Adaptation Changes Stereoscopic Depth Selectivity in Visual Cortex

Thang Duong, Bartlett D. Moore IV, and Ralph D. Freeman

Group in Vision Science, School of Optometry, Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, California 94720-2020

Exposure to specific visual stimuli causes a reduction in sensitivity to similar subsequent stimulation. This adaptation effect is observed behaviorally and for neurons in the primary visual cortex. Here, we explore the effects of adaptation on neurons that encode binocular depth discrimination in the cat's primary visual cortex. Our results show that neuronal preference for binocular depth is altered selectively with appropriate adaptation. At the preferred depth, adaptation causes substantial suppression of subsequent responses. Near the preferred depth, the same procedure causes a shift in depth preference. At the null depth, adaptation has little effect on binocular depth coding. These results demonstrate that prior exposure can change the depth selectivity of binocular neurons. The findings are relevant to the theoretical treatment of binocular depth processing. Specifically, the prevailing notion of binocular depth encoding based on the energy model requires modification.

Introduction

Repeated or extended use of identical stimulation has been used in different sensory systems to investigate various aspects of neural connectivity. This adaptation process has been used in perceptual and neurophysiological studies to explore coding of different visual stimulus parameters (Blakemore and Campbell, 1969a,b; Blakemore and Julesz, 1971; Blakemore and Hague, 1972; Movshon and Lennie, 1979; Marlin et al., 1991, 1993; Müller et al., 1999; Dragoi et al., 2000). In the early visual pathway, this process occurs on different timescales. Rapid adaptation of V1 neurons operates on the order of hundreds of milliseconds to seconds (Müller et al., 1999; Sanchez-Vives et al., 2000b; Chung et al., 2002; Felsen et al., 2002). This phenomenon is thought to be mediated by a combination of Ca^{2+} -activated K^{+} current (Sanchez-Vives et al., 2000b), short-term plasticity of corticocortical synapses (Felsen et al., 2002), and rapid depression of thalamo-cortical synapses (Chung et al., 2002). Intracellular studies show that adaptation is accompanied by a membrane potential hyperpolarization that is likely to be mediated by Na^{+} -activated K^{+} current (Carandini and Ferster, 1997; Sanchez-Vives et al., 2000a,b). Prolonged adaptation occurs over tens of seconds, and its effects last for seconds (Movshon and Lennie, 1979; Ohzawa et al., 1982, 1985; Duong and Freeman, 2007).

Adapted neurons show two clear properties. First, responses to similar subsequent stimuli are greatly reduced, and this effect is much more robust in V1 compared with LGN (Movshon and Lennie, 1979; Ohzawa et al., 1982, 1985; Carandini and Ferster, 1997; Sanchez-Vives et al., 2000a,b; Duong and Freeman, 2007).

Second, adaptation changes orientation, spatial frequency, and direction selectivity of cortical neurons (Movshon and Lennie, 1979; Marlin et al., 1988, 1991, 1993; Saul and Cynader, 1989a,b; Müller et al., 1999; Dragoi et al., 2000, 2001). For V1 neurons, adaptation causes a shift in the preferred value away from that of the adapting stimulus. This effect is a cortical phenomenon and is likely to be mediated by intracortical circuits (Duong and Freeman, 2007). Adaptation at both short and long temporal scales serves to decorrelate stimulus input and may improve coding efficiency (Müller et al., 1999; Wang et al., 2003).

In the current study, we examine the effects of adaptation on disparity coding neurons in the cat's primary visual cortex. We adapt neurons to a prolonged period of dichoptically presented drifting sinusoidal gratings at various relative interocular phases. We determine interocular phase tuning curves before and after adaptation to gratings at optimal, near-optimal, and null interocular phases. Our findings show that adaptation at the optimal phase substantially reduces response to subsequent stimuli. At the null phase, adaptation has minimal effects on subsequent disparity-related responses and does not change the preferred interocular phase. However, adaptation at intermediate phases causes a reduction in response and a shift in the tuning curve away from the adapting phase. These adaptation properties may have perceptual consequences and might also improve disparity coding efficiency in the primary visual cortex.

