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.

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
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 simple 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 \( \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{max}} + L_{\text{min}}} \), where \( L_{\text{max}} \) and \( L_{\text{min}} \) 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.

*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.

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.
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:

\[ L(x, t) = A_\ell \cos(2\pi(x + \omega t)) + L_m, \]

where \( L \) = luminance, \( x \) = spatial position, \( t \) = time, \( L_m \) = mean luminance, \( A_\ell \) = 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:

\[ R(p, t) = A_0(\mu, \omega) \cdot \cos(2\pi(\omega t) + P_0(\mu, \omega)); \] (1)

where \( A_0 \) and \( P_0 \) 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 \( A_0(\mu, \omega) \) and \( P_0(\mu, \omega) \), 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:

\[ R(x, t) = A_0(\mu, \omega) \cdot \cos(2\pi(x + \omega t) + P_0(\mu, \omega) + 2\pi\mu p). \]

Therefore, the amplitude of the output spatiotemporal sine-wave is \( A_0(\mu, \omega) \) and its phase is \( P_0(\mu, \omega) + 2\pi\mu p \). 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:

\[ A(\mu, \omega) = A_0(\mu, \omega); \]
\[ P(\mu, \omega) = P_0(\mu, \omega) + 2\pi\mu p. \]

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

\[ T(\mu, \omega) = A(\mu, \omega) e^{-2\pi i P(\mu, \omega)}; \] (2)

(see Bracewell, 1978). Thus, from the raw amplitude and phase values \( (A_0 \) and \( P_0 \)), 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 \( A_0(\mu, \omega) e^{-2\pi i P(\mu, \omega)} \)) gives the correct shape
of the spatiotemporal receptive field. Although the position \( p \) of the receptive field is unknown, it turns out that \( p \) can be estimated from the phase data because simple cells have rather linear phase functions (see Results).

**Separable and quadrature models of the spatiotemporal transfer function**

Several types of models have been proposed for the spatiotemporal receptive fields of neurons in the visual pathway. The simplest class of model assumes that the receptive fields are linear and separable. These models provide a reasonably accurate characterization of some receptive fields. However, linear separable models are not appropriate for many cells in the visual cortex because such models cannot produce direction selectivity. While it is possible to achieve direction selectivity using nonlinear mechanisms, the simplest class of model that can produce direction selectivity is the linear quadrature models such as the one proposed by Watson and Ahumada (1983, 1985). The two sections that follow define the linear separable and linear quadrature models and derive the predictions of both for the phase and amplitude responses to drifting sine-wave gratings.

**Linear separable models.** Consider a receptive field that is linear and separable in space and time. In this case, there is a rather simple relationship between the receptive field and the transfer function. If a spatiotemporal receptive field, \( r(x, t) \), is separable then it can be described as the product of a spatial receptive field, \( g(x) \), and a temporal receptive field, \( h(t) \):

\[
r(x, t) = g(x) \cdot h(t).
\]

To obtain, the spatiotemporal transfer function, \( T(\mu, \omega) \), associated with a given spatiotemporal receptive field, the receptive field is first converted into an impulse response function by negating the arguments, and then it is Fourier transformed (Gaskill, 1978). Therefore:

\[
T(\mu, \omega) = G(\mu) \cdot H(\omega);
\]

where \( \mu \) and \( \omega \) are spatial and temporal frequency, respectively, and \( G \) and \( H \) are Fourier transforms of the spatial and temporal impulse response functions. (Note that \( G(\mu) \) and \( H(\omega) \) are the transfer functions corresponding to the component spatial and temporal receptive fields, \( g(x) \) and \( h(t) \).) Because the receptive field, \( r(x, t) \), is real-valued, the following symmetry relations must hold (Bracewell, 1978; Gaskill, 1978):

\[
A(\mu, \omega) = A(-\mu, -\omega);
\]
\[
P(\mu, \omega) = -P(-\mu, -\omega).
\]

That is, the ATF must have even symmetry about the spatial and temporal frequency origin, and the PTF must have odd symmetry. These symmetries hold generally, and are not dependent on the assumption of separability.

Further constraints are implied by separability. Note first that the component transfer functions, \( G(\mu) \) and \( H(\omega) \), can also be expressed in terms of their amplitude and phase transfer functions:

\[
G(\mu) = A_g(\mu) e^{-j2\pi f_x(\mu)};
\]
\[
H(\omega) = A_h(\omega) e^{-j2\pi f_y(\omega)};
\]

where \( A_g \) and \( A_h \) are the component ATFs, and \( P_g \) and \( P_h \) are the component PTFs. Substituting these expressions into equation (3) and comparing with equation (2) shows that the spatiotemporal ATF is the product of the component ATFs, and the spatiotemporal PTF is the sum of the component PTFs:

\[
A(\mu, \omega) = A_g(\mu) \cdot A_h(\omega);
\]
\[
P(\mu, \omega) = P_g(\mu) + P_h(\omega).
\]

Now because \( g(x) \) and \( h(t) \) are real-valued functions, the following symmetry relations must also hold (Bracewell, 1978; Gaskill, 1978):

\[
A_g(\mu) = A_g(-\mu);
\]
\[
A_h(\omega) = A_h(-\omega);
\]
\[
P_g(\mu) = -P_g(-\mu);
\]
\[
P_h(\omega) = -P_h(-\omega).
\]

In other words, the component ATFs must have even symmetry about the origin of their frequency axis and the component PTFs must have odd symmetry. By examining equations (4) and (5), we see that the spatiotemporal ATF and PTF for separable receptive fields have the following symmetries:

\[
A(\mu, \omega) = A(-\mu, \omega);
\]
\[
A(\mu, \omega) - A(\mu, -\omega);
\]
\[
P(\mu, \omega) - P(0, \omega)
\]
\[
= -[P(-\mu, \omega) - P(0, \omega)];
\]
\[
P(\mu, \omega) - P(\mu, 0)
\]
\[
= -[P(\mu, -\omega) - P(\mu, 0)].
\]
Thus, as Dawis et al. (1984) note, separability implies that a slice of the spatiotemporal ATF obtained at any fixed temporal frequency must be even symmetric about zero spatial frequency, and that a comparable slice of the spatiotemporal PTF must be odd symmetric about the phase value at zero spatial frequency. These equations also show that similar symmetries hold for slices at a fixed spatial frequency.

