

**Nonlinear Properties of Visual Cortex Neurons:
Temporal Dynamics, Stimulus Selectivity, Neural Performance**

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I. Introduction

A. Analysis of visual cortex neurons

The primary visual cortex plays a very important role in vision and visual perception. To begin with, consider the fact that without area V1, all of the many visual cortical areas (which constitute approximately half of the cerebral cortex in the macaque monkey) are deprived of the visual information relayed through the thalamus from the retina. It has been known for more than a century that damage to this area produces almost total blindness. However, area V1 is not merely a relay station between the thalamus and the other cortical regions. On the contrary, V1 clearly transforms the lateral geniculate nucleus input: In comparison to the relatively simple center/surround receptive fields of geniculate cells, the receptive fields of V1 neurons are considerably more complex and, as will be emphasized in this chapter, the cells are considerably more selective for specific visual features. Finally, consider the anatomical size of the region and the complexity of the neural tissue. In the macaque monkey, V1 constitutes approximately 10% of the entire cerebral cortex, and, in comparison to all of the other cortical areas, the primary visual cortex has about twice as many neurons per unit volume, with perhaps half a billion neurons per hemisphere. Given all of these facts, analysis of both the structures and the functions of the primary visual cortex stands as an important challenge to visual neuroscientists in their quest to understand vision and visual perception.

Beginning with the work of Hubel and Wiesel (1962), measurements of the responses of V1 neurons (in the form of action potentials) have provided a wealth of information concerning both the potential biophysical and biochemical mechanisms as well as the ultimate visual information processing functions of these neurons. Nonetheless, in spite of this wealth of scientific information that has accumulated

over the decades, in many respects we have only taken a very small step toward a complete understanding of how the visual cortex contributes to visual perception.

In an attempt to analyze the structures and the functions of visual cortex neurons, many researchers have utilized the well-developed conceptual and mathematical techniques of what can be termed a “systems analysis.” This quantitative approach was introduced to visual neuroscience in principle by Hartline, who was studying the *Limulus* visual system (e.g., Ratliff et al., 1974); it has since been utilized to study the retina, lateral geniculate nucleus, and visual cortex of the primate, and related species (e.g., Enroth-Cugell and Robson 1966; Movshon, Thompson and Tolhurst 1978; Shapley and Victor 1979; De Valois, Albrecht and Thorell 1982; Ohzawa, Sclar and Freeman 1985; for reviews see Robson 1975; Shapley and Lennie 1985; De Valois and De Valois 1988; Palmer, Jones and Stepnoski 1991; Carandini, Heeger and Movshon 1999; Ferster and Miller 2000; Geisler and Albrecht 2000).

Over the past several decades, much research has been devoted to describing both the linear and the nonlinear properties of V1 neurons using a systems analysis. Within this framework, one begins by assessing what aspects of the behavior can be accounted for on the basis of simple linear equations and what aspects require nonlinear equations. In this chapter, we describe linear and nonlinear response properties that have been measured within V1 neurons. We then discuss these measurements (and others) within the context of functional transformations of the visual information that ultimately produce high degrees of reliable stimulus selectivity. Finally, we consider several models, at different levels of analysis, of the neural operations that can potentially account for the linear and the nonlinear behaviors that have been measured.

B. Stimulus selectivity: features, filters, and functions

Research over the past several decades indicates that stimulus selectivity plays a fundamental role in the analysis of visual information within the visual systems of humans, primates, and related species. Within the visual cortex, each neuron is quite selective for a specific “visual feature.” Currently, there is not an agreed upon intuitive name that adequately captures the presumed function associated with this selectivity (e.g., edge detector, line detector, spatial frequency detector, and so forth). Nonetheless, it is possible to summarize and quantify the selectivity by measuring the responses as a function of many different stimulus dimensions that describe visual stimuli: for example, spatial position, spatial orientation, spatial frequency, temporal frequency, direction of motion, contrast, color, and so forth. These stimulus dimensions are relatively easy to manipulate within the laboratory to measure stimulus selectivity in a systematic, quantitative, and replicable fashion. Further, it is possible to develop descriptive mathematical equations that can adequately describe and summarize the measured responses along these various dimensions. Finally, these descriptive equations can be combined with other equations and analyses to assess the performance characteristics of visual cortex neurons within this multi-dimensional space and to investigate the ultimate functional consequences of the measured stimulus selectivity.

Rather than attempting to characterize the function of visual cortex neurons using simple intuitive visual feature detection (e.g., edge detection), it is possible to conceptualize the function of each neuron, in a somewhat more neutral fashion, by thinking of the function as a filtering operation. A neuron in the primary visual cortex only responds to a specific range of values within a complex (and not necessarily intuitive) multi-dimensional feature space. In so doing, the neuron filters out the overwhelming majority of unique subsets

within the total set and only passes (or signals) the presence of a very small and unique subset. It seems reasonable to assume that whatever this particular type of stimulus selectivity might be, it will probably be closely related to the statistics of natural images (Barlow 1961).

The observation that cortical neurons are selective for a specific subset of possible visual stimuli has important implications for the overall performance capabilities of cortical neurons: Because of this stimulus selectivity, the response of each neuron contains specific information about the presence or absence of a particular feature within the visual stimulus that could be utilized by a subsequent brain mechanism to detect, discriminate, and identify that specific visual feature. For example, the response magnitude could be utilized to identify, with a high level of confidence, a specific oriented spatial contour, demarcated by a specific color contrast, moving across a particular location in space, at a particular rate, in a particular direction, and so forth.

This high degree of stimulus selectivity at the level of the visual cortex has led to several different hypotheses regarding the ultimate functional significance of the selectivity. One hypothesis is that the selectivity reflects a sparse code that is well matched to the statistics of natural images (Field 1987; Olshausen and Field 1987). A second hypothesis is that the selectivity for local image feature/attributes is a critical step towards the goal of object-segregation (Geisler and Albrecht 2000). A third hypothesis is that the selectivity reflects the sequential hierarchical progression towards neurons within higher cortical regions that are selective for real-world objects (Barlow 1995). As noted some time ago, sequential filtering is functionally equivalent to pattern recognition (Craik 1966).

Regardless of whether one, or all, of these hypotheses proves to be accurate, it seems clear that the stimulus selectivity of cortical neurons plays an important role in visual information processing. With this observation in mind, the major focus of this chapter will be those linear and nonlinear

properties (and mechanisms) that could potentially have a beneficial influence, or a deleterious influence, on stimulus selectivity.

C. Spatiotemporal filters and systems analysis

In an attempt to characterize both the structures and the functions of visual cortex neurons, from the subcellular level to the behavioral level, many neuroscientists have utilized the well-developed techniques of a systems analysis. The basic principles of this analytical approach have been fully described for the physical sciences as well as the life sciences (e.g., Schwarz and Friedland 1965; Marmarelis and Marmarelis 1978) and need not be formally described in this chapter. Stated simply, one attempts to identify and characterize the linear as well as the nonlinear properties of a complex system with the goal of developing a quantitative model that can potentially describe the behavior of the system under a wide range of diverse circumstances. Within this framework, visual cortex neurons can be conceptualized as spatiotemporal filters that respond selectively along several different stimulus dimensions.

There are different methodologies that can be used to investigate a physical system of interest: For example, one can utilize a frequency domain analysis, a space and/or time domain analysis, a white noise domain analysis, and so forth. All of these methods have been applied to visual cortex neurons. As noted above, this quantitative systems approach was initially introduced to visual neuroscience by Hartline (and colleagues) but over the past three decades, many different laboratories have adopted this approach, and as a consequence we have a rich understanding of both the linear and nonlinear properties of visual cortex neurons (for recent reviews of this literature, see Carandini, Heeger and Movshon 1999; Ferster and Miller 2000; Geisler and Albrecht 2000).