Materials and Methods

Electrophysiological preparation. All procedures complied with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals*. Details of our recording procedures are given in previous publications (Ohzawa and Freeman, 1986a,b; Duong and Freeman, 2007). Briefly, extracellular recordings were made using epoxy-coated tungsten microelectrodes in area 17 of 3 male and 13 female anesthetized and paralyzed mature cats. Electrodes are placed at Horsley–Clarke coordinate P4L2 angled 20° anterior and 10° medial (Horsley and Clarke, 1906). Cats are anesthetized with sodium thiopental at a level determined individually for each animal (typically ~ 1.0 – $1.5 \text{ mg} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$) and paralyzed with pancuronium bromide (0.2

Received Aug. 15, 2010; revised May 2, 2011; accepted May 26, 2011.

Author contributions: T.D. and R.D.F. designed research; T.D. and R.D.F. performed research; T.D., B.D.M., and R.D.F. analyzed data; T.D., B.D.M., and R.D.F. wrote the paper.

This work was supported by National Eye Institute Research and Core Grants EY01175 and EY03176.

Correspondence should be addressed to Ralph D. Freeman, School of Optometry, University of California, Berkeley, 360 Minor Hall, Berkeley, CA 94720-2020. E-mail: freeman@neurovision.berkeley.edu.

DOI:10.1523/JNEUROSCI.4267-10.2011

Copyright © 2011 the authors 0270-6474/11/3112198-10\$15.00/0

$\text{mg} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$). Single units are isolated in real time by the shape of their action potentials. Optimal parameters are obtained for spatial frequency, temporal frequency, orientation, and receptive field size. Subsequent tests are made using gratings with optimal orientation, spatial frequency, and temporal frequency that are slightly larger than receptive field sizes.

Visual stimulation. Visual patterns are presented on a large CRT at a frame rate of 75 Hz. The 47.8-cm-diameter CRT is positioned at an optical distance of 41.8 cm in front of the cat's eyes. For binocular stimulation, a setup similar to that described previously is used (Ohzawa and Freeman, 1986a). Mirrors are placed so that the left and right halves of the display stimulate left and right eyes, respectively. Luminance of the CRT is calibrated to provide linear steps with maximum and minimum values of 90 and 0.1 cd/m^2 , respectively. To obtain high signal-to-noise levels, we stimulate neurons with drifting gratings, which generally elicit high spike rates. These gratings have optimal spatial and temporal frequencies and orientation. To measure disparity tuning, phase difference is varied between gratings presented to left and right eyes. Binocular disparity values correspond to differences in responses at various relative interocular phases (Freeman and Robson, 1982; Ohzawa and Freeman, 1986a,b; Chino et al., 1994; Smith et al., 1997). Neurons that are excited or inhibited by different depth planes have clear phase tuning curves as illustrated in Figure 1, *A* and *B*. To measure the nonadapted tuning curve, gratings at different interocular phases chosen randomly from a set of 12 test phases spanning 360° are presented for 2 s each following 4 s of rest during which the animal is stimulated with a blank screen at mean luminance. The adapted phase tuning curve is measured by a standard adaptation paradigm as depicted in Figure 1C (Movshon and Lennie, 1979; Ohzawa et al., 1982, 1985). During each repetition, an initial adaptation grating is presented for 60 s. After this initial adaptation period, 2 s test stimulations at different interocular phases are presented randomly following 4 s of top-up adaptation as represented in Figure 1C. Contrast for both the adaptation and test stimuli is kept at 50%. At least five repetitions are presented for every experiment. Before each adaptation experiment, the neuron is exposed to 15 min of mean luminance stimulation to neutralize any effects of previous tests.

Data analysis. All data analysis is done in MATLAB (MathWorks). Neurons are classified as either simple or complex based on the F1/F0 ratio. The F1 or F0 component is used for subsequent analysis of simple or complex cells (Skottun et al., 1991). Adapted and nonadapted interocular phase tuning curves are each fit with a truncated sine function as follows:

$$r(\phi) = \max(a \cdot \sin(\phi + \theta) + m, 0), \quad (1)$$

where ϕ is interocular phase, $r(\phi)$ is the response, and a and m are free parameters corresponding to the amplitude and offset of the tuning curve, respectively. θ is an arbitrary phase parameter that is used to calculate the optimal and null phases. Optimal phase is defined as the phase that maximizes response. Null phase is separated by 180° from optimal. Note that stimulation at the null phase can elