

# Visual cortex neurons in monkey and cat: Effect of contrast on the spatial and temporal phase transfer functions

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## Abstract

The responses of simple cells (recorded from within the striate visual cortex) were measured as a function of the contrast and the frequency of sine-wave grating patterns in order to explore the effect of contrast on the spatial and temporal phase transfer functions and on the spatiotemporal receptive field. In general, as the contrast increased, the phase of the response advanced by approximately 45 ms (approximately one-quarter of a cycle for frequencies near 5 Hz), although the exact value varied from cell to cell. The dynamics of this phase-advance were similar to the dynamics of the amplitude: the amplitude and the phase increased in an accelerating fashion at lower contrasts and then saturated at higher contrasts. Further, the gain for both the amplitude and the phase appeared to be governed by the magnitude of the contrast rather than the magnitude of the response. For the spatial phase transfer function, variations in contrast had little or no systematic effect; all of the phase responses clustered around a single straight line, with a common slope and intercept. This implies that the phase-advance was not due to a change in the spatial properties of the neuron; it also implies that the phase-advance was not systematically related to the magnitude of the response amplitude. On the other hand, for the temporal phase transfer function, the phase responses fell on five straight lines, related to the five steps in contrast. As the contrast increased, the phase responses advanced such that both the slope and the intercept were affected. This implies that the phase-advance was a result of contrast-induced changes in both the response latency and the shape/symmetry of the temporal receptive field.

**Keywords:** Visual cortex, Receptive field, Phase transfer function, Contrast, Spatial frequency, Temporal frequency

## Introduction

Over the past several decades (following the experiments of Hubel & Wiesel, 1962, 1968), the responses of neurons in the visual cortex of monkeys and cats have been measured as a function of the spatial frequency and the temporal frequency of drifting sine-wave grating patterns. These measurements result in a spatiotemporal transfer function, which is composed of an amplitude transfer function and a phase transfer function. A complete transfer function provides a systematic method for quantitatively characterizing some of the basic receptive-field properties of visual cortex neurons. Further, comparisons of the measured responses to those expected from a linear system are generally informative. (Progress within this general framework has been reviewed: e.g. Robson, 1975, 1983; Shapley & Lennie, 1985; De Valois & De Valois, 1988; Palmer et al., 1991; Skottun et al., 1991; DeAngelis et al., 1993; Jagadeesh et al., 1993; McLean & Palmer, 1994.)

In certain respects, the *phase transfer function* for simple cells is similar to the phase transfer function of a comparable bandpass linear filter. For such a filter, the phase of the response to drifting sine-wave gratings is determined by four different spatiotemporal properties of the filter: the spatial position, the spatial shape/symmetry, the temporal latency, and the temporal shape/symmetry (Hamilton, 1987; Hamilton et al., 1989). These four components add in a simple fashion such that the spatiotemporal phase transfer function can be described using a pair of linear equations, with the four parameters determined by the four spatiotemporal properties of the filter. Hamilton et al. (1989) have shown that these linear equations provide a good description of the measured phase transfer function of visual cortex simple cells (recorded from both cat and monkey) and that the four parameters provide a quantitative metric for describing the spatial and temporal properties of the receptive field. (For related work on the phase transfer function in the retina, lateral geniculate nucleus, and the visual cortex, see Shapley & Victor, 1978, 1979, 1981; Lee et al., 1981*a,b*; Enroth-Cugell et al., 1983; Dawis et al., 1984; Hamilton, 1987; Reid et al., 1992.)

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In other respects, the phase transfer function for simple cells is different from the phase transfer function of a linear filter. In a linear filter, the phase of the response is not affected by contrast. For simple cells, the phase of the response advances as the contrast is increased (Albrecht, 1978; Dean & Tolhurst, 1986; Carandini & Heeger, 1994), similar to neurons in the retina (Shapley & Victor, 1978, 1979, 1981) and the lateral geniculate nucleus (Sclar, 1987).

