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Are primate lateral geniculate nucleus (LGN) cells really sensitive to orientation or direction?

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Abstract

There is considerable controversy over the existence of orientation and direction sensitivity in lateral geniculate nucleus (LGN) neurons. Claims for the existence of these properties often were based upon data from cells tested well beyond their peak spatial frequencies. The goals of the present study were to examine the degree of orientation and direction sensitivity of LGN cells when tested at their peak spatial and temporal frequencies and to compare the tuning properties of these subcortical neurons with those of visual cortex. For this investigation, we used conventional extracellular recording to study orientation and direction sensitivities of owl monkey LGN cells by stimulating cells with drifting sinusoidal gratings at peak temporal frequencies, peak or higher spatial frequencies, and moderate contrast. A total of 110 LGN cells (32 koniocellular cells, 34 magnocellular cells, and 44 parvocellular cells) with eccentricities ranging from 2.6 deg to 27.5 deg were examined. Using the peak spatial and temporal frequencies for each cell, 41.8% of the LGN cells were found to be sensitive to orientation and 19.1% were direction sensitive. The degree of bias for orientation and direction did not vary with eccentricity or with cell class. Orientation sensitivity did, however, increase, and in some cases orientation preferences changed, at higher spatial frequencies. Increasing spatial frequency had no consistent effect on direction sensitivity. Compared to cortical cell orientation tuning, the prevalence and strength of LGN cell orientation and direction sensitivity are weak. Nevertheless, the high percentage of LGN cells sensitive to orientation even at peak spatial and temporal frequencies reinforces the view that subcortical biases could, in combination with activity-dependent cortical mechanisms and/or cortical inhibitory mechanisms, account for the much narrower orientation and direction tuning seen in visual cortex.

Keywords: Owl monkey, Magnocellular, Parvocellular, Koniocellular, Receptive fields

Introduction

Since the pioneering work of Hubel and Wiesel (1962, 1968), the properties of orientation and direction tuning in cortical neurons have been some of the most intensively investigated receptive-field attributes in the nervous system. The properties of orientation and direction tuning also have been identified as fundamental properties for neurons in the mammalian visual system, because these properties are likely to be critical to the perception of form and motion. In spite of the volume of data published regarding the neural processes involved in orientation and direction selectivity, the underlying neural mechanisms are still not fully understood (see Vidyasagar et al., 1996; Ferster & Miller, 2000 for review).

Most of the models proposed to account for cortical orientation selectivity assume that the properties of orientation and direction selectivity emerge within cortex and do not exist in the subcortical inputs to cortical neurons (Ferster & Miller, 2000; Alonso et al., 2001). Nevertheless, a growing number of studies in cats and macaque monkeys have shown that some LGN relay cells are sensitive to stimulus orientation or direction (Vidyasagar & Urbas, 1982; Vidyasagar & Heide, 1984; Soodak et al., 1987; Shou & Leventhal, 1989; Smith et al., 1990; Jones & Sillito, 1994; Thompson et al., 1994*a*; Zhou et al., 1995). Most of those studies, however, tested LGN cell orientation sensitivity by using much higher than peak spatial frequencies, close to the cells' cutoff thresholds, where response rates are low. Thus, it has been argued that the reports of orientation and direction bias within LGN cells

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are an artifact of the stimulus conditions (e.g. Chapman et al., 1991). Moreover, none of the studies in primates reporting on orientation or direction sensitivity in LGN cells made direct comparisons between the degree of LGN and visual cortical tuning under similar conditions.

In the present study, we used owl monkeys (*Aotus trivigatus*) to examine orientation and direction sensitivities of LGN cells. Owl monkeys are New World nocturnal simian primates with a well-developed visual system. We had three specific questions: (1) How sensitive are LGN cells to orientation and direction tested at their peak spatial and temporal frequencies? (2) How do other properties such as eccentricity and spatial frequency affect orientation and direction tuning in LGN neurons? (3) How selective are LGN cells to orientation and direction in comparison to cells in primary visual cortex (V1)?

Some of the findings reported here were published previously in abstract form (Xu et al., 2000).

Method and materials

General procedures

Standard extracellular electrophysiological methods were used. Recordings were made with 5–10 MΩ Parylene-coated tungsten electrodes (FHC Inc., Bowdoinham, ME) in paralyzed, anesthetized animals. A total of 11 adult owl monkeys were used for the present study. We recorded directly from LGN cells in nine owl monkeys. In the remaining two monkeys, recordings were made from LGN cell afferent axons in primary visual cortex (V1) where intrinsic neuronal activity was inhibited by the $GABA_A$ agonist muscimol (Chapman et al., 1991; Boyd et al., 1998; Xu et al., 2001). All monkeys were handled and cared for according to the National Institutes of Health Guide for the Care and Use of Animals under an approved protocol from the Vanderbilt University Animal Care and Use Committee. Details concerning the surgical preparation, V1 silencing procedures, and physiological maintenance of the monkeys are provided in an earlier paper (Xu et al., 2001). In brief, monkeys were anesthetized with halothane during surgical removal of the skull overlying either the LGN or V1. Following surgery, the monkeys were paralyzed with an intravenous injection of 1–1.5 mg/kg vecuronium bromide (Norcuron) and artificially ventilated with a mixture of 75% N_2O, 23.5% O_2, and 1.5% CO_2 delivered at a rate sufficient to maintain the peak end tidal CO_2 level at 4%. Paralysis and anesthesia were maintained by intravenous infusion of vecuronium bromide (0.2 $mg \cdot kg^{-1} \cdot h^{-1}$) and sufentanil citrate (Sufenta: 12–15 $\mu g \cdot kg^{-1} \cdot h^{-1}$) mixed in 5% dextrose lactated Ringer's delivered at a rate of 2.7 ml/h. To ensure that adequate levels of anesthesia were maintained throughout the experiment, heart rate, CO_2 levels, and EEG activity were monitored continuously after paralysis. If the animal exhibited any signs (fluctuating heart rate, CO_2, or low voltage fast EEG records) indicating that the anesthesia levels were inadequate, the percentage of Sufenta in the infusion line was immediately increased.

Pupils were dilated with atropine eye-drops (1% ophthalmic atropine sulfate). Individually fitted clear gas-permeable contact lenses were used to bring the retina into focus with the viewing screen located at 57 cm in front of the monkey. In some animals, lenses with 3.0 mm artificial pupils were used. No differences were seen in degree of sensitivity for orientation or the percentage of cells that were sensitive to orientation between monkeys in which pupils were used and those in which they were not used. Retinal landmarks (optic disk and area centralis) were projected onto a plotting screen with a reversible ophthalmoscope.

Visual stimulation and data acquisition

The receptive fields of units were first plotted by manually controlled stimuli displayed on a tangent screen. Eye dominance was then determined and the receptive-field center boundaries were drawn. Appropriate corrections were made for all receptive fields to convert receptive-field size and distance from the projections of the area centralis to degrees of retinal angle.

Stimuli consisted of drifting sine-wave gratings presented at different spatial and temporal frequencies, contrasts, and orientations. Stimuli were generated by an image-processing board (Pepper PRO 1280) with a capacity of 1,024 × 1,280 pixels by 8 bits of modulation and presented on a CRT screen that subtended an angle of 10 deg with a background luminance of 110 cd/m^2. This level is likely to be in the photopic range for these animals. Data were collected, and data analysis was achieved primarily through construction of 2-s, 128 bin/s poststimulus time histograms. The interleaved histogram technique of Henry et al. (1973) with randomization was employed to reduce artifacts from the inherent nonstationarity of the visual system. A stimulus set was specified and comprised each measured condition as well as a null condition (a blank screen at the mean luminance of the gratings) to assess the maintained discharge. Each element in the stimulus set was presented once in random order with a 1-s blank screen interval between each stimulus presentation. Presentation of the stimulus set was then repeated in a random order until each stimulus condition had been tested completely (5–10 times). With 4-s presentation periods, data are based on 20–40 s of averaging for each condition. The poststimulus time histograms for each cell were Fourier transformed and subsequently analyzed. The responses to the gratings were defined as the amplitude of the fundamental Fourier component. The peak or "optimal" response for the cell for each parameter was defined as the maximum amplitude response for that parameter. For this study, the following receptive-field properties were measured for each cell: sensitivity to a range of spatial and temporal frequencies, sensitivity to stimulus orientation and direction (described below), and response to contrasts varied from 3% to 56% contrast. Data about the spatial and temporal resolution and contrast sensitivity of different classes of owl monkey LGN cells were reported earlier (Xu et al., 2001).

