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Receptive field properties of neurons in the primary visual cortex under photopic and scotopic lighting conditions

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Abstract

Knowledge of the physiology of the primate visual cortex (area V-1) comes mostly from studies done in photopic conditions, in which retinal cones are active and rods play little or no part. Conflicting results have come from research into the effects of dark adaptation on receptive field organization of cells in the retina and the lateral geniculate nucleus. These studies claim either that the effect of the surround disappears with dark adaptation or that it does not. The current study has as its objective a comparison of responses of V-1 cells in awake-alert macaque monkeys under conditions of light and dark adaptation. We reasoned that basic receptive field properties of V-1 cells such as orientation selectivity, direction selectivity, and end-stopping should be preserved in scotopic conditions if the receptive field organization of antecedent cells is maintained in dim light. Our results indicate that dark adaptation does not alter basic V-1 receptive field characteristics such as selectivity for orientation, direction, and bar length.

Keywords: Adaptation; Scotopic; Cortex; Receptive field; Monkey

1. Introduction

Knowledge of the physiology of mammalian visual cortex is largely based on studies in photopic conditions, in which rods make little or no contribution. Studies within the scotopic range have mostly been done at the retinal ganglion cell and lateral geniculate levels, and most of this work has been done in anesthetized cats. The earliest receptive-field studies of rod inputs to single cells in mammalian nervous systems were made by Barlow, Fitzhugh, and Kuffler (1957). The records were made from cat retinal ganglion cells and represented a continuation of work in light-adapted cats (Kuffler, 1953), in which ganglion cells were shown to have receptive fields that were center-surround, with an on-center and off-surround, or the reverse. Barlow et al. extended Kuffler's work to examine the behavior of cat retinal ganglion cells after dark adaptation. Cell receptive fields were assessed by measuring threshold as a function of stimulus area and were found to change after dark adaptation, with a dropping out of the surround and some enlargement of the center. The authors interpreted these results as indicating a reorganization of the receptive field under scotopic conditions, and as suggesting that rods made little or no contribution to the receptive-field surround (Barlow et al., 1957).

In a survey of lateral geniculate responses in anesthetized macaque monkeys, Wiesel and Hubel (1966) confirmed the original results of Barlow et al. (1957) that in dark adaptation the area-threshold curve failed to turn up as the stimulus size exceeded the center region but did not support their conclusion that rods make no contribution to the surround. For the parvocellular cells studied in light and dark adaptation, at various non-zero eccentricities, a spot bright enough to evoke a response, when it filled the center, always evoked a weaker response on being made larger (Wiesel & Hubel, 1966). It was concluded that in scotopic conditions, at threshold, and only at threshold,

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it is not possible to bring out the effects of a field surround. For the surround to assert itself the center must evidently be illuminated at suprathreshold intensities, either by the stimulus itself or by the background.

The findings of Barlow et al. (1957) have been supported by several studies of dark adaptation (e.g. Kaplan, Marcus, & So, 1979; Muller & Dacheux, 1997; Peichl & Wassle, 1983; Rodiek & Stone, 1965; Wrobel, 1981), while others found a maintenance of the surround effects in the dark adapted state (e.g. Enroth-Cugell & Lennie, 1975; Troy, Bohnsack, & Diller, 1999; Virsu, Lee, & Creutzfeldt, 1977; Wiesel & Hubel, 1966). Additional support that the surround does not disappear in scotopic conditions comes from an examination of a perceptual illusion, simultaneous contrast, that Barlow et al. (1957) predicted would disappear upon dark adaptation due to its presumed contingency on center-surround interaction. Maffei and Fiorentini (1972) tested this prediction and determined that simultaneous contrast persists even at low luminance. Fig. 1 presents a stimulus demonstrating simultaneous contrast that the reader can view under dim light conditions to verify the observation of Maffei and Fiorentini (1972).