To simplify this chapter, the frequency domain analysis will be the major focus, although other analyses will be discussed when appropriate. In a frequency domain analysis of visual cortex neurons, the visual stimulus is a spatiotemporal sine wave grating pattern, which can be systematically varied along many different stimulus dimensions. These measurements, and the equations that can be used to describe the responses along the various stimulus dimensions, have provided a quantitative description of the stimulus-response characteristics of visual cortex neurons under a wide and diverse set of circumstances.

D. Linear systems analysis can reveal both linear and nonlinear properties

Over the past half century, linear systems analysis has played a major role in the quantitative analysis of the visual system. As will be described in this chapter, there is overwhelming evidence that visual cortex neurons exhibit a variety of nonlinear properties. Although there are specific mathematical methods that have been developed to study nonlinear systems (e.g., Victor, Shapley and Knight 1977; Victor and Knight 1979; see Marmarelis and Marmarelis 1978), we have learned a great deal about the nonlinear properties of visual cortex neurons by applying linear systems techniques and analyzing the deviations from what would be expected from a linear system.

In a linear system the response to the sum of several inputs is equal to the sum of the responses to each input individually and as the amplitude of the stimulus increases the response increases proportionately. There are many standard techniques for characterizing a linear system that could be applied (see Schwarz and Friedland 1965), and have been applied, to characterize visual cortex neurons. For example, one could measure either the spatiotemporal receptive field or the spatiotemporal transfer function (e.g., Palmer, Jones and Stepnoski 1991; DeAngelis, Ohzawa and Freeman 1993). If

a system is linear, then all of the different techniques give equivalent results and the measurements made with any one of the techniques can be used to predict the responses of the system to arbitrary inputs. However, when a system is nonlinear, two different techniques may give different results; in this case, it becomes essential to utilize several different techniques and then compare what is similar and what is not. For example, in the case of visual cortex neurons (as will be described below), the spatiotemporal receptive field and the spatiotemporal transfer function are not exactly equivalent. Finally, note that oftentimes, a specific nonlinear mechanism can only be revealed, isolated, and studied using a specific technique. In the case of visual cortex neurons, different nonlinear properties have been discovered and characterized by using different linear systems techniques.

E. Temporal dynamics, stimulus selectivity, neural performance

During natural viewing, eye movements create a rapid progression of diverse images, and because of this, the spatiotemporal contrast can change rapidly over the course of a few hundred milliseconds (for a comprehensive review see Carpenter 1991). The average duration of a single fixation (during normal saccadic inspection of a visual scene) is approximately 200 ms. This is an important observation to keep in mind when considering the potential effects of a specific linear or nonlinear mechanism on stimulus selectivity and neural performance. If the temporal dynamics of the mechanism are relatively fast, then the mechanism might be able to influence selectivity and performance during a single fixation, based upon the spatiotemporal contrast contained within that single fixation. On the other hand, if the temporal dynamics are relatively slow, then the mechanism will not be able to influence stimulus selectivity during a single fixation, based upon the spatiotemporal contrast within that fixation.

Over the past several decades, many different laboratories have measured the responses of V1 neurons using drifting spatial frequency gratings, across a wide array of stimulus dimensions, using stimulus durations that are relatively long, to approximate a steady-state condition. These measurements, along with other measurements, have revealed some of the fundamental linear and nonlinear properties of V1 neurons (e.g., Movshon, Thompson and Tolhurst 1978; De Valois, Albrecht and Thorell 1982; for recent reviews see Carandini, Heeger and Movshon 1999; Ferster & Miller 2000; Geisler and Albrecht 2000).

The drifting steady-state measurements can be supplemented by measurements of the responses to transient stationary stimuli, where the stimulus durations approximate the fixation durations during natural viewing. Consider using a stationary grating that is presented for a brief interval (200 ms) to measure the responses as a function of some stimulus dimension of interest (e.g., contrast). The measured post stimulus time histograms offer a unique opportunity to examine the temporal dynamics of specific linear and nonlinear properties on a fine time scale. With such a set of measurements, one can ask a wide range of different experimental questions and compare the results of the experiments to what we have learned from the steady-state experiments. Consider the following, somewhat overlapping, subset of possible questions:

- In general, are the basic response properties that have been measured using drifting steady-state stimuli similar under transient stationary conditions?
- What is the temporal onset of the stimulus selectivity along each of the fundamental stimulus dimensions?
- Do the selectivities change over the course of the brief interval?
- How long does it take for the nonlinear properties (e.g., contrast-set gain control) to build up through time?

- How do the temporal dynamics compare to the average fixation duration during natural viewing?
- Does the well-established relationship between the mean and the variance of cortical neurons hold under these transient stationary conditions?
- Does the discrimination performance change?

Recently, several different laboratories have measured the responses to brief stimuli and analyzed the time course of some of the fundamental properties (e.g., Frazor et al. 1997; Ringach, Hawken and Shapley 1997; Gillespie et al. 2001; Muller et al. 2001; Albrecht et al. 2002). Within this chapter, we will consider measurements using drifting steady-state stimuli and measurements using stationary transient stimuli. The results of both types of measurements will be discussed within the context of the effects of the various nonlinearities on stimulus selectivity within a time frame that is comparable to natural viewing.

II. Linear and nonlinear properties

A. Some linear properties of simple cells

Hubel and Wiesel (1962) described two basic types of neurons in the visual cortex: *simple cells* and *complex cells*. Since then, some have elaborated the original binary classification with subsidiary and supplementary sub-classifications (e.g., Henry 1977) and others have argued that simple and complex cells reflect opposite ends of a virtual continuum (Geisler and Albrecht 2000; Mechler and Ringach 2002). However, the basic distinction between simple and complex cells remains an important part of the published literature. Stated simply, simple cells have a variety of linear properties that are not generally seen in most complex cells. Specifically, in the original report, Hubel and Wiesel (1962)

described four basic linear properties of simple cells:

- distinct excitatory and inhibitory sub-regions within the receptive field;
- spatial summation within a given sub-region;
- mutual antagonism between sub-regions;
- responses to novel stimuli could be predicted (qualitatively) on the basis of the arrangement of the subregions.

These four properties are what one would expect from a linear spatiotemporal filter. Complex cells, on the other hand, failed to display these properties and were therefore defined by exclusion. For example, a typical complex cell will produce excitatory responses to both white and black contrasts in the same spatial location. This is clearly not what one would expect from a linear spatiotemporal filter. Nonetheless, it is important to emphasize that notwithstanding the various linear and nonlinear properties of simple and complex cells, both types of neurons are highly selective for specific stimulus attributes (e.g., orientation).

Many different laboratories have measured a variety of different properties of simple cells, using many different types of stimulus protocols. On the basis of this research, it is possible to list a set of linear properties that have been reported in simple cells. Note that in each case, the implied comparison is between (a) the measured neural response behavior of simple cells and (b) the known theoretical behavior of a linear spatiotemporal filter. Finally, bear in mind that the comparison between the measured behavior of the neurons, and the known behavior of a linear filter, is always approximate, and never exact.

1. The receptive field and the optimal stimulus

The receptive field can be mapped using flashing white and black spots (or bars/lines). This map (which is analogous to the impulse response of a linear spatial filter) provides one characterization of the stimulus selectivity for the dimension of space. Thus, for example, one can

qualitatively predict the optimal spatial position (say, 2° above the optic axis), spatial orientation (say, horizontal), and spatial configuration of the contrast (say, one narrow white line flanked by two narrow black lines). This observation suggests that the spatial variations in luminance contrast are summed in a linear fashion.

