

## VISUAL CORTICAL RECEPTIVE FIELDS IN MONKEY AND CAT: SPATIAL AND TEMPORAL PHASE TRANSFER FUNCTION

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**Abstract**—The response *amplitude* of simple cortical cells to spatiotemporal sine-wave patterns has been thoroughly documented in both cat and monkey. However, comparable measurements of response *phase* are not available even though phase measurements are essential for estimating the complete transfer function of a cell, and thus its spatiotemporal receptive field. This report describes a simple procedure for measuring both the amplitude and the phase transfer functions of striate cells. This technique was applied to 15 monkey and 27 cat simple cells. The spatiotemporal phase response functions were found to be adequately described by linear equations in four parameters. Both the amplitude and phase responses were found to satisfy several strong constraints implied by the class of linear quadrature models proposed recently in theories of biological motion sensitivity. Because the data satisfied these constraints, it was possible to determine four important receptive field properties from the phase data: the spatial symmetry, the temporal symmetry, the response latency, and the spatial position. The receptive fields were found to have a wide range of spatial symmetries, but a more narrow range of temporal symmetries. Spatiotemporal receptive fields reconstructed from complete transfer functions are used to illustrate some of the differences between direction selective and nondirection selective cells. Finally, the effects of linear and nonlinear mechanisms on amplitude, phase, and direction selective responses are considered.

Striate cortex	Simple cells	Linear systems	Response phase	Direction selectivity
Spatial frequency	Temporal frequency	Gratings	Receptive fields	Latency

### INTRODUCTION

Ever since Hubel and Wiesel first recorded the responses of simple cells in the visual cortex of monkeys and cats (1959, 1962, 1968), it has been known that a simple cell's sensitivity to light and dark across space—its receptive field—has a specific shape which varies from cell to cell. Early qualitative procedures for mapping receptive fields provided some indication of the dependence of the responses of cortical cells on the spatial, temporal, and directional aspects of the visual stimulus. These procedures, however, did not provide sufficient detail for developing and testing rigorous models of cortical processing.

To obtain more quantitative descriptions of receptive fields, researchers have employed many of the established techniques for analyzing linear systems (e.g. Enroth-Cugell &

Robson, 1966; Cooper & Robson, 1968; Campbell, Cooper & Enroth-Cugell, 1969; for recent reviews see: Shapley & Lennie, 1985, or De Valois & De Valois, 1988). In the linear systems approach, the working hypothesis is that the physiological mechanisms underlying a cell's response satisfy the linearity assumption: the output to a composite stimulus is the sum of the outputs to the individual components present in the stimulus. When this assumption is correct, a cell's response to arbitrary stimuli can be predicted by its response to sine-wave gratings of various spatial and temporal frequencies. Even when the linearity assumption does not hold precisely, it is generally recognized that responses to sinusoidal stimuli provide a useful characterization of a cell's behavior.

The response of a linear system to drifting gratings, measured as a function of spatial and temporal frequency, is the spatiotemporal transfer function. A transfer function can be converted to an equivalent receptive field in space and time by an inverse Fourier transform.† Both the spatiotemporal transfer function, and the spatiotemporal receptive field, completely

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†Inverse Fourier transformation of the transfer function produces the impulse response function; negating the space-time coordinates of the impulse response function produces the receptive field.

characterize a linear system; either can be used to predict its responses to arbitrary stimuli.

In a linear system, sinusoidal input produces sinusoidal output which can differ from the input only in amplitude and phase. Thus, the transfer function can be obtained by measuring the amplitude and phase of the response to drifting sine-waves as a function of spatial and temporal frequency, in other words, by measuring the amplitude-transfer function (ATF), and the phase-transfer function (PTF).