The symmetry relations given in equations (5.3) and (5.4) also imply a simple and useful relationship between the spatiotemporal PTF and the component PTFs. Specifically, by comparing equations (4.2), (5.3) and (5.4) we see that:

\[ P_x(\mu) = \frac{[P(\mu, \omega) - P(-\mu, \omega)]}{2}; \]  
\[ P_x(\omega) = \frac{[P(\mu, \omega) + P(-\mu, \omega)]}{2}; \]

or equivalently,

\[ P_x(\mu) = \frac{[P(\mu, \omega) + P(\mu, -\omega)]}{2}; \]  
\[ P_x(\omega) = \frac{[P(\mu, \omega) - P(\mu, -\omega)]}{2}. \]

Thus, the component spatial and temporal PTFs at any given spatial and temporal frequency can be directly determined from the measured values of the spatiotemporal PTF.

Equations (7) show that measurements must be obtained for drifting gratings with spatial and temporal frequencies of \((\mu, \omega)\) and \((-\mu, \omega)\), or with frequencies of \((\mu, \omega)\) and \((\mu, -\omega)\). (Changing the sign of either the spatial frequency or the temporal frequency reverses the direction of a drifting sine-wave grating.) Thus, equations (7) show that even for separable receptive fields, measurement of the spatial PTF requires measurement of response phase for gratings drifting in opposite directions. As noted earlier, Glezer et al. (1980) only measured response phase to gratings drifting in one direction. Unless the temporal phase happened to be zero, which is unlikely even if time delay is factored out, their measurements would not be sufficient to determine either the spatial or temporal PTF.

Although the spatial PTF and the temporal PTF can be determined precisely from the composite spatiotemporal PTF, the same is not true for the component ATFs. Equation (4.1) shows that the spatial ATF is proportional to the spatiotemporal ATF evaluated at a fixed temporal frequency. Similarly, the temporal ATF is proportional to the spatiotemporal ATF evaluated at a fixed spatial frequency. It is only possible to determine the product of the gain factors on the spatial and temporal components—all pairs of factors that produce the same product will produce identical spatiotemporal ATFs. For example, increasing the amplitude of the spatial ATF by a factor of two and decreasing the amplitude of the temporal ATF by a factor of two would not change the composite spatiotemporal ATF.

Linear quadrature models. Linear quadrature receptive fields are obtained by combining pairs of separable receptive fields:

\[ r(x, t) = q \cdot g(x) \ast h(t) + (1 - q) \cdot g(x) \ast h(t); \]

where the spatial components \(g(x)\) and \(g(x)\), are in approximate quadrature and the temporal components \(h(t)\) and \(h(t)\), are in approximate quadrature as well. The parameter \(q\) is a relative weighting factor between 0.5 and 1.0, and the “+” sign determines the preferred direction of motion. If two functions are in quadrature, they are identical except that all the frequency components in one of them have been shifted by 90 deg.*

Note that if \(q\) in equation (8) is 1.0, the quadrature receptive field is separable—that is, the spatiotemporal receptive field is the simple product of the spatial and temporal components, \(g(x)\) and \(h(t)\). In this case, equivalent responses are produced in both directions, and thus the spatial and temporal ATFs are the same for both drift directions. When \(q < 1.0\) the receptive field is not separable, and produces direction selective responses. However, even in this case the linear quadrature receptive field remains separable for a given direction of motion.

The transfer function associated with the quadrature receptive field is given by the following equation:

\[ T(\mu, \omega) = A_s(\mu) \cdot A_t(\omega) \times \left[ q \pm (1 - q) \text{sgn}(\mu) \text{sgn}(\omega) \right] \times e^{-j\pi_p(\mu) + p_q(\omega)}, \]

The functions \(\text{sgn}(\mu)\) and \(\text{sgn}(\omega)\) are “sign” functions; they are +1 for positive frequencies and −1 for negative frequencies. This equation can be obtained from equation (8) using well

*Strictly speaking receptive fields cannot be accurately described by sub-components that are in exact quadrature because, in general, the resulting receptive field would be noncausal (Watson & Ahumada, 1985). However, this is not a serious problem because causal receptive fields are easily produced by sub-components that are in approximate quadrature (Adelson & Bergen, 1985).
known properties of the Fourier transform. Inspection of equation (9) shows that the ATF and PTF of the quadrature receptive field are given by:

\[ A(\mu, \omega) = A_s(\mu) \cdot A_h(\omega) \times [q \pm (1 - q) \text{sgn}(\mu) \text{sgn}(\omega)]; \]  

(10.1)

\[ P(\mu, \omega) = P_s(\mu) + P_h(\omega). \]  

(10.2)

Interestingly, the PTF of a quadrature receptive field is identical to that of a separable receptive field [c.f. equation (10.2) and equation (4.2)]. Thus, all the properties of the PTF for separable receptive fields described earlier hold for the quadrature PTF. Specifically, the strong symmetry constraint on the PTF given by equations (6) must hold, and equations (7) can still be used to compute the phase functions of the spatial and temporal components \( g(x) \) and \( h(t) \) of the receptive field.

If \( q = 0.5 \), the quadrature receptive field responds only to motion in one direction. To see this, note that an arbitrary drifting sine-wave grating is represented in the Fourier domain as a pair of impulses (\( \delta \) functions) located symmetrically about the origin of the spatiotemporal frequency plane. Drift velocity determines the slope of the imaginary line through the origin connecting the pair of impulses. Thus, a stationary grating is represented by a pair of impulses lying on the spatial-frequency axis. If a grating is drifting one way the pair of impulses move so that one falls in the first quadrant and one in the third (i.e. the slope of the line is positive). If the grating is drifting the other way, the impulses fall into the second and fourth quadrants (i.e. the slope of the line is negative). Inspection of equation (10.1) shows that when \( q \) is 0.5 the ATF completely vanishes in either quadrants 1 and 3 or quadrants 2 and 4, depending on whether the sign in the equation is positive or negative. In other words, when \( q \) is 0.5 the quadrature receptive field can respond to only one of the two opposite drift directions, regardless of spatial and temporal frequency.