Physiological studies of dark adaptation have mostly come from work done in anesthetized cats at the level of the retina (e.g. Barlow et al., 1957; Enroth-Cugell & Lennie, 1975; Rodiek & Stone, 1965; Troy et al., 1999) and in cat and monkey LGN (e.g. Maffei & Fiorentini, 1972; Virsu et al., 1977; Wiesel & Hubel, 1966; Wrobel, 1981). In the visual cortex little is known about the effect of dark adaptation on receptive field properties of cells. Two studies in cats have looked at the effects of dark adaptation on orientation selectivity in V-1: both found a persistence of orientation tuning (Bisti, Clement, Maffei, & Mecacci, 1977; Ramoa, Freeman, & Macy, 1985). The cat visual system is rod dominated and may not provide an ideal model for understanding human visual function in dim light. No one seems to have compared photopic and scotopic orientation tuning, direction selectivity, or end-stopping in cortical cells of the monkey. If in scotopic conditions the receptive field organization of ganglion cells or geniculate cells dramatically changed, one might expect to see marked effects on the behavior of the cortical cells to which they project. We therefore ask the question: do basic receptive field properties of monkey V-1 cells change with dark adaptation?

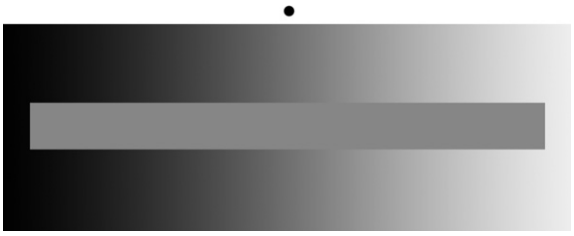

Fig. 1. The perception of simultaneous brightness contrast remains strong at low luminance. This can be demonstrated to the reader by dark-adapting for 10–15 min and then fixating slightly above or below the stimulus while positioning it at a distance of about 20 cm. Dark adaptation can be confirmed if the dot above the stimulus disappears when fixated due to its projection onto the rod-free fovea. When the inset bar is viewed with averted gaze under photopic or scotopic conditions, the region positioned to the left of center will appear lighter than the region positioned to the right, despite the bar having equal luminance across its length.

2. Methods

Monkeys were anesthetized and prepared for chronic recording by implanting a head post, scleral search coil, and a recording chamber that was positioned so as to permit access to neurons within the right primary visual cortex. Surgical procedures were the same as those previously reported (Livingstone, Freeman, & Hubel, 1996) with the exception that we used isoflurane as the general anesthetic. All procedures were approved by the Harvard Medical Area Standing Committee on Animal Care.

We assessed receptive field characteristics of neurons in the primary visual cortex of two rhesus macaques by extracellular recording using fine tungsten electrodes coated with a vinyl lacquer (Hubel, 1957) (Frederick Haer, Bowdoinham, ME). During recording, monkeys were awake and secured in an isolation chamber and faced a monitor (Barco Display Systems, Kortrijk, Belgium) that displayed visual stimuli at variable luminance within the photopic and scotopic range. Throughout the recording period, monkeys fixated a red dot that was positioned at the center of the monitor. Motivation for fixation came in the form of a juice reward given automatically at regular intervals provided that fixation was maintained. Data were collected only while the animal fixated within 1 degree of the fixation spot; the scleral eye coil permitted a continuous assessment of eye position throughout the recording period.

We recorded from 64 neurons located within part of V-1, the operculum, mapping the fovea and parafovea. Single unit responses were amplified and then isolated using a window discriminator (Bak Electronics, Germantown, MD). Optimal stimulus orientation, selectivity for movement direction, and end-stopping were evaluated in photopic and scotopic lighting conditions. Under room lit conditions, assessment of the cell's response properties was done using a computer program that enabled display of a white bar whose orientation, direction of motion, and length could be varied. We determined the optimum slit position, orientation, direction and speed of motion, bar length and width, and best direction of contrast (black vs. white). Orientation selectivity was assessed by presenting the monkey with an array of 25–50 like-orientated bars every other second, with bar orientation changing randomly across 50–70 trials. Direction selectivity was measured with a single moving bar whose orientation was set perpendicular to the preferred axis of motion, and whose velocity was set to obtain maximum response. Between 30 and 40 bar excursions were used to assess the cell's direction preference. The computer program plotted orientation selectivity and preferred direction of motion, and average responses vs. bar length ('length-summation curves') was plotted to evaluate end-stopping. The monkey viewed stimuli binocularly and our sampling did not include assessment of ocular dominance or color selectivity. Luminance measurements were made using a Prichard spot photometer.

