Dim-Light Sensitivity of Cells in the Awake Cat’s Lateral Geniculate and Medial Interlaminar Nuclei: A Correlation With Behavior

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Kang I, Malpeli JG. Dim-light sensitivity of cells in the awake cat’s lateral geniculate and medial interlaminar nuclei: a correlation with behavior. J Neurophysiol 102: 841–852, 2009. First published May 20, 2009; doi:10.1152/jn.90642.2008. Contrast thresholds of cells in the dorsal lateral geniculate (LGNd) and medial interlaminar (MIN) nuclei of awake cats were measured for scotopic and mesopic vision with drifting sine gratings (1/8, 2, and 4 cycles/deg [cpd]; 4-Hz temporal frequency). Thresholds for mean firing rate (F0) and temporally modulated responses (F1) were derived with receiver-operating-characteristic analyses and compared with behavioral measures recently reported by Kang and colleagues. Behavioral sensitivity was predicted by the neural responses of the most sensitive combinations of cell class and response mode: Y-cell F1 responses for 1/8 cpd, X-cell F1 responses for 2 cpd, and Y-cell F0 responses for 4 cpd. All previous estimates of neural scotopic increment thresholds in animal models fell between Weber’s law (proportional to retinal illuminance) and the deVries–Rose law (proportional to the square root of illuminance). However, psychophysical experiments suggest that under appropriate conditions human scotopic vision follows the deVries–Rose law. If behavioral sensitivity is assumed to be determined by the most sensitive class of cells, this discrepancy is resolved. Under scotopic conditions, off-center Y cells were the most sensitive and these followed the deVries–Rose law fairly closely. MIN Y cells were, on average, 0.25 log units more sensitive than LGNd Y cells under scotopic conditions, supporting a previous proposal that the MIN is a specialization of the carnivore for dim-light vision. We conclude that both physiologically and behaviorally, cat and human scotopic vision are fundamentally similar, including adherence to the deVries–Rose law for detection of Gabor functions.

INTRODUCTION

The subject of this study is the dim-light sensitivity of the cat’s lateral geniculate complex, which consists of the dorsal lateral geniculate nucleus (LGNd) and medial interlaminar nucleus (MIN). The former is the homolog of the primate LGNd, the latter a small satellite of the LGNd present in carnivores. Our object was to characterize the sensitivity of single cells in awake cats under conditions as close as possible to a parallel study of behavioral sensitivity (Kang et al. 2009). We asked three questions: 1) which cell categories and response modes account for behavioral sensitivity?; 2) do neural increment thresholds follow the deVries–Rose law?; and 3) do the LGNd and MIN differ in sensitivity?

The stimuli were sinusoidal gratings drifting at a fixed temporal frequency. Neuronal sensitivity was measured for two aspects of evoked activity: changes in average firing rate and responses temporally modulated at the stimulus frequency. Because of the considerable time required to determine threshold for a single spatial frequency, the investigation was limited to three: 1/8, 2, and 4 cpd (cycles/deg). We selected 1/8 cpd to probe vision near absolute luminance threshold, 2 cpd as a high spatial frequency well within the cat’s acuity limit, and 4 cpd because it is at the cat’s acuity limit for parafoveal vision (Kang et al. 2009).

By correlating contrast thresholds of X and Y cells with the behavioral data of Kang et al. (2009), we show that the cell classes and neural response modes supporting behavioral sensitivity vary with adaptation level and spatial frequency and that the most sensitive cell class for any given stimulus condition best explains behavioral sensitivity. Perhaps the most surprising outcomes are the extent to which one cell class dominates for a given stimulus condition and the critical contribution of Y cells at the highest spatial frequency used.

Of particular interest is the regulation of contrast sensitivity under scotopic conditions because previous physiological experiments with laboratory species have failed to explain this aspect of human rod vision. In contrast to photopic conditions, where Weber’s law describes the relationship between sensitivity and retinal illuminance, in dim light, human contrast sensitivity has been shown to follow the deVries–Rose law, which holds that the increment threshold is proportional to the square root of retinal illuminance (Rose 1948), at least for small uniform stimuli of short duration (Barlow 1957) and for sine gratings (Smith Jr 1973; van Nes and Bouman 1967). Kang and colleagues (2009) showed that for low spatial frequencies at scotopic adaptation levels, cat behavioral sensitivity is regulated in accordance with the deVries–Rose law. The scotopic sensitivity of the rhesus monkey is apparently similarly regulated (Oehler and Sharpe 1989). However, prior physiological measurements of scotopic visual sensitivity are at variance with the deVries–Rose law (see DISCUSSION). We show here that if the data are obtained in awake animals, and if one assumes that behavioral sensitivity is determined by the most sensitive category of cells (off-center Y cells), there is no discrepancy between behavior and physiology and scotopic neural increment thresholds follow the deVries–Rose law.

Relying on data from anesthetized cats, Lee et al. (1984) reported that the density of inputs from nontapetal retina to the MIN is very low, and combining this observation with evidence from the preexisting literature of a high degree of retinal-thalamic convergence on MIN cells, they proposed that the MIN of carnivores is a dim-light specialization. Subsequently, Lee et al. (1992) showed in anesthetized cats that MIN cells are more sensitive than LGNd cells in the scotopic range. Here we revisited this issue in the awake cat and confirmed...
METHODS

Animal preparation, display apparatus, and behavioral paradigm

Three adult female cats were used, including the two tested by Kang et al. (2009). Eye positions were monitored at 500 Hz. Surgical procedures, method of recording eye movements, and general behavioral procedures were identical to those of Kang et al. (2009), with the addition of microdrive bases implanted on the skull to allow quartz-coated, platinum–tungsten microelectrodes to be inserted into the thalamus, using procedures identical to those of Lee and Malpeli (1998). Care and use of animals were in accordance with the guidelines of the American Physiological Society, the Society for Neuroscience, and the University of Illinois Institutional Animal Care and Use Committee.

The display apparatus and methods of verifying display luminance and stimulus contrast were those used by Kang et al. (2009). All measurement of display luminance and retinal illuminance will be reported in human photopic units. Neural thresholds were obtained with extended sine gratings (15°×15°), drifting upward at 4 Hz. Uniform gratings were used, as opposed to the Gabor functions used to determine behavioral sensitivity in Kang et al. (2009), because of the technical difficulties of aligning Gabor functions exactly at the center of the receptive field and keeping them perfectly aligned during eye movements. The gratings were dynamically repositioned with each refresh cycle of the display to keep them centered on the receptive field in real time as the animal made small eye movements around the fixation point. Specifically, at every vertical refresh the displacement of the eye from the fixation point was added to the stimulus coordinates. Because the vertical refresh rate was 60 Hz and the velocity criterion to screen out epochs of unstable eye positions was 15°/s (see Estimating contrast thresholds from neurometric functions), the maximum error would be 0.25°. However, because eye movements were usually much slower than this (Supplemental Material, section B), the average error would be a lot smaller, probably on the order of 0.04°. The mean luminance of the gratings was identical to the background luminance of the display. All stimuli were binocularly viewed.