Orientation and direction sensitivities were tested by presenting a series of drifting sinusoidal gratings at different orientation angles at the cell's peak and/or higher spatial frequencies and at its peak temporal frequency with a moderate contrast (i.e. 28%). By definition, the orientation of each grating is orthogonal to its direction of movement. Since each orientation can have two directions of movement, the 0–360 deg stimulus set represents 180 deg of orientation and two directions for each orientation. Gratings of orientation 0 deg drift downward (with a drift direction of 270 deg) and gratings of orientation 90 deg drift leftward (with a drift direction of 0 deg). For each cell, we initially measured orientation and direction sensitivity using a global test with 12 "angles" at 30-deg increments over the entire 360-deg range (i.e. 6 orientations and 2 directions for each orientation). A more refined test of local orientation/direction tuning was then performed using more closely spaced angles centered on the peak orientation based on the results of the global test. Typically, nine to

18 angles with 10-deg increments around the cell's peak orientation/direction were examined. For each angle in the global and local test, 20–80 cycles of grating stimuli were drifted across the receptive field to compile the tuning curves.

Data analysis

The preferred orientation, direction, and a measure (index) of the degree of orientation and direction sensitivity were calculated for each cell using statistical methods described in Batschelet (1981) and Zar (1999). These methods have been used in calculations of the orientation and direction sensitivity in both retinal ganglion cells (Levick & Thibos, 1980, 1982) and in LGN cells (Shou & Leventhal, 1989; Smith et al., 1990; Thompson et al., 1994*a*,*b*). According to these methods, responses of each cell to different orientations and directions are stored as vectors. The vectors are added and then divided by the sum of the absolute values of the vectors. The resultant vector length, termed the orientation or direction bias, provides a measure of the degree of orientation and direction sensitivity of each cell. Mathematically, the response amplitude for different orientations can be represented in phasor notation as $R_o = r * \exp(j * 2\theta)$, where the response amplitude (R_o) for an orientation (θ) is described by a vector with a length of r at an angle of 2θ, j is the square root of -1. The degree of orientation sensitivity can be summarized by the mean response vector for all stimulus orientations. The normalized resultant vector phasor for all the orientations can be computed by $\Sigma R_o/\Sigma r$, and represented by $A * \exp(j * 2\theta_{po})$, where the resultant normalized amplitude (A) of the phasor can be used as an orientation-bias index, and the angle θ_{po} is the preferred orientation. In like manner, the response amplitude for directions (R_d) can be represented in phasor notation as $R_d = r * \exp(j * \theta)$. The normalized resultant vector phasor for all stimulus directions can be computed by $\Sigma R_d/\Sigma r$, and represented by $B * \exp(j * \theta_{pd})$, where the resultant normalized amplitude (B) of the phasor can be used as the direction-bias index, and the angle θ_{pd} is the preferred direction. In this calculation, the orientation or direction indices can range from 0 to 1.0, with 0 being completely nonoriented or insensitive to orientation or direction, and 1.0 indicating response to only a single orientation or direction. We defined LGN cells as orientation or direction sensitive if they exhibited an index of $\geq$0.08 when tested with gratings at the cells' peak spatial and temporal frequencies and at moderate contrast. An orientation- or direction-bias index of 0.08 or greater indicates that the distribution of the cell's response to the stimulus differs significantly from a random distribution, that is, the cell's responses are clustered about some angle (Rayleigh test, $P < 0.05$). An index of $\geq$0.1 indicates a high degree of sensitivity (Rayleigh test, $P < 0.005$). Since it had previously been reported that orientation sensitivity of LGN cells is strongest at high spatial frequencies near the cell's spatial-frequency cutoff (Shou & Leventhal, 1989; Smith et al., 1990; Thompson et al., 1994*a*,*b*), and since that direction sensitivity may be affected by spatial frequency (Thompson et al., 1994*a*,*b*), we also examined the impact of spatial frequency on orientation and direction bias in the present study.

The fundamental components of the Fourier-transformed cell responses were plotted to obtain each orientation tuning curve. These curves were displayed graphically on either polar plots where the cell responses were represented as the radial amplitudes of vectors at the angular coordinates corresponding to the orientations and directions of stimulus, or a rectilinear plot of response amplitude versus stimulus orientation.

Histology

The position of each recorded cell was noted by the depth indicated on the microdrive. At least two electrolytic lesions (5 μA $\times$ 5 s) were made to mark the location of each electrode track to aid in reconstruction of cell locations and to calculate tissue shrinkage. Using methods described in detail earlier (Xu et al., 2001), the laminar location of each cell in the LGN or axon in cortex was reconstructed from serial sections. For reconstructions, sections were stained alternately for Nissl bodies and cytochrome oxidase to show the magnocellular (M) and parvocellular (P) LGN layers and the layers of V1, and immunostained for calbindin to reveal the koniocellular (K) LGN cells.

Results

Our chief finding is that a significant fraction of the LGN cells were sensitive to stimulus orientation (41.8%) or direction of movement (19.1%) under peak stimulus conditions for each cell tested. In the results presented below, we begin by describing the general characteristics of orientation and direction sensitivity in the LGN. Next, we consider the impact of spatial frequency on the sharpness of tuning and on orientation and direction preference. Finally, we compare the selectivity for orientation and direction found in the LGN with that found in visual cortex.

General characteristics of orientation and direction sensitivity

Results are based upon quantitative examination of orientation and direction sensitivity in 110 LGN units that included 104 LGN cells and six LGN afferent axons recorded from silenced V1. Average orientation and direction sensitivities recorded from cells did not differ from those recorded from afferent axons. Based upon reconstructions, 32 of the units recorded were K cells, 34 were M cells, and 44 were P cells. The receptive-field eccentricities of the cells studied ranged from 2.6 deg to 27.5 deg.

The distribution of indices for orientation sensitivity and direction sensitivity tested at peak spatial and temporal frequencies are shown in Figs. 1A and Fig. 1B, respectively. The orientation-bias indices ranged from 0.009 to 0.477, and the direction-bias indices from 0.001 to 0.311. The mean orientation-bias index was 0.095 ($\pm$ 0.081, SD), median 0.07; for direction bias the mean was 0.055 ($\pm$ 0.052), median 0.04. There was a weak but significant correlation between orientation bias and direction bias ($r = 0.22$, $P = 0.02$).

When cells were tested at their peak spatial and temporal frequencies, the orientation bias was 0.112 $\pm$ 0.10 (median 0.07) for P cells, 0.083 $\pm$ 0.063 (median 0.064) for M cells, and 0.084 $\pm$ 0.053 (median 0.08) for K cells. The mean orientation biases for P, M, and K cells did not differ significantly (one-way ANOVA, $P = 0.20$). The direction bias was 0.054 $\pm$ 0.054 (median 0.039) for P cells, 0.051 $\pm$ 0.049 (median 0.039) for M cells, and 0.062 $\pm$ 0.051 (median 0.049) for K cells. The mean direction-bias indices for P, M, and K cells also did not differ significantly (one-way ANOVA, $P = 0.65$).