2. Responses to drifting gratings

When a linear spatiotemporal filter is stimulated with a drifting sine wave the response is a sinusoidal modulation in synchrony with the temporal frequency of the stimulus. Similarly, when a simple cell is stimulated with a drifting sine wave the response of the cell modulates in synchrony with the temporal frequency of the input. However, the shape of the temporal response (i.e., the post stimulus time histogram) is not sinusoidal. Specifically, all of the negative values of the sine wave are absent. This observation is not terribly surprising given that simple cells generally have little or no maintained activity (and, of course, there are no “negative action potentials”). In sum, the responses of simple cells to drifting sine waves are similar to what one would expect from a linear filter followed by half-wave rectification.

3. Responses as a function of spatial phase

Using a stationary spatial frequency grating, whose contrast is modulated in time (i.e., a counterphase flickering grating), it is possible to measure the responses as a function of spatial phase. If this measurement is performed on a linear spatiotemporal filter, the response is a sinusoidal function of spatial phase. Similarly, if this measurement is performed on a simple cell, the response (i.e., the post stimulus time histogram) is approximately a sinusoidal function of spatial phase. There is a specific relationship between the direction selectivity of a linear filter and the responses as a function of spatial phase. The responses of simple cells follow these

linear expectations, to a first approximation (Albrecht and Geisler 1991; Reid, Soodak and Shapley 1991; Tolhurst and Dean 1991).

4. Spatiotemporal transfer function

There are several strong constraints that are implied by the linear model for the spatiotemporal receptive field (e.g., amplitude symmetry and phase additivity) and many of these constraints hold, to a first approximation, for simple cells. Because these constraints hold, it is possible to describe the spatiotemporal phase transfer function using a simple four-parameter linear equation (Dawis et al. 1984; Hamilton, Albrecht and Geisler 1989; Albrecht 1995).

5. Null phase position

Enroth-Cugell and Robson (1966) introduced a clever method to test for linear spatial summation in retinal ganglion cells whose center-surround receptive fields are approximately circularly symmetric. The logic of this test is simple. A white-black edge is positioned on the center of the receptive field and then flashed on and off. If the cell sums its inputs in a linear fashion, then the response of the cell should be unaffected by the flashing edge because the increased luminance over half of the receptive field is canceled by an equivalent decrease in the luminance over the other half. The method is clever for the following reason: No response is evoked and hence the linearity of spatial summation can be tested even if there are response nonlinearities. This method for testing the linearity of spatial summation has been applied to simple cells and the linear prediction holds, to a first approximation (e.g., Movshon, Thompson and Tolhurst 1978; De Valois, Albrecht and Thorell 1982).

6. Receptive field and spatial frequency tuning

It is possible to characterize the properties of a complex unknown system by measuring either the “impulse response” or

the “frequency response.” If the system is linear, either set of measurements would provide a complete description of the system, and further, one would be able to predict the impulse response from the frequency response (and vice versa). Measurements of the spatial receptive field and the spatial frequency tuning are analogous to the impulse and frequency response. Movshon, Thompson and Tolhurst (1978) have demonstrated that it is possible to predict the shape of the spatial receptive field profile on the basis of the measured spatial frequency response function, to a first approximation.

7. Spatiotemporal receptive field and motion

If the receptive field is measured as a function of both space and time using stationary flashed bars or spots, and if the cell is linear, it is possible to use the resulting spatiotemporal receptive field to determine (a) whether the cell is direction selective, (b) the optimal direction of motion, and (c) the degree of direction selectivity.

It has been demonstrated that these linear expectations hold for simple cells, to a first approximation (McLean and Palmer 1989; DeAngelis, Ohzawa and Freeman 1993).

B. Some nonlinear properties of both simple and complex cells

1. Response refractory period

As the firing rate of a given neuron increases, the absolute and relative refractory period will produce response saturation that is solely determined by the magnitude of the firing rate, regardless of what particular stimulus produced that high rate of firing. The temporal dynamics for this nonlinearity are on the order of a few milliseconds, or less. It is worth noting that from the perspective of neural performance there are potential costs and benefits associated with this nonlinearity. In particular, response saturation that is caused by the absolute or relative refractory period

is deleterious on stimulus selectivity because it makes the neuron less selective at high firing rates. Interestingly, however, the regularization in the spike trains that occurs during this type of saturation has beneficial consequences on detection, discrimination, and identification performance because, for most cells, the regularization decreases the variance in the firing pattern, relative to the mean (Geisler et al. 1991). One might speculate that these two factors could potentially offset each other to some extent.

2. Response rectification

Hubel and Wiesel (1962) were the first to observe the effects of rectification: They reported that many complex cells responded in an excitatory fashion to both white and black lines (or bars) in the same spatial location, throughout all positions of the receptive field. Similarly, as illustrated in Figure 1A, when stimulated with a counterphase flickering sine wave grating pattern, excitatory responses are observed regardless of whether the luminance is increasing or decreasing over a particular spatial region (e.g., Movshon, Thompson and Tolhurst 1978; De Valois, Albrecht and Thorell 1982). This type of behavior can be described as full-wave rectification. When a sine wave is passed through a linear filter followed by full-wave rectification, the output is the absolute value of the input.

In comparison, as illustrated in Figure 1B, when simple cells are stimulated with a drifting or flickering sine wave grating, only half of the modulation appears in the response waveform (e.g., Movshon, Thompson and Tolhurst 1978; Albrecht and De Valois 1981). This type of nonlinear behavior can be described as half-wave rectification: When a linear filter, followed by half-wave rectification, is stimulated with a sine wave, the output does not contain any of the values of the sine wave that are below zero. As will be described below, rectification, in both simple and complex cells, appears to be fully operational within 200 ms and thus it can exert its influence within the time frame of a single fixation.

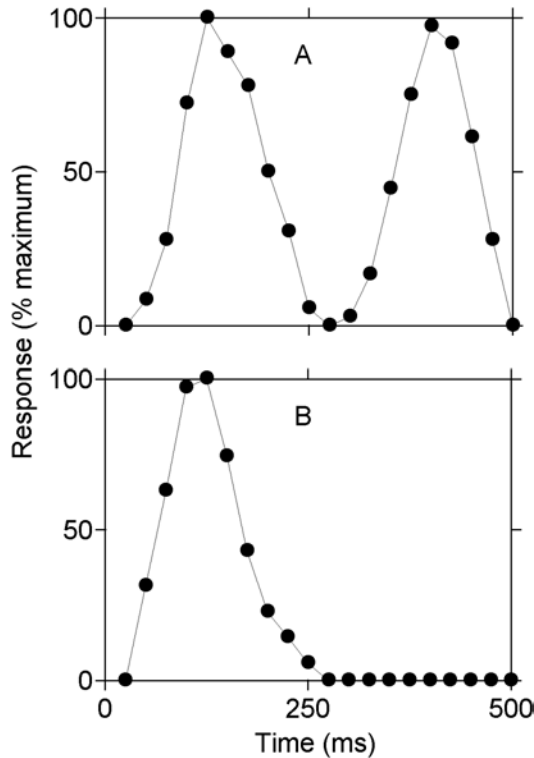


Figure 1. Responses of two monkey cells to a counterphase flickering sine wave grating pattern, to illustrate response rectification in complex cells (A) and simple cells (B). (Adapted from De Valois, Albrecht and Thorell 1982.)

