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Luminance-contrast mechanisms in humans: Visual evoked potentials and a nonlinear model

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Abstract

Isolated-checks were luminance-modulated temporally to elicit VEPs. Bright or dark checks were used to drive ON or OFF pathways, and low or high-contrast conditions were used to emphasize activity from magnocellular or parvocellular pathways. Manipulation of stimulus parameters and frequency analysis of the VEP were performed to obtain spatial and contrast–response functions. A biophysical explanation is offered for why the opposite polarity stimuli drive selectively ON and OFF pathways in primary visual cortex, and a lumped biophysical model is proposed to quantify the data and characterize changes in the dynamics of the system with contrast given a limited number of parameters. Response functions were found to match the characteristics of the targeted pathways.

Keywords: Visual evoked potential; Magnocellular; Parvocellular; ON pathway; OFF pathway; Contrast gain control; Shunting inhibition; Nonlinear model

1. Introduction

Luminance-contrast[1] information is critical for perception of form, motion, and depth (Livingstone & Hubel, 1987, 1988; Ratliff, 1965; Shapley, 1990). Differences have been observed psychophysically in brightness and darkness perception (Fiorentini, Baumgartner, Magnussen, Schiller, & Thomas, 1990), and also in low and high-contrast perception (Bowker, 1983; Georgeson & Sullivan, 1975; Zemon, Conte, & Camisa, 1993). One aim of this study is to measure electrophysiological responses to stimuli that elicit each of these perceptual responses. Parallel neural pathways appear to govern these different aspects of contrast perception. Thus, a second aim is to determine the properties of these pathways with stimuli designed to emphasize contributions from select pathways. We attempt to explain in biophysical terms how positive- and negative-contrast information is processed separately in primary visual cortex, and we introduce a lumped biophysical model with a few free parameters to quantify the observed changes in dynamics of the system with contrast, referred to phenomenologically as contrast gain control (CGC).

Early neurophysiological studies demonstrated a functional dichotomy in the processing of positive- and negative-contrast (Hartline, 1938a, 1938b; Kuffler, 1953). On-center (ON) and off-center (OFF) cells form this pair of parallel pathways, which remain independent up to primary visual cortex (Schiller, 1982) and which appear to mediate the separate perceptions of brightness and darkness (Fiorentini et al., 1990; Hartline, 1938b; Jung, 1973). In previous studies, we used bright or dark check stimuli to emphasize contributions to the VEP from either ON or OFF subsystems (Zemon, Gordon, & Welch, 1988;

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[1] Throughout the remainder of this report, luminance-contrast will be referred to simply as contrast.

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Zemon et al., 1995a). This work yielded physiological evidence for differences in the processing of positive- and negative-contrast information.

Another important functional dichotomy exists within the primate visual system: the M-magnocellular (M) pathway exhibits high-contrast sensitivity and the P-parvocellular (P) pathway exhibits low contrast sensitivity (Kaplan & Shapley, 1986). The M and P streams, each of which is subdivided into ON and OFF subsystems, remain segregated at the initial cortical level (Hendrickson, Wilson, & Ogren, 1978; Hubel & Wiesel, 1972), beyond which interactions occur (Merigan & Maunsell, 1993; Nealey & Maunsell, 1994). Cortical neurons are known to exhibit essential nonlinearities such as rectification (De Valois, Albrecht, & Thorell, 1982; Movshon, Thompson, & Tolhurst, 1978; Spitzer & Hochstein, 1985) and contrast gain control (Carandini & Heeger, 1994; Ohzawa, Sclar, & Freeman, 1982, 1985). This latter nonlinearity was shown to be present in M but not P neurons (Benardete, Kaplan, & Knight, 1992).

Here, we used stimuli of low or high and positive- or negative-contrast to explore the characteristics of these pathways in humans. Differences in the responses were found to be consistent with differences in anatomical and physiological properties of neurons in the retino-geniculocortical pathway, and the lumped biophysical model provided good fits to all of the contrast functions. A preliminary description of this work was presented elsewhere (Zemon & Gordon, 1988, 2002).

2. Materials and methods

2.1. Rationale for the separation of activity from parallel pathways

To emphasize contributions from ON or OFF subsystems to the VEP, arrays of bright or dark isolated-checks (Fig. 1) were used (Zemon et al., 1988). Similar kinds of opposite polarity, positive- and negative-contrast stimuli, have been shown to be processed predominantly by respective ON and OFF pathways in monkeys (Schiller, 1982; Schiller, Sandell, & Maunsell, 1986).