The cats were trained to fixate a central laser spot that remained on throughout each trial. A trial began with a 500-ms warning tone, followed immediately by the central fixation spot, which the cat was required to fixate for 5 to 6 s. Successful performance was rewarded with food. In contrast to the psychophysical study by Kang et al. (2009), the cats were trained to ignore the gratings and fixate the laser spot throughout the trial. The tolerance window for fixation varied from 8°×8° to 15°×15°. The larger windows were most often used for the lower adaptation levels, where the drifting gratings were more likely to evoke eye drifts.

Data collection

We recorded from retinotopic locations as comparable as possible to those of the Gabor functions used by Kang et al. (2009) to assess behavioral sensitivity (i.e., 8° on the horizontal meridian). The locations of recording sites were physiologically determined based on retinotopy and ocular dominance (Supplemental Material, section A).

Once a single neuron was isolated, its ocular dominance and center polarity (on-center vs. off-center) were determined. Receptive fields were located with a computer-generated series of briefly flashed horizontal and vertical bars (light or dark, depending on center polarity) dynamically stabilized on the retina of the dominant eye. Cells were classified as X or Y based on their responses to 15°×15°, horizontally oriented sinusoidal gratings centered on the receptive field, counterphased at a temporal frequency of 2 or 4 Hz, with spatial frequencies varying from 1/2 to 4 cpd (see Cell classification). Initial characterizations were usually carried out at a display luminance of 0.70 cd/m². When the results were ambiguous, as judged from on-line Fourier analysis of spike trains, the test was repeated at a 1 or 2 log-unit higher adaptation level.

After the cell was characterized, the cats were dark-adapted for 30 min before collection of contrast-threshold data began. For a given combination of spatial frequency and adaptation level, responses were typically collected for four to seven contrast levels in separate blocks of trials. Each stimulus contrast was presented for five trials (stimulus trials), temporally flanked alternately by two or three trials with no stimulus (nonstimulus trials). Using on-line Fourier analyses of spike trains as a guide, stimulus contrasts were chosen to bracket threshold and to ensure that stimulus contrasts were evenly spread over the neurometric function.

When data collection was completed for one adaptation level, display luminance was raised to the next level and at least 2 min were allowed for light adaptation before trials resumed. When a neuron was held sufficiently long to allow data collection up to mesopic adaptation levels, the cell was usually rechecked for center polarity, receptive-field location, and cell class. On occasion, a characterized cell was lost toward the end of the dark-adaptation period and, if another was isolated without significantly advancing the microelectrode, contrast-threshold data were taken and the cell was characterized once adaptation levels reached the mesopic range. Fifteen LGNd X cells, 11 LGNd Y cells, and 3 MIN Y cells were thus obtained. Data for such cells would have been discarded had the subsequently mapped receptive field not been in the expected location but, because of the regular retinotopy of the LGNd and MIN, this never occurred.

Cell classification

The test for cell classification was that proposed by Hochstein and Shapley (1976), based on the observation that for high spatial frequencies, X cells tend to respond to only one phase of a counterphased grating, whereas Y cells respond to both phases. Thus the ratio of the first harmonic component (F1) to the second harmonic component (F2) can be used as an index to distinguish X cells (low ratio) from Y cells (high ratio). Usually, we used 2- to 4-cpd gratings for this purpose, although for a few cells it was necessary to use lower spatial frequencies to get adequate responses.

The trials collected with counterphased gratings were divided into 1,000-ms epochs and spike trains in each epoch were subjected to a discrete Fourier transform (Matlab Version 7, The MathWorks). To minimize confounding effects of eye movements or misalignment of the stimulus with respect to the receptive field, those epochs for which instantaneous eye velocity (i.e., velocity measured at every 2 ms) exceeded 15°/s, or for which gaze deviated from the central fixation point >5°, were excluded from analysis. The magnitudes of the F1 and F2 components were averaged over epochs and the F2:F1 ratio was calculated. When the ratio varied with spatial frequency, the highest spatial frequency was used (So and Shapley 1979). If trials were collected for both temporal frequencies (2 and 4 Hz), the ratio was calculated for the one that evoked a stronger modulation. Neurons were classified as X if the F2:F1 ratio was <0.9 and Y if it was >1.1.

Cells with intermediate ratios were considered of ambiguous type and excluded from further analysis. This procedure is illustrated for an X and a Y cell and the overall F2:F1 ratio distribution is presented in Fig. 1.

For the LGNd, we concentrated mainly on the dorsal layers (layers A and A1), although a few cells were recorded in layer C, immediately below layer A1. We did not seek and did not encounter LGNd W cells, which should lie below layer C. For the MIN, we excluded cells with particularly sluggish responses and those with poorly

1 The online version of this article contains supplemental data.
defined receptive fields or center polarity. We suspect these may have been W cells but, because conduction velocity was not measured, this could not be verified. With the exception of one X cell, all identified MIN cells were Y cells.

Estimating contrast thresholds from neurometric functions

Discrete Fourier transforms were applied to spike trains to quantify response magnitude in two ways: unmodulated changes in mean firing rate (F0 response) and modulation of activity at the temporal drift frequency of the stimuli (F1 response). Contrast threshold for each response was defined using signal detection theory (Green and Swets 1966), as illustrated in Fig. 2. For a given combination of spatial frequency and adaptation level, trials collected both with and without the stimulus were binned into 500-ms epochs and spike trains of

FIG. 1. Cell classification. A: single trials illustrating responses to counterphased gratings (2 cpd, 4 Hz, 0.70 cd/m²) for an off-center X cell (top) and an on-center Y cell (bottom). The top 2 traces in each panel show horizontal (Hor) and vertical (Ver) eye positions. Bottom traces in each panel are spike trains, along with spike density (derived from Gaussian convolution; SD = 20 ms). Alternating phases of the gratings are indicated by white and gray patches. Trials lasted 5–6 s, but only the first 3 s are shown. The X cell responded to only one phase of the grating, the Y cell to both. B: discrete Fourier transforms of spike train for the same cells, showing average magnitudes of Fourier components for 5,100-ms epochs for the X cell and 17,000-ms epochs for the Y cell. The F1 component (at 4 Hz) predominates for the X cell, whereas the F2 component (at 8 Hz) predominates for the Y cell. C: histogram of F2:F1 ratio for 139 neurons on a logarithmic scale. The criteria used to classify cells are marked with dashed lines; 4 additional cells (2.8% of the total) that fell between these lines were discarded from all analyses.