Based upon sensitivity, our sample of LGN cells could be divided into four categories similar to those described previously (Thompson et al., 1994*a*): (1) cells with orientation sensitivity but without direction sensitivity; (2) cells with direction sensitivity but not orientation sensitivity; (3) cells with both orientation and direction sensitivity; (4) cells with neither orientation nor direction

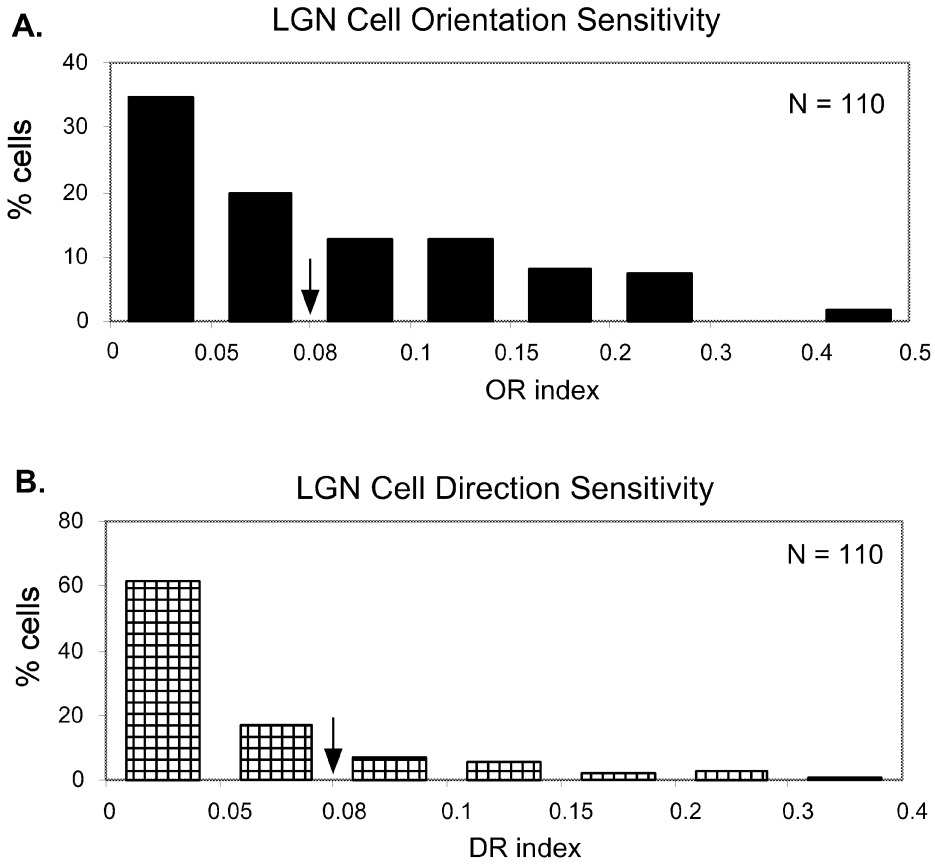

Fig. 1. Distributions of orientation-bias (OR) and direction-bias (DR) indices from 110 LGN units. The orientation-bias index ranged from 0.009 to 0.477; the direction bias from 0.001 to 0.311. The mean bias index for orientation is 0.095 (± 0.081, SD), median 0.07; for direction the mean bias is 0.055 (± 0.052), median 0.04. The arrows in the graphs point to the threshold value (0.08) for significant orientation and direction sensitivity. See text for details.

sensitivity. Fig. 2 illustrates the orientation response functions of four representative LGN cells, one from each category. Fig. 2A shows an ON-center P cell that exhibited obvious orientation tuning. Although it showed good orientation sensitivity with an orientation-bias index of 0.41 and a preferred orientation at 85 deg/265 deg, it showed little directional preference (direction-bias index 0.03). Approximately one-third (34 out of 110) of the sample population fell into this category, including ten K, eight M, and 16 P cells. Fig. 2B shows another ON-center P cell with poor orientation sensitivity (orientation-bias index 0.05) but with good direction sensitivity (direction-bias index of 0.23; preferred direction at 110 deg). Only nine out of the 110 cells fell into this category (3 K, 1 M, and 5 P cells). Fig. 2C shows an OFF-center M cell that was well tuned for both orientation and direction (orientation-bias index 0.15, preferred orientation at 64 deg/244 deg; direction-bias index 0.25, preferred direction at 41 deg). A small minority, 12 out of 110, of the population fell into this category (5 K, 4 M, and 3 P cells). Finally, Fig. 2D shows an OFF-center K cell which showed no bias for either orientation or direction (orientation-bias index 0.02 and direction-bias index 0.02). Half of the population (55 out of 110) fell into this category (14 K, 21 M, and 20 P cells).

When tested at their peak spatial and temporal frequency, all but five of the LGN cells (29 out of 34) that showed orientation sensitivity without direction sensitivity had their preferred orientations within 20 deg of either a horizontal (0 deg/180 deg) or vertical (90 deg/270 deg) orientation. Seven out of the nine LGN cells, that were exclusively sensitive to direction, preferred horizontal directions (0 deg or 180 deg). For those cells that exhibited biases for both orientation and direction, ten out of 12 had preferred orientations around horizontal (0 deg/180 deg) or vertical (90 deg/270 deg). Of the latter cells, nine of 12 had orthogonal preferred orientations and directions; the remaining three exhibited nonorthogonal preferences.

The orientation and direction biases of LGN cells did not vary with the eccentricity of the receptive field with a nonsignificant correlation between LGN cell orientation/direction-bias index and receptive-field location (orientation bias, $r = 0.22$, $P = 0.065$; direction bias, $r = -0.09$, $P = 0.223$).

Effects of spatial frequency

Orientation sensitivity of LGN cells is reported as strongest at high spatial frequencies near the cell's spatial-frequency cutoff (Vidyasagar & Heide, 1984; Shou & Leventhal, 1989; Smith et al., 1990; Thompson et al., 1994*a*), and that direction sensitivity improves at lower spatial frequencies (Thompson et al., 1994*a*). We found a similar effect. Fig. 3 shows an ON-center M cell that exhibited changes in orientation and direction sensitivities with higher spatial frequencies. Fig. 3A shows the LGN cell's spatial-