The first aim of the research reported here was to provide a more thorough understanding of the contrast-induced phase-advance, and if possible, to characterize the contrast-phase relationship with a quantitative mathematical formulation. Previous work has shown that the Naka-Rushton relationship provides a good description of the response amplitude as a function of contrast (Albrecht & Hamilton, 1982; Albrecht & Geisler, 1991; Sclar et al., 1990; Geisler & Albrecht, 1992, 1995; DeAngelis et al., 1993). The results of the present analysis show that the same relationship provides a good description of the response phase as a function of contrast. Thus, the descriptive parameters of this equation were utilized to compare the dynamics of the amplitude with the dynamics of the phase, and to summarize the sample of cells as a whole.

The second aim of this study was to explore the effect of contrast on the spatiotemporal receptive-field properties. To this end, the spatiotemporal phase transfer function was measured at multiple contrasts. As noted above, when measured at a fixed contrast, the phase transfer function is adequately described by linear equations with four parameters, and each parameter is individually influenced by a specific receptive-field property. For the spatial phase transfer function, the slope is determined by the spatial position of the receptive field and the intercept is determined by the spatial shape/symmetry of the receptive field. (Related work on these properties of the receptive fields can be found in Pollen & Ronner, 1981; Field & Tolhurst, 1986; Hawken & Parker, 1987; Jones & Palmer, 1987; Ferster, 1988.) For the temporal phase transfer function, the slope is determined by the temporal latency and the intercept is determined by the temporal shape/symmetry of the receptive field. (Related work on these properties of the receptive fields can be found in Lee et al., 1981*a,b*; Lennie, 1981; Reid et al., 1992; DeAngelis et al., 1993.) Therefore, by measuring the slopes and the intercepts of the spatial and temporal phase transfer functions at multiple contrasts, it should be possible to determine what aspect of the space-time receptive-field changes as a function of contrast. The results of the analysis imply that variations in contrast produce a change in both the latency and the shape/symmetry of the temporal receptive field.

The third aim of this study was to evaluate the effects of contrast on the phase transfer function, within the context of other known properties of the contrast response function of visual cortex neurons. Previous work has shown that as contrast increases, the response amplitude for most cortical cells increases over some range of contrasts and then remains static, at a maximum saturated value; further, the point of saturation in the contrast response function is not determined by the overall magnitude of the response, but rather by the overall magnitude of the contrast (Albrecht & Hamilton, 1982; Sclar & Freeman, 1982; Li & Creutzfeldt, 1984; Skottun et al., 1987; Albrecht & Geisler, 1991, 1994; Bonds 1991, 1993; Geisler & Albrecht, 1992, 1995; Heeger, 1992*a*; Carandini & Heeger, 1994; see Appendix). In the present analysis, the phase transfer function was measured at multiple contrasts to determine whether the phase-

advance was a consequence of the magnitude of the contrast, the magnitude of the response, or both. The results of the analysis imply that the phase-advance was primarily determined by the overall level of the contrast and not the overall level of the response.

## Methods

Procedures for the electrophysiological recording, the display of stimuli, and the measurement of neural responses using linear systems analysis have been described (Albrecht & Hamilton, 1982; Albrecht et al., 1984; Hamilton et al., 1989; Albrecht & Geisler, 1991; Geisler et al., 1991). The stimuli were drifting spatiotemporal sine-wave grating patterns presented on a Conrac studio monitor. The mean luminance was held constant at 27.4 cd/m<sup>2</sup>. Contrast (Michelson contrast) was defined as  $100 \cdot (L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$ . Both hardware and software methods were utilized to compensate for display nonlinearities.

The contrast, spatial frequency, temporal frequency, and direction of stimulus motion were varied in a systematic fashion, such that each of the different stimulus conditions were randomly interleaved. One presentation at a fixed spatiotemporal contrast consisted of a block of 10 or 12 contiguous temporal cycles. Each block was separated by a period of time equal to the block length; during these separations, the contrast was zero. Thus, for example, for the responses shown in Fig. 1, 12 contiguous temporal cycles were presented at one contrast, followed by zero contrast, followed by a randomly selected second contrast, followed by zero contrast, etc. Similarly, for the responses shown in Fig. 10, a given spatiotemporal frequency was drifted in one direction, followed by zero contrast, followed by a second randomly selected spatiotemporal frequency, direction, etc. A minimum of four blocks were obtained for each stimulus condition, which resulted in 40 or 48 repeated temporal cycles. Action potentials were collected in 0.1-ms time bins and the resulting spike trains were then Fourier analyzed. Once a single neuron had been isolated and classified as a simple cell, its optimal orientation was determined and held constant throughout the experiment.

