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

DUANE G. ALBRECHT, WILSON S. GEISLER, AND ALISON M. CRANE

Introduction

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 taken only 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 used 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 used to study the retina, lateral geniculate nucleus, and visual cortex of the primate and related species (e.g., De Valois et al., 1982; Enroth-Cugell and Robson, 1966; Movshon et al., 1978; Ohzawa et al., 1985; Shapley and Victor, 1979; for reviews see Carandini et al., 1999; De Valois and De Valois, 1988; Ferster and Miller, 2000; Geisler and Albrecht, 2000; Palmer et al., 1991; Robson, 1975; Shapley and Lennie, 1985).

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 by 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 nonlinear behaviors that have been measured.

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 no 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 multidimensional 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) multidimensional 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 used by a subsequent brain mechanism to detect, discriminate, and identify that specific visual feature. For example, the response magnitude could be used 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 features/attributes is a critical step toward the goal of object segregation (Geisler and Albrecht, 2000). A third hypothesis is that the selectivity reflects the sequential hierarchical progression toward 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.

**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 used the well-developed techniques of 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., Marmarelis and Marmarelis, 1978; Schwarz and Friedland, 1965) 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 use a frequency domain analysis, a space and/or time domain analysis, a white noise domain analysis, and so forth (see Marmarelis and Marmarelis, 1978). 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 et al., 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 across a wide and diverse set of circumstances.

**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 specific mathematical methods have been developed to study nonlinear systems (e.g., Victor and Knight, 1979; Tsvetkov et al., 1977; see also 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., DeAngelis et al., 1993; Palmer et al., 1991). 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 use 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 sometimes, 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.

**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 msec. 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 on 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 on 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., De Valois et al., 1982; Movshon et al., 1978; for recent reviews see Cavanagh and Marmarelis, 1999; Ferster and 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 msec) to measure the responses as a function of some stimulus dimension of interest (e.g., contrast). The measured poststimulus 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 the responses 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., Albrecht et al., 2002; Frazor et al., 1997; Gillespie et al., 2001; Muller et al., 2001; Ringach et al., 1997). Within this chapter, we will consider measurements using drifting steady-state stimuli and measurements using stationary 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.

**Linear and nonlinear properties**

**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 investigators have elaborated the original binary classification with subsidiary and supplementary subclassifications (e.g., Henry, 1977) and others have argued that simple and complex cells reflect opposite ends of a virtual continuum (Chance et al., 1998; 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 their original report, Hubel and Wiesel (1962) described four basic linear properties of simple cells:

- Distinct excitatory and inhibitory subregions within the receptive field
- Spatial summation within a given subregion
- Mutual antagonism between subregions
- Responses to novel stimuli can 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 stimuli 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 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 (1) the measured neural response behavior of simple cells and (2) 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.

**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 degrees 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.

**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 poststimulus time histogram) is not sinusoidal. Specifically, all of the negative values of the sine wave are absent. This observation is not particularly 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.

**Responses as a function of spatial phase.** Using a stationary spatial frequency sine wave 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 poststimulus 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 et al., 1991; Tolhurst and Dean, 1991).

**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 (Albrecht, 1995; Dawis et al., 1984; Hamilton
et al., 1989).

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 nonlin-
erities. This method for testing the linearity of spatial sum-
mation has been applied to simple cells, and the linear
prediction holds to a first approximation (e.g., De Valois
et al., 1982; Movshon et al., 1978).

Receptive field and spatial frequency tuning. It is possible to char-
acterize 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 response and frequency
response. Movshon et al. (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.

Spatiotemporal receptive field and motion. If the receptive field is
measured as a function of both space and time using sta-
nary flashed bars or spots, and if the cell behaves in a
linear fashion, it is possible to use the resulting spatiotem-
poral receptive field to determine (1) whether the cell is
direction selective, (2) the optimal direction of motion, and
(3) the degree of direction selectivity.

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

Some Nonlinear Properties of Both Simple
and Complex Cells

Response refractory period. As the firing rate of a given neuron
increases, the absolute and relative refractory periods will
produce response saturation that is solely determined by the
magnitude of the firing rate, regardless of what particular
stimulus produced the high rate of firing. The temporal
dynamics for this nonlinearity are on the order of a few mil-
iseconds 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 refrac-
tory period is deleterious on stimulus selectivity because
it makes the neuron less selective at high firing rates. Inter-
estingly, however, the regularization in the spike trains
that occurs during this type of saturation has beneficial
consequences for detection, discrimination, and identifica-
tion 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.