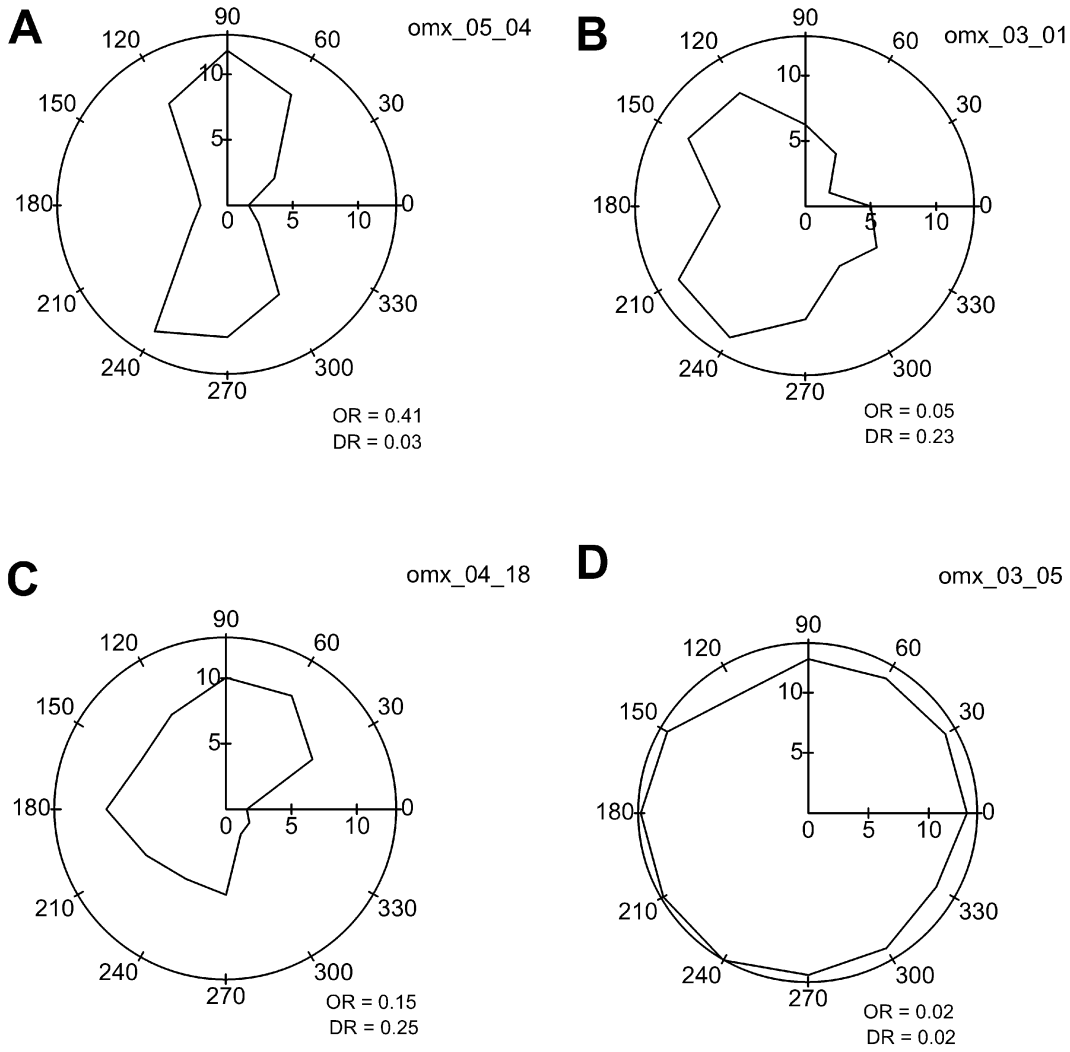

Fig. 2. Examples of orientation and direction sensitivity for four neurons whose numbers are indicated by omx_#_#. All cells shown were tested at their peak spatial and temporal frequencies at moderate contrast (28%). The data are plotted in polar coordinates, where the distance from the origin represents the amplitude of the fundamental Fourier response component in spikes/s, the angles correspond to stimulus orientation and the direction of drift. Gratings of orientation 0-deg drift downward (with a drift direction of 270 deg) and gratings of orientation 90-deg drift leftward (with a drift direction of 0 deg). **A:** A P ON-center cell that exhibited good orientation sensitivity with an OR index of 0.41 and a preferred orientation at 85 deg/265 deg, but without obvious direction sensitivity (DR index 0.03). **B:** A P ON-center cell that demonstrated good direction sensitivity with a DR index of 0.23 and a preferred direction at 110 deg, but not much orientation sensitivity (OR index 0.05). **C:** An M OFF-center cell that exhibited both orientation and direction sensitivity. Its OR index was 0.15 with a preferred orientation of 64 deg/244 deg, and its DR index was 0.25 with a preferred direction of 41 deg. **D:** A K OFF-center which exhibited neither orientation nor direction sensitivity (OR index 0.02 and DR index 0.02).

frequency tuning curve with a peak spatial frequency at 0.4 cycles/degree (c/deg), and a cutoff close to 3.2 c/deg. As shown in Fig. 3B, when the cell was tested at its peak spatial frequency of 0.4 c/deg, it did not show significant orientation or direction sensitivity with an orientation-bias index of 0.07 and direction-bias index of 0.03. When the cell was retested at twice its peak spatial frequency (0.8 c/deg), it exhibited both orientation and direction sensitivity with an orientation-bias index of 0.17 and a direction-bias index of 0.10 (preferred orientation at 78 deg/258 deg and preferred direction at 161 deg), as shown in Fig. 3C. Then based upon the global tuning curve, we centered on the firing response peak of 240 deg with 10-deg increments to test the same cell's local tuning curve. The local curve of the cell shown in Fig. 3D indicates its peak orientation response was around 240 deg, but the tuning curve was broad. As seen in Figs. 3E and 3F, when the cell was tested at three times its peak spatial frequency (1.2 c/deg), it showed much stronger tuning with an orientation-bias index of 0.36 and a direction-bias index of 0.082 (preferred orientation at 78 deg/258 deg and preferred direction at 109 deg). The local tuning curve at three times its peak spatial frequency produced a peak orientation response at 240 deg. With higher spatial frequencies, the cell's orientation and direction sensitivity got stronger, but its peak response rate dropped from 30 spikes/s at its peak spatial frequency, to 24 spikes/s at twice the peak spatial frequency, and to 15 spikes/s at three times the peak spatial frequency. This suggests that the increased tuning may simply reflect the loss of response at neighboring nonpeak orientations and directions (i.e. tip-of-the-iceberg effect).