Equation (10.1) also shows that when \( q \) is between 0.5 and 1.0 the response is stronger for one of the drift directions. Note, however, that there is a rather strong symmetry constraint on the shape of the ATF. In particular, the ATF in quadrants 1 and 3 is identical to that in quadrants 2 and 4 except for a scaling factor that depends on \( q \). Specifically:

\[ A(\mu, \omega) = (2q - 1) \cdot A(-\mu, \omega); \]  

(11.1)

In sum, the linear quadrature receptive fields are sufficiently general to predict any level of direction selectivity, and they include, as a special case, the separable receptive fields. Thus, they make a reasonable starting point in the analysis of the phase (and amplitude) response of cortical simple cells. Furthermore, if a receptive field is well described by a linear quadrature model then equations (7) can be used to determine the phase spectra of the component spatial and temporal receptive fields.

We have seen that the linear quadrature model makes strong symmetry predictions for the raw amplitude and phase data. Later we will see that these symmetry predictions hold to a first approximation for many cortical cells, validating the use of equations (7), and leading us to a very simple four-parameter model of cortical cell response phase.

RESULTS

The first goal of this study was to measure the phase transfer function of striate simple cells. The basic stimulus was a drifting sine-wave grating pattern; spatial frequency, temporal frequency, and drift direction were varied. Figure 1 shows the average responses of a typical simple cell (recorded from monkey striate cortex) during one temporal period of the stimulus for several spatial and temporal frequency combinations. The left panel (1A) shows the PSTHs produced by five different spatial-frequency gratings, each drifted at a constant temporal frequency of 5 Hz. The right panel (1B) shows the PSTHs produced by a spatial frequency of 1.42 c/deg at five different temporal frequencies. The amplitude and phase of the first harmonic are indicated in the top right corner. As can be seen, both the amplitude and the phase vary with the spatiotemporal combination presented. As spatial frequency increases the PSTHs shift to the left, indicating a decrease in phase. Similarly as temporal frequency increases the PSTHs shift to the left, again indicating a decrease in phase.

These trends are better illustrated in Fig. 2 where the raw phase data for all fifty spatial and temporal frequency combinations tested are plotted as a function of spatial frequency (Fig. 2A) and temporal frequency (Fig. 2B). (Positive frequencies indicate gratings drifting from right to left, and negative frequencies left...
Fig. 1. Responses (averaged PSTHs) of a direction selective simple cell recorded from the striate cortex of a monkey. These responses were averaged over 40 presentations of a given spatiotemporal combination; the PSTHs represent the first six harmonic components of the response. (A) Responses to five different spatial frequencies (indicated to the left of each PSTH) at a fixed temporal frequency of 5 c/sec. (B) Responses to five different temporal frequencies at a fixed spatial frequency of 1.42 c/deg. The amplitude and phase of the first harmonic are indicated in the upper right of each PSTH. Note that as spatial or temporal frequency increases the responses shift to the left indicating that the phase of the response decreases.

This particular cell showed a response bias for gratings moving from right to left. (For the remainder of the paper, this cell will be referred to as the "direction selective" cell.) To quantify this directional bias, the ratio of the responses in the non-preferred direction to those in the preferred direction was subtracted from one, and then multiplied by 100 (Kato, Bishop & Orban, 1978; Albus, 1980; De Valois, Yund & Hepler, 1982). For this cell, the average response was 31 spikes/sec for all 25 stimuli moving in the preferred direction, and 15 spikes/sec for all 25 stimuli moving in the nonpreferred direction. Thus, the directionality index was 52.

For comparison, Fig. 3 shows the phase data for a monkey simple cell which produced almost equivalent responses to gratings moving in opposite directions. (For the remainder of the paper this cell will be referred to as the "non-direction selective" cell.) The average response was 39 spikes/sec for gratings drifting in the preferred direction and 30 spikes/sec for gratings drifting in the nonpreferred direction. Thus, the directionality index was 23. (The directionality index for the entire sample of cells to right.) These data have clear linear trends as a function of both spatial and temporal frequency. We will show later that the slope of the functions in Fig. 2A indicate the spatial position of the receptive field, the slope of the functions in Fig. 2B indicate the latency of the cell's response, and the intercepts indicate the spatial and temporal receptive field symmetries.*

*It is important to understand that the linear quadrature model does not require that the phase data (e.g. Figs 2 and 3) fall on straight lines (although it does require the data to fall on parallel curves). The term linear (with respect to the quadrature model) refers to the way the receptive field integrates light across space and time.

Fig. 2. Phase responses for all 50 spatiotemporal stimulus combinations for the direction selective simple cell shown in Fig. 1. The solid lines are the fit of the four parameter linear phase model [equation (12)]. As described in the text, these four parameters index the following receptive field properties: spatial symmetry, temporal symmetry, spatial position, response latency. (A) Response phase as a function of spatial frequency for the five different temporal frequencies tested. The positive spatial frequencies represent drift from right to left (the preferred direction), and the negative spatial frequencies drift from left to right (the nonpreferred direction). (B) Response phase as a function of temporal frequency for the five different spatial frequencies tested. (These are the same data as in A, but are represented in another quadrant of spatiotemporal frequency space.)
Phase transfer function

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Fig. 3. The phase response functions for a nondirection selective simple cell recorded from monkey striate cortex. The solid lines are the fit of the four parameter linear phase model [equation (12)]. (A) Response phase as a function of spatial frequency for the five different temporal frequencies tested. (B) Response phase as a function of temporal frequency for the five different spatial frequencies tested. The pattern of results for this nondirection selective cell are similar to those of the direction selective cell shown in Fig. 2. The cells in Figs 2 and 3 are quite representative of the population as a whole.

is shown in Table 1.) Like the direction selective cell shown in Fig. 2, the phase data for this nondirection selective cell fall on straight lines. The phase response data illustrated in Figs 2 and 3 are representative of the 42 cat and monkey cells examined. In the sections which follow, we assess the degree to which the amplitude and phase data conformed to the symmetry constraints implied by the separable and quadrature models. Because the cells satisfied, to a close approximation, the constraints of the linear quadrature model, the phase response data could be used to estimate the position and symmetry of the spatial component of the receptive field, and the latency and symmetry of the temporal component of the receptive field.