Half-wave rectification could, in part, be a simple consequence of the fact that cortical cells tend to have little or no maintained spontaneous discharge; the net result can be thought of as a threshold nonlinearity. Although half-wave rectification forces a doubling of the number of elements that are required to transmit both the positive and the negative values, it does have beneficial consequences. First, it conserves metabolic energy within the cortex by reducing the number of action potentials produced, the amount of neurotransmitter substance released, and so forth. Second, it increases the stimulus specific identification performance of a neuron: Given that the cell produces no action potentials unless a very specific stimulus is present at a very specific location within the visual field, just a few action potentials can strongly constrain the most likely set of potential visual features at that location (Barlow et al. 1987; Geisler and Albrecht 1995; 1997). Third, full-wave

rectification can be useful for computing “motion energy” (Adelson and Bergen 1985; Watson and Ahumada 1985) and “texture energy” in the stimulus (Bergen 1991).

3. Response expansion

Measurements of the responses as a function of luminance contrast using drifting gratings have shown that, in general, as the contrast increases from zero, the response increases in an accelerating fashion (e.g., Albrecht and Hamilton, 1982; Sclar, Maunsell and Lennie 1990). Figure 2 shows measurements of the contrast response function from a representative cell to illustrate the response expansion that can be seen at the lower values of contrast. The smooth curve shows the fit of a Naka-Rushton equation. The exponent of this equation can be utilized to quantify the response expansion. The average value in the primary visual cortex is approximately 2.5.

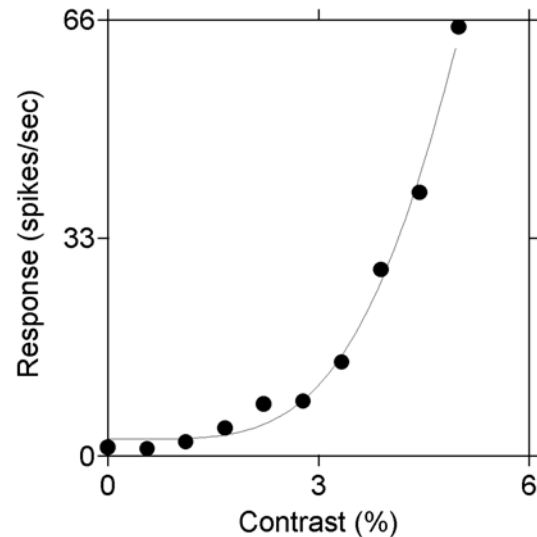


Figure 2. Responses as a function of contrast for a representative neuron to illustrate the response expansion that can be seen in the contrast response function at lower contrasts, prior to the compression and saturation that is induced by the contrast-set gain control. (Albrecht and Geisler, unpublished observations.)

Note that in measurements of the contrast response function, the acceleration is most easy to visualize at the lower values of contrast (prior to any compression and

saturation). However, it would be incorrect to conclude that the effects of the accelerating nonlinearity are only expressed at low contrasts. Indeed, there are many other types of experimental observations, which demonstrate that the response acceleration operates across the full range of contrast and response, even after the response is fully saturated. For example, as noted above, the responses of simple cells as a function of spatial phase are approximately sinusoidal, but not exactly. Specifically, the responses appear more narrow and peaked than a sine wave, across the full range of contrasts, even contrasts that evoke fully saturated responses. A linear filter that is followed by an accelerating nonlinearity produces exactly this sort of behavior. Interestingly, if the value of the expansive exponent, determined from the measured contrast response function for a given cell, is taken into consideration (i.e., by applying the acceleration to a sinusoidal function), the predicted responses provide a reasonably good fit to the measured responses of that cell.

There are other observations that cannot be predicted by a linear filter alone, but can be accounted for reasonably well if a linear filter is followed by an accelerating nonlinearity. Several of these observations are listed below. In each case, the accelerating nonlinearity diminishes the discrepancy between the linear prediction and the measured properties.

- The measured spatial frequency selectivity is narrower than expected, based upon the measured receptive field (e.g., De Valois, Thorell and Albrecht 1985; Tadmor and Tolhurst, 1989).
- The measured direction selectivity is greater than expected, based upon the responses as a function of spatial phase (Albrecht and Geisler 1991; Reid, Soodak and Shapley 1991; Tolhurst and Dean 1991; Murthy et al. 1998).
- The measured direction selectivity is greater than expected, based upon the spatiotemporal receptive field

(DeAngelis, Ohzawa and Freeman 1993; McLean and Palmer 1994).

- The measured orientation selectivity is greater than expected, based upon the measured receptive field (Gardner et al. 1999).
- Vernier acuity is greater than expected based upon measurements of length summation (Swindale and Cynader 1989).
- Direction selectivity is greater when action potentials are measured and compared to intracellular synaptic potentials (Jagadeesh et al. 1997).

4. Response Saturation

Measurements of the contrast response function have shown that cortical neurons generally have a limited dynamic response range followed by response saturation. Figure 3 plots the responses as a function of contrast to illustrate response saturation. Measurements illustrated below (Figures 7-10) have demonstrated that the saturation can occur well with the time frame of a single fixation. In a later section (Section IIIB) we will consider the potential effects of saturation on stimulus selectivity.

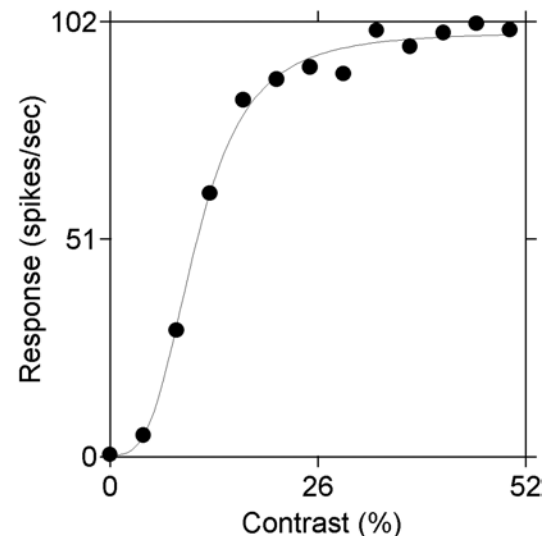


Figure 3. Responses as a function of contrast for a representative neuron recorded from the monkey cortex to illustrate response saturation. (Albrecht and Geisler, unpublished observations.)

5. Contrast-set gain control

As shown in Figure 3, the responses of cortical cells saturate as the contrast increases, oftentimes at very low contrasts. This saturation could be determined by either (a) the magnitude of the response, or (b) the magnitude of the contrast. Measurements performed over the past several decades have shown that this saturation is only one manifestation of a scaling of the response based upon the magnitude of the contrast: a contrast-set gain control. Recent measurements (e.g., section IIIB) have shown that this nonlinearity is operational well within the time frame of a single fixation. Interestingly, this contrast-set gain control affords the maintenance of stimulus selectivity and high differential sensitivity along many dimensions; however, this beneficial consequence comes at the expense of differential sensitivity along the dimension of contrast.

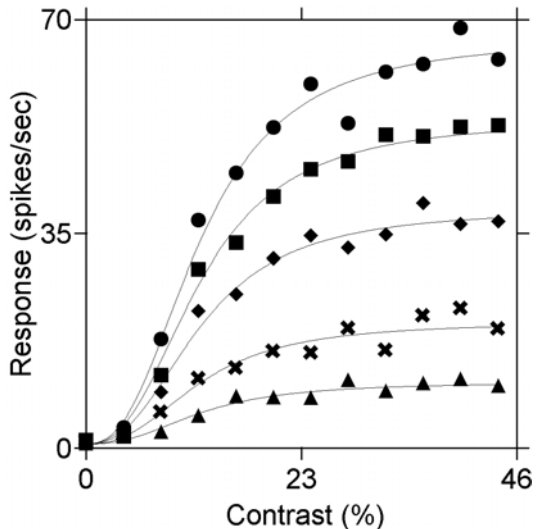


Figure 4. Contrast response function measured at five different spatial frequencies to illustrate contrast-set gain control: The scaling and the saturation is determined by the magnitude of the contrast and not the magnitude of the response. (Albrecht and Geisler, unpublished observations.)