To separate the contributions to the VEP from M and P streams with the use of luminance-contrast, we applied the knowledge, obtained from the work of Kaplan & Shapley (1982, 1986), that: (1) the contrast sensitivity (or contrast gain as defined by the slope of the linear segment of the contrast–response function) of M cells is nearly 10 times greater than that of P cells; and (2) the response magnitudes of M cells nearly saturate at moderate contrasts (above 16%), whereas the responses of P cells increase approximately linearly with increases in contrast throughout the entire contrast range.

We used isolated-check stimuli that varied from zero contrast to a maximum positive- or negative-contrast (*appearance–disappearance*) within the low contrast region to emphasize contributions from the M pathway to the VEP (Fig. 2). To emphasize P contributions, a high static contrast (*pedestal*) was used along with a temporal contrast component to modulate isolated-checks such that their minimum absolute value was equal to or greater than 16%. This type of stimulation avoids the low contrast region where the magnitudes of M-cell responses rise steeply with increases in contrast. Under this stimulus condition, M cells are expected to respond steadily with little modulated discharge. This high standing contrast is expected to generate strong shunting inhibition, which should limit responses from the M pathway (see nonlinear model below). Thus, its contribution to the VEP should be small or negligible. The more numerous P cells, however, are expected to produce a sizable modulated (summed) response under this condition, and therefore yield a dominant contribution to the VEP. (Unfortunately, there are no comparable, published single-unit data obtained under similar high-contrast pedestal conditions.) Psychophysical responses to low and high luminance-contrast stimuli are known to differ and recent work has attempted to explain these differences in terms of the physiological distinctions between M and P pathways (e.g., Pokorny & Smith, 1997).

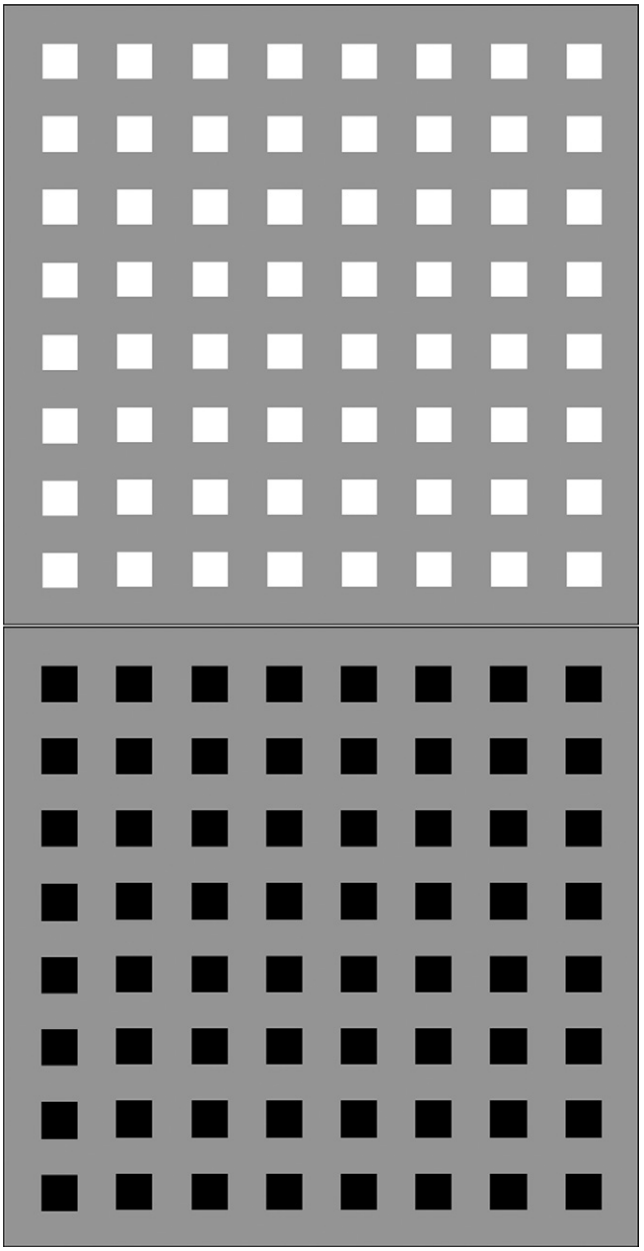

Fig. 1. Examples of the bright and dark isolated-check patterns used in this study. Check size was manipulated, and the intercheck spacing was always equal to the width of a check. The luminance of the checks was sinusoidally modulated in time at 6 Hz while the uniform background field remained stationary.

2.2. A biophysical model

A biophysical model is proposed to demonstrate how, through the process of rectification, the arrays of bright or dark isolated-checks might be processed separately by cortical neurons with low maintained discharge rates that receive input directly from ON or OFF cells, respectively