FIG. 2. Method of estimating contrast thresholds demonstrated for the F0 (left) and F1 (right) responses of a dorsal lateral geniculate (LGNd) Y cell. The stimulus was a 1/8 cpd grating drifting at 4 Hz presented at a background luminance of −3.67 log cd/m². Spike trains were divided into 500-ms epochs and F0 and F1 responses for each epoch were determined from discrete Fourier transforms. Top panels: Distributions of F0 and F1 responses for stimulus (open histogram) and nonstimulus (shaded histogram) epochs, in order of increasing stimulus contrast (stimulus contrasts indicated beside histograms; n = number of 500-ms epochs). Middle panels: receiver-operating-characteristic (ROC) curves derived from the distributions of stimulus and nonstimulus responses. Each curve was generated by choosing a decision criterion for detection of a stimulus and counting the number of stimulus (open) and nonstimulus (shaded) trials for response magnitudes ≥ that criterion to determine the probabilities of a correct response and false alarm with that decision criterion. This was repeated for decision criteria spanning the range of 0%–90% correct, resulting in a family of ROC curves. The area under each ROC curve provides an estimate of the proportion of correct decisions expected from an ideal observer of the spike trains (for either F0 or F1 responses) for that stimulus contrast. The entire procedure was repeated for each stimulus contrast to produce a family of ROC curves. The area under each ROC curve provides an estimate of the proportion of correct decisions expected from an ideal observer of the spike trains (for either F0 or F1 responses) for that stimulus contrast. Bottom panels: neurometric functions used to estimate contrast threshold. The proportions of correct decisions derived from the ROC curves are plotted as functions of stimulus contrast. The horizontal lines mark the threshold criterion (75% correct) and the downward-pointing arrows mark the estimated contrast threshold. As is typical for Y cells at this spatial frequency, both F0 and F1 thresholds were reliably estimated and the F1 threshold was the lower of the two.
individual epochs were Fourier-analyzed to calculate the magnitude of F0 and F1 components. For each stimulus contrast, the distribution of F0 or F1 responses obtained from the stimulus trials was used to derive the probability distribution of the evoked neural response. Likewise, the probability distribution of spontaneous activity was estimated from the distribution of F0 or F1 responses collected from the nonstimulus trials. To minimize effects of slow fluctuations in excitability, samples comprising the nonstimulus distributions were taken from the five nonstimulus trials bracketing each block of five stimulus trials (either two before and three after the stimulus trials or vice versa).

As in classification of cell types, epochs for which instantaneous eye velocity exceeded 15°/s were excluded from analysis. Also, epochs during which the eyes deviated >10° from the central fixation point were excluded to ensure that the sine grating was well within the screen borders (see section B and Table S1 in Supplemental Material for statistics on eye positions during epochs included in analysis). From the response distributions for stimulus and nonstimulus conditions, an empirical receiver-operating-characteristic (ROC) curve was obtained for each stimulus contrast. The proportion correct for an empirical ROC curve was taken from the five nonstimulus trials bracketing each block of five stimulus trials. To minimize effects of slow fluctuations in excitability, samples comprising the nonstimulus distributions were taken from the five nonstimulus trials bracketing each block of five stimulus trials (either two before and three after the stimulus trials or vice versa).

To quantify contrast sensitivity for a particular adaptation level and spatial frequency, we subtracted contrast threshold from 100%. Zero sensitivity was assigned if the fitting function estimated a threshold ≥100% or if the cell was unresponsive to the highest contrast stimulus as confirmed with post hoc analyses of the Fourier spectra (Supplemental Material, section C). If a neurometric function could not be fit to the data, but the cell was not tested with the highest contrast so that the post hoc tests could not be performed, sensitivity was not defined and the data were excluded from further analysis. In almost all such cases it was clear that sensitivity would have been at or near zero had the cell been tested with the highest contrast because there was no monotonic increase in area under the ROC curve with increasing stimulus contrast.

RESULTS

Sampled populations

In all, 141 cells were recorded from the LGNd and MIN. Among these, 139 (122 LGNd, 17 MIN) were fully characterized for location, cell class, receptive-field center location, and polarity of center (Table 1). Two additional cells isolated from the MIN in the dark-adapted state were lost before luminance was raised sufficiently for classification as X or Y. These are included in the comparison of dim-light sensitivity of MIN and LGNd cells only and treated as Y cells because MIN cells that were characterized were almost entirely Y cells and these two unclassified cells were typical of identified MIN Y cells in all respects. Most cells were not held long enough for contrast thresholds to be determined for all three spatial frequencies at each adaptation level, so the data are biased toward lower adaptation levels and thus toward the lowest spatial frequency.

The eccentricity of receptive-field centers ranged from 2.8 to 13.8°, with a mean of 7.2° (mean absolute value of azimuth = 6.7°, SD 2.2°; mean value of elevation = −1.5°, SD 2.2°), which is close to the nominal center of the Gabor functions used by Kang et al. (2009) for determining behavioral thresholds (8°) and 74% had eccentricities between 5.5 and 10.5°. The retinal eccentricity of the Gabor functions used by Kang et al. (2009) varied from 5.5 to 10.5° because the maximum tolerance window placed around the central fixation point in that study was 5 × 5°, so the overlap of receptive fields with the Gabor functions was excellent. Therefore any sensitivity difference due to retinal eccentricity probably does not play a significant role in the comparison of neural sensitivity with behavioral sensitivity. This is a moot point in any event because, as will be shown in Effects of other variables on dim-light sensitivity of Y cells, sensitivity was not correlated with eccentricity for this sample.

Contrast sensitivity compared with behavioral sensitivity

The dominant cell type and response mode varied dramatically with adaptation level and spatial frequency. We first illustrate this with contrast thresholds for two of the several cells held long enough to be tested for the three spatial frequencies at all adaptation levels (Fig. 3). The X cell (Fig. 3A) modulated its firing rate at the drift frequency of the gratings (F1 component) for 1/8, 2, and 4 cpd, although very insensitively for 4 cpd. It did not respond with an unmodulated increase in activity (F0 component) for any combination of adaptation level and spatial frequency. The Y cell (Fig. 3B) responded with both F0 and F1 responses at 1/8 cpd, although the threshold of the F1 response was lower. At 2 and 4 cpd, it responded with unmodulated increases in firing rate.