Consider the effect of response-set saturation determined by the absolute and relative refractory periods: In this case, the saturation would diminish stimulus

selectivity because at contrasts that produce response saturation, optimal and non-optimal stimuli could produce equivalent responses. However, measurements of the contrast response function using optimal and non-optimal stimuli have shown that the saturation is not determined by the magnitude of the response (e.g., Figure 4); instead, the saturation is determined by the magnitude of the contrast (Albrecht and Hamilton 1982; Sclar and Freeman 1982; for a review see Carandini, Heeger and Movshon 1999; Geisler and Albrecht 2000). Further, the saturation is just one manifestation of an overall scaling of the entire contrast response function by the magnitude of the contrast.

6. Latency shift

As contrast increases and the response magnitude increases, there is a decrease in the latency of the response. This latency shift could be determined by either (a) the magnitude of the response, or (b) the magnitude of the contrast. Measurements have demonstrated that the shift is determined by the contrast and not the response (Dean and Tolhurst 1986; Carandini and Heeger 1994; Albrecht 1995; Gawne et al. 1996; Carandini, Heeger and Movshon 1997; Reich et al. 2001). Figure 5 shows the shift for a representative cell at an optimal and a non-optimal spatial frequency. The magnitude of the response to the optimal stimulus was approximately three times the magnitude of the response to the non-optimal stimulus, therefore if the latency was determined by the magnitude of the response then the latency shift should be greater for the optimal stimulus. However, as can be seen, the shift appears to be equivalent for both the optimal and the nonoptimal stimulus.

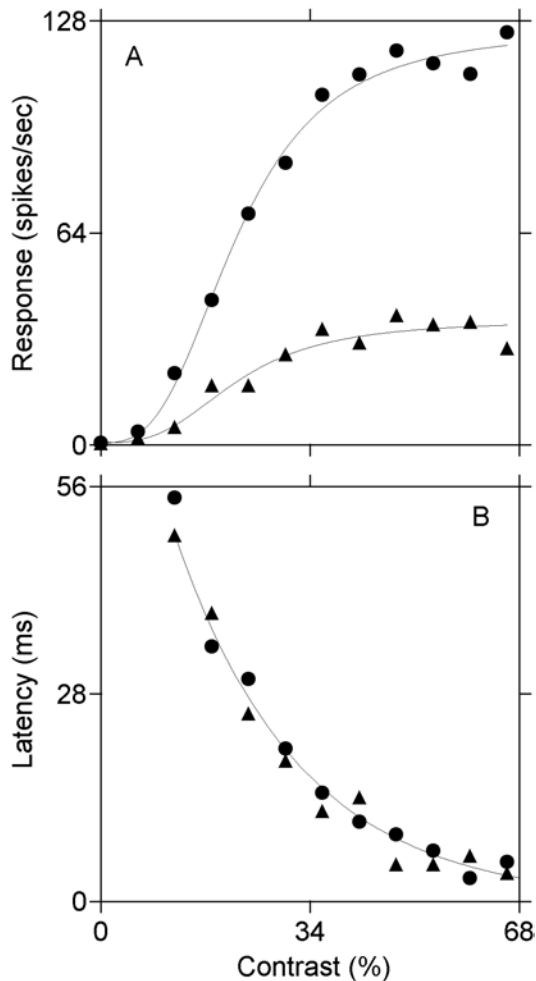


Figure 5. Response amplitude (A) and response latency (B) plotted as a function of contrast, to illustrate that the latency shift is determined by the magnitude of the contrast and not the magnitude of the response. (Albrecht and Geisler, unpublished observations.)

7. Contrast adaptation

When a V1 neuron is presented with a high contrast grating for an extended period of time (e.g., 30 seconds) the response magnitude decreases (Movshon and Lennie 1979; Albrecht, Farrar and Hamilton 1984; Saul and Cynader 1989; McLean and Palmer 1996). The temporal dynamics of this nonlinearity are too slow to have an influence on stimulus selectivity within a single fixation, based upon the level of stimulus contrast within that single fixation. To the extent that there is some degree of contrast adaptation during a single fixation,

this adaptation has been induced over the course of many fixations.

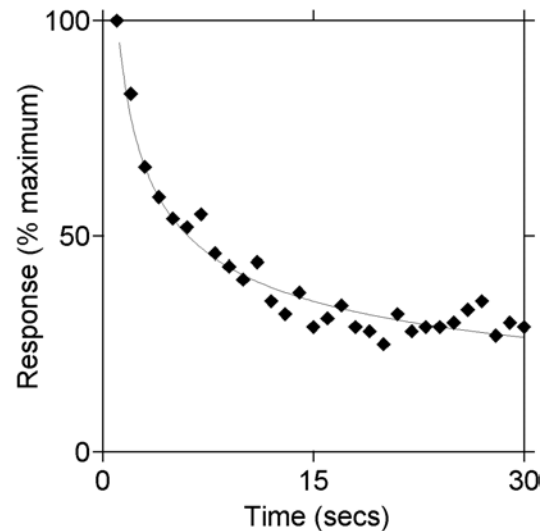


Figure 6. Responses of a cortical cell to a high contrast spatial frequency grating drifting over the course of 30 secs, to illustrate contrast adaptation. (Adapted from Albrecht et al., 1984.)

8. Other nonlinear behaviors

- Nonlinear spatial summation (Movshon, Thompson and Tolhurst 1978).
- Spatial frequency inhibition (De Valois and Tootell 1983)
- Surround effects, outside classic receptive field (De Valois, Thorell and Albrecht 1985)
- Non-Fourier envelope responses (Zhou and Baker 1994).
- Supersaturation (Li and Creutzfeldt 1984; Bonds 1991).
- Cross-orientation inhibition (Bonds 1989).
- Nonspecific suppression (e.g., Nelson 1991; DeAngelis et al. 1992; Carandini, Heeger and Movshon 1997).

III. Temporal dynamics

It is worth considering the temporal dynamics of the various nonlinear properties, described above, within the context of the potential effects upon stimulus selectivity and neural performance during natural viewing. For example, if the onset of a specific nonlinear mechanism is

slow relative to the duration of a single fixation, then it will not affect the selectivity and neural performance within a single fixation, based upon the spatiotemporal contrast within that fixation.

A. Rapid and slow nonlinearities

It is clear that some of the nonlinearities operate rapidly enough to exert their influence on stimulus selectivity and performance, based upon the response to a stimulus during a single fixation. It is equally clear that other nonlinearities could not have a significant influence on the selectivity and performance, based upon the stimulus within a single fixation because the onset occurs over the course of many seconds. Consider the temporal dynamics of the absolute refractory period, half-wave rectification, the latency shift, and contrast adaptation.

1. Response refractory period

Any refractory effects on selectivity, and performance, would surely be fully expressed within the time frame of a single fixation, given that they would operate on the order of a few milliseconds.

2. Response rectification

To the extent that rectification is based upon the transduction from the voltage potential within the neuron to the production of action potentials, any rectification effects would also be fully expressed within a single fixation.

3. Latency shift

The average value of the contrast induced latency shift is approximately 45 ms (Dean and Tolhurst 1986; Carandini and Heeger 1994; Albrecht 1995; Carandini, Heeger and Movshon 1997). Therefore, the effects of the latency shift can be expressed within the time frame of a single fixation and the shift will be based upon the contrast within that fixation.