Receptive fields were characterized first under photopic lighting conditions and then, after at least 15 min in the dark, the same cell was examined with stimulus luminance in the scotopic range. We achieved this with adjustment of the monkey's monitor to 20% brightness, a level at which we could detect only the faintest diffuse glow from the monitor even when fully dark adapted. We set the red 1/4 degree fixation spot at a level no brighter than necessary to permit fixation by the dark-adapted monkey. To be sure we were dark-adapted, we set the stimulus intensity to well below the level at which (1) a 1/4 degree spot disappeared when fixated, and (2) a green-phosphor spot of the same size lost any trace of green color and became gray. The monkey's state of dark adaptation was confirmed by its inability to fixate a low luminance moving spot (<-2.0 log cd/m^2) that was still bright enough to provoke an attempt at fixation when detected by its rod-dominant peripheral vision.

3. Results

We examined receptive field properties of 64 V-1 neurons from two alert rhesus macaques, sampling at eccentricities ranging from 1/2 to 7 degrees. For each cell, we began by establishing its main response properties in photopic conditions using a photopic (>-2.0 log cd/m^2) background.

Most of the cells we recorded produced a stronger response to bright stimuli on a dark background than to stimuli of reversed contrast. To avoid the difficulties involved in maintaining dark adaptation while adjusting background luminance, we restricted our examination to cells responsive to stimulation with bright slits on a dark background. For each cell, we first determined the receptive-field position and orientation preference using a computer program that presented a bar whose orientation and length, among other parameters, could be varied manually. We next mapped out the borders of the receptive field and established optimal bar length and width. Orientation and direction plots were then made, and end-stopping was assessed by plotting a length summation-curve.

For a subset of cells ($n = 32$) we determined response threshold by turning off the room lights, setting the background level to zero and, for cells whose response extended into the scotopic range, waiting about 15 min before taking measurements. Our assessment of threshold should not be interpreted as the cell's absolute threshold, which would likely have required longer dark adaptation (Hecht & Mandelbaum, 1940). Using stimulus parameters that had been optimal in photopic conditions (position, length, movement rate, and so on) we gradually decreased stimulus brightness (within the scotopic range) until a response could no longer be heard. The stimulus luminance at which the cell just failed to respond was considered its threshold. The results are shown in the scatter plot of Fig. 2. Of the cells whose fields were less than 2 degrees from the fovea, two had thresholds of -2.0 log cd/m^2 and the remaining 8 were -1.0 to -1.7 log cd/m^2. Based on the lack of response to stimuli of scotopic luminance we concluded that these cells had little or no rod input. For the 22 cells with eccentricities greater than 2 degrees, all but one (whose eccentricity was 2.5 degrees) had thresholds indicating that they had rod inputs. The four least sensitive of these cells responded at -2.4 log cd/m^2, well below cone threshold. All of the cells we recorded in this study were revealed by their response to photopic stimuli, so it is not surprising that all responded to stimuli of high luminance. The existence of a population of V-1 cells that receive input from rods but not cones is unlikely because rods have been shown to share the cone pathway through AII type ama-

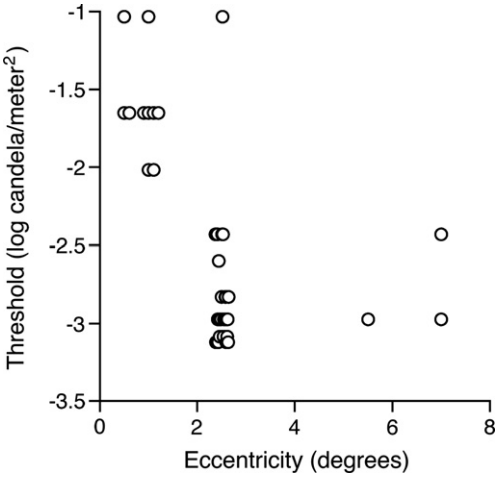

Fig. 2. Response threshold of dark-adapted V-1 neurons as a function of receptive field eccentricity. None of the cells we recorded within 2 degrees eccentricity ($n = 10$) responded to low luminance stimuli, likely because of a lack of rod input. Neurons with receptive fields beyond 2 degrees were found to be more sensitive to low light levels compared to those near the fovea. All but one of these cells, whose eccentricity was 2.5 degrees, responded to scotopic stimuli. Where eccentricities are identical, points in the scatter plot are shown slightly offset to make all data points visible.