Over the past 20 years, many investigators have measured ATFs of cortical cells as a function of spatial and/or temporal frequency (e.g. Cooper & Robson, 1968; Campbell, Cooper & Enroth-Cugell, 1969; Maffei & Fiorentini, 1973; Glezer, Ivanoff & Tscherbach, 1973; Ikeda & Wright, 1975; Tolhurst & Movshon, 1975; Schiller, Finlay & Volman, 1976; Bisti, Clement, Maffei & Mecacci, 1977; Albrecht, 1978; Movshon, Thompson & Tolhurst, 1978a, b; Pollen, Andrews & Feldon, 1978; Andrews & Pollen, 1979; Holub & Morton-Gibson, 1981; Kulikowski & Bishop, 1981a, b; De Valois, Albrecht & Thorell, 1982; Kulikowski, Marcelja & Bishop, 1982; Hawken & Parker, 1984; Foster, Gaska, Nagler & Pollen, 1985; Kulikowski & Vidyasagar, 1986; Jones, Stepnoski & Palmer, 1987; Hawken & Parker, 1987; Robson, Tolhurst, Freeman & Ohzawa, 1988). However, none of these studies attempted to make comparable measurements of the PTFs for cortical cells.

The PTF is crucial for a complete description of the cell's transfer function (see Westheimer, 1984), thus it has many important ramifications for a cell's receptive field structure. The PTF determines the type of symmetry of the spatial and temporal receptive field profiles (e.g. whether they are even-symmetric, odd-symmetric, or asymmetric). It also determines the response latency and the spatial location of the receptive field. These properties cannot be determined by measuring only the ATF. Furthermore, the PTF, in conjunction with the ATF, determines the number of excitatory and inhibitory regions in the receptive field. There are, of course, many other effects of the PTF on receptive field structure.\*

This article reports measurements of both response amplitude and response phase, of sim-

ple cells recorded from the striate cortex of monkey and cat, to gratings drifting first in one direction of motion and then in the opposite direction. There have been several other attempts to measure the response phases of visual neurons. The method used here for measuring response phase was similar to that of previous investigators, however the method of analyzing and interpreting the data was different.

Glezer, Tsherback, Gauselman and Bondarko (1980) wanted to examine the relationship between the spatial receptive field, and the responses to drifting sine-wave gratings. To this end, they measured the amplitude and the phase of the response to gratings of various spatial frequencies, drifting in one direction. As they noted, accurate prediction of the spatial receptive field from the responses to gratings requires measurement of both the amplitude and the phase (see also Pollen & Ronner, 1981). However, because they only measured responses to gratings moving in one direction, their estimates of the response phase reflected not only the spatial but also the temporal properties of the cell. Indeed, they acknowledged that their analysis did not take into account the temporal characteristics of the cells (other than the latency of the response). As will be demonstrated here, one must measure the response phase to gratings drifting in opposite directions in order to separate those phase components related to the spatial receptive field from those components related to the temporal receptive field.

Lee, Elepfandt and Virsu (1981a, b) measured the phase responses of neurons in the retina, lateral geniculate nucleus (LGN) and striate cortex to drifting sine-wave gratings. Their goal was to compare the spatial receptive fields of simple cells in the cortex with the receptive fields found in the retina and LGN. Lee et al. used the same basic technique as Glezer et al. (1980) with the important addition of measuring the responses to gratings drifting in opposite directions. They assumed that the measured response phases were only determined by the spatial receptive field. However, response phases are determined by both the spatial and temporal receptive fields. Ignoring the influence of the temporal receptive field may not produce large errors of interpretation for cells that are approximately even-symmetric and not direction selective (such as those in the retina and LGN). On the other hand, as will be shown later, one cannot ignore the effect of the temporal recep-

\*Oppenheim and Lim (1981) present a related discussion, concerning the importance of phase in representing images.

tive field for cells that are direction selective, or for cells that lack even-symmetry (such as those in the cortex).

Enroth-Cugell, Robson, Schweitzer-Tong and Watson (1983) and Dawis, Shapley, Kaplan and Tranchina (1984) used a similar technique to measure the PTF of ganglion and LGN cells. Like Lee et al. (1981a) and Glezer et al. (1980), they did not explicitly take into account the separate effects of both the spatial and temporal receptive field on the measured response phases. The approach of Enroth-Cugell et al. (1983) and Dawis et al. (1984) has been valuable for investigating the response properties of retinal ganglion and LGN cells. However, as mentioned above, different methods of analysis are required for cortical cells because many are direction selective and are not even symmetric.