Tests of separability and quadrature constraints

The linear separable model and the linear quadrature model, described in the methods section, imply symmetry constraints on the raw phase and amplitude data. Thus, the validity of these models for different types of cells can be tested by examining the degree to which these constraints hold.

To begin with, both models predict that the phase measurements for gratings drifting in opposite directions should be odd-symmetric about a point on the origin. If this odd-symmetry constraint holds, the responses measured in one direction should map onto those measured in the opposite direction when equations (6.3) and (6.4) are applied to the raw phase data. Figures 4 and 5 show the results of applying these equations to the data in Figs 2 and 3. The phase responses are seen to satisfy
Table 1. Estimates of the latency (I) in msec, spatial phase (\(\theta_s\)) in degrees, temporal phase (\(\theta_t\)) in degrees, and direction selectivity in percent, for all 42 cat and monkey cells tested in the study.

<table>
<thead>
<tr>
<th>Cell No.</th>
<th>Latency</th>
<th>Spatial phase</th>
<th>Temporal phase</th>
<th>Directional index</th>
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<td><strong>Cat</strong></td>
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<td></td>
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<td>57</td>
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<td>3</td>
<td>41</td>
<td>51</td>
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<td>53</td>
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<td><strong>59</strong></td>
<td></td>
<td><strong>50</strong></td>
<td><strong>63</strong></td>
</tr>
</tbody>
</table>

| **Monkey** |         |               |                |                   |
| 1          | 78      | 152           | 8              | 9                 |
| 2          | 83      | 146           | 26             | 52                |
| 3          | 66      | 300           | 0              | 31                |
| 4          | 58      | 249           | 5              | 16                |
| 5          | 87      | 186           | 25             | 26                |
| 6          | 74      | 107           | 54             | 43                |
| 7          | 64      | 311           | 20             | 21                |
| 8          | 68      | 315           | 29             | 23                |
| 9          | 61      | 186           | -4             | 74                |
| 10         | 62      | 289           | -1             | 18                |
| 11         | 29      | 161           | 21             | 28                |
| 12         | 50      | 172           | 53             | 36                |
| 13         | 117     | 228           | -6             | 24                |
| 14         | 139     | 116           | 8              | 36                |
| 15         | 92      | 160           | 9              | 23                |
| **Average** | **75** |               | **17**         | **32**            |
| **Total (N = 42)** | **65** |               | **38**         | **52**            |

this odd-symmetry constraint to a close approximation.

The separable model implies similar symmetry constraints for the response amplitude data: the amplitudes at every fixed temporal frequency should be even symmetric about the spatial frequency origin [equation (6.1)], or vice versa, [equation (6.2)]. Most cortical cells (including the ones in our sample, see Table 1) do not respond equally well to stimuli drifting in opposite directions (e.g. De Valois, Yund & Hepler, 1982a), and thus do not satisfy the constraint. Therefore, the separable model must be rejected for most cortical cells.

The quadrature model implies the somewhat weaker constraint given by equations (11): the amplitude data should be even symmetric about the spatial frequency origin, up to a scaling factor. To test this constraint, we determined the single multiplicative constant \((2q - 1)\) that minimized the squared error between all the amplitudes for the two drift directions. We then plotted, for each temporal frequency, the amplitudes for one direction onto the amplitudes for...
Phase transfer function

As can be seen in Fig. 6 (where the data for both cells are plotted) the amplitudes are approximately even symmetric once scaled. Thus, the quadrature model remains plausible.

The quadrature model implies additional constraints on the phase and amplitude data. As shown in equation (10.2), the phase data must satisfy a strong additivity constraint: the composite spatiotemporal PTF should be the sum of the spatial PTF and temporal PTF. Thus, the change in response phase as a function of spatial frequency should be independent of temporal frequency, and vice versa. This constraint can be tested by subtracting the average phase at each temporal frequency from all the phase data at that temporal frequency. If the additivity constraint holds then all the data should collapse onto one curve. The results of these calculations are shown in Fig. 7. The phase data clearly satisfy the additivity constraint.

Equation (10.1) implies that the amplitude data should be separable when each drift direction is considered individually. This type of separability was first tested in cortical cells by Tolhurst and Movshon (1975). If the data are consistent with this type of separability, the

![Figure 5](image1.png)

**Fig. 5.** Test of the phase symmetry constraint implied by the linear separable and quadrature models for the nondirection selective simple cell shown in Fig. 3 (conventions are the same as those described for Fig. 4). Again, the phase symmetry constraint is satisfied.

![Figure 6](image2.png)

**Fig. 6.** Test of the amplitude symmetry constraint implied by the quadrature model. Log relative amplitude is plotted as a function of log spatial frequency for the five temporal frequencies tested. (A) The amplitude data for the direction selective cell shown in Fig. 2 have been plotted and tested for even symmetry. To do this we determined the single multiplicative constant which minimized the squared error between all the amplitudes for the two drift directions. The response amplitudes for the positive spatial frequencies are plotted as solid circles. The response amplitudes for the negative spatial frequencies were scaled by the multiplicative constant, reflected about the ordinate, and then plotted as open triangles. Each pair of curves was shifted vertically for ease of viewing. (B) The same procedure was performed on the amplitude data for the nondirection selective cell shown in Fig. 3. As can be seen, the responses for both cells approximately satisfy the amplitude symmetry constraint.
Fig. 7. Test of the phase additivity constraint implied by the linear separable and quadrature models. Equation (10.2) implies that subtracting the average phase at each temporal frequency from the phase data at that frequency, should collapse all the data from all temporal frequencies onto a single curve. (A) Results of this calculation applied to the data for the direction selective cell shown in Fig. 2. For each constant temporal frequency curve in Fig. 2, the average phase response was determined and then subtracted from the curve measured at that frequency. (B) The same procedure was performed on the phase data for the nondirection selective cell shown in Fig. 3. As can be seen, the phase data for these two cells satisfy the additivity constraint.