4. Contrast adaptation

It takes approximately 15 seconds for contrast adaptation to achieve two-thirds of its full strength (e.g., Albrecht, Farrar and Hamilton 1984). Therefore, the effects of contrast adaptation cannot be expressed within the time frame of a single fixation.

B. Contrast response nonlinearities

Most of the nonlinear properties described above can be seen in the steady-state measurements of the contrast response function. However, the steady-state measurements are not well suited for analysis of the temporal dynamics that occur on the time frame of a single fixation. As described in the Introduction (Section IE), the responses to transient stationary gratings are useful for examining the temporal dynamics of linear and nonlinear properties. Recently, there have been several different laboratories measuring the responses to brief stimuli and analyzing the time course of some of the fundamental properties (e.g., Frazor et al. 1997; Ringach, Hawken and Shapley 1997; Gillespie et al. 2001; Muller et al. 2001; Albrecht et al. 2002).

In this section we show the responses as a function of contrast when the stimulus is a stationary grating, presented for a brief interval (200 ms), in order to illustrate how the contrast response function develops over the course of the first 200 ms after stimulus onset. Further, we consider some of the general questions posed in the Introduction, within the context of this specific set of transient stationary measurements. For example, one can ask: How long does it take for the two nonlinearities, response expansion and contrast-set gain control, to build up? If the expansion and gain control take more than a few hundred milliseconds they will have little or no influence on the responses during a single fixation, based upon the level of contrast within that fixation, and therefore, these two nonlinearities will have little or no influence on stimulus selectivity during a single fixation.

1. Post stimulus time histogram as a function of contrast

Figure 7 shows the responses of a neuron recorded from within the monkey visual cortex to stationary gratings that were presented for a 200 ms interval at 10 different levels of contrast. Each set of data points plots the responses as a function of time, every 4 ms (i.e., the post stimulus time histogram), for 10 different levels of contrast (from 0% to 90%, in linear increments). The smooth curves through the data points plot the average post stimulus time histogram that has been scaled for the amplitude of the response at a given level of contrast and shifted for the latency of the response at a given level of contrast. For ease of viewing the rapid variations across time and contrast, only 100 ms of the responses are plotted and the contrast induced latency shift has been removed, such that the responses at each level of contrast are optimally aligned (i.e., they begin at the same time, peak at the same time, and so forth). There are several trends that are easy to see when the responses are plotted in this fashion:

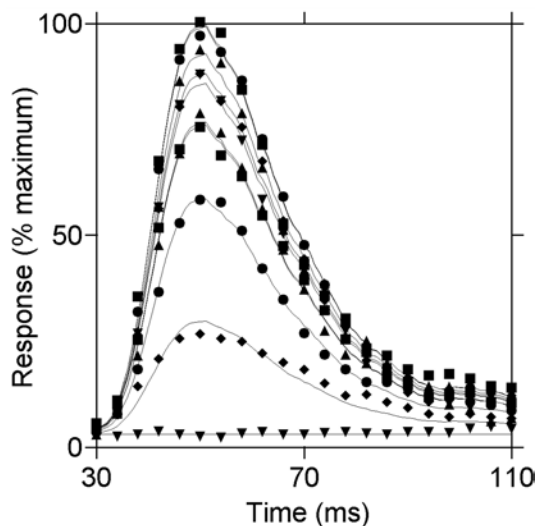


Figure 7. Responses of a neuron recorded from the monkey visual cortex as a function of time and contrast. (Adapted from Albrecht et al., 2002.)

- The magnitude of the response increases rapidly from the base rate to the maximum firing rate in approximately 20

ms and then declines to approximately one third the maximum firing rate within approximately 30 ms after the peak.

- The overall shape of the post stimulus time histogram appears to be relatively similar across the different levels of contrast.
- Simply scaling and shifting the average temporal response profile accounts for much of the variation in the data (over 95% on average across a population of cells).
- Although the stimulus remains on for 200 ms, the response is considerably more transient.

It is important to note that there is a great deal of heterogeneity from cell to cell.

2. Responses as a function of contrast through time

Figure 8 plots the responses as a function of contrast for six different times during the course of the responses shown in Figure 7: 58 (◆), 62 (■), 70 (▲), 78 (●), 86 (▼), and 102 ms (✕). The smooth curves through each set of data points plot the parameter optimized fits of a single scaled Naka-Rushton equation, with the same half-saturation contrast (29.6%) and the same expansive response exponent (3.1); the equation was simply scaled in amplitude for the different time intervals. There are several trends that are easy to see when the responses are plotted in this fashion:

- A single scaled Naka-Rushton equation accounts for a large percentage of the variation in the data (over 95% across a population of cells).
- The expansive response exponent and the contrast-set gain control appear to be present in every time interval, even the first interval, which occurs only 8 ms after the onset of the response.
- The saturation does not appear to be determined by the magnitude of the response given that the saturation occurs at the same contrast, independent of the magnitude of the response.

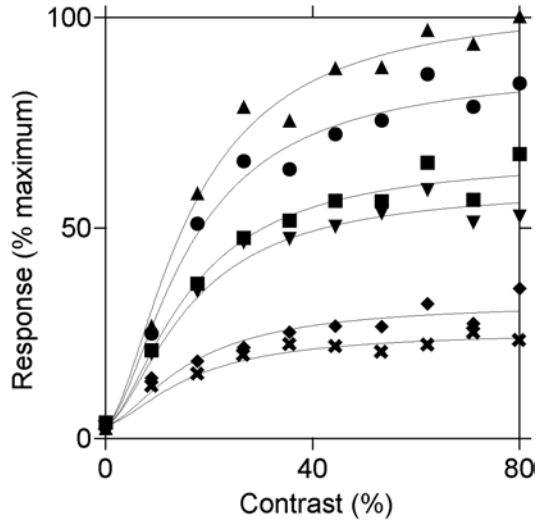


Figure 8. Responses as a function of contrast during the first 50 ms after the onset of the response to a stationary grating. (Adapted from Albrecht et al., 2002.)

3. Responses during the first 16 ms

Figure 9 plots the responses as a function of contrast during the first 16 ms after the onset of the response to a transient stationary grating. Each set of data points plots the responses in sequential 2 ms time bins after the onset of the response. The sequential order of the symbols is as follows: (■), (▲), (◆), and (●), with dashed lines, and (■), (▲), (◆), and (●), with solid lines. The curves through each set of points show the parameter-optimized fit of a single scaled Naka-Rushton equation, with the same expansive response exponent (3.1) and half-saturation contrast (31.0). There are several trends that are easy to see in this plot:

- The responses are quite systematic and appear to be qualitatively similar across the different time intervals.
- A single scaled Naka-Rushton equation accounts for a large percentage of the variation in the responses across contrast and through time (over 95%); this quantitatively demonstrates that the shape of the contrast response function is relatively invariant through time.
- The two important nonlinearities (expansive response exponent and contrast-set gain control) appear to be

fully operational at the onset of the response (well within 10 ms after the onset of the response).

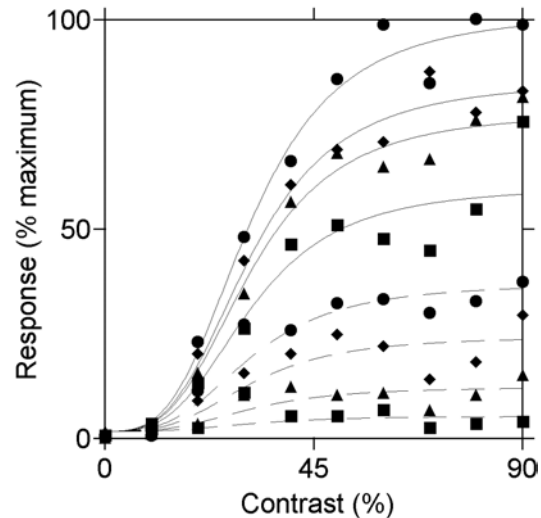


Figure 9. Responses as a function of contrast during the first 16 ms after the onset of the response to a stationary grating. (Adapted from Albrecht et al., 2002.)