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 47.1A, when stimulated with a coun-
terphase 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., De Valois et al., 1982; Movshon et al., 1978). This type

![Figure 47.1](image)

**Figure 47.1.** Responses (poststimulus time histograms) 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 et al., 1982.)

ALBRECHT, GEISLER, AND CRANE: VISUAL CORTEX: NONLINEAR PROPERTIES 751
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 47.1B, 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., Albrecht and De Valois, 1981; Movshon et al., 1978). 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 msec, and thus it can exert its influence within the time frame of a single fixation.

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, 1983; Watson and Ahumada, 1985) and texture energy in the stimulus (Bergen, 1991).

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 et al., 1990). Figure 47.2 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:

\[ r_c = \frac{c^a}{c^{\alpha} + c_50} \]

where \( \alpha \) is the response exponent, \( c_50 \) is the half-saturation contrast, and \( c \) is luminance contrast. Many studies have shown that this function provides a good fit to the contrast response function of striate cortex neurons (e.g., Albrecht and Hamilton, 1982; Albrecht et al., 1984; DeAngelis et al., 1993; Geisler and Albrecht, 1997; McLean and Palmer, 1996; Sclar et al., 1990; Tolhurst and Heeger, 1997). The exponent of this equation can be used to quantify the response expansion. The average value in the primary visual cortex is approximately 2.5.

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 expressed only 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 frequency are approximately sinusoidal, but not exactly. Specifically, the responses as a function of spatial position 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 on the measured receptive field (e.g., De Valois et al., 1985; Tadmor and Tolhurst, 1989).
• The measured direction selectivity is greater than expected, based on the responses as a function of spatial phase (Albrecht and Geisler, 1991; Murthy et al., 1998; Reid et al., 1991; Tolhurst and Dean, 1991).
• The measured direction selectivity is greater than expected, based on the spatiotemporal receptive field (DeAngelis et al., 1993; McLean and Palmer, 1994).
• The measured orientation selectivity is greater than expected, based on the measured receptive field (Gardner et al., 1999).
• Vernier acuity is greater than expected, based on 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).

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 47.3 plots the responses as a function of contrast to illustrate response saturation. Measurements illustrated below (Figs. 47.7 to 47.10) have demonstrated that the saturation can occur well within the time frame of a single fixation. In a later section (“Contrast Response Nonlinearities”) we will consider the potential effects of saturation on stimulus selectivity.

Contrast-set gain control. As shown in Figure 47.3, the responses of cortical cells saturate as the contrast increases, oftentimes at very low contrasts. This saturation could be determined by either (1) the magnitude of the response or (2) 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 on the magnitude of the contrast: a contrast-set gain control. Recent measurements (e.g., the section “Contrast Response Nonlinearities”) 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.

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 nonoptimal stimuli could produce equivalent responses. However, measurements of the contrast response function using optimal and nonoptimal stimuli have shown that the saturation is not determined by the magnitude of the response (e.g., Fig 47.4); instead, the saturation is determined by the magnitude of the contrast (Albrecht and Hamilton, 1982; Sclar and Freeman, 1982; for a review see Carandini et al., 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.

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
(1) the magnitude of the response or (2) the magnitude of the contrast. Measurements have demonstrated that the shift is determined by the contrast, and not the response (Albrecht, 1995; Carandini and Heeger, 1994; Carandini et al., 1997; Dean and Tolhurst, 1986; Gawne et al., 1996; Reich et al., 2001). Figure 47.5 shows the shift for a representative cell at an optimal and a nonoptimal spatial frequency. The magnitude of the response to the optimal stimulus was approximately three times the magnitude of the response to the nonoptimal 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.

**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, as illustrated in Figure 47.6 (Albrecht et al., 1984; McLean and Palmer, 1996; Movshon and Lennie, 1979; Saul and Cynader, 1989). The temporal dynamics of this nonlinearity are too slow to have an influence on stimulus selectivity within a single fixation, based on 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.

**Other types of nonlinear behaviors**
- Nonlinear spatial summation (Movshon et al., 1978)
- Spatial frequency inhibition (De Valois and Tootell, 1983)
- Surround effects, outside the classic receptive field (Cavanaugh et al., 2002a, 2002b; De Valois et al., 1985)
- Non-Fourier envelope responses (Zhou and Baker, 1994)
- Supersaturation (Bonds, 1991; Li and Creutzfeldt, 1984)
- Cross-orientation inhibition (Bonds, 1989)
- Nonspecific suppression (e.g., Carandini et al., 1997; DeAngelis et al., 1992; Nelson, 1991).

