

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

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(Received 15 July 1988; in revised form 31 January 1989)

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, μ = spatial frequency, and ω = temporal frequency. The drift velocity, v , equals ω/μ . If a neuron behaves linearly, its response to a drifting grating will be a sinusoidally modulated spike train of frequency ω 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 (Δt) earlier or later. Thus, $R(x, t) = R(p, t + \Delta t)$. Because time = distance/velocity, Δt 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

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:

$$T(\mu, \omega) = G(\mu) \cdot H(\omega); \quad (3)$$

where μ and ω 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:

$$G(\mu) = A_g(\mu) e^{-j2\pi P_g(\mu)};$$

$$H(\omega) = A_h(\omega) e^{-j2\pi P_h(\omega)};$$

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:

$$A(\mu, \omega) = A_g(\mu) \cdot A_h(\omega); \quad (4.1)$$

$$P(\mu, \omega) = P_g(\mu) + P_h(\omega). \quad (4.2)$$

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

$$A_g(\mu) = A_g(-\mu); \quad (5.1)$$

$$A_h(\omega) = A_h(-\omega); \quad (5.2)$$

$$P_g(\mu) = -P_g(-\mu); \quad (5.3)$$

$$P_h(\omega) = -P_h(-\omega). \quad (5.4)$$

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:

$$A(\mu, \omega) = A(-\mu, \omega); \quad (6.1)$$

$$A(\mu, \omega) = A(\mu, -\omega); \quad (6.2)$$

$$\begin{aligned} P(\mu, \omega) - P(0, \omega) \\ = -[P(-\mu, \omega) - P(0, \omega)]; \end{aligned} \quad (6.3)$$

$$\begin{aligned} P(\mu, \omega) - P(\mu, 0) \\ = -[P(\mu, -\omega) - P(\mu, 0)]. \end{aligned} \quad (6.4)$$

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:

$$P_g(\mu) = [P(\mu, \omega) - P(-\mu, \omega)]/2; \quad (7.1)$$

$$P_h(\omega) = [P(\mu, \omega) + P(-\mu, \omega)]/2; \quad (7.2)$$

or equivalently,

$$P_g(\mu) = [P(\mu, \omega) + P(\mu, -\omega)]/2; \quad (7.3)$$

$$P_h(\omega) = [P(\mu, \omega) - P(\mu, -\omega)]/2. \quad (7.4)$$

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 (μ, ω) and $(-\mu, \omega)$, or with frequencies of (μ, ω) 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:

$$r(x, t) = q \cdot g(x) \cdot h(t) \pm (1 - q) \cdot \hat{g}(x) \cdot \hat{h}(t); \quad (8)$$

where the spatial components $g(x)$ and $\hat{g}(x)$, are in approximate quadrature and the temporal components $h(t)$ and $\hat{h}(t)$ are in approximate quadrature as well. The parameter q is a relative weighting factor between 0.5 and 1.0, and the “ \pm ” 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:

$$\begin{aligned} T(\mu, \omega) &= A_g(\mu) \cdot A_h(\omega) \\ &\times [q \pm (1 - q) \operatorname{sgn}(\mu) \operatorname{sgn}(\omega)] \\ &\times e^{-j2\pi P_r(\mu) + P_h(\omega)}. \end{aligned} \quad (9)$$

The functions $\operatorname{sgn}(\mu)$ and $\operatorname{sgn}(\omega)$ 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 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:

$$A(\mu, \omega) = A_g(\mu) \cdot A_h(\omega) \times [q \pm (1 - q) \operatorname{sgn}(\mu) \operatorname{sgn}(\omega)]; \quad (10.1)$$

$$P(\mu, \omega) = P_g(\mu) + P_h(\omega). \quad (10.2)$$

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 is 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 (δ 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:

$$A(\mu, \omega) = (2q - 1) \cdot A(-\mu, \omega); \quad (11.1)$$

$$A(\mu, \omega) = (2q - 1) \cdot A(\mu, -\omega). \quad (11.2)$$

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

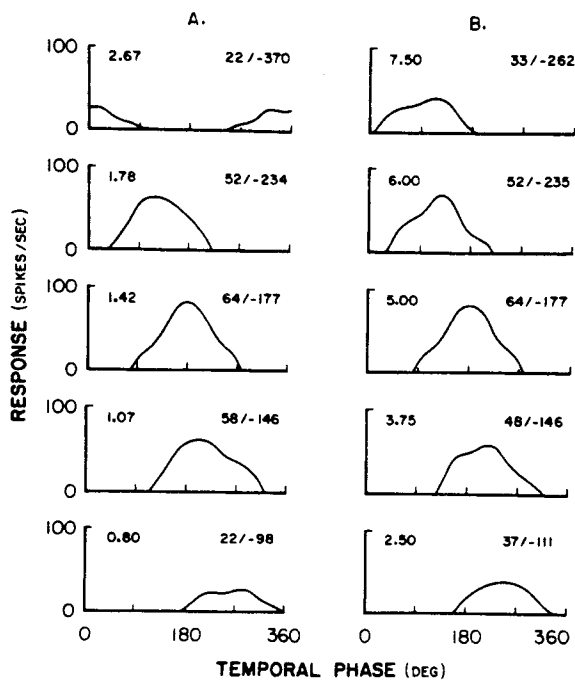


Fig. 1. Responses (averaged PSTHs) of a direction selective simple cell recorded from the striate cortex of a monkey. These responses were averaged over 40 presentations of a given spatiotemporal combination; the PSTHs represent the first six harmonic components of the response. (A) Responses to five 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.

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.*

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

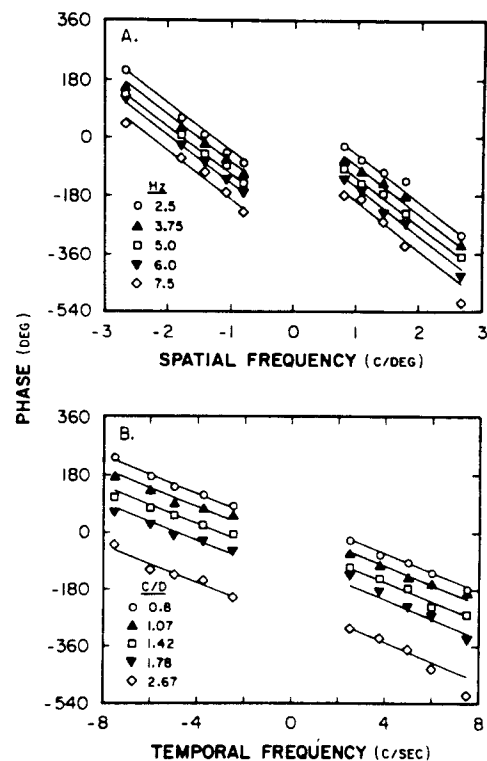


Fig. 2. Phase responses for all 50 spatiotemporal stimulus combinations for the direction selective simple cell shown in Fig. 1. The solid lines are the fit of the four parameter linear phase model [equation (12)]. As described in the text, these four parameters index the following receptive field properties: 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.)

*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.

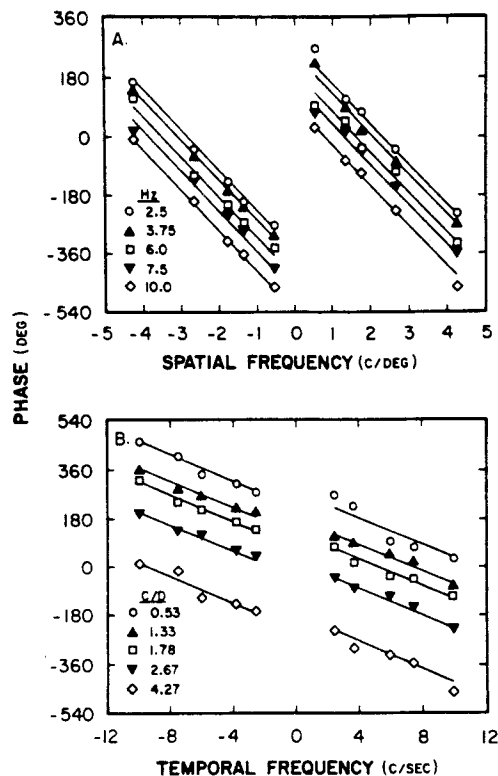


Fig. 3. The phase response functions for a nondirection selective simple cell recorded from monkey striate cortex. The solid lines are the fit of the four parameter linear phase model [equation (12)]. (A) Response phase as a function of spatial frequency for the five different temporal frequencies tested. (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

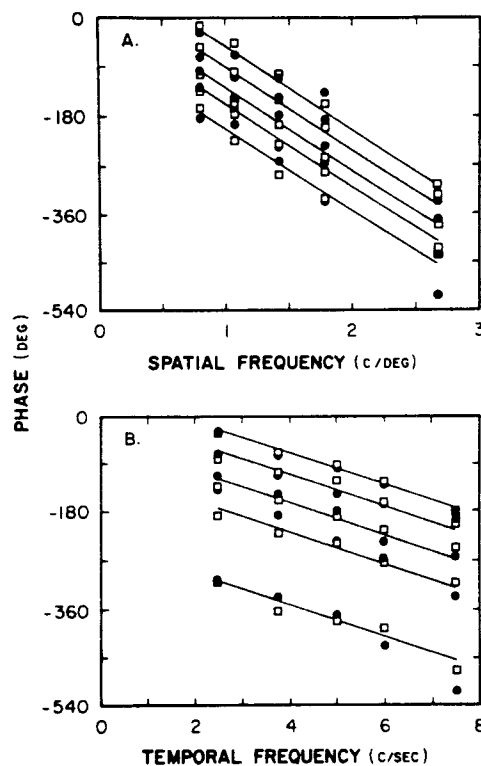


Fig. 4. Test of the phase symmetry constraint implied by both the separable and quadrature models. The phase response data for the direction selective simple cell shown in Fig. 2 have been replotted to test for odd symmetry about a point on the ordinate. (A) Response phase as a function of spatial frequency for the five temporal frequencies tested. The original data in Fig. 2A at positive frequencies are plotted as solid circles and have not been transformed. The data at negative frequencies were reflected about a point on the ordinate, as per equation (6), and are plotted as open squares. (B) Results of the analysis plotted as a function of temporal frequency. If the phase responses from the negative frequencies superimpose upon the responses from the positive frequencies, then the symmetry constraint holds. As can be seen, the phase responses satisfy the symmetry constraint to a close approximation. The straight lines were derived from the lines in Fig. 2 using the same transformation.