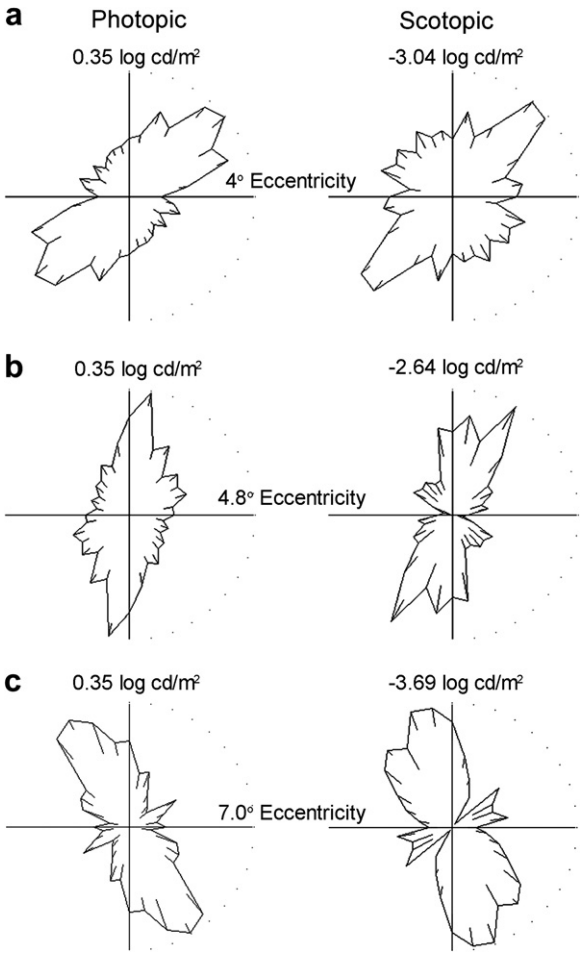

Fig. 3. Orientation tuning in photopic and scotopic conditions plotted for three V-1 neurons (a, b, and c). Length of the line joining the origin to each point represents the normalized response to flashed bars whose orientation was parallel to the line. These maps demonstrate that orientation tuning does not change after dark adaptation. The variability in sensitivity to scotopic luminance is illustrated by the cell with a 7 degree eccentricity (c) whose response was well below any of the thresholds plotted in Fig. 2, including those at the same eccentricity.