Interpretation of the phase data using the linear quadrature model

When the quadrature model holds, equations (7) can be used to estimate, from the raw phase data, the PTFs of the spatial and temporal components of the receptive field. For example, the spatial PTF can be obtained by subtracting the raw phase responses in one direction of motion from the responses in the other direction of motion, and dividing by two [see equation (7.1)]. This operation cancels the effects of the temporal PTF.

Figure 9A shows the spatial PTF, and Fig. 9B the temporal PTF obtained by applying equations (7), point for point, on all of the phase data for the direction selective cell shown in Fig. 2. Figure 10 shows a similar analysis of the phase data for the nondirection selective cell shown in Fig. 3. In each figure, the phase data are seen to cluster around a single straight line. This result is consistent with the linear quadrature model [equations (7)] which predicts that the spatial PTF should be independent of temporal frequency and that the temporal PTF should be independent of spatial frequency.

The data shown in Figs 9 and 10 are adequately described by straight lines. It is important to note, however, that the linear quadrature model only constrains the data points to fall on a single curve, which need not be a straight line. The fact that the phase data in each figure fall on a straight line suggests that the spatial and temporal PTFs of these cells are only dependent upon a few simple factors.

In the Methods section, it was shown that a spatial offset of the stimulus reference point from the center of the receptive field adds a linear phase component (+2πμp) to the measured phases as a function of spatial frequency. Because the observed phase changes as a function of spatial frequency are described by a linear function, the slope of the function can be interpreted as a consequence of the spatial offset. The spatial offset (p) was estimated by dividing the slope by 2π (i.e. 360 deg). For the cells in Figs 9A and 10A, the distance between the reference point and the center of the receptive field was estimated to be 0.42 and 0.34 deg of visual angle, respectively.

Similarly, because all the phase changes as a function of temporal frequency are described by a linear function, the slope of the temporal PTF can be interpreted as a consequence of a fixed latency or temporal offset between stimulus
Fig. 8. Test of the spatiotemporal separability constraint implied by the quadrature model. Equation (9.1) implies the amplitude data should show spatiotemporal separability when each drift direction is considered individually. (A) The amplitude data for the direction selective cell have been plotted here as a function of positive and negative spatial frequency. The curves in Fig. 6A for each drift direction were scaled and then plotted in log-log coordinates. (B) Results of the same analysis applied to the nondirection selective cell. As can be seen, these curves are approximately the same shape and thus satisfy the quadrature separability constraint.

onset and the cell’s response (which can also be thought of as the temporal position of the receptive field). From the slope of the functions in Figs 9B and 10B, the latencies for the two cells were estimated to be 83 and 68 msec, respectively. The latencies for the entire population of cells can be found in Table 1.

As noted earlier, the changes in phase, as a function of either spatial or temporal frequency, are entirely due to fixed spatial and temporal offsets. This indicates that all frequency components are in the same phase with respect to the spatiotemporal center of the receptive field. These relative phase values are given by the intercepts of the phase functions at zero spatial and temporal frequency. Because the phases are constant, it is reasonable to interpret the intercepts as the symmetry of the component spatial and temporal receptive fields. The spatial phase intercept, or spatial phase, was estimated to be 146 deg for the direction selective cell and 315 deg for the nondirection selective cell. The temporal phase intercept, or temporal phase, was estimated to be 26 deg for the direction selective cell and 29 deg for the nondirection selective cell.

Figure 11 shows the distribution of spatial phase for the entire population. Note that spatial phase is widely distributed across the entire range (0–360 deg) indicating that the spatial receptive field symmetries do not fall into the canonical categories of even-symmetric (0 or 180 deg) or odd-symmetric (90 or 270 deg). The entire distribution of temporal phase is presented in Fig. 12. In contrast to the distribution of spatial phase, temporal phase clusters in the range from 0 to 90 deg. This indicates much more similarity in the temporal symmetries relative to the spatial symmetries.

The range of temporal phases plotted in
Fig. 9. Component phase transfer functions for the direction selective cell. (A) The spatial phase transfer function obtained by applying equation (7.1) to all the data in Fig. 2A. The solid line was fit by the method of least squares. The slope determines the spatial position of the receptive field with respect to the stimulus reference point (0.42 deg); the intercept determines the spatial symmetry of the receptive field (146 deg). (B) The temporal phase transfer function obtained by applying equation (7.2) to all the data in Fig. 2A. The slope determines the latency (83 msec); the intercept determines the temporal symmetry (26 deg).

Fig. 10. Component phase transfer functions for the non-direction selective cell obtained by applying equations (7) to all of the data in Fig. 3A (see Fig. 9). (A) The spatial phase transfer function. (B) The temporal phase transfer function. The values of the estimated receptive field parameters were as follows: 0.34 deg (spatial position), 315 deg (spatial symmetry), 68 msec (latency), 29 deg (temporal symmetry).

Fig. 11. Distribution of the spatial phase parameter for all cells and for the populations of cat and monkey cells considered separately. As described in the text, the spatial phase parameter provides a quantitative index of the symmetry of each cell's spatial receptive field. A wide range of spatial symmetries are evident in these distributions.

Fig. 12 was restricted to a range of 180 deg, because it is not possible to determine the polarity of the underlying spatial and temporal impulse response functions associated with a given receptive field. Consider a receptive field region which inhibits to white. Such a region could be the product of either a positive spatial impulse response and a negative temporal impulse response, or a negative spatial impulse response and a positive temporal impulse response. Because the polarities are experimentally indeterminate, we have adopted the convention that the initial polarity of the temporal impulse response will always be positive. Note that there is no indeterminacy in the composite spatiotemporal receptive field, only in our ability to resolve the polarity of the underlying components.

DISCUSSION

The major goal of this investigation was to describe and characterize the spatial and temporal phase responses of striate simple cells. To this end, we measured the responses to gratings
drifting in one direction and then the opposite direction, as a function of spatial and temporal frequency. We found that the phase response functions were quite orderly; they were adequately described by linear equations depending upon only four factors. In addition, the phase and amplitude responses were found to be consistent with the symmetry and separability predictions of the linear quadrature model. The validity of these predictions allowed us to derive a number of fundamental properties of the receptive field from the phase responses: (a) the symmetry of the spatial component of the receptive field; (b) the symmetry of the temporal component of the receptive field; (c) the temporal latency; and (d) the spatial position.