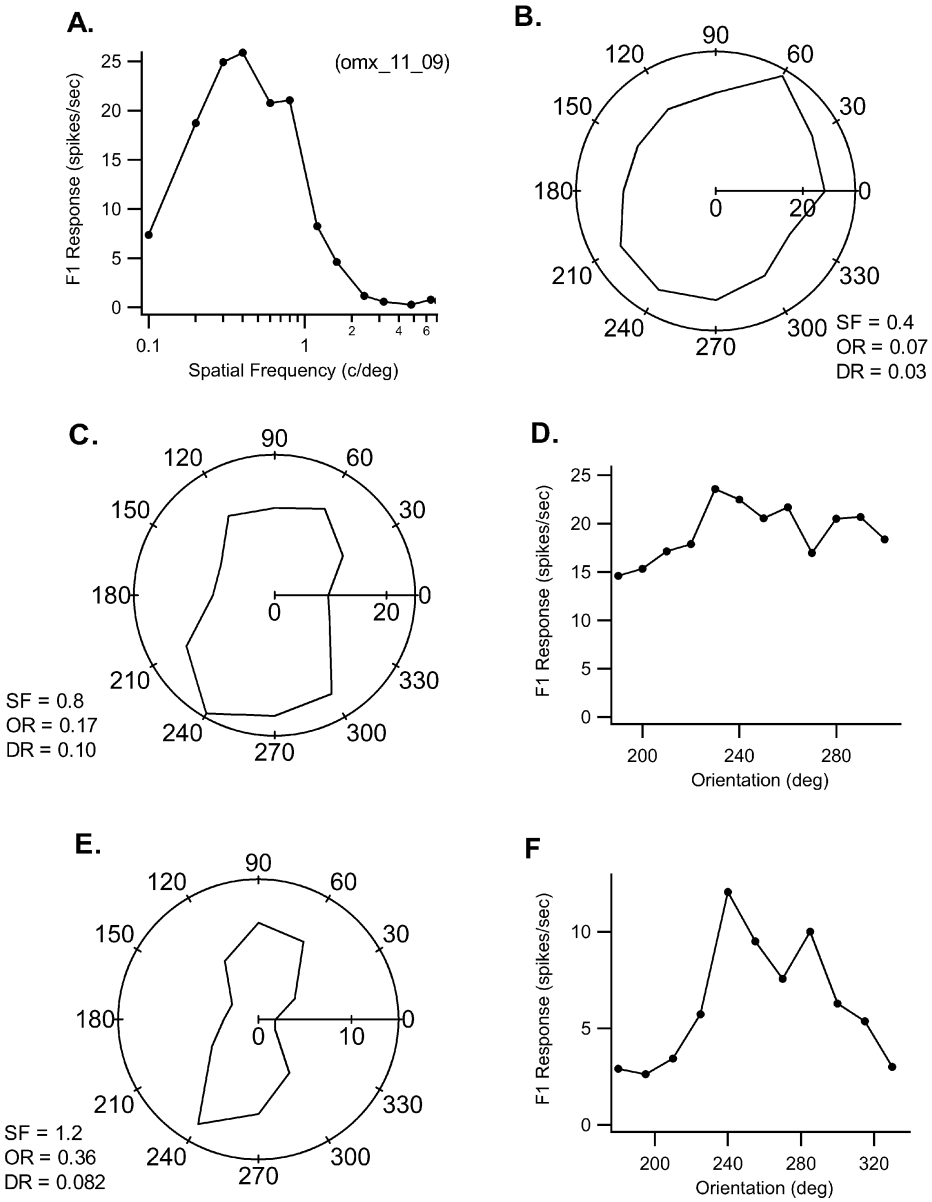

Fig. 3. Effects of higher spatial frequencies on LGN cell orientation and direction sensitivity. **A:** The spatial-frequency tuning curve for an ON-center M cell. This cell had a peak spatial frequency at 0.4 cycles/deg (c/deg) and a cutoff around 3.2 c/deg. **B:** The orientation-response function for the same cell tested at its peak spatial frequency of 0.4 c/deg. Note that at its peak spatial frequency this cell shows no orientation sensitivity with an OR index of 0.07 and no direction sensitivity with a DR index of 0.03. **C:** When this cell is tested at twice its peak spatial frequency (i.e. 0.8 c/deg), the global tuning curve is narrower with a peak at 240 deg. The cell showed significant sensitivities to both orientation and direction with an OR index of 0.17 with its preferred orientation at 78 deg/258 deg, and a DR index of 0.10 with a preferred direction at 161 deg. **D:** A rectilinear plot of response versus stimulus orientation for this cell's local orientation tuning curve tested with 10-deg angle increments centered on 240 deg. The peak response is around 240 deg. **E:** The polar plot for the cell's global tuning curve at three times its peak spatial frequency. Although the overall response of the cell drops, the orientation tuning sharpens with a peak remaining at 240 deg. Its OR index is 0.36 with the cell's preferred orientation at 78 deg/258 deg. Its DR index is 0.082 with a preferred direction of 109 deg. **F:** A local test of this cell's orientation sensitivity at three times peak spatial frequency. The peak response is at 240 deg. Other conventions are as in Fig. 2.

Although the cell in Fig. 3 showed the same preferred orientation with different spatial frequencies, we also found that for some cells, spatial frequency could affect the preferred orientation. Fig. 4 shows a cell that exhibited different preferred orientation and direction sensitivities with different spatial frequencies. Fig. 4A shows the spatial-frequency tuning curve of an M cell. The peak spatial frequency was at 0.6 c/deg, and the cutoff was close to 5 c/deg. In Fig. 4B, when the cell was tested at its peak spatial frequency of 0.6 c/deg, it showed orientation sensitivity and broad tuning with an orientation-bias index of 0.14 and a direction-bias index of 0.079. Its preferred orientation was at 45 deg/225 deg. Fig. 4C shows the local tuning curve centered on 240 deg for the

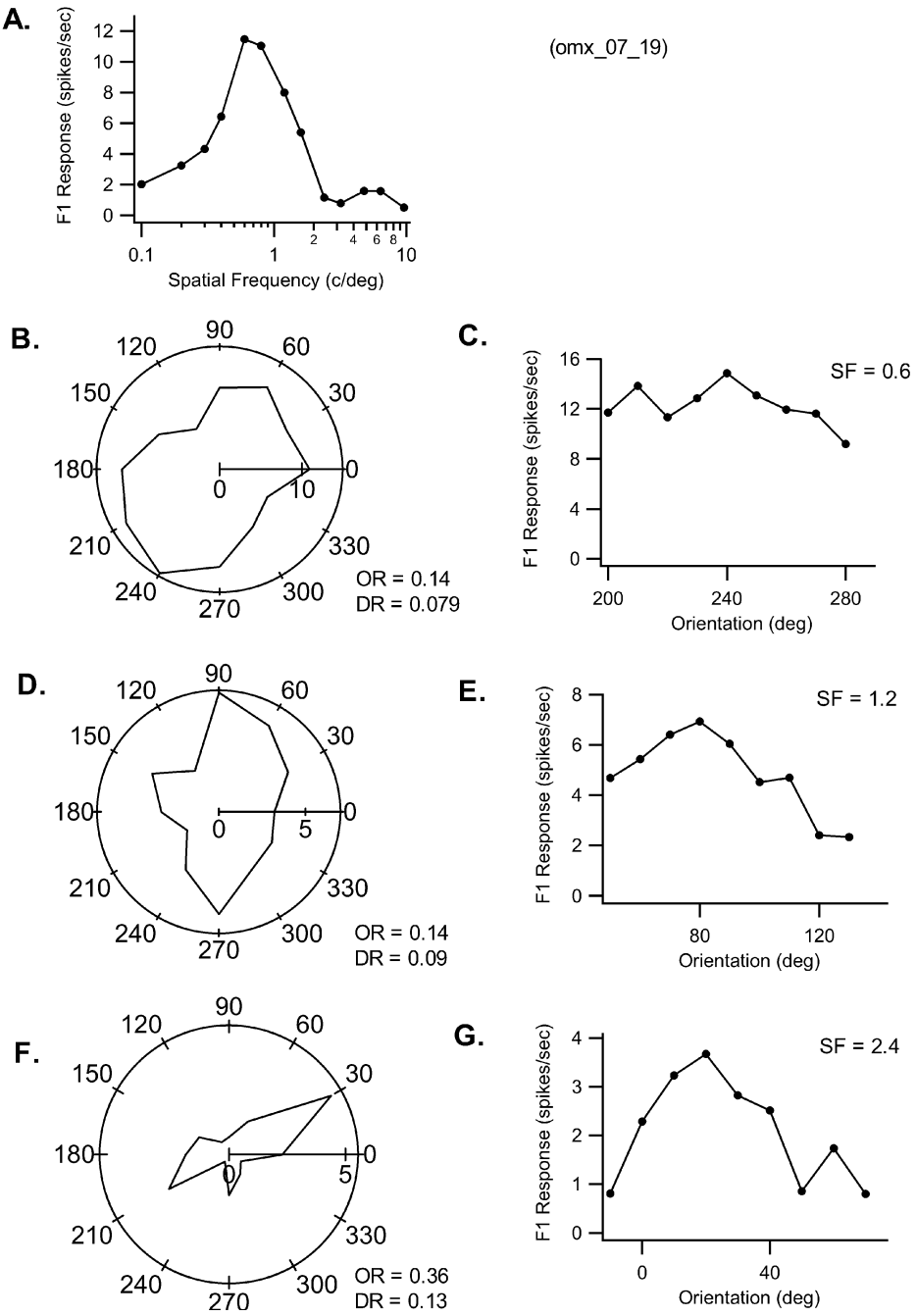

Fig. 4. Orientation and direction preferences can shift at higher spatial frequencies. **A:** The spatial-frequency tuning curve of an ON-center M cell. This cell had a peak spatial frequency at 0.6 c/deg and a cutoff around 5 c/deg. **B:** The orientation-response function in polar coordinates for this same cell tested at its peak spatial frequency of 0.6 c/deg. The cell's peak response is at 240 deg. Its OR index is 0.14 with a preferred orientation at 45 deg/225 deg, and its DR index is 0.079. **C:** The local tuning curve centered on 240 deg for the cell tested at its peak spatial frequency. The cell's peak response is at 240 deg. **D:** The orientation-response function of the same cell tested at twice its peak spatial frequency (1.2 c/deg). The cell's peak response is at 90 deg. Its OR index is 0.14 with the preferred orientation at 84 deg/264 deg; and its DR index is 0.09 with the preferred direction at 321 deg. **E:** The rectilinear plot that shows local orientation tuning and a peak response at 80 deg. **F:** The orientation-response functions in polar coordinates for the cell at four times its peak spatial frequency (2.4 c/deg). The cell's peak response is at 30 deg. Its OR index is 0.36 with the preferred orientation at 24 deg/204 deg; and its DR index is 0.13 with the preferred direction at 300 deg. **G:** The rectilinear plot that shows a good local orientation tuning. The cell responds poorly and its peak response has now shifted to 20 deg.