4. Responses to optimal and non optimal stimuli during the first 20 ms

Figure 10 plots the responses as a function of contrast during the first 20 ms after the onset of the response for an optimal and nonoptimal spatial position. The smooth curves through the data points plot the fit of a single Naka-Rushton equation that is simply scaled for each spatial position (i.e., the same exponent and half-saturation contrast). The single scaled equation indicates that the scaling is determined by the magnitude of the contrast and not the magnitude of the response.

5. Response expansion and contrast-set gain control

In summary, using transient stationary gratings, it is possible to track the temporal dynamics of various linear and nonlinear properties to assess whether these properties could, or could not, play a role in shaping stimulus selectivity and performance on the time frame of single fixations during natural viewing. Based upon the measurements illustrated in Figures 7-10, it appears as though the two nonlinearities revealed

within the measurements of the contrast response function operate rapidly enough to have a significant impact on stimulus selectivity and neural performance. The functional implications of these virtually instantaneous nonlinearities are discussed in greater detail below.

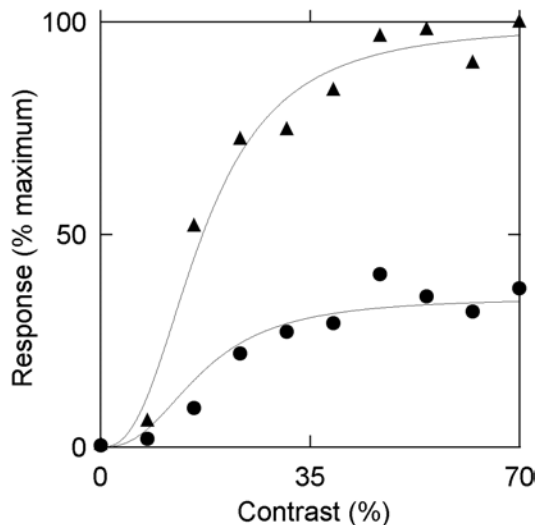


Figure 10. Responses as a function of contrast during the first 20 ms of the response for an optimal and nonoptimal spatial phase. (Adapted from Albrecht et al., 2002.)

C. Temporal nonlinearities

The temporal properties of V1 neurons have been measured using drifting gratings as well as stationary gratings; in addition, the stimuli have been presented for relatively prolonged durations (several seconds, to approximate a steady-state condition) as well as for relatively brief durations (to more closely approximate natural viewing). The results from these different types of measurements do not always conform to what would be expected within the framework of a linear system. Further, these discrepancies are not easily explained, even when the other known nonlinearities are taken into consideration.

1. Steady-state stimuli vs. impulsive stimuli

Consider several discrepancies between the properties that are measured using

drifting steady-state stimuli as opposed to transient stationary stimuli:

- The responses to transient stationary stimuli decay more rapidly than expected from the steady-state temporal frequency transfer function (Tolhurst et al. 1980; Muller et al. 2001).
- The steady-state temporal frequency tuning changes substantially as contrast increases (e.g., Albrecht 1995; Hawken, Shapley and Gross 1992; Holub and Morton-Gibson 1981) whereas the temporal response profile for transient stationary gratings is relatively invariant as contrast increases (Albrecht et al. 2002).
- Under steady-state conditions, the variability of cortical neurons is approximately proportional to the mean firing rate (e.g., Tolhurst, Movshon and Dean 1983; Softky and Koch 1993; Geisler and Albrecht 1997) whereas this relationship does not hold for the initial transient response to stationary gratings (Muller et al. 2001).

2. Transient stationary stimuli vs. transient drifting stimuli

There are several discrepancies between the responses measured for transient drifting stimuli vs. transient stationary stimuli (Frazor et al. 1997; Muller et al. 2001; Albrecht et al. 2002).

- Responses to stationary gratings are more transient than the responses to drifting gratings.
- Both detectability and discriminability are better for drifting gratings as opposed to stationary gratings.
- Transient stationary gratings generally produce large off-responses whereas transient drifting gratings generally do not.
- Transient stationary gratings often evoke complex secondary oscillations whereas transient drifting gratings generally do not.

IV. Conclusion

A. Models at different levels of analysis

There are many different laboratories measuring the properties of visual cortex neurons and then developing models at many different levels of analysis. In preparation for this Chapter, we searched the literature to learn more about the different types of models that have been proposed for neurons in the visual cortex. We tried to be as inclusive as possible. As one might expect, there are hundreds of unique types of models that have been proposed over the past several decades to account for a variety of different linear and nonlinear properties of visual cortex neurons, at many different levels of analysis. In order to organize this vast literature (which cannot be reviewed here), we have found that it is useful to distinguish three different levels of models: *descriptive models*, *functional models*, and *structural models*.

1. Descriptive models

Consider performing systematic measurements of the responses across a large population of visual cortex neurons as a function of some important stimulus dimension; say, for example, the dimension of contrast. At this stage of the investigation (i.e., after performing the measurements) it is useful to have a *descriptive model*. The goal of a *descriptive model* is to summarize and interpolate the measured responses using an atheoretical mathematical equation. For example, the Naka-Rushton equation provides a reasonably accurate description of the contrast response function for the overwhelming majority of visual cortex neurons using only three free parameters.

If the *descriptive model* provides an accurate description of the trends in the data across the entire sample of neurons, it becomes a very powerful tool that can be used in many different applications. To begin with, the function can be used to describe important characteristics of the responses across the entire sample of cells in a unified and quantitative fashion.

Oftentimes, the parameters of the equation directly quantify the property of interest (e.g., the exponent of the Naka-Rushton equation); even if the parameters themselves are not useful, it is easy to use the equation to solve for the value of interest, as long as the equation provides an accurate description.

Beyond this initial summary of the data, a *descriptive model* can be used in many other applications. Consider the following applications of the Naka-Rushton equation:

- To quantitatively test the hypothesis that response saturation is determined by the magnitude of the response or the magnitude of the contrast (see above).
- To quantitatively test the hypothesis that the contrast-set gain control and the expansive response exponent are present virtually instantaneously (see above).
- To quantitatively test the hypothesis that the latency shift is determined by the magnitude of the contrast or the magnitude of the response (see above).
- To assess the degree to which the variation in the measured responses are more likely a result of systematic variation as opposed to the inherent stochastic variation of cortical neurons, by performing randomization tests of specific null hypotheses (e.g., Albrecht et al. 2002).
- As one final example, the equation has been effectively incorporated into many different higher level models at both the functional level and the structural level (e.g., Heeger 1991; 1992a; 1992b; Albrecht and Geisler 1991; Carandini, Heeger and Movshon 1999).

Several examples of *descriptive models* are given in Albrecht et al. (2002).

2. Functional models

Upon completing systematic measurements and the quantitative description and summary using a *descriptive model* (or models), it then becomes useful, at this stage of the investigation, to consider analyzing the systematic trends within a functional context and to develop a

functional model. The goal of a *functional model* is to characterize the response properties within the context of a visual information processing algorithm.

Consider, for example, systematic measurements of the responses of a simple cell as a function of contrast (in both directions of motion) and spatial position. The responses can be summarized using the Naka-Rushton equation. Then, as trends are observed, analyzed, and quantified, one can begin to speculate about possible functions that are revealed within a given set of measurements. Given the measurements described in this example, several important trends reveal possible functions.