**Temporal dynamics**

It is worthwhile to consider 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 on the spatiotemporal contrast within that fixation.

**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 on the response to a stimulus during a single fixation. It is equally

**Figure 47.5.** 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. (D. G. Albrecht and W. S. Geisler, unpublished observations.)

**Figure 47.6.** Responses (mean firing rate) of a cortical cell to a high-contrast spatial frequency grating drifting over the course of 30 sec, to illustrate contrast adaptation. (Adapted from Albrecht et al., 1984.)

754 PROCESSING IN PRIMARY VISUAL CORTEX
clear that other nonlinearities could not have a significant influence on the selectivity and performance, based on 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.

- 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.

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

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

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

**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 preceding section “Temporal Dynamics, Stimulus Selectivity, Neural Performance,” the responses to transient stationary gratings are useful for examining the temporal dynamics of linear and nonlinear properties. Recently, several different laboratories have been measuring the responses to brief stimuli and analyzing the time course of some of the fundamental properties (e.g., Albrecht et al., 2002; Frazor et al., 1997; Gillespie et al., 2001; Muller et al., 2001; Ringach et al., 1997).

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 msec), in order to illustrate how the contrast response function develops over the course of the first 200 msec after stimulus onset. Further, we consider some of the general questions posed in the Introduction, within the context of this specific set of transient measurements. For example, one can ask: How long does it take for the two nonlinearities, response expansion and contrast 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 on the level of contrast within that fixation. Therefore, these two nonlinearities will have little or no influence on stimulus selectivity during a single fixation.

**Poststimulus time histogram as a function of contrast.** Figure 47.7 shows the responses of a neuron recorded from within the monkey visual cortex to stationary gratings that were presented for a 200 msec interval at 10 different levels of contrast. Each set of data points plots the responses as a function of time, every 4 msec (i.e., the poststimulus 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 poststimulus 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 msec 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:

- The magnitude of the response increases rapidly from the base rate to the maximum firing rate in approximately 20 msec and then declines to approximately one-third of the maximum firing rate within approximately 30 msec after the peak.

- The overall shape of the poststimulus 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).

![Figure 47.7](image-url)
• Although the stimulus remains on for 200 msec, the response is considerably more transient. It is important to note that there is a great deal of heterogeneity from cell to cell (Albrecht et al., 2002).

Responses as a function of contrast through time. Figure 47.8 plots the responses as a function of contrast for six different times during the course of the responses shown in Figure 47.7: 38 (○), 62 (□), 70 (▲), 78 (●), 86 (▼), and 102 msec (●). The smooth curves through each set of data points plot the parameter-optimized fit 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 msec 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.

Responses during the first 16 msec. Figure 47.9 plots the responses as a function of contrast during the first 16 msec after the onset of the response to a transient stationary grating. Each set of data points plots the responses in sequential 2 msec 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 qualitatively similar across the different time intervals.

• A single, scaled Naka-Rushton equation accounts for large percentage of the variation in the responses across contrast and through time (over 95%); this demonstrates qualitatively that the shape of the contrast response function 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 msec after the onset of the response).

Responses to optimal and nonoptimal stimuli during the first 20 msec. Figure 47.10 plots the responses as a function of contrast during the first 20 msec after the onset of the response to stationary grating. (Adapted from Albrecht et al., 2002.)
during the first 20 msec after the onset of the response for an optimal and a 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.

**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 on the measurements illustrated in Figures 47.7 to 47.10, 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.

**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 approximate natural viewing more closely). The results of 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.

**Steady-state stimuli versus 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 (Muller et al., 2001; Tolhurst et al., 1980).
- The steady-state temporal frequency tuning changes substantially as contrast increases (e.g., Albrecht, 1995; Hawken et al., 1992; Holub and Morton-Gibson, 1981), whereas the temporal response profile of 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., Geisler and Albrecht, 1997; Sofiky and Koch, 1993; Tolhurst et al., 1983), whereas this relationship does not hold for the initial transient response to stationary gratings (Muller et al., 2001).

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

- Responses to stationary gratings are more transient than responses to drifting gratings.
- Both detectability and discriminability are better for drifting gratings than for 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.