The four parameter linear phase model

Because the phase response of simple cells has been shown to depend upon only four factors, it is possible to derive a four parameter phase model to describe raw phase data, such as those illustrated in Figs 2 and 3. Recall that the spatial PTF \( P_s(\mu) \) for simple cells is described by a linear equation whose slope is determined by the spatial position \( \mu \) of the receptive field and whose intercept is the spatial phase \( \theta_s \), thus:

\[
P_s(\mu) = \text{sgn}(\mu)\theta_s - 2\pi\mu p.
\]

(The sgn function, which is +1 for positive frequencies and −1 for negative frequencies, is required because the phase function is odd-symmetric about the origin.) Similarly, the temporal PTF \( P_t(\omega) \) is described by a linear equation whose slope is determined by the latency \( l \) and whose intercept is the temporal phase \( \theta_t \), thus:

\[
P_t(\omega) = \text{sgn}(\omega)\theta_t - 2\pi\omega l.
\]

Because the constraints of the linear quadrature model were satisfied, the composite spatio-temporal PTF \( P(\mu, \omega) \) must be the sum of these component PTFs [see equation (10)]; therefore:

\[
P(\mu, \omega) = \text{sgn}(\mu)\theta_s + \text{sgn}(\omega)\theta_t - 2\pi\mu p - 2\pi\omega l. \tag{12}
\]

We refer to equation (12) as the four parameter linear phase model.* The solid lines in Figs 2 and 3 illustrate the fit of this model to the raw phase data. As can be seen, the model provided an excellent fit for these two cells. To test how well the model describes the phase data for the entire sample studied, equation (12) was fitted, using least squares criteria, to the PTFs of all 42 cells. Results of this analysis showed that the model accounted for at least 90% of the variance for all cells and 95% of the variance for all but 6 of the cells. These statistics quantitatively demonstrate that the four parameter linear phase model provides an adequate description of the phase responses of simple cells, and further, that the two cells used throughout this report are representative of the entire sample.

If the phase responses of a given cell are accurately described by the four parameter linear phase model, then it is possible to use equation (12) to determine the spatial phase,
temporal phase, latency, and position of a given cell. (Notice that spatial frequency must be varied in order to estimate $p$, temporal frequency must be varied to estimate $l$, and gratings must be drifted in two directions to estimate $\theta_1$ and $\theta_2$. ) However, it is worth reiterating that even if the four parameter model were not to fit the phase responses of a particular cell (e.g. if the responses did not fall on straight lines), it may still be possible to derive the spatial PTF and temporal PTF by applying equations (7). The validity of using these equations depends only upon the validity of the linear quadrature model and not the four parameter phase model.

**Spatiotemporal receptive field**

As discussed earlier in the methods section, the spatiotemporal receptive field of a neuron can be reconstructed by inverse Fourier transformation of the raw amplitude and phase data. To do this, the measured amplitude and phase responses were fitted with the particular form of the linear quadrature model proposed by Watson and Ahumada (1983, 1985). In their model, the spatial component of the receptive field is a Gabor function, and the temporal component is a difference of two gamma functions. Figure 13A shows the reconstructed spatiotemporal receptive field for the direction selective cell. Figure 13B shows the reconstructed receptive field for the nondirection selective cell. In these figures, time runs vertically and space horizontally. The vertical location of each receptive field is determined by the response-latency parameter ($l$). The horizontal location is determined by the spatial-offset parameter ($p$). (The receptive field is located in negative time, because the cell's response can only depend upon past stimulation.) These spatiotemporal receptive fields describe how light distributed over space and time is summed to produce a response at a particular moment. In these pictures, lighter regions indicate excitation to light and darker regions indicate inhibition to light.

Consider first the receptive field of the nondirection selective cell. As expected from the analysis of Adelson and Bergen (1985), such a receptive field has a checkerboard pattern of regions which alternately excite and inhibit to light. Across space, the pattern of alternating preferences for white and black correspond to a particular spatial symmetry for the receptive field. Recall that the estimate of the spatial symmetry parameter for this cell was $315^\circ$. The fact that the parameter is between $270^\circ$ and $360^\circ$ (i.e. the symmetry is neither even nor odd) is evident in the figure. Similarly, across time, the pattern of excitation and inhibition produces a temporal symmetry. The temporal symmetry for this cell was $29^\circ$, which falls near the middle of the narrow range of temporal phases observed in the population as a whole.

Unlike the broad distribution of spatial phases, this narrow range of temporal phases implies that for most cells the light and dark pattern through time would be similar to that in the figure.

Now consider the receptive field of the direction selective cell in Fig. 13A. Like the nondirection selective cell, it too has regions which alternately excite and inhibit to light. However, the regions do not form a checkerboard pattern but rather a striped pattern oriented in space-time (as expected from the analysis of Watson & Ahumada, 1983, 1985; and Adelson & Bergen, 1985). The oriented, striped pattern indicates that this cell is selective to direction of motion. The counter-clockwise orientation from vertical indicates a preference for right-to-left motion.

The manifestation of the spatial symmetry parameter is not as evident in the spatiotemporal receptive field of direction selective cells. What is evident is that the spatial symmetry of the complete receptive field changes continuously through time. The spatial phase parameter, which reflects only one of the spatial quadrature components, determines the spatial symmetry near time zero, because here, the influence of the second component is minimal. Through time, the contribution of the second component increases, causing the spatial symmetry to shift. These trends can be seen in Fig. 13A—the spatial symmetry of the receptive

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Fig. 13. Spatiotemporal receptive fields for two monkey striate neurons. Lighter regions indicate excitation to light and darker regions indicate inhibition. (A) Direction selective neuron shown in Fig. 2. This cell's spatial receptive field shifts from left to right through time indicating a preference for movement in that direction. (B) Nondirection selective cell shown in Fig. 3. This cell's spatial receptive field does not shift to any great extent through time indicating an approximately equivalent sensitivity to movement in both directions.
Fig. 13

(A)

Time (msec)

Space (deg)

(B)

0 0.5°
-120 0.4°
-240
-75
-150
field agrees with the estimated phase parameter (146 deg) near time zero, and then shifts towards the phase of the quadrature component.