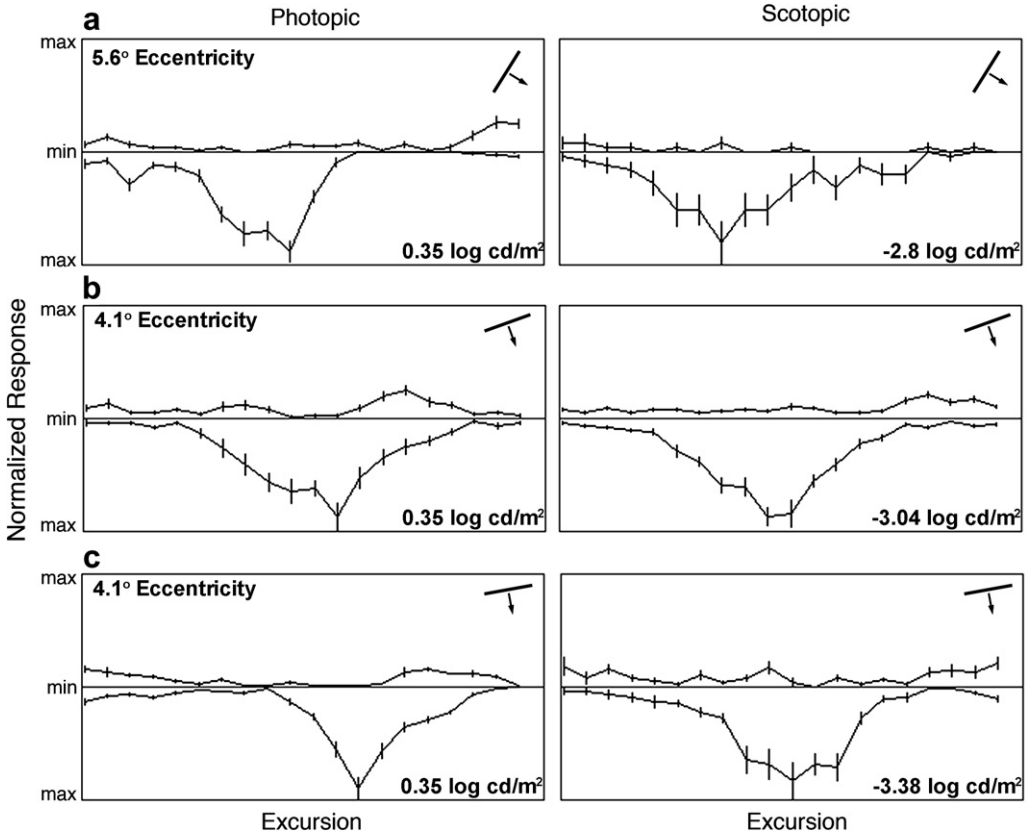

Fig. 4. Plots of direction selectivity for three cells (a, b, and c) in which the moving bar's excursion is plotted along the horizontal axis. The bottom trace in each plot shows response to movement in the preferred direction. Data points are normalized average responses to bar movement over many excursions. Stimulus luminance is indicated in the lower right quadrant of each plot. Receptive field eccentricity is presented in the upper left quadrant of the 'photopic' plots. Selectivity for direction of motion, indicated in the upper right quadrant of each plot, was not altered when stimulus luminance was changed from photopic to scotopic. Bar velocity was adjusted to maximize the cell's response, and for each cell the chosen speed was maintained across scotopic and photopic conditions.

crine cells (Strettoi, Dacheux, & Raviola, 1994; Strettoi, Raviola, & Dacheux, 1992). If such a cell type exists, its discovery would require screening with low luminance stimulation.

None of the cells we recorded responded briskly to diffuse light (large spots), in either photopic or scotopic conditions. Most of the cells had a clear orientation preference that was revealed upon stimulation with flashed or moving bars. Fig. 3 illustrates this result for 3 cells that were stimulated with an array of flashed bars whose orientation varied in random fashion. Cells that responded to scotopic stimuli invariably displayed an orientation preference that was indistinguishable from the one recorded under photopic conditions, though firing rate was about 30% reduced under scotopic luminance. The stimuli we used to map receptive field properties in the scotopic range were always of suprathreshold luminance because close to threshold responses were sometimes unreliable, fluctuating in the degree of selectivity. For many of the cells, orientation selectivity dropped off abruptly as luminance was lowered to a level near response threshold.

Directional selectivity was likewise unchanged under low luminance conditions. This is shown in Fig. 4 where direction-selectivity plots are presented for three cells that were stimulated with a moving bar whose directions of motion were set perpendicular to the cell's determined orientation preference. None of the cells that were direction selective under high luminance conditions showed a change in selectivity when examined after dark adaptation, though, as with orientation selectivity, firing rate was reduced by about 40% under scotopic luminance.

Length summation was assessed for several cells first in the presence of high luminance stimuli and then again after dark adaptation with low luminance stimuli. A typical result was plotted and is shown in Fig. 5 where a cell's response to different bar lengths demonstrates no difference in optimal length between photopic and scotopic conditions (although response to optimal length was reduced in dim light).

4. Discussion

Results from this study demonstrate that basic receptive field properties of monkey V-1 neurons do not change between photopic and scotopic lighting conditions. Orientation preference, directional selectivity, and end-stopping mapped photopically were found not to change when luminance was reduced for dark-adaptation. This study confirms in monkey what has been reported in cat, namely

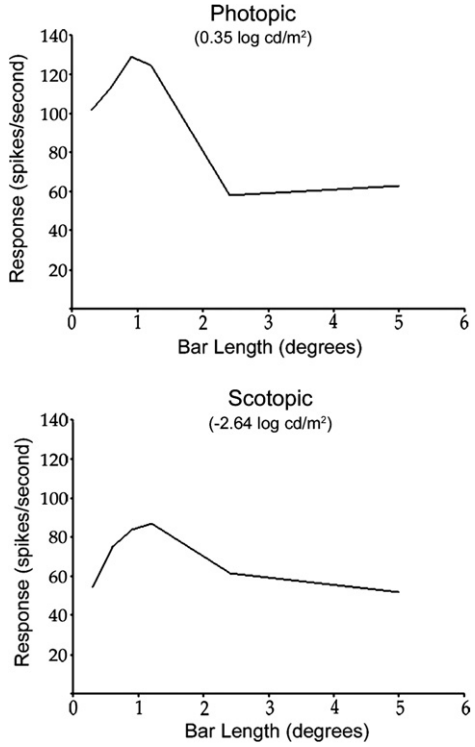

Fig. 5. Responses as a function of bar length are plotted for an ''end-stopped'' neuron in V-1. This cell responded maximally to a bar length of approximately 1 degree for both photopic and scotopic conditions. The receptive field eccentricity of this cell was 3.21 degrees. The stimulus luminance is indicated at the top of each plot.