cell tested at its peak spatial frequency. The cell's peak response is at 240 deg locally. When the cell was tested at twice its peak spatial frequency (1.2 c/deg) as shown in Fig. 4D, it exhibited better tuning than at the peak spatial frequency with an orientation index of 0.14 (preferred orientation at 84 deg/264 deg) and a direction index of 0.09 (preferred direction at 321 deg). The local tuning curve at twice the peak spatial frequency showed that the peak orientation was at 80 deg (Fig. 4E). As shown in Fig. 4F,

when the cell was tested at four times its peak spatial frequency (2.4 c/deg), its orientation tuning got much stronger with an orientation-bias index of 0.36 (preferred orientation at 24 deg/204 deg) and a direction-bias index of 0.13 (preferred direction at 300 deg) but the response rate of the cell dropped significantly. The local tuning curve in Fig. 4G suggests that the peak orientation shifted to 20 deg. Thus, increasing spatial frequency not only sharpened the tuning of some LGN cells, but also changed the orientation preference of some of these cells. Of the 25 cells that were examined at different spatial frequencies, we found that eight cells with increased orientation sensitivity to higher spatial frequencies shifted their orientation preferences by an average of 40 degrees.

Although only higher spatial frequencies were tested, our results suggest that varying spatial frequency has variable effects on direction sensitivity. One third of the LGN cells tested showed increases in direction sensitivity with increases in spatial frequency (e.g. the cells in Figs. 3 and 4), but two thirds exhibited the opposite effect, namely, they showed less direction sensitivity at higher spatial frequencies. As an example of the latter case, the cell in Fig. 5 exhibited worse direction sensitivity when the spatial frequency increased from the peak spatial frequency to twice the peak spatial frequency, although this same cell showed stronger orientation sensitivity. For these cells, when the spatial frequency used for testing orientation sensitivity increased from the peak spatial frequency to twice the peak spatial frequency, the average change in the orientation-bias index was 0.07 ± 0.09 ($N = 25$); the average change in the direction-bias index was 0 ± 0.06.

Finally, we examined to see if cells sensitive to common orientations or directions tended to cluster in the LGN. Since our penetrations through the LGN were at oblique angles to the layers, our sample was restricted to just five groups of cells that had overlapping receptive fields within single penetrations. A total of 27 cells were recorded within these clusters. Seventeen of these 27 cells had sufficient orientation bias for this comparison; too few of these cells had a direction bias sufficient for separate comparison. Each cluster included more than two orientation-sensitive cells. Our results show that cells in three out of the five clusters had similar orientation preferences to their neighbors; cells in the other two clusters exhibited different orientation preferences from their neighbors. These ambiguous results suggest that a larger N will be required to determine if orientation sensitivity is organized in any regular way in the owl monkey LGN.

Relation to cortical orientation tuning

Since LGN cell signals will ultimately impact cortical cell responses, it becomes important to know how the orientation selectivities of these populations compare. In a study of the functional organization of V1 in owl monkeys, O'Keefe et al. (1998) used experimental techniques comparable to ours and reported that there exists a broad range of orientation selectivity across layers. All layers contain nonoriented cells and all layers contain at least some relatively narrowly tuned cells. After excluding the nonoriented cells (10.4% of their cell sample), they found that the median orientation bandwidth (half-width at half-height) for simple and complex cells (189 cells) was about 27.4 deg, 30.8 deg (79 cells) for simple cells, and 26.9 deg (110 cells) for complex cells.

Compared to cortical cell orientation tuning, LGN cell orientation sensitivity in owl monkey is weak. When the cells were tested at their peak spatial and temporal frequency, we found that a total of 25 out of the 110 LGN cells (22.7%) had an orientation tuning bandwidth of less than or equal to 90 deg, a bandwidth we considered to be orientation selective. Twenty-one cells were orientation biased with broad tuning. Finally, 64 cells did not exhibit any significant bias in response to stimulus orientation. The

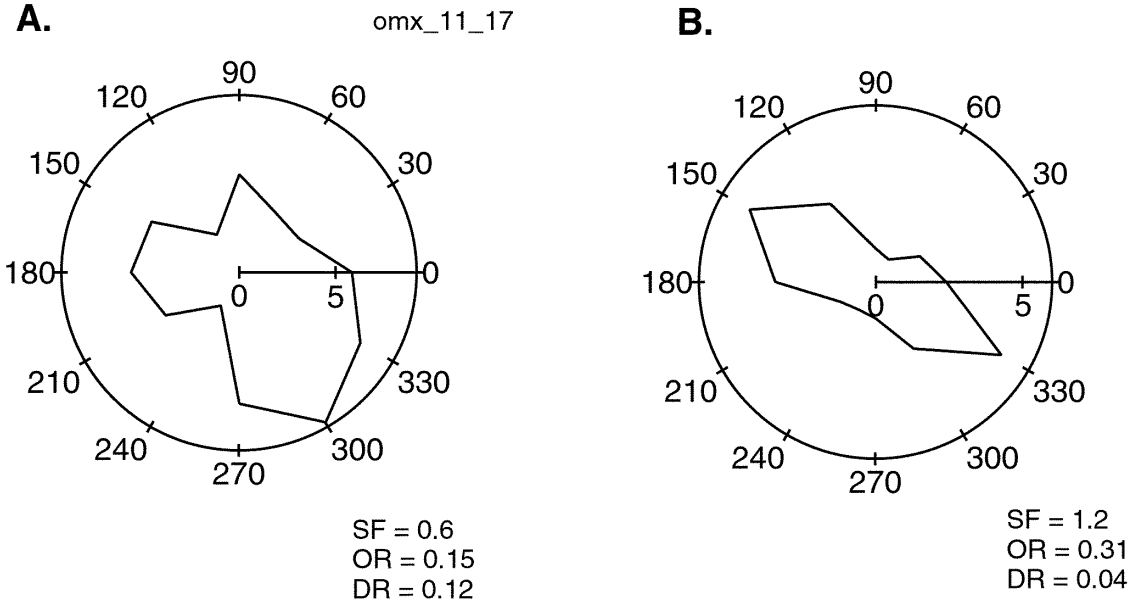

Fig. 5. Higher spatial frequencies have different effects on orientation and direction sensitivity. **A:** The orientation-response function in polar coordinates for an ON-center K cell at its peak spatial frequency of 0.6 c/deg. The cell shows sensitivity to both orientation and direction. Its OR index is 0.15; and its DR index is 0.12. **B:** The orientation-response functions in polar coordinates for the cell at twice its peak spatial frequency (1.2 c/deg). The cell exhibits better orientation sensitivity but much worse direction sensitivity than at the peak SF (0.6 c/deg). Its OR index is 0.31. Its DR index is 0.04, below the critical value of 0.08.

tuning bandwidth of our 25 best tuned LGN cells was about 2.5 times broader (median 67.5 deg) than that of V1 cortical cells (27.4 deg) recorded by O'Keefe et al. (1998). Some of our LGN cells, nevertheless, were surprisingly well tuned for orientation. An example of such a well-tuned cell (P cell, ON-center) is shown in Fig. 6A. The global tuning curve of this cell exhibited two peaks at 90 deg and 240 deg. The orientation tuning width measured at this cell's peak spatial and temporal frequency was about 45 deg. Fig. 6B shows the distribution of orientation tuning bandwidths of the subpopulation of 25 LGN orientation-tuned LGN cells. Tuning widths ranged from 32 deg to 90 deg, and the mean width was 65 deg ± 16 deg.