All of the neural contrast-sensitivity data, pooled across the LGNd and MIN, are presented in Fig. 4, along with behavioral data of Kang et al. (2009). For 1/8 cpd, Y cells account for behavioral sensitivity (red, Fig. 4, A and B). The most sensitive F0 responses match behavioral sensitivity, but F1 responses are significantly more sensitive than F0 responses, with average F1

<p>| TABLE 1. Distribution of cells by geniculate layer, functional class, and center polarity |
|------------------------------------------|--------|--------|--------|--------|--------|--------|
| X Cell (n = 63)                          |        |        |        |        |        |        |</p>
<table>
<thead>
<tr>
<th>ON</th>
<th>OFF</th>
<th>Sum</th>
<th>ON</th>
<th>OFF</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>LGNd (n = 122)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Layer A</td>
<td>18</td>
<td>14</td>
<td>32</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>Layer A1</td>
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<td>15</td>
<td>29</td>
<td>16</td>
<td>11</td>
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<tr>
<td>Layer C</td>
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<td>1</td>
<td>1</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Sum</td>
<td>32</td>
<td>30</td>
<td>62</td>
<td>37</td>
<td>23</td>
</tr>
<tr>
<td>MIN (n = 19*)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Layer 1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Layer 2</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
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<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Sum</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>7</td>
<td>11</td>
</tr>
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</table>

Total: n = 141. *These include two MIN cells that were not objectively classified (both off-center, one each in layers 1 and 3), but were included as Y cells for the comparison of LGNd/MIN sensitivity (see text).

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2 We use this subtraction measure rather than the more common alternative of inverting the contrast threshold (i.e., 1/T) for several reasons. Sensitivity measured by subtraction is bounded at both ends, whereas the alternative is unbounded for lower thresholds. To avoid greatly compressing the data in the region of most interest for this study (high thresholds that characterize scotopic vision), the 1/T measure requires presentation on a log scale. Logarithmic scaling of the 1/T measure has the advantage that the data are typically well fit by straight lines, but the disadvantage of obscuring the convergence of MIN and LGNd sensitivity at high and low luminances. Finally, we compare these data to those of Lee et al. (1992), who used the subtractive measure.
sensitivity tracking behavior (Fig. 4B; see also Supplemental Material, Fig. S1A). Y cells are much more sensitive than X cells for 1/8 cpd and for F1 responses there is virtually no overlap in the distributions (red vs. blue, Fig. 4B). X cells only occasionally responded with an F0 component for 1/8 cpd (blue, Fig. 4A).

For 2 cpd, the F1 response of X cells predominates, with the most sensitive cells tracking behavioral sensitivity (blue, Fig. 4D). The F0 and F1 sensitivities of Y cells (red, Fig. 4, C and D) and the F0 sensitivity of X cells (blue, Fig. 4C) fall far short of behavioral sensitivity. For both X and Y cells, behavioral and F1 neural sensitivity dropped to zero at approximately −3 log cd/m² (see also Fig. 4 of Kang et al. 2009), which is probably in the high scotopic region. This suggests that rod pathways can support perception at 2 cpd, although sensitivity for this spatial frequency is clearly much higher in the mesopic range, presumably due to the contributions of cones.

For 4 cpd, the F0 component of Y-cell responses supports behavioral sensitivity (red, Fig. 4E). Those cells that respond tend to surpass behavioral sensitivity, but when sensitivity is averaged across all Y cells (i.e., including those that were unresponsive), the results track behavioral sensitivity fairly closely (red line, Fig. 4E), except at the highest luminance levels where there is a sudden increase in behavioral sensitivity. This increase coincides with the appearance of F0 and F1 responses of X cells, which are absent at lower luminance levels (blue, Fig. 4, E and F).

Contrast sensitivity for high spatial frequencies appears to be much higher in awake than that in anesthetized cats. Figure 5 presents a comparison of the average sensitivity of cells for F1 responses obtained in the current study with those obtained by Lee et al. (1992) from the anesthetized cat. Although the agreement for Y cells at 1/8 cpd is fair, X-cell sensitivity at 2 cpd is vastly higher in the awake cat. This discrepancy would presumably be even larger at higher spatial frequencies, but the comparison could not be made for 4 cpd because neural sensitivity at this spatial frequency depended on the F0 response, whereas Lee et al. (1992) measured contrast thresholds only for the F1 response.4

The neurometric functions for both X and Y cells had consistently lower slopes at the 75% threshold level than the psychometric functions measured by Kang et al. (2009) for all spatial frequencies, as illustrated by plots of slope as a function of threshold (Fig. 6). The ratios of the average neurometric slope to the average psychometric slope were 2.47, 3.44, and 3.94 at 1/8, 2, and 4 cpd, respectively. Such differences would be expected if the variances of the underlying noise and signal-plus-noise response distributions are greater for the cells than for the animal, which in turn implies that the brain averages over a number of cells to make a decision.

Contrast sensitivities of geniculate cells in this study were derived from F0 and F1 responses sampled from 500-ms epochs and thus each trial contributed more than one epoch (the number varied depending on how often the eye stability criteria were violated). This sampling interval was chosen to best match the time that the cats typically had for detecting Gabor functions in Kang et al. (2009). To evaluate how sensitive our measurements were to choice of sampling epochs, we repeated the calculations of F0 and F1 neural sensitivity with 250-, 750-, and 1,000-ms sampling epochs. Overall, estimates of neural sensitivity increased with sampling epoch, but the improvement was not enough to affect the comparisons of behavioral and neural sensitivity based on the 500-ms sampling epoch used for the analysis in Fig. 4 (Supplemental Material, section D).

Comparison of MIN and LGNd scotopic sensitivity

Lee et al. (1992) reported that at low spatial frequencies (<1/2 cpd), MIN cells are more sensitive than LGNd cells in the anesthetized cat. We examined the F1 response for our 1/8-cpd data to see whether this result holds up in the awake cat. The comparison was confined to Y cells because there was only one MIN X cell in our sample and because Y cells appear to be the most sensitive elements at scotopic adaptation levels in both structures (Lee et al. 1992). The two unclassified MIN cells (Fig. 7A, 4 In the study of Lee et al. (1992), one author (blind to the stimulus contrast) estimated contrast threshold for the F1 response by listening to the auditory monitor. Similar estimates of threshold made by the same individual in the current experiment were consistently about 10% lower than those obtained with Fourier analyses. This is because a human observer can readily detect modulation below the 75% threshold level that was used to extract threshold from the neurometric functions, particularly when allowed to mentally average over several seconds of responses, or even several trials. Thus, the extent to which neural sensitivity is higher in the awake cat is probably understated here.
FIG. 4. Comparison of neural and behavioral sensitivity. Behavioral sensitivities (solid lines) are from the data of Kang et al. (2009). Each of the data points that these lines connect is 100% minus the average of the contrast thresholds of the 2 cat subjects, except for the zero-sensitivity points, which mark the luminance at the absolute thresholds in Fig. 4 of Kang et al. (2009). Left and right panels show results for the F0 and F1 responses, respectively. X cells are indicated by blue filled circles, Y cells by red open circles. The shaded bars at the top and bottom of each panel mark contrasts above or below the range of available stimulus contrasts (see Supplemental Material, section C, for estimation of contrast threshold in these regions). Spatial frequency increases from the top row down: A and B, 1/8 cpd; C and D, 2 cpd; E and F, 4 cpd. For the F0 response of Y cells at 4 cpd only, zero-sensitivity points are displaced right and left for greater visibility and the average neural contrast sensitivity is plotted (E, red line). However, all panels include luminance ranges where the density of zero-sensitivity points is too high to indicate graphically, particularly near absolute luminance threshold. The number of such points for X and Y cells, respectively, are: A, 175 and 108; B, 51 and 67; C, 49 and 75; D, 19 and 86; E, 55 and 50; and F, 57 and 94. Note that for certain cell types and spatial frequency, there are not as many F0 sensitivity estimates as F1 estimates or vice versa (e.g., compare the blue dots in A and B). Missing points are those for which sensitivity could not be assigned for the reasons given in Estimating contrast thresholds from neurometric functions of methods. In general, these cells were clearly unresponsive for the condition in question, although they did not meet the strict criteria for assignment of zero sensitivity.