Receptive field symmetry

In the past, investigators have attempted to characterize receptive fields in terms of a single spatial symmetry parameter (Albrecht, 1978; Movshon et al., 1978a; De Valois, Albrecht & Thorell, 1978; Pollen & Ronner, 1981; for a recent review see Field & Tolhurst, 1986). Such a description may be adequate for cells which respond equivalently to movement in both directions. In this case, one of the two quadrature components drops-out [see equation (8)] and thus the spatial symmetry of the receptive field corresponds directly with the remaining component. However, a single symmetry parameter is harder to define for cells with any degree of direction selectivity because the spatial symmetry of the complete receptive field changes continuously through time. Within the framework of the linear quadrature model, the spatial symmetry of the complete receptive field of direction selective cells is determined by a pair of components separated by 90 deg. Because the two components are fixed in quadrature, it is then possible to define the spatial symmetry of the complete receptive field by the phase of just one of the components (i.e. by the spatial phase intercept parameter, \( \theta \)).

An additional implication of the direction selectivity of simple cells is that the classic receptive field plotting procedures may not be adequate for measuring spatial symmetry. Specifically, the symmetry estimated by flashing bars at different positions changes depending upon the duration of the bars. For example, computing the responses to flashing bars of various durations for the cell in Fig. 13A, shows that the estimates of symmetry would vary by more than 45 deg. For cells with greater direction selectivity, varying the duration of the flashing bars would result in an even larger range of symmetry estimates.

Cortical representations of visual information

It has been suggested that spatial information might be represented in the cortex by pairs of neurons with even and odd symmetric receptive fields (Robson, 1975, 1983; Pollen & Ronner, 1981; Kulikowski & Bishop, 1981a, b; Sakitt & Barlow, 1982). These encoding schemes have the advantage that with the appropriate choice of receptive field parameters (bandwidths, center frequencies, and spatial locations), they are capable of representing the visual image completely with a minimum number of units (i.e. a number of units given by the Nyquist rate). Presumably, it is the optimal efficiency of such encoding schemes that prompted the search for them in the visual cortex.

While it is certainly true that the receptive fields of some simple cells can be qualitatively described as either even-symmetric or odd-symmetric (e.g. Albrecht, 1978; Movshon et al., 1978a; De Valois et al., 1978), the results of the present measurements suggest that, when the population as a whole is considered, neither monkey nor cat simple cells fall into canonical groups of even and odd spatial symmetry, or into any particular pair of orthogonal symmetries (see Fig. 11). Thus, the results appear to rule out the hypothesis of a single encoding strategy of matched pairs of units with fixed symmetries. However, this does not rule out the possibility that cortical representations of spatial information are of optimal efficiency. For example, there could be multiple matched pair representations, each of optimal efficiency. Note that by current estimates, the number of cells in layer IV alone is approximately 40 times greater than the number in the dorsal lateral geniculate nucleus (Barlow, 1981). Thus, it is possible that entire optimal matched-pair encodings could be implemented by subsets of simple cells that comprise only a small fraction of the total number of cells. Such subpopulations would be difficult to discern in a given sample of cells (see related discussion in Hamilton, 1987).

On the other hand, it is important to note that matched pairs of orthogonal units are not required for efficient coding of spatial information; there are many possible efficient encoding schemes (Geisler & Hamilton, 1986). Some of these require only a single symmetry for all units, while others require a wide range of symmetries for the different units. It is possible that the neurons in area V1 contain multiple efficient encodings, each designed to provide complete information in a form appropriate for some later visual processing stage or module.

Nonlinear mechanisms

It is well known that simple cells display certain nonlinear characteristics such as response rectification and response compression (e.g. Movshon & Tolhurst, 1975; Albrecht, 1978; Movshon et al., 1978a; Albrecht & De Valois, 1981; Dean, 1981; De Valois,
Albrecht & Thorell, 1982b; Tolhurst, Movshon & Thompson, 1981; Albrecht & Hamilton, 1982). How would such nonlinearities affect responses to the stimuli used in the present linear systems analysis? To get an answer to this question, consider two types of nonlinear systems each containing the following three components in a different sequence: (a) a band-limited spatiotemporal linear mechanism, (b) a static (zero-memory) nonlinear response function, and (c) a thresholding mechanism which produces half-wave rectification. The first type of system has the spatiotemporal linear mechanism, followed by the nonlinear response function, and finally the threshold. The second has the nonlinear response function, followed by the linear mechanism and then the threshold.

Static nonlinearities have no effect on a phase transfer function measured using the procedures described in the methods section. Thus the estimated PTF, for both of the nonlinear systems, would be simply that of the linear mechanism. This is because instantaneous nonlinearities, such as rectification and compression, cannot alter the temporal position of the fundamental of the response, regardless of whether they precede or follow the linear mechanism.

The effect of static nonlinearities on the amplitude transfer function is somewhat more complicated and depends on the method used for measuring the ATF. The two common methods for measuring ATFs are (a) measuring the amplitude of the response to constant-contrast gratings, and (b) measuring the contrast required to evoke a constant-criterion response. If the nonlinear response function precedes the linear stage, then the constant-contrast procedure will accurately measure the shape of the ATF of the linear stage. This holds because the nonlinear response function has identical effects at all frequencies; thus, the amplitude of the fundamental at the output of the nonlinear stage will be constant. It follows that the amplitudes of the fundamental at the output of the linear stage will describe the ATF of the linear stage (up to a scale factor). The effect of the half-wave rectification is simply to scale the ATF by a known amount.

On the other hand, if the nonlinear response function follows the linear stage, the constant-contrast procedure will not accurately measure the ATF of the linear stage. This occurs because the response amplitudes at the output of the linear stage would be different and hence would be affected differently by the subsequent compressive nonlinearity. Specifically, a compressive nonlinearity would attenuate the response to frequencies near the peak of the ATF more than in the tails. The appropriate procedure for measuring the linear stage when a nonlinear response function follows the linear stage is to measure the stimulus contrast required for a fixed criterion response (Enroth-Cugell & Robson, 1966; Robson, 1975).