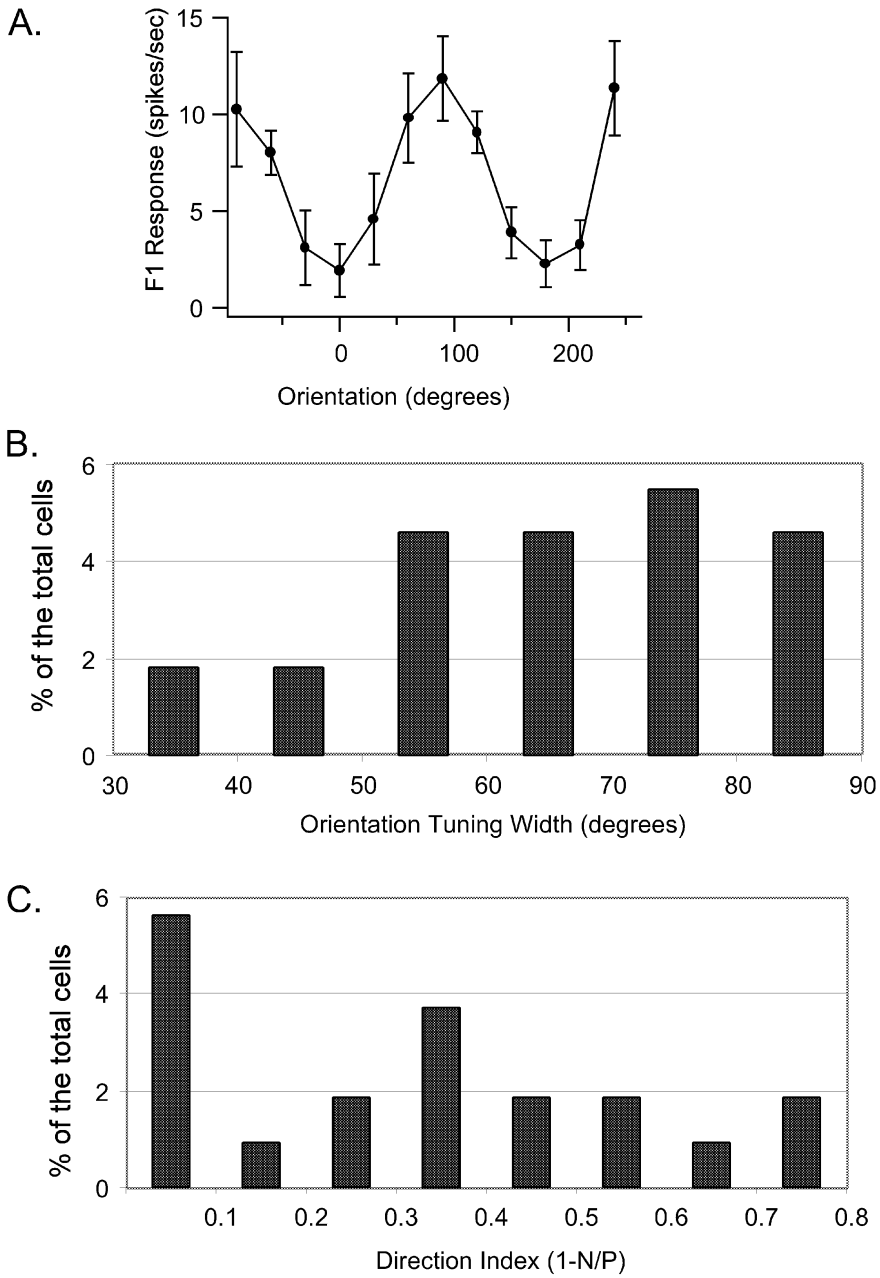

Fig. 6. Orientation-tuned LGN cells and their tuning bandwidth distribution. **A:** The orientation-response function of one well-tuned LGN cell on rectilinear coordinates at its peak spatial frequency. Data points are plotted with ± 1 SD error bars. **B:** The distribution of orientation-tuning bandwidth for the LGN cells that are well tuned at their peak spatial frequency. The orientation-tuning bandwidth ranges from 32 deg to 90 deg. The mean width was 65 deg ± 16 deg, median 67.5 deg. Out of the total of 110 LGN cells, 25 cells had orientation tuning band widths of less than or equal to 90 deg (considered orientation selective), 21 cells were broadly tuned, and 64 cells did not have significant bias to stimulus orientation. **C:** The distribution of direction index (*DI*) of the direction-biased LGN cells, with the *DI* ranging from 0.02 to 0.8. To be considered direction selective the *DI* needs to be greater than 0.67. Using this criterion only about 3% of our sample cells are considered direction selective. See text for details.

In their study of V1 cells, O'Keefe et al. (1998) also examined the direction selectivity of their cells. They calculated a direction index ($DI = 1 - Rn/Rp$) for each of their cells, where Rp is the net response in the preferred direction and Rn is the net response to the nonpreferred direction. If a cell had a $DI \geq 0.67$, they defined it as direction selective. According to this criterion, about 34% of the cells in their sample were direction selective. Applying this much more stringent criterion of $DI \geq 0.67$, only about 3% of our sample can be considered direction selective, although 19.1% of the LGN cells showed a direction bias using our original criterion. Fig. 6C shows the distribution of owl monkey direction-biased LGN cells with a DI between 0.02–0.8.

Discussion

Our major finding in this study is that a significant percentage (41.8%) of owl monkey LGN cells, including cells in all three classes (M, P, and K), are sensitive to stimulus orientation and to the direction of stimulus movement (19.1%). These data in owl monkeys can be added to a growing collection of studies in other species (cats, macaque monkeys, and marmosets) showing that a surprisingly large fraction of LGN cells in adult mammals show response biases for orientation and direction. In the discussion that follows, we compare the results reported in some of these studies with our current findings. We next consider the source of these subcortical response biases. Finally, we address the question of whether LGN orientation and direction sensitivity could contribute to cortical selectivity for these properties.

General features of LGN orientation and direction sensitivity

The dominant view of orientation and direction sensitivity is that these properties first emerge in visual cortex, although there are a number of reports detailing similar observations to ours in other species, including cats, macaque monkeys, and marmosets (cats: Vidyasagar & Urbas, 1982; Vidyasagar & Heide, 1984; Soodak et al., 1987; Shou & Leventhal, 1989; Jones & Sillito, 1994; Thompson et al., 1994*a*,*b*; Zhou et al., 1995; macaque monkeys: Lee et al., 1979; Smith et al., 1990; marmosets: White et al., 2001). In the latter studies, a variety of stimuli including bars, drifting and counterphased gratings, and drifting spots were used to test the degree of orientation and direction bias in LGN cells. Although some LGN cells showed orientation biases to bars and gratings and direction biases to all drifting stimuli, it was clear that drifting gratings (similar to those we used in the present study) produced the strongest biases.

As we found in owl monkey, the degree of orientation and direction bias reported in cat and macaque monkey LGN cells is influenced strongly by the spatial frequency of the stimulus (Smith et al., 1990; Thompson et al., 1994*a*; Zhou et al., 1995). Thus, LGN cells in all species tested exhibit a greater bias when tested at higher than their preferred spatial frequency. In cats, it has been reported that 75% of the cells show an orientation-bias index of greater than 0.1 (Thompson et al., 1994*a*); however, this high percentage of cells is based upon cells tested at higher than the cell's peak spatial frequency; no percentages were given for cells tested at their peak spatial frequency. Similarly, Smith et al. (1990) reported that 89% of LGN cells in macaque monkeys exhibit a significant bias for orientation. Again this high percentage is calculated based upon the maximum bias obtained at the highest spatial frequencies to which these cells would respond. In owl monkeys more than 60% of our cells were estimated to show orientation sensitivity when tested at the highest spatial frequency to which they would respond, compared to 41.8% when cells were tested at their peak frequency. As shown for the cells in Figs. 3 and 4, the increase in orientation bias at higher spatial frequencies could simply reflect the "tip of the iceberg" phenomenon since LGN cell responses are much lower at their nonpeak spatial frequencies. In this context, it would be interesting to know the impact of increases in contrast on LGN response bias since it is known that cortical cells show contrast invariance in their orientation tuning.