green symbols) were included because their sensitivities for 1/8 cpd in dim-light conditions were within the sensitivity range of Y cells, which was much higher than that of X cells at any given adaptation level with almost no overlap (see Fig. 4B). Layer C was excluded because only four Y cells from layer C were available for the comparison range of adaptation levels and because C-layer cells may be intermediate in sensitivity between A-layer and MIN cells (Lee et al. 1992).

MIN cells were, on average, more sensitive than LGNd cells, although sensitivities of neurons from the two structures largely overlapped at all adaptation levels (Fig. 7A). This difference is more obvious when the average sensitivity at each adaptation level was compared (Fig. 7B). There was a range of scotopic adaptation levels for which the average sensitivity of MIN and LGNd cells differed and, outside that range, their sensitivity converged. The low end of this range, $10^{-6}$ cd/m$^2$, coincided with the behavioral absolute threshold for 1/8 cpd (Kang et al. 2009) and the high end was about $4 \times 10^{-3}$ cd/m$^2$ (Fig. 7B).

To quantify differences in dim-light sensitivity, the average sensitivity of LGNd cells was subtracted from that of MIN cells at each tested adaptation level from $2.40 \times 10^{-6}$ to $2.15 \times 10^{-4}$ cd/m$^2$ (seven levels whose range is marked by vertical dashed lines in Fig. 7B). The mean value of these differences for seven adaptation levels was 9.43% in favor of the MIN. Horizontal differences between the two average sensitivity curves provide a more intuitive comparison, since they quantify the MIN’s advantage in terms of ambient light level. These were calculated at 5% intervals from 5 to 85% contrast sensitivity (Fig. 7C). The MIN’s average luminance advantage in this range is 0.25 log units. The differences in contrast sensitivity (9.43% in Fig. 7B) and luminance sensitivity ($0.25 \log \text{cd/m}^2$ in Fig. 7C) were statistically significant (permutation tests, $P = 0.0134$ and 0.0164, respectively). To see whether the two cells assumed to be in the MIN, but not rigorously classified, significantly influenced the results, this procedure was repeated without them, yielding virtually the same result: a contrast-sensitivity advantage of the MIN of 9.48% ($P = 0.0179$) and a luminance-sensitivity advantage of 0.25 log cd/m$^2$ ($P = 0.0183$).

Effects of other variables on dim-light sensitivity of Y cells

To see whether factors other than structure per se might contribute to the MIN’s sensitivity advantage relative to the
LGNd, a multiple linear regression analysis was performed on contrast sensitivity for Y cells with four parameters as independent variables: polarity of receptive-field center, structure (MIN vs. LGNd), receptive-field eccentricity, and spontaneous firing rate. This required that two variables that varied with adaptation level—overall sensitivity and spontaneous firing rate—be quantified over the range of adaptation levels for which the analysis was carried out.

For the regression analyses that follow, we estimated the extent to which each cell had greater or lesser sensitivity than the mean sensitivity of the entire sample. This can be considered a cell’s “global-sensitivity advantage” (or disadvantage) relative to the average cell. Global-sensitivity advantage was calculated over the same range of adaptation levels for which MIN and LGNd cells were compared (i.e., 2.40 \times 10^{-6} to 4.46 \times 10^{-5} cd/m^2, marked by vertical dashed lines in Fig. 8B). Average sensitivity was obtained by fitting an exponential function to the contrast sensitivities of all MIN and LGNd Y cells for 1/8 cpd. An excellent fit was provided by an exponential function with four free parameters (see legend of Fig. 8A for details). The global-sensitivity advantage of a given cell was defined by the average (signed) deviation of contrast sensitivities from this function at all adaptation levels for which sensitivity of the cell was evaluated, so that a cell consistently more (less) sensitive than the average would be assigned a positive (negative) global-sensitivity advantage.

The spontaneous firing rate of Y cells, another predictor variable in the regression analysis, monotonically changed with adaptation level for many geniculate neurons and diverged for ON- and OFF-center cells at higher luminance (Fig. 8B). However, such differences were inconsequential for the dimmer adaptation levels. To remove receptive-field polarity as a factor in the analysis of spontaneous activity, the spontaneous firing rate of a given cell was taken as the average rate over adaptation levels from 2.40 \times 10^{-5} to 4.46 \times 10^{-5} cd/m^2, a range marked by vertical dashed lines in Fig. 8B, for which cells with different receptive-field polarities had similar spontaneous firing rates.

Having defined the parameters of interest, a multiple linear regression analysis was performed to identify variables other than structure that were correlated with sensitivity. In particular, spontaneous activity had a contribution comparable to that of structure (the higher the spontaneous firing rate, the higher the sensitivity) and the contribution of receptive-field center polarity was also significant, although substantially smaller (OFF-center more sensitive than ON-center). Sensitivity was not

![Fig. 5](http://jn.physiology.org/)

Comparison of neural contrast sensitivity of awake (filled circles) and anesthetized (open squares) cats for F1 responses of Y cells at 1/8 cpd (top) and X cells at 2 cpd (bottom). Data from anesthetized cats are from Lee et al. (1992); F0 responses were not examined in that study, so we cannot compare their estimates of contrast sensitivity for 4 cpd with ours.