that V-1 orientation selectivity is preserved in scotopic luminance (Bisti et al., 1977; Ramoa et al., 1985). Furthermore, this is the first investigation to reveal that direction selectivity and end-stopping of V-1 neurons do not change under scotopic conditions.

Our investigation has demonstrated that response threshold of V-1 neurons to scotopic visual stimuli falls at eccentricities beyond about 2 degrees of the fovea, about where rod density has been shown to rise sharply (Wikler, Williams, & Rakic, 1990). Most cells in the visual cortex at eccentricities beyond about 2 degrees were shown to receive input from rods and cones, and more rarely from cones alone. This is in stark contrast to cells with eccentricities up to 2 degrees, which appeared to receive little, if any, input from rods as evidenced by their insensitivity to low luminance stimuli. That a single cell can receive input from both rods and cones has been demonstrated in the retina (Barlow et al., 1957) and in the LGN (Wiesel & Hubel, 1966), making it likely that V-1 cells responsive to photopic and scotopic visual stimuli connect to antecedent cells that receive input from both rods and cones. Support for this notion comes from an examination of retinal connectivity that has demonstrated convergence of rod and cone signals in the retina through the narrow-field, bistratified AII amacrine cell (Strettoi et al., 1992, 1994). A less likely alternative is that afferents from LGN cells fed exclusively by rods or by cones first converge on single V-1 cells.

There seems to be a common belief that a shift to scotopic luminance, thereby engaging rod-driven vision, is necessarily accompanied by a marked reduction of acuity. Such a reduction is obviously to be expected in and near the fovea, but beyond a few degrees visual performance is remarkably robust across changing luminance levels. For instance, investigations of extrafoveal vision under photopic and scotopic conditions demonstrate only slight changes in form acuity (Low, 1946), orientation acuity (van Hoff, Legein, & Reuter, 1969), minimum angle of resolution (Yap, Levi, & Klein, 1989), and motion detection (van de Grind, Koenderink, & van Doorn, 2000). We add to this body of research results that indicate stability of basic receptive field properties, measured physiologically, between high and low luminance conditions. Our results also provide some evidence of differences between luminance conditions. Response magnitude of cells, for example, was reduced in the dark-adapted state. More sophisticated analyses of the response of V-1 cells to low luminance stimuli may reveal additional changes that can account for observed scotopic impairments with stereopsis (Livingstone & Hubel, 1994) and perception of speed of motion (Gegenfurtner, Mayser, & Sharpe, 1999).

In the cat visual system there is considerable disagreement on the effect of dark adaptation on receptive field organization. At the level of the retina several studies have confirmed the finding of Barlow et al. (1957) that there is significant diminution of the surround's antagonism (e.g. Muller & Dacheux, 1997; Peichl & Wassle, 1983; Rodiek & Stone, 1965), while other studies have found persistence of surround effects in dim light (Enroth-Cugell & Lennie, 1975; Troy et al., 1999). Work on dark adaptation in the cat LGN has likewise produced mixed results, some studies finding a loss of the receptive field surround (Kaplan et al., 1979; Ramoa et al., 1985; Wrobel, 1981), and others reporting no such effect (Bisti et al., 1977; Maffei & Fiorentini, 1972; Virsu et al., 1977; Wiesel & Hubel, 1966). The large degree of method variability between studies makes it difficult, if not impossible to reconcile these seemingly opposed results. A plausible explanation for the discrepancy is that the surround's effect falls off only at about the cell's absolute detection threshold. Support for this comes from a report in which the receptive field surround of LGN cells in monkey was found to fall off with luminance intensity at absolute threshold, but was clearly present when intensity was suprathreshold and in the scoptopic range (Wiesel & Hubel, 1966). It was concluded that loss of the surround at absolute threshold derives from its having a slightly higher threshold compared to the center, and that center activation must be at or above threshold before the surround can be revealed.

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