- The contrast response function reveals an accelerating nonlinearity.
- The contrast response function reveals a saturating nonlinearity.
- The responses scale and saturate at the same contrasts for both optimal and nonoptimal spatial positions, even though the response magnitude is very different for these two positions.
- The cell is direction selective.
- The responses as a function of contrast saturate at the same contrast for the two directions of motion, even though the response amplitude is very different for the optimal vs. nonoptimal direction of motion.
- The degree of direction selectivity is related to the responses as a function of spatial phase but the selectivity is much larger than would be expected.
- The phase response function is approximately sinusoidal.
- There is a null phase position even though the cell is direction selective.
- The phase response function is more narrow and peaked than a sine wave.

Within the context of the *descriptive model*, these are all separate facts that are quantified with the Naka-Rushton equation. However, these apparently disparate facts can be unified within the context of a relatively simple *functional model*: a linear spatial filter, whose gain is set by the overall

magnitude of the contrast, followed by an expansive response exponent (e.g., Heeger 1991; 1992a; 1992b; Albrecht and Geisler 1991; Carandini and Heeger 1994; Ferster 1994; for reviews see Carandini, Heeger and Movshon 1999; Geisler and Albrecht 2000). The linear filter accounts for (a) the sinusoidal responses as a function of spatial position, (b) the direction selectivity and (c) the relationship between the two. The contrast gain control accounts for the saturation at the same contrast, independent of response amplitude. The expansive exponent accounts for (a) the mismatch between the direction selectivity and the responses as a function of spatial phase as well as (b) the narrow and peaked pattern. Several examples of *functional models* are given in Albrecht et al. (2002).

3. Structural models

Upon completing systematic measurements and analyzing the systematic trends within a functional context it is then useful to develop a *structural model*. The goal of a *structural model* is to characterize the biophysical and biochemical neural mechanisms that are responsible for some specific property. Consider for example two of the nonlinear properties that have been identified in many different laboratories in many different stimulus situations: contrast-set gain control and the expansive response exponent. Many different laboratories are currently working to understand these nonlinearities within the context of various structural models.

Structural models for response expansion and contrast gain control include: expansive voltage-spike transduction, noisy membrane potential, recurrent excitation, intracortical inhibition, correlation-based inhibition, synaptic depression, nonspecific suppression, shunting inhibition, tonic hyperpolarization, strong push-pull inhibition, and changes in membrane conductance. Some models rely upon feedforward inputs, some rely upon feedback inputs, and others rely upon lateral inputs through local connections and through the far-reaching interconnectivity

among cortical neurons. For recent discussions and reviews of this literature, and related issues, see the sources listed in Table 1.

Table 1.

Abbott et al., 1997
Adorjan et al., 1999
Anderson, Carandini and Ferster, 2000
Carandini, Heeger and Movshon, 1999
Chance, Nelson and Abbott, 1998
Douglas et al. (1995)
Ferster and Miller, 2000
Gilbert, Hirsch and Wiesel, 1990
Hirsch et al., 1998
Kayser, Priebe and Miller, 2001
Miller, Pinto and Simons, 2001
Murthy and Humphrey, 1999
Nelson et al., 1994
Somers, Nelson and Sur, 1995
Stetter, Bartsch and Obermayer 2000
Troyer et al., 1998
Wielarrd et al., 2001
Worgotter et al., 1998

B. Contrast gain control

1. Gain control, amplifiers, light adaptation

The gain control that occurs within electrical systems in general, and electronic amplifiers in particular, has provided a useful analogy for the type of gain control that occurs at various levels of the visual system. Consider for example the ammeter analogy discussed by Craik (1938), or consider a simple amplifier. The purpose of a traditional amplifier is to take a small input voltage and make it larger by multiplying the input by a constant factor. The “gain” of an amplifier refers to this multiplicative factor: It relates the magnitude of the output to the magnitude of the input. To optimize the limited dynamic response range of the amplifier, across a wide range of input values (while attempting to minimize distortions), “gain control” systems can be introduced to adjust the magnitude of the multiplicative factor, based upon the magnitude of the input, the output, or both:

If the input values are small, the gain is adjusted to be large; whereas, if the input values are large, the gain is adjusted to be small.

The amplifier analogy and terminology have been applied to the light adaptation characteristics of the visual system (e.g., Shapley and Enroth-Cugell 1984; Hood 1998). Conceptually, within this analogy, the gain of the system is adjusted based upon the prevailing, ambient range of luminance intensities available within the visual stimulus at any point in time. The gain control in this case shifts the sensitivity to light, based upon the average amount of light available. The goal is to effectively utilize the limited response range so as to optimize high differential sensitivity (to luminance increments and decrements) and other such performance characteristics. The amplifier analogy and terminology have also been applied to the contrast response characteristics of visual cortex neurons.

2. Cortical contrast-set gain control

It seems reasonable to take the traditional notions of gain control that have been applied to light adaptation and brightness discrimination and apply the same basic concepts to the virtually instantaneous type of contrast-set gain control that occurs within the visual cortex. However, one must apply the analogy carefully because the direct application to the dimension of contrast and contrast discrimination performance is not particularly useful. It may lead one to think that the contrast gain control has the beneficial consequence of improving contrast discrimination. It does not. In fact, it is deleterious in the sense that the responses as a function of contrast saturate at low contrasts (due to the contrast gain control).

In the light adaptation analogy, one might suppose that the gain control in the cortex is designed to position the limited dynamic response range of V1 neurons around the ambient level of contrast for optimal contrast discrimination performance. If one attempts to apply the analogy, as formulated

above, one is immediately confronted with a number of properties of the gain control that are to some extent counterintuitive. Specifically, the gain control produces response saturation that is virtually instantaneous, oftentimes at very low levels of contrast, for both optimal and nonoptimal stimuli, even though the latter do not produce large amplitude responses. These properties have a deleterious effect on contrast discrimination: Obviously, when the cell saturates, contrast discrimination is eliminated.

3. Gain control in a multidimensional feature space

As emphasized many times within this chapter, one hallmark property of cortical neurons is stimulus selectivity. To characterize this selectivity, visual neuroscientists measure the responses along a variety of different stimulus dimensions. Although these measurements are fundamental in our analysis of V1 neurons, it is important not to lose sight of the fact that the stimulus selectivity of any given neuron reflects many stimulus dimensions simultaneously. We study the selectivity within the multidimensional feature space varying each stimulus dimension individually, but the visual feature itself is the simultaneous combination along all of the dimensions.

The traditional notions of gain control can be applied to cortical contrast-set gain control; however, it is necessary to consider more than the single stimulus dimension of contrast. Specifically, one must consider all of the *other* stimulus dimensions. Within this framework, the gain control does improve discrimination performance, but not along the dimension of contrast. Instead, the gain control improves performance within a multidimensional feature space. The contrast gain of the cell's dynamic response range is set such that the optimal stimulus (within this feature space) will always produce the maximum response, and the nonoptimal stimuli will simply scale-down accordingly, independent of the overall

ambient prevailing level of contrast. In so doing, the discrimination performance is optimized along all of the stimulus dimensions within this feature space, with the exception of contrast, and deviations from the optimum will produce maximum discriminability. Further, when the cell produces saturated responses, it identifies the presence of a specific feature with a high degree of certainty.

In sum, for the traditional analogy of gain control to be useful, the dimension of luminance needs to be compared to a multidimensional feature space: The contrast gain control scales the responses, based upon the average prevailing contrast, such that differential sensitivity is optimized within the multidimensional feature space.

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