![Fig. 6](http://jn.physiology.org/)

Slopes of fitted psychometric (red) and neurometric (blue) functions at threshold plotted against contrast threshold for 1/8, 2, and 4 cpd stimuli. The cat psychometric data are from the study of Kang and colleagues (2009). Neurometric functions are shown only for the cell class and response mode accounting for behavioral sensitivity: F1 for Y cells at 1/8 cpd, F1 for X cells at 2 cpd, and F0 for Y cells at 4 cpd. Mean slopes are indicated in each panel (red numerals for psychometric, blue for neurometric). Kang et al. (2009) excluded from their analyses contrast thresholds significantly outside the range of the actual stimulus contrasts used (i.e., shaded regions in Fig. 4) and, for this comparison, we have done the same for the neural data.
cells could detect stimuli of the same contrast, but at a dimmer adaptation level (marked by 2 horizontal dashed lines). Thus a positive index means that MIN curves (LGNd minus MIN) at every 5% contrast sensitivity from 5 to 85% was obtained by averaging horizontal distances between the 2 sensitivity comparison. An index of luminance advantage of MIN cells over LGNd cells advantage of the MIN. All 23 LGNd and 18 MIN cells contributed to this analysis revealed no interactions of structure with either spon-

dent with data from anesthetized cats (Lee et al. 1992). The correlated with receptive-field eccentricity, a result in agree-

ment with data from anesthetized cats (Lee et al. 1992). The analysis revealed no interactions of structure with either spon-

taneous activity or receptive-field center polarity in their con-

tributions to global-sensitivity advantage, so the comparisons of dim-light sensitivity of the MIN with LGNd made in Fig. 7 are not confounded by those variables. In particular, MIN cells were not more sensitive because they had higher spontaneous activity, nor because the MIN sample had relatively larger receptive-field eccentricity, nor because of the excess of off-

center cells in the MIN sample. MIN on-center cells had a global-sensitivity advantage over LGNd off-center cells (4.24 vs. 0.47%), which clearly obviates the possibility that the overall MIN sample was more sensitive than the LGNd sample solely because it had more off-center than on-center cells. The numerical results of the regression analyses are presented in section E of Supplemental Material.

FIG. 7. Comparison of scotopic sensitivity of MIN and LGNd cells as functions of adaptation level. A: contrast sensitivity for 1/8 cpd estimated from F1 responses for 23 LGNd Y cells (blue open circles), 16 MIN Y cells (red open squares), and 2 MIN cells not formally classified, but assumed to be Y cells (green open squares). B: contrast sensitivity advantage of the MIN. Twenty of 23 LGNd cells and 17 of 18 MIN cells contributed to this comparison; data for the others were outside the comparison range of adapta-

tion levels. The curves show average contrast sensitivity of the cells in A (LGNd, blue circles; MIN, red squares). An index of contrast-sensitivity advantage of MIN cells over LGNd cells was obtained by averaging sensitivity differences (MIN minus LGNd) at 7 adaptation levels from 2.40 × 10⁻⁶ to 2.15 × 10⁻⁴ cd/m² (marked by 2 vertical dashed lines). C: luminance advantage of the MIN. All 23 LGNd and 18 MIN cells contributed to this comparison. An index of luminance advantage of MIN cells over LGNd cells was obtained by averaging horizontal distances between the 2 sensitivity curves (LGNd minus MIN) at every 5% contrast sensitivity from 5 to 85% (marked by 2 horizontal dashed lines). Thus a positive index means that MIN cells could detect stimuli of the same contrast, but at a dimmer adaptation level than that of LGNd cells.

FIG. 8. A: estimation of global sensitivity advantage. Open circles are contrast sensitivities of 20 LGNd and 17 MIN Y cells measured in the range of adaptation levels indicated by dashed vertical lines in Fig. 7B. An exponential function, \( S = a - b \exp[-(L - c)/d] \), was fitted to the data points (solid curve), where \( S \) is contrast sensitivity and \( L \) is the display luminance in log cd/m². The values of the 4 free parameters were \( a = 96.54, b = 1.92, c = -2.29, \) and \( d = 0.88 \). The \( R^2 \) of the fit was 0.74, with a root mean square error of 15.8%. To demonstrate the quality of the fit, the average sensitivity at each adaptation level is indicated by open squares. The global-sensitivity advantage of a given cell was defined by the average (signed) deviation of contrast sensitivities from this function at all adaptation levels for which sensitivity of the cell was evaluated. B: spontaneous firing rate of ON- and OFF-center Y cells as a function of display luminance. For the multiple linear regression analyses described in RESULTS and Supplemental Material (section E), the spontaneous firing rate of a given cell was defined by its average firing rate across the range of adaptation levels bracketed by the 2 vertical dashed lines. This interval was chosen because the data density is high and the spontaneous activity is similar for ON- and OFF-center cells. Vertical bars at each symbol indicate the SE.
Increment threshold

For detection of sine gratings, increment threshold is contrast threshold multiplied by retinal illuminance. If sensitivity is regulated according to the deVries–Rose law, the increment threshold will be proportional to the square root of retinal illuminance (Rose 1948) and increment thresholds plotted against retinal illuminance on a log-log scale will fall on a line with a slope of 0.5. If the increment threshold follows Weber's Law, it will be proportional to retinal illuminance and the slope will be 1. There are potentially 12 such functions for the data in this study: for all combinations of 2 cell types (X and Y), 2 response modes (F0 and F1), and 3 spatial frequencies. Of these, we have adequate data to examine for 7 combinations (Fig. 9); for the remaining 5 combinations (F0 for X cells at 1/8 cpd, F0 and F1 for X cells at 4 cpd, and F1 for Y cells at 2 and 4 cpd), cells were insufficiently responsive to provide these data.

The F1 response of Y cells, which best matches behavioral sensitivity for 1/8 cpd, approximately follows the deVries–Rose law throughout scotopic adaptation levels, with a log increment-threshold slope for the overall sample of 0.58 (Fig. 9, top right, open blue circles). This analysis was confined to the scotopic range because for the mesopic range most F1 thresholds of Y cells were either extrapolated or assigned (Fig. 4B, top shaded bars). The slope is somewhat steeper than the cat behavioral increment-threshold slope of 0.52 for 1/8 cpd (see Fig. 8 of Kang et al. 2009), which was also obtained in the scotopic range. However, it is plausible that behavioral increment-threshold is determined not by Y cells in general, but by the most sensitive class of Y cells and, as was shown earlier, MIN Y cells are more sensitive than LGNd Y cells and OFF-center Y cells are more sensitive than ON-center Y cells. When increment threshold is examined for the population responses of various groups of Y cells defined by structure and center polarity (Fig. 10), it can be seen that the more sensitive groups have increment-threshold functions closer to the behavioral increment-threshold function, with the slope for MIN OFF-center Y cells most closely approximating the behavioral slope (0.54 vs. 0.52). Although it is undoubtedly the population response that underlies the behavioral increment-threshold function, it is also instructive to consider increment-threshold functions of individual cells and their relationship to the global-sensitivity advantage (Fig. 11). Here the sample is significantly smaller because not all cells contributed data over a sufficient luminance range for the increment-threshold slope and global-sensitivity advantage to be estimated. Individual slopes are quite variable, but MIN off-center cells (red solid squares) have the highest sensitivity and lowest slopes (mean slope = 0.51). Thus whether one considers the population response of all Y cells or the responses of individual Y cells, the neural increment-threshold functions are reasonably similar to the deVries–Rose behavior of the cat and converge on deVries–Rose behavior for the most sensitive group.