One of the major goals of the present study was to gain some understanding of the relationship between a striate neuron's spatiotemporal PTF and its receptive field. For example, what aspect of the PTF corresponds to the spatial symmetry of the neuron's receptive field? Or, what aspect of the PTF corresponds to the latency of the neuron's response? To answer questions such as these, we considered how the spatiotemporal transfer function and the receptive field of simple cells might be related within the framework of two general models. The first is the simple linear separable model. Because this model cannot predict direction selective responses, we also examined the linear quadrature model (Watson & Ahumada, 1983, 1985) which in various forms has been proposed as a biological motion sensor (Reichardt, 1961; Watson & Ahumada, 1983, 1985; Adelson & Bergen, 1985; Van Santen & Sperling, 1985). Both models impose a number of constraints on the phase and the amplitude data. These constraints, which are derived in the methods section, can be used to assess the usefulness and validity of the models as descriptors of cortical cell responses.

The Results section will show that most simple cell phase and amplitude responses do

not satisfy the constraints implied by the linear separable model, but do approximately satisfy the constraints implied by the linear quadrature model.\* In addition, we show that within the framework of the linear quadrature model, it is possible to determine the unique contributions of the spatial receptive field and the temporal receptive field on the phase transfer function of the cell.

The approach used here is based upon the theory of linear systems. However, simple cells display some clearly nonlinear behaviors, such as response rectification and response compression. In the Discussion section, we consider several simple types of nonlinear mechanisms and show that the most plausible types would have a minimal effect on the conclusions drawn from a linear systems analysis.

## METHODS

The procedures for electrophysiological recording and stimulus display have been described elsewhere (Albrecht & Hamilton, 1982; Albrecht, Farrar & Hamilton, 1984). Once a single neuron was isolated and classified as a simple cell, its optimal orientation was determined, and held constant throughout the experiment. The contrast of the gratings (defined as  $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$ , where  $L_{\max}$  and  $L_{\min}$  are the maximum and minimum luminance levels) was also held constant throughout the experiment. The stimulus protocol consisted of 50 unique items presented in random order (5 spatial frequencies  $\times$  5 temporal frequencies  $\times$  2 directions). An individual stimulus presentation consisted of 10 contiguous cycles of a given grating.

### *Measurement of response phase and amplitude*

The procedure for measuring the phase and amplitude of the response of simple cortical cells was based on linear systems analysis. It was assumed that the output of a simple cell could be modeled as a linear system followed by a threshold mechanism that produces half-wave rectification. When this assumption holds, the complete transfer function (i.e. the ATF and PTF) of a simple cell's linear mechanism can be obtained by measuring its amplitude and phase responses to drifting sine-wave gratings of various spatial and temporal frequencies. Half-wave rectification is a nonlinear mechanism that does not interfere with the measurement of the linear mechanism.

\*It is important to distinguish two types of separability. A direction selective cell is, by definition, not separable in space and time for opposite directions of motion. Nevertheless, such a cell can be separable in space and time for motion in one direction. The results of our experiments agree with previous reports (e.g. Tolhurst & Movshon, 1975), that most simple cells are, to a first approximation, spatiotemporally separable for motion in one direction: the shape of the spatial ATF is similar when measured at different temporal frequencies.

The technique used for calculating the raw response phase and amplitude from the spike train is well known. Peri-stimulus time histograms (PSTHs) were recorded for each spatial- and temporal-frequency combination tested. These histograms were then Fourier transformed to obtain the amplitude and the phase of the first six harmonics as well as the mean response rate (the d.c. component). As expected from simple cells, most of the power in the response was located at the temporal frequency of the drifting grating. Because most of the spectral power in the d.c. component and the higher-order harmonics could be accounted for by rectification, only the fundamental was considered in the analysis. These measurements of the raw amplitude and phase of the fundamental were used to estimate the value of the cell's spatiotemporal ATF and PTF at the tested frequencies.

