.44 degrees/s, $n = 25$ vs. 9.87 ± 5.75 degrees/s, $n = 34$; $P < 0.01$, t -test). These differences are reminiscent of the differences between the behaviors of cat retinal Y and X cells. Y cells have larger RFs and prefer lower SFs and higher speeds than X cells and X cells display linear spatial summation, whereas Y cells do not. These differences are also seen in LGN Y and X cells. In addition, a portion of retinal and LGN W cells have relatively large RFs, low spatial resolution, and nonlinear spatial response properties (see Sherman and Spear 1982; Shapley and Lennie 1985; Shapley and Perry 1986; Troy and Shou 2002; Van Hooser et al. 2005). That Y cells tend to exhibit more transient response than X cells is also consistent with that the finding that luminance-contrast cells prefer temporal frequencies higher than those of contrast cells. One possible hypothesis underlying the relationships between LGN and V1 cells in regard to these response properties is that luminance-contrast cells mainly receive inputs from LGN Y and a portion of LGN W cells, while contrast cells mainly receive inputs from LGN X cells. That cat retinal Y cells respond vigorously to diffuse light (Fukada 1971; Hochstein and Shapley 1976; Shapley and Perry 1986) also supports the idea. By this argument, however, we do not mean that luminance-contrast cells only receive Y-like inputs and contrast cells only receive X-like inputs. It is possible that X-like inputs contribute to contrast responses of contrast cells and luminance-contrast cells more than Y-like inputs, while Y-like inputs contribute to luminance responses of luminance-contrast cells more than X-like inputs. It is quite possible that the large melanopsin-containing intrinsically photosensitive retinal ganglion cells having large dendrites (Dacey et al. 2005; Semo et al. 2005) also contribute to the responses to large uniform luminance.

On the other hand, LGN cells receive most of their retinal inputs from one or a very small number of retinal axons (Van Horn et al. 2000) and their RF organizations are almost identical to that of their retinal inputs (DeAngelis et al. 1995). In addition, it is the general consensus that LGN cells weakly respond to large stimuli in comparison to small stimuli, although a full-field luminance change can elicit responses from LGN cells (Reinagel and Reid 2000; Sherman 2001; Tucker and Fitzpatrick 2006) which might be simply because the center mechanism is stronger than the surround one. These facts imply that the independent responses of cortical cells to the temporally modulated luminance or contrast in a large field might be largely generated in the cortex. The process must rely on convergent inputs of many LGN cells that signal an increment or a decrement in local luminance or contrast. The ON and OFF signals originating from retinal bipolar cells have been demonstrated to remain largely segregated until they converge on single cortical cells (Schiller 1992; Martinez et al. 2005; Jin et al. 2008) and contribute to the perceptual detection of light increments and decrements (Schiller 1992). Thus, it seems likely that the independent responses to luminance and contrast we see reflect a combination of the originally separate ON and OFF signals seen subcortically with biases in different LGN X, Y, and W channels, as well as, a direct cortical contribution.

Regarding cortical contributions, another possibility is that these differences reflect the contribution of the RF far surround

in setting spike thresholds at the center of an RF of a cortical cell. It is known that stimulation of the far surround can enhance or suppress the responses to a centrally presented stimulus. One hypothesis is that subthreshold potential inputs from the far surround activated by a luminance change in a large uniform region may enhance intracellular membrane potentials evoked by a luminance changes inside an RF or may reduce the membrane potential to fall below the threshold. This enhancement would result in luminance-contrast cells and luminance cells, which increase their response to a large uniform luminance stimulus, while the suppression would occur in contrast cells unresponsive to uniform luminance. Actually both facilitative and suppressive effects of a large uniform stimulus on the responses of V1 cells have been observed (Komatsu et al. 1996; MacEvoy et al. 1998). Similarly, facilitative effects of contrast in the far surround of the classical RF (MacEvoy et al. 1998) could enable contrast cells and luminance-contrast cells to respond to a large contrast stimulus, and suppressive effects enable luminance cells not to respond to the large contrast stimulus. These neural processes then could eventually result in the different responses to a large uniform luminance stimulus or a contrast stimulus among these cells. In order to be effective, this far surround mechanism would be expected to recruit LGN feedforward, V1 horizontal, and extrastriate feedback connections as all of these connections are involved in these interactions. Among the 3 sources, the intrinsic long-range horizontal connections of V1 may play a central role in the transmission of the facilitative and suppressive signals from the surround to the center.

It is interesting in light of the above proposal that horizontal connections in V1 have been proposed to be involved in the process of the contrast edge-induced brightness (Komatsu et al. 1996, 2000, 2002; Roe et al. 2005; Hung et al. 2007; Huang and Paradiso 2008). This induced brightness plays a primary role in object brightness perception (Reid and Shapley 1988). These facts also raise a final possibility that luminance responses of luminance cells and luminance-contrast cells are generated first from responses to the difference in luminance at the proximal contrast edge and then propagated away from the edge to the uniform luminance region (Hung et al. 2007; Huang and Paradiso 2008) through the long-range horizontal connections in V1 (Gilbert and Wiesel 1983, 1989; Bringuier et al. 1999; Smith and Kohn 2008). Cortical circuitry may play a role in this processing (Komatsu et al. 2000, 2002; Roe et al. 2005; Hung et al. 2007). However, the horizontal spread of luminance information from the contrast edge to the surface interior is a relatively slow process (Huang and Paradiso 2008), which cannot account for the perception of surface luminance in the case of rapid eye movements. Presumably multiple mechanisms are involved in generating responses of cortical cells to uniform surface luminance that depends on context under conditions of natural viewing.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>

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Notes

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