For all other combinations of cell class, response mode, and spatial frequency, increment threshold either adhered closely to Weber’s law or was intermediate between deVries–Rose and Weber behaviors (Fig. 9). Notably, for combinations determining behavioral sensitivity in the mesopic range, slopes of increment-threshold functions were comparable to the corresponding slopes of behavioral increment-threshold functions: the F1 response of X cells at 2 cpd displayed intermediate behavior (slope = 0.77) and the F0 response of Y cells at 4 cpd closely adhered to Weber’s law (slope = 0.99). The slopes of behavioral increment-threshold functions for these two spatial frequencies were 0.70 and 0.97 (see Figs. 7 and 8 of Kang et al. 2009). Note that the F0 response for Y cells at 2 cpd is derived only from grouped data; no individual cells supplied sufficiently sensitive responses to define an increment-threshold function.

Discussion

Cell class, neural codes, and behavioral sensitivity

This study demonstrates that behavioral contrast sensitivity in dim light is supported by distinct geniculate cell classes and response modes for different stimulus conditions. For detection of 1/8 cpd in the scotopic range and 4 cpd in the mesopic range, the cat appears to rely mainly on Y cells, but with different response modes: temporal modulation of firing rate at low spatial frequency and unmodulated elevation of mean firing rate near the acuity limit. At 2 cpd, temporally modulated responses of X cells likely mediate behavioral sensitivity.
Because the neural and behavioral data were not simultaneously collected with exactly the same task and visual stimuli, as was done in some previous studies using monkeys (Britten et al. 1992; Cook and Maunsell 2002; Hernández et al. 2000; Liu and Newsome 2005; Uka and DeAngelis 2003), we cannot definitively determine how many geniculate cells need to be pooled to achieve behavioral sensitivity. However, the observations that the sensitivity of many geniculate cells derived from responses during short intervals (i.e., 500 ms) matched behavioral sensitivity (Fig. 4), whereas the slopes of neurometric functions were significantly shallower than those of psychometric functions (Fig. 6), suggest that behavioral sensitivity is the outcome of subsequent (probably cortical) processing stages that suboptimally combine a pool of geniculate activity (Palmer et al. 2007). In this regard it should be noted that two factors may have contributed to an underestimation of neural sensitivity. First, to the extent that attention increases neuronal responsiveness (and thereby sensitivity; see McAdams and Maunsell 1999), we may have underestimated sensitivity of our geniculate cells because the cats presumably ignored the stimuli during the collection of neural data, but attended target locations during the behavioral sessions of Kang et al. (2009). Spatial attention does modestly increase the visual responses of magnocellular and parvocellular neurons in the macaque LGN (McAlonan et al. 2008; but see also Bender and Youakim 2001) and it is reasonable to suppose that the same is true for the cat. Second, it is possible that the uniform sine gratings used in the physiological experiments reduced neural sensitivity relative to behavioral sensitivity by more strongly activating surround mechanisms. If either or both of these factors were in play, this would further support the notion of suboptimal pooling at postgeniculate stages.

Estimates of the lower end of the cat mesopic vision vary from −0.5 to 1.0 log td (Kang et al. 2009). This coincides with the lowest adaptation level for which behavioral and neural sensitivity for 4 cpd rose above zero, suggesting that detection of spatial frequencies ≥4 cpd depends on cones. Over most of the mesopic range, behavioral contrast sensitivity for 4 cpd was low, relatively constant, and supported by Y-cell F0 responses. The elevation of mean firing rate of retinal Y cells in response to spatial frequencies beyond their Nyquist limit has been attributed to out-of-phase responses of nonlinear retinal subunits (Hochstein and Shapley 1976; for a review see Lennie 1980). The coincidence of a sharp increase in sensitivity for 4 cpd near the top of the mesopic range with appearance of X-cell responses implicates cone signals transmitted through X cells. The density of β ganglion cells, averaged for nasal and temporal retina, is about 1,600/mm² (Fig. 7A of Stein et al. 1996). If one assumes that β ganglion cells form a hexagonal lattice and that 1 mm on the retinal surface corresponds to 4.6° visual angle (Vakkur and Bishop 1963), then the Nyquist limit of β retinal ganglion cells (which presumably drive LGN X cells) at 8° retinal eccentricity is about 4.7 cpd, consistent with a behavioral acuity limit just above 4 cpd at this luminance.

Kang et al. (2009) found that cats can perceive 4 cpd at 8° eccentricity, whereas some previous physiological studies in anesthetized cats suggested lower high-spatial frequency cutoffs for both X and Y cells (Derrington and Lennie 1982; Lee et al. 1992; see also Fig. 5). We do not know whether the low neural sensitivity in anesthetized cats is due to direct effects of anesthesia on retinal sensitivity [Derrington and Lennie (1982) and Lee et al. (1992) used urethane and sodium thiopental, respectively] or to degradation of optics in the anesthetized preparation, but either way, these results suggest that caution be exercised when interpreting sensitivity measures obtained from anesthetized animals, particularly when they are to be correlated with behavioral data.

FIG. 10. Increment-threshold functions of Y cells for F1 responses at 1/8 cpd, grouped by structure and receptive-field center polarity. Top panels: Y cells grouped by structure (LGNd vs. MIN) and center polarity (ON vs. OFF). Bottom panels: ON- and OFF-center Y cells grouped by structure (left, LGNd; right, MIN). Slopes of linear regressions with 95% confidence intervals estimated from t distributions and the number of cells contributing to the data are shown in each panel.

FIG. 11. Increment-threshold slopes for F1 responses at 1/8 cpd stimuli in the scotopic range as a function of global-sensitivity advantage for 25 Y cells. Slopes were determined by linear regressions of increment threshold vs. retinal illuminance for all Y cells for which there were ≥3 data points. Global-sensitivity advantage is a measure of the extent to which a cell’s sensitivity in the scotopic range is higher or lower than the average (see Fig. 8A). The most sensitive class of cells (MIN OFF–center) has the lowest increment-threshold slopes.
Control of sensitivity across illumination levels

The visual system can operate over a spectacularly wide range of luminance because a series of retinal mechanisms maximizes sensitivity in dim light while preventing response saturation in bright light (Dunn et al. 2006). Under appropriate conditions, both human and cat increment thresholds are proportional to the square root of retinal illuminance at scotopic luminance levels (Kang et al. 2009), in agreement with the deVries–Rose law (Rose 1948). Our data show that Y-cell responses, but not X-cell responses, are consistent with these behavioral results. The highest spatial frequency for which cats show deVries–Rose behavior is between 1 and 2 cpd (Kang et al. 2009). We did not test cells with spatial frequencies between 1/8 and 2 cpd, but presumably the deVries–Rose behavior of the cat observed at spatial frequencies ≤1 cpd would also be evident in Y cells, although we cannot exclude the possibility that X cells follow the deVries–Rose law at some spatial frequencies in that range. We cannot say whether the deVries–Rose responses of Y cells are specifically linked to low spatial frequencies because for spatial frequencies ≥2 cpd, geniculate cells are insensitive at the adaptation levels for which this law holds.