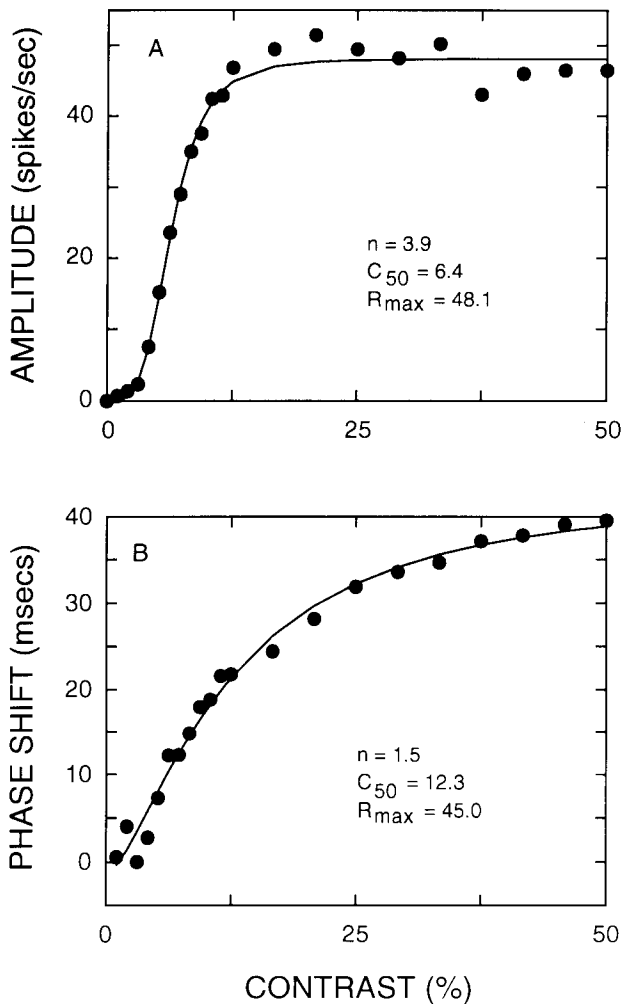
### Analysis of the contrast response functions

The responses as a function of contrast,  $R(C)$ , were fitted to the Naka-Rushton equation using least-squares criteria:

$$R(C) = R_{\max} C^n / (C^n + C_{50}^n) \quad (1)$$

The amplitude and the phase of the first harmonic component were fitted separately. When  $R(C)$  refers to the amplitude of the response as a function of contrast,  $R_{\max}$  is the maximum saturated response,  $C_{50}$  is the contrast that evoked 50% of  $R_{\max}$ , and  $n$  is the power function exponent.\* When  $R(C)$

\*In comparison to neurons in the retina and LGN, neurons in the visual cortex have a rather low spontaneous discharge. The spontaneous discharge for most simple cells is generally much less than one action potential per second. Further, this spontaneous discharge is generally not rhythmically periodic at the fundamental frequency of the stimulus. Thus, there is generally little or no spontaneous activity at the amplitude of the first harmonic of the stimulus. However, whenever there was spontaneous activity at the first harmonic, it was subtracted from the responses prior to fitting eqn. (1).



**Fig. 1.** Contrast response function for a representative neuron, recorded from within the visual cortex of a cat. The stimulus was a drifting sine-wave grating pattern (at the optimal spatial and temporal frequency, 0.44 cycle/deg, 6.25 cycle/s), presented at various contrasts. In (A), the amplitude of the response of the first harmonic component is plotted as a function of contrast. The smooth curve through the measured responses is the best fit of the Naka-Rushton relationship [see eqn. (1)]; the optimized values of the three parameters are listed. As the contrast increased, the response increased and then saturated. In (B), the phase of the response is plotted as a function of contrast. The phase responses are expressed as a shift in time (milliseconds), relative to the lowest value. The smooth curve through the measured responses is the best fit of the Naka-Rushton relationship [see eqn. (1)]; optimized values of the three parameters are listed. As the contrast increased, the phase of the response advanced (or shifted) in time. So, for example, the response of the cell to a 30% contrast occurred approximately 30 ms sooner than the response of the cell to a 3% contrast. The phase and the amplitude of the contrast response function were similar (the phase and the amplitude were dynamic at lower contrasts and static at higher contrasts), although not identical.