We chose to use constant-contrast stimuli because of the evidence that the compressive nonlinearity controlling the contrast response of simple cells is located prior to the stages responsible for the spatial ATF. Specifically, Albrecht and Hamilton (1982; see Figs 7–10) found that response saturation of cortical cells occurs at approximately the same physical contrast independent of spatial frequency. Consistent with this finding is the fact that ATFs measured at different fixed contrasts are approximately shape invariant on log-log coordinates (Albrecht & Hamilton, 1982; Skottun, Bradley, Sclar, Ohzawa & Freeman, 1987; see also, Sclar & Freeman, 1982). These results are most easily explained by a saturating nonlinear response function operating prior to the mechanisms responsible for the spatial-frequency tuning of cortical cells.

In general, if the major nonlinearities affecting a given cell’s responses are static nonlinearities, then it follows that the spatiotemporal properties, such as spatial frequency tuning and direction selectivity, are due to the linear stages. For cells with static nonlinearities, the procedure outlined in the methods section correctly measures the phase transfer function. Further, for cells in which the nonlinear response function precedes the linear stages, the procedure also correctly measures the amplitude transfer function. However, if the nonlinear mechanisms underlying a cell’s responses are more complex and dynamic, then they may play a more fundamental role in the spatiotemporal responses of cortical cells. In this case, linear systems analysis might be less appropriate than some form of nonlinear systems analysis.

**Direction selective mechanisms**

Since the early work of Barlow and Levick (1965), there has been a great deal of research directed towards understanding the biological mechanisms of direction selectivity in mammals. Although the experiments of Barlow and Levick led them to conclude that direction selectivity
All of the energy would be found in the first kernel; there would be no energy in the higher kernels. The first-order kernel is the “linear kernel”; it is equivalent to the spatiotemporal impulse response profile, and is thus directly comparable to a spatiotemporal receptive field (such as the one in Fig. 13A, of this report). The space–time interaction in the first-order kernel would be diagonally oriented, reflecting the inherent lack of separability for a direction selective mechanism [see equation (6.1), (6.2), and the related discussion presented earlier].

Next, consider the outcome of a Wiener analysis given a linear direction selective mechanism followed by half-wave rectification (and/or a nonlinear response function, as described earlier). Although most of the energy would remain in the first-order kernel, there would be considerable energy present in the second-order kernel. The energy present in this nonlinear kernel (a consequence of the rectification nonlinearity) would carry with it the property of direction selectivity, even though the direction selectivity was produced by linear summation. Thus, a single space–time interaction profile, pulled from the second-order kernel, would show the diagonally oriented energy, characteristic of a direction selective mechanism.

Finally, consider the outcome given a linear spatiotemporal filter (with no directional preference) coupled with some nonlinear direction selective mechanism. There would be energy present in the first-order kernel which would reflect the nondirectional selective linear spatiotemporal filter; the space–time interaction would not be diagonally oriented. There would also be energy in the higher order kernels which would reflect the nonlinear direction selective mechanism, and thus a single space–time interaction profile, pulled from the second-order kernel, would be diagonally oriented.

The space–time interaction profile shown in Fig. 2 of Emerson et al. (1987), is a slice of a Wiener-like second-order kernel. Similarly, the space–time interaction profile shown in Fig. 3 of Baker and Cynader (1988) is a slice of a second-order Volterra-like kernel. Because these profiles are not first-order kernels, they cannot be directly compared to the spatiotemporal receptive fields shown in Fig. 13 of this report, or to the spatiotemporal impulse responses of the linear direction selective mechanism of Watson and Ahumada (1985; Fig. 9A) and Adelson and Bergen (1985; Figs 8 and 10). For
both the Wiener and the Volterra analysis, energy present in the higher-order interactions must reflect some type of nonlinearity. However, the presence of energy in the higher-order kernels of a direction selective cell (whether it is diagonally oriented or not)* does not in and of itself imply that the direction selectivity of a given cell is determined by a nonlinear mechanism. The energy present in these second order kernels could be the result of a linear direction selective mechanism coupled with other nonlinearities, such as response rectification and response compression.†

Summary and conclusions

This article reported the measurements of the spatiotemporal transfer function (amplitude and phase responses as a function of spatial frequency, temporal frequency, and direction of motion) of monkey and cat simple cells. These measurements and the associated theoretical analysis can be summarized as follows. First, phase measurements from monkey and cat simple cells were found to be well described by linear equations in four parameters. Second, the phase and amplitude responses satisfied the symmetry constraints implied by the linear quadrature model. This allowed us to derive four important properties of the receptive field from the four phase parameters: the spatial position, the latency, the temporal symmetry, and the spatial symmetry. Third, simple-cell receptive fields were found to display a wide range of spatiotemporal shapes. In particular, they displayed a wide range of spatial symmetries (even symmetric, odd symmetric, asymmetric) and a relatively narrow range of temporal symmetries. Fourth, many of the direction selective simple cells have spatiotemporal shapes similar to the mechanisms proposed recently for biological motion processing. Indeed, as noted earlier, the cells behave as expected from the linear quadrature model (Watson & Ahumada, 1983, 1985; Adelson & Bergen, 1985). Fifth, we showed that the well-known nonlinearities of simple cells (response rectification and response compression) should have little effect on the PTF or the shape of the ATF. Given only these nonlinearities, the measured ATFs and PTFs reflect only the linear spatiotemporal mechanisms.

The procedures outlined here should make it possible to quantitatively catalog the shapes and distributions of spatial and temporal receptive fields, thus allowing strong tests of specific models of visual processing (e.g. Robson, 1975; Marcelja, 1980; Sakitt & Barlow, 1982; Geisler & Hamilton, 1986).

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*The second-order interaction plots of Emerson et al. are diagonally oriented while those of Baker and Cynader are not. Possible reasons for the differences between these two reports are discussed in Emerson et al., pp. 48–50, and in Baker and Cynader, pp. 244–245.

†For a related discussion of how simple nonlinearities such as response rectification can affect the interactions between pairs of lines, see Tolhurst and Dean, 1987.

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