

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

Kevin R. Duffy ^a, David H. Hubel ^{b,*}

^a *Department of Psychology, Dalhousie University, Life Sciences Centre, Halifax, NS, Canada B3H 4J1*

^b *Department of Neurobiology, Harvard Medical School, 220 Longwood Ave, Boston, MA 02115, USA*

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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.

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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,

* Corresponding author. Fax: +1 617 432 0210.

E-mail address: david_hubel@hms.harvard.edu (D.H. Hubel).

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 & Wässle, 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

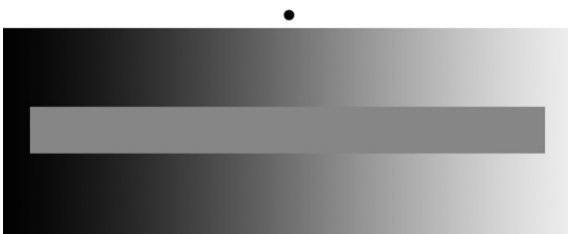


Fig. 1. The perception of simultaneous brightness contrast remains strong at low luminance. This can be demonstrated to the reader by dark-adapting for 10–15 min and then fixating slightly above or below the stimulus while positioning it at a distance of about 20 cm. Dark adaptation can be confirmed 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.

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?

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 ($< -2.0 \log \text{cd/m}^2$) that was still bright enough to provoke an attempt at fixation when detected by its rod-dominant peripheral vision.

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