#### *Estimation of the spatiotemporal ATF and PTF*

Some care is required in estimating the spatiotemporal ATF and PTF from the raw amplitude and phase data. There are two reasons for this. First, the stimulus is a spatial and temporal modulation, whereas a given cell's response is a simple temporal modulation. Second, because the exact spatial position of the receptive field's center is not known (*a priori*), the phase measurements are only known relative to an arbitrary, but constant, spatial reference point. These complexities are considered here. We show (a) that the raw amplitudes can be directly interpreted as the cell's ATF and (b) that the raw phases can be interpreted as the cell's PTF plus a linear term which represents the spatial offset of the receptive field relative to the constant spatial reference point.

To begin with, note that a drifting sine-wave grating is defined by the following equation:

$$L(x, t) = A_i \cdot \cos[2\pi(\mu x + \omega t)] + L_m;$$

where  $L$  = luminance,  $x$  = spatial position,  $t$  = time,  $L_m$  = mean luminance,  $A_i$  = amplitude,  $\mu$  = spatial frequency, and  $\omega$  = temporal frequency. The drift velocity,  $v$ , equals  $\omega/\mu$ . If a neuron behaves linearly, its response to a drifting grating will be a sinusoidally modulated spike train of frequency  $\omega$  that can vary only in amplitude and phase. Thus, the response function  $R$ , of a cell located at position,  $p$ , is:

$$R(p, t) = A_o(\mu, \omega) \cdot \cos[2\pi(\omega t) + P_o(\mu, \omega)]; \quad (1)$$

where  $A_o$  and  $P_o$  are the raw response amplitude and phase values obtained in the drifting grating experiment.

Recall that the position of the receptive field ( $p$ ) is unknown. From the experimental measurements of  $A_o(\mu, \omega)$  and  $P_o(\mu, \omega)$ , we would like to estimate the spatiotemporal transfer function of the cell. To do this, consider a continuum of cells, identical to the one being recorded, arrayed along the spatial axis. The output of this array is a function of space and time,  $R(x, t)$ . Thus, in this array, a drifting sine-wave input produces a drifting sine-wave output. The phase and amplitude of the output of this array, as a function of spatial and temporal frequency, is the spatiotemporal transfer function of the cell.

To calculate the temporal response in the whole spatial array,  $R(x, t)$ , from the recorded response of the cell at position  $p$ , consider the response of an arbitrary cell at spatial position  $x$ . This cell would produce the same response as the cell placed at position  $p$ , but at some time ( $\Delta t$ ) earlier or later. Thus,  $R(x, t) = R(p, t + \Delta t)$ . Because time = distance/velocity,  $\Delta t$  can be expressed as  $(p - x)\mu/\omega$ . Substituting into equation (1) we obtain:

$$R(x, t) = A_o(\mu, \omega) \cdot \cos[2\pi(\mu x + \omega t) + P_o(\mu, \omega) + 2\pi\mu p].$$

Therefore, the amplitude of the output spatiotemporal sine-wave is  $A_o(\mu, \omega)$  and its phase is  $P_o(\mu, \omega) + 2\pi\mu p$ . In other words, the cell's amplitude transfer function,  $A(\mu, \omega)$ , and phase transfer function,  $P(\mu, \omega)$ , are given by the following relations:

$$A(\mu, \omega) = A_o(\mu, \omega);$$

$$P(\mu, \omega) = P_o(\mu, \omega) + 2\pi\mu p.$$

The complete spatiotemporal transfer function,  $T(\mu, \omega)$ , is a complex-valued function containing the ATF and PTF:

$$T(\mu, \omega) = A(\mu, \omega) e^{-j2\pi P(\mu, \omega)}; \quad (2)$$

(see Bracewell, 1978). Thus, from the raw amplitude and phase values ( $A_o$  and  $P_o$ ), the complete transfer function can be determined up to a linear phase term whose slope depends on the position ( $p$ ) of the receptive field. The shift property of the Fourier transform (see Bracewell, 1978) implies that the inverse Fourier transform of the measured amplitudes and phases (that is, the inverse Fourier transformation of  $A_o(\mu, \omega) e^{-jP_o(\mu, \omega)}$ ) gives the correct shape