The deVries–Rose law follows from the assumption that at very dim light levels sensitivity will be limited by random fluctuations in the photon density of the stimulus (Rose 1948; for a brief primer, see Kang et al. 2009). As pointed out by Shapley and Enroth-Cugell (1984), this is not actual regulation of sensitivity, but a lack of regulation that should occur when biological gain is maximal, leaving increment threshold to be determined by the physics of the stimulus. It is thus curious that we observed deVries–Rose behavior throughout the entire scotopic range, at least the upper portion of which should be subject to biological gain adjustments. As pointed out by Walraven et al. (1990), adherence to the deVries–Rose law does not prove that photon noise is the direct determinant of scotopic sensitivity. They speculate that it may be desirable for the visual system to keep the effects of photon noise constant across adaptation levels, and so neural gain-control mechanisms might enforce deVries–Rose behavior independently of photon-noise limitations. The current study was designed to determine which, if any, geniculate cells follow the deVries–Rose law and not the mechanisms by which this relationship or that predicted by Weber’s law are enforced, so we cannot directly address this issue. We can only note that since all classes of geniculate cells receive their scotopic inputs from the same shared population of rods, the difference between those that show deVries–Rose behavior and those that do not is determined by postreceptor circuits.

As spatial frequency and luminance levels increase through the mesopic range, regulation of increment threshold shifts to that predicted by Weber’s law, with increment threshold becoming proportional to retinal illuminance for the cat at 4 cpd in the mesopic range (Kang et al. 2009). Our data show that this relationship is probably mediated by F0 responses of Y cells, although they do not address the question of what cell classes and response modes may be responsible for Weber-like behavior at higher illuminance levels (and for other spatial frequencies). All X cells showed increment-threshold behavior intermediate between the deVries–Rose and Weber’s laws and, presumably, these account for the cat’s increment-threshold function for 2 cpd.

Previous examinations of retinal ganglion cells in the cat, monkey, and mouse have uniformly produced neural increment thresholds that are in agreement with Weber’s law or are intermediate between those predicted by Weber’s law and the deVries–Rose law. In particular, none reported neural responses that follow the deVries–Rose law in the scotopic range: the slopes of increment-threshold functions on a log-log scale were all significantly >0.5 and often closer to 1.0 than to 0.5. The bulk of these experiments used the anesthetized cat and, although most used flashing, stationary spots (for a recent example and a review of other studies using stationary spots, see Troy et al. 1999), one is comparable to the present study in that it used drifting gratings and Fourier analysis (Derrington and Lennie 1982). Data in the scotopic range are much less common for other species, but recent work in the excised retinas of mice and monkeys has also produced increment-threshold slopes >0.5 (Dunn et al. 2006). No increment-threshold data for LGNd cells across a comparable scotopic range are available in the literature, but we have extracted increment thresholds from the study by Lee et al. (1992) of LGNd and MIN cells in the anesthetized cat and the slopes of the increment-threshold functions were also well above 0.5 (e.g., 0.80, overall, for Y cells; Supplemental Material, Fig. S2).

There are many possible explanations for the apparent discrepancy between behavioral and prior neural data. For example: the regulation of retinal sensitivity could be distorted by retinal excision, anesthesia or stimulus conditions; analysis methods used in physiological and behavioral experiments might differ in critical ways; or sensitivity may be additionally regulated at higher neural levels. Although any or all of these factors could play a role, here we show that at the geniculate level the discrepancy is largely resolved by adhering to the assumption that for any given set of conditions, behavioral sensitivity is determined by the most sensitive population of cells. The retinal studies cited earlier dealt predominately or exclusively with on-center cells and often primarily with X cells [an exception may be Dunn et al. (2006), who targeted large cells that were presumably alpha cells, but which were not identified by physiological class]. However, for conditions under which cats have been shown to display deVries–Rose behavior (i.e., those of Kang et al. 2009), on-center X cells are the least sensitive category and are unlikely to be the determinant of behavioral sensitivity. Off-center Y cells, and particularly MIN off-center cells, are the most sensitive and these more closely follow the deVries–Rose law.

Medial interlaminar nucleus and dim-light vision

Our results support the proposal of Lee et al. (1984) that the MIN is a specialization related to dim-light sensitivity. In the lower scotopic range, individual MIN Y cells were, on average, significantly more sensitive than LGNd Y cells for 1/8-cpd stimuli, having contrast sensitivities equivalent to those of LGNd cells at adaptation levels 0.25 log unit dimmer (Fig. 7C). This replicates results of Lee et al. (1992) obtained from anesthetized cats, who reported MIN luminance-sensitivity advantage of about 0.3 log units at 1/8 cpd.

One may wonder whether it would be worth maintaining the MIN merely to achieve an improvement of about 10% in
contrast sensitivity or 0.25 log units of ambient luminance (Fig. 7, B and C). As pointed out by Lee et al. (1992), this question is answered by the ultimate arbiter: evolution. The cat’s tapetum, an adaptation whose sole function is to enhance sensitivity, results in a sensitivity improvement of only 0.11 log units in retinal illuminance (Kang et al. 2009), so an adaptation resulting in a sensitivity improvement of 0.25 log units clearly provides a meaningful selective advantage. The MIN’s advantage is likely even greater at spatial frequencies <1/8 cpd, given that it was nearly one full log unit at 0 cpd in the study of Lee et al. (1992) and that anesthesia does not appear to suppress sensitivity at low spatial frequencies and adaptation levels (see Fig. 5). This being said, we do not seek to imply that MIN cells by themselves support cat vision at even the dimmest adaption level. There are many more LGNd cells than MIN cells and thus there may be more opportunity for postthalamic signal averaging for activity relayed thorough the former.

Kang et al. (2009) suggest that most of the cat’s dim-light advantage comes from optics, implying that neural sensitivities of the two species are similar in para-central retina. This may not seem well reconciled with the MIN’s sensitivity advantage given that the human lacks an MIN, but there is no contradiction. It is not necessarily thalamic sensitivity, but neural sensitivity as a whole that is similar for cats and humans. The behavioral comparison excludes neither the possibility that a specialized visual stream equivalent to the cat MIN pathway exists in the human visual system (e.g., the magnocellular pathway) nor the possibility that signal averaging in later stages of visual processing plays a significant role in achieving human behavioral sensitivity. Furthermore, the neural sensitivity of cats may indeed be somewhat higher than that of humans. Although factoring out the cat’s optical advantages accounted for most of the sensitivity differences between the species in low scotopic conditions, the cats’ sensitivity was still higher for 0 cpd, by about 0.22 log td (Fig. 6; Kang et al. 2009). Finally, measurement errors may have obscured modest interspecies differences. There are opportunities for such errors at several stages of analysis and there are no ready means to quantify their overall possible effects. However, at present, there are no empirical or theoretical reasons to assume that there is a substantial difference in basic sensitivity between cat and human rod pathways.

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