**Selectivity along other dimensions** Figures 47.7 to 47.10 indicate that the properties of the contrast response function are fully established at the very onset of the response and remain relatively invariant throughout the entire time course of the response, during an interval comparable to natural fixation (i.e., a 200 msec interval). These findings lead one to ask whether the response properties along other stimulus dimensions are similar. For example, is the stimulus selectivity along other stimulus dimensions fully established at the onset of the response? Similarly, is the stimulus selectivity along other stimulus dimensions relatively invariant throughout the entire time course of the response during an interval comparable to natural fixation?

With these questions in mind, it is important to note that several different lines of evidence appear to indicate that this type of behavior (i.e., rapid development and invariance through time) may not generalize to other stimulus dimensions. However, it is equally important to note that this is an emerging line of research and that the results across laboratories are not yet entirely reconcilable. In brief, it appears as though some important aspects of stimulus selectivity develop over the course of the first 50 msec after the onset of the response.

**Spatial frequency and orientation selectivity measured with a reverse correlation procedure.** Ringach et al. (1997) have measured the temporal dynamics of orientation tuning using a new reverse correlation procedure (where gratings are presented for very brief intervals: 20 msec). Their measurements indicate that orientation tuning changes through time for some V1 neurons: specifically, the preferred orientation changes and the selectivity increases (however, see Gillespie et al., 2001; Mazer et al., 2002; Muller et al., 2001).
Bredfeldt and Ringach (2002) used a similar procedure to measure the temporal dynamics of spatial frequency selectivity. Their measurements indicate that spatial frequency selectivity also changes through time. Specifically, the measurements indicate that (1) the preferred spatial frequency shifts from low frequencies to high frequencies and (2) the selectivity increases (however, see Albrecht et al., submitted).

Spatial frequency and orientation selectivity measured in an awake, behaving monkey. Mazer et al. (2002) have measured the responses of V1 neurons using the awake, behaving preparation, in which a monkey is trained to fixate while visual stimuli are presented (for a duration longer than 20 msec). Unlike the measurements of Ringach et al. (1997), their measurements indicate that orientation selectivity is relatively invariant through time. However, similar to Bredfeldt and Ringach (2002), the measurements of Mazer et al. indicate that the preferred spatial frequency increases through time.

Spatial frequency selectivity measured with transient stationary stimuli. We have measured spatial frequency selectivity using stationary gratings that are turned on for 200 msec and off for 300 msec (Albrecht et al., submitted). In agreement with Bredfeldt and Ringach (2002) and Mazer et al. (2002), we find that spatial frequency selectivity changes through time. Specifically, our measurements indicate that the latency of the response increases as spatial frequency increases. This latency shift causes the peak of the spatial frequency response function to shift through time, and it also causes the spatial frequency selectivity to decrease as the responses are integrated over the course of 200 msec: the spatial frequency peak and the bandwidth change as the responses are integrated over the first 50 msec, and then they both become relatively stable and remain invariant thereafter.

Spatial frequency, spatial phase, and direction selectivity during natural fixation. Given that all three laboratories discussed in the preceding sections, using very different measurement techniques, have reported that spatial frequency tuning changes through the course of an interval comparable to natural fixation, it is important to consider the functional consequences of these changes. Although these changes may help us understand the underlying structural components that produce high degrees of stimulus selectivity, it seems unlikely that these changes will have important functional consequences for the discrimination and identification performance, if one assumes that subsequent neurons integrate the responses over more than just a few milliseconds. Specifically, if the response to a given stimulus is integrated through time following the onset of the response, the stimulus selectivity should become relatively stable within 50 msec.

In addition, it is important to keep in mind the effect of the integration interval on the signal-to-noise ratio when considering neural discrimination and identification performance. We know from signal detection theory that performance should improve as the integration interval increases. In the case of V1 neurons, as the integration interval increases, the number of action potentials increases, and because the variance is proportional to the mean of the response, the longer the integration interval the larger the signal-to-noise ratio. We have found that, on average, it takes approximately 50 msec to reach 50% of the total number of action potentials when a stationary grating is presented for 200 msec (Albrecht et al., 2002, submitted). Thus, for example, integrating over the entire 200 msec would, on average, double the number of action potentials, which would increase the signal-to-noise ratio by approximately 50% (assuming a variance proportionality constant of 1.3).

Even if stimulus selectivity is dynamic over the first 50 msec of the response, measurements indicate that if the integration interval is extended to 200 msec (comparable to natural fixation), the selectivity for many stimulus dimensions is stable and essentially equivalent to the selectivity that is measured with steady-state stimuli (Frazor, 2002; Frazor et al., 1997). This observation holds not only for spatial frequency, but also for direction selectivity and spatial position selectivity. Figure 47.11 illustrates the responses as a function of spatial frequency and the direction of stimulus.