refers to the phase of the response as a function of contrast,  $R_{\max}$  is the maximum saturated phase,  $C_{50}$  is the contrast that evoked 50% of  $R_{\max}$ , and  $n$  is the power function exponent.

For the results presented in Part I of this study, the spatial frequency and the temporal frequency were held constant at, or near, the optimal values for each cell and the phase as a function of contrast data (e.g. Figs. 1–9) were normalized across cells

by expressing the phase responses as a shift in time (in ms) relative to the lowest value. Alternatively, the shift can be expressed as a fraction of the period of the stimulating temporal frequency (in degrees, or in  $\pi$  radians); the normative statistics were summarized in this fashion at the end of Part I and in the discussion section.† For the sample of cells as a whole, the stimulating temporal frequency ranged from 1–10 Hz. For nearly 75% of the cells, the stimulating temporal frequency fell within a range of 4.0–8.0 Hz. The average stimulating temporal frequency was 5.5 Hz, for both cat and monkey.

*Analysis of the phase transfer function*

*The four-parameter linear model*

Consider measuring the response of a linear filter, with band-pass spatiotemporal characteristics similar to a simple cell (e.g. a linear quadrature spatiotemporal filter, Watson & Ahumada, 1983, 1985; Adelson & Bergen, 1985), as a function of time.‡ The measured phase response,  $P$ , at a particular spatial frequency,  $\mu$ , and temporal frequency,  $\omega$ , can be described by the following equation (Hamilton, 1987; Hamilton et al., 1989):

$$P(\mu, \omega) = \text{sgn}(\mu)\theta_s - \mu p + \text{sgn}(\omega)\theta_t - \omega l \quad (2)$$

Eqn. (2) generates a pair of straight lines. One line describes the spatial phase transfer function, with slope  $p$  and intercept  $\theta_s$ ; the other line describes the temporal phase transfer function, with slope  $l$  and intercept  $\theta_t$ . The phase symmetries about the spatiotemporal origin are introduced by the  $\text{sgn}$  function, which is +1 for positive frequencies and -1 for negative frequencies.

These four parameters correspond to four separate properties of the spatiotemporal filter.

1. The *spatial position* of the filter introduces a fixed spatial displacement and thus a phase shift which increases with spatial frequency; the spatial position of the filter is given by the slope of the spatial phase transfer function ( $p/360$  deg).
2. The *spatial phase* of the filter (the spatial shape/symmetry) introduces a fixed phase shift independent of frequency; the spatial phase of the filter is given by the intercept of the spatial phase transfer function ( $\theta_s$ ).

†Consider the potential effect of the stimulating temporal frequency on these conventions within the framework of the four-parameter model of the phase transfer function. When the phase-advances are expressed as a fixed delay in time then any changes in the latency (as a function of contrast) should have a constant effect, independent of stimulating temporal frequency, while any changes in the shape/symmetry (as a function of contrast) should have a larger effect as the temporal frequency decreases. Conversely, when the phase-advances are expressed as a fixed fraction of the period of the stimulating temporal frequency (in degrees, or  $\pi$  radians) then any changes in the latency (as a function of contrast) should have a larger effect as the stimulating temporal frequency increases, while any changes in the shape/symmetry (as a function of contrast) should have a constant effect, independent of frequency.

‡It is easy to show that the phase transfer function of a bandpass linear filter similar to a simple cell can be adequately described by eqn. (2). For example, eqn. (2) would describe the phase transfer function of a bandpass Gabor-like filter (i.e. the product of a cosine and a Gaussian). However, it is important to note that the phase transfer function of a linear filter at very low frequencies may not be adequately described by eqn. (2) (see Hamilton et al., 1989, p. 1299).