We did not find a consistent effect of spatial frequency on LGN cell direction bias in owl monkeys. Some cells exhibited a stronger bias at higher frequencies while others lost their bias for direction at higher frequencies. We, however, did not specifically examine spatial frequencies lower than the cell's peak spatial frequency. In cats the majority of LGN cells showed their strongest sensitivity for direction of motion when tested at or below the peak spatial frequency (Thompson et al., 1994*a*). Nevertheless, 30% of LGN cells that exhibited a directional bias in the latter study actually showed a stronger bias at higher than the peak spatial frequency (Thompson et al., 1994*a*,*b*). In cats, directional sensitivity of LGN cells also was reported to improve when tested with longer rather than shorter bars; it is unclear whether increasing the size of a grating would have a similar effect (Jones & Sillito, 1994).

In owl monkeys, we also examined orientation and direction bias in all three classes of relay cells (K, M, and P) and did not find any significant difference in the degree of bias between these classes. In macaque monkeys, orientation bias has been examined only in M and P LGN cells and, as in owl monkeys, cells in both classes exhibited an equal amount of bias for orientation (Smith et al., 1990). In the prosimian primate, bush baby, some elongated receptive fields were found among M, P, and K cell classes and some K cells were reported to be highly directionally selective although these properties were not examined systematically (Norton & Casagrande, 1982; Irvin et al., 1986). In cats, X and Y LGN cells also were found to exhibit equivalent degrees of orientation and direction bias (Thompson et al., 1994*a*,*b*). W cells in cats have not been examined in exactly the same way but studies have reported that W cells in the retina have elongated fields suggesting that they are biased for orientation (Leventhal & Schall, 1983); some W cells also have been reported to show a high degree of direction sensitivity (e.g. Stone & Fabian, 1966). Taken together, these data suggest that bias for orientation and direction is a general feature of LGN relay cells in all classes in a variety of mammalian species.

Origin of LGN biases

Since LGN cell receptive fields reflect their retinal inputs, the most likely source of a bias is the retina. Cortical influence can be ruled out in our experiments since LGN axons recorded in silenced V1 showed the same degree of bias as LGN cells recorded directly. In owl monkeys, we do not have any direct information on the degree of orientation or direction sensitivity of retinal ganglion cells. In cats and macaque monkeys, however, there is data suggesting that retinal ganglion cells show biases for orientation and direction. The strongest evidence for such a bias comes from a direct comparison of the orientation tuning characteristics of LGN cells and their retinal inputs (S potentials) in macaque monkeys (Smith et al., 1990). For the subset of LGN cells in which S potentials and an orientation tuning bias could clearly be demonstrated, Smith et al. (1990) were able to show that the S potentials always

reflected the same bias as their target LGN cells. Additionally, comparisons between retinal ganglion cell anatomy and physiology and orientation biases in the LGN support a correspondence. The degree of dendritic-field elongation of cat ganglion cells appears to correspond to physiological measures of orientation bias in these cells (Hammond, 1974; Leventhal & Schall, 1983; Schall et al., 1986*a*,*b*). Both the preferred orientations determined physiologically (Levick & Thibos, 1980; 1982) and the dendritic-field orientations measured anatomically vary in a systematic fashion with receptive-field position (Leventhal & Schall, 1983; Schall et al., 1986*a*,*b*). At a given peripheral retinal position, most retinal ganglion cells prefer stimuli that are radially oriented and exhibit radially oriented dendritic fields (Leventhal & Schall, 1983; Schall et al., 1986*a*,*b*). A similar preference for radial orientation has been reported for cat LGN cells (Shou & Leventhal, 1989), although we and others working in owl monkey and cat LGN, respectively, have reported a bias toward horizontal and vertical orientations (Vidyasagar & Urbas, 1982; Vidyasagar, 1984) suggesting that the LGN itself may make an additional contribution.

Since we see increases in orientation sensitivity with increases in spatial frequency, the bias we see in the LGN likely reflects the shape of the center mechanism of retinal ganglion cell inputs. In some cases, however, no increases in orientation sensitivity were seen with increases in spatial frequency suggesting that other factors contribute besides an elliptical shape of the receptive-field center. Since direction specificity tended to worsen at higher spatial frequencies in most cells, it is possible that asymmetry in the inhibitory surrounds could contribute as proposed by others (Thompson et al., 1994*b*)

Could LGN cell biases contribute to cortical cell selectivity?

A key question is whether orientation or direction biases could contribute to orientation and direction tuning of cortical cells. The alternatives are that such biases are ignored by cortical cells altogether and instead the precise alignment of untuned LGN afferent axons creates sharp orientation tuning at the first synapse, or that a weak alignment of untuned LGN afferent axons is sharpened by cortical circuitry (reviewed in Ferster & Miller, 2000). Both of the latter alternatives still require some developmental mechanisms to establish the sharp tuning seen in adult visual cortex. Since it is generally believed that other properties of cortical cells (i.e. ocular dominance) are set up during development through mechanisms that involve competitive preservation of connections that exhibit correlated patterns of firing, subcortical biases originating at the retina and transmitted through the LGN may be important to launch this process.

If retinal biases are transmitted through the LGN to cortex to aid in setting up orientation selectivity in cortex, then one would predict similarities in the distributions of biases at each level. In fact several such similarities can be identified. Radial orientations established in the cat retina appear to be preserved in the distribution of biases seen in the LGN and the arrangement of orientation tuning in cortex (Schall et al., 1986*b*). In owl monkey LGN, we see an overrepresentation of biases for horizontal and vertical orientations. Although we do not have data for owl monkey V1, in the central vision representation of macaque V1 more neurons prefer horizontal and vertical orientations than the oblique orientations (Mansfield, 1974; Mansfield & Ronner, 1978). Finally, as mentioned above, Shou and Leventhal (1989) provide good evidence that orientation biases in cat LGN are arranged in an orderly way very similar to that seen in cat cortex. Our data in owl monkey were too limited to determine if cells with similar orientation are clustered in the same way as was shown in the cat.

If orientation and direction biases constructed subcortically are responsible for setting up these properties in cortex, then how does this take place given that orientation and direction selectivity is seen at birth in monkeys and develops prior to eye opening in the ferret (see Chapman et al., 1999 for review)? The cerebral cortex appears especially well designed to detect correlations in its inputs (Linsker, 1990). Moreover, waves of synchronous retinal activity are proposed to be important in cortical development (Mastronarde, 1983; Meister et al., 1991; Miller, 1994). Within this context one can easily imagine how biases in the retina could impact LGN cells and subsequent cortical organization since ganglion cells with common dendritic orientations would tend to fire most during waves of retinal activity moving parallel to their common orientations. A variant on this model was proposed by Tavazoie and Reid (2000) who argue that imprecise retinogeniculate connections set up oriented LGN cell fields that, in turn, are responsible for initiating orientation tuning in cortex. In their model, the bias in the ferret LGN is transient and disappears in the adult. Regardless, both models depend upon elongated receptive fields in the LGN initiating the process of orientation tuning in cortex. LGN afferents with common orientations should, according to this scenario, converge with their long axis aligned with the long axis of the receptive fields of cortical cells. Of course, the weak bias exhibited by LGN cells would then need to be sharpened in cortex either based upon the alignment of commonly tuned LGN afferents or *via* cortical circuits, or both mechanisms.

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