**Figure 47.11.** Responses (mean firing rate per 200 msec) as a function of spatial frequency for the preferred direction of motion (A) and the nonpreferred direction of motion (B). The responses and fitted curve for steady-state stimuli are shown with the • and solid curve; the responses and fitted curve for transient stimuli are shown with the ● and dashed curve. (Adapted from Frazor, 2002.)
motion for transient and steady-state methods of stimulus presentation; Figure 47.12 illustrates the responses of the selectivity for spatial position. In sum, the stimulus selectivity for these three dimensions for integration over 200 ms is very similar to the stimulus selectivity that has been measured using steady-state stimuli.

Conclusion

Models at different levels of analysis. There are many different laboratories measuring the properties of visual cortex neurons and developing models at many different levels of analysis. In preparation for writing 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.

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.

In addition to providing 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 test quantitatively the hypothesis that response saturation is determined by the magnitude of the response or the magnitude of the contrast (see above).
- To test quantitatively the hypothesis that the contrast gain control and the expansive response exponent are present virtually instantaneously (see above).
- To test quantitatively 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 is 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., Albrecht and Geisler, 1991; Carandini et al., 1999; Heeger, 1991, 1992a, 1992b).

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

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 amplitudes are very different for the optimal versus 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., Albrecht and Geisler, 1991; Carandini and Heeger, 1994; Ferster, 1994; Heeger, 1991, 1992a, 1992b; for reviews see Carandini et al., 1999; Geisler and Albrecht, 2000). The linear filter accounts for (1) the sinusoidal responses as a function of spatial position, (2) the direction selectivity, and (3) the relationship between the two. The contrast-set gain control accounts for the saturation at the same contrast, independent of response amplitude. The expansive exponent accounts for (1) the mismatch between the direction selectivity and the responses as a function of spatial phase as well as (2) the narrow and peaked pattern. Several examples of functional models are given in Albrecht et al. (2002).

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-set gain control include: expansive voltage-spike transduction, noisy membrane potential, recurrent excitation, intracellular inhibition, correlation-based inhibition, synaptic depression, nonspecific suppression, shunting inhibition, tonic hyperpolarization, strong push-pull inhibition, and changes in membrane conductance. Some models rely on feedback inputs, others rely on feedback inputs, and still others rely on 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 47.1.

**Contrast-set Gain Control**

*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 con-

**Table 47.1**

<table>
<thead>
<tr>
<th>Examples of contemporary structural models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abbott et al. (1997)</td>
</tr>
<tr>
<td>Adorjan et al. (1999)</td>
</tr>
<tr>
<td>Anderson et al. (2000)</td>
</tr>
<tr>
<td>Carandini et al. (1999)</td>
</tr>
<tr>
<td>Chance et al. (1998)</td>
</tr>
<tr>
<td>Douglas et al. (1995)</td>
</tr>
<tr>
<td>Ferster and Miller (2000)</td>
</tr>
<tr>
<td>Gilbert et al. (1990)</td>
</tr>
<tr>
<td>Hirsch et al. (1998)</td>
</tr>
<tr>
<td>Kayser et al. (2001)</td>
</tr>
<tr>
<td>Miller et al. (2001)</td>
</tr>
<tr>
<td>Murthy and Humphrey (1999)</td>
</tr>
<tr>
<td>Nelson et al. (1994)</td>
</tr>
<tr>
<td>Somers et al. (1995)</td>
</tr>
<tr>
<td>Stetter et al. (2000)</td>
</tr>
<tr>
<td>Troyer et al. (1998)</td>
</tr>
<tr>
<td>Wieland et al. (2001)</td>
</tr>
<tr>
<td>Worogotov et al. (1998)</td>
</tr>
</tbody>
</table>

760  PROCESSING IN PRIMARY VISUAL CORTEX
stant 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 on 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., Hood, 1998; Shapley and Enroth-Cugell, 1984). Conceptually, within this analogy, the gain of the system is adjusted based on 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 on the average amount of light available. The goal is to use effectively 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.

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-set 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-set gain control).

In the light adaptation analogy, one might suppose that the gain control in the cortex is positioned 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.

Gain control in a multidimensional feature space. As emphasized many times within this chapter, one hallmark of cortical neurons is stimulus selectivity. To characterize this selectivity, visual neuroscientists measure the responses along many 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-set gain control scales the responses, based on the average prevailing contrast, such that differential sensitivity is optimized within the multidimensional feature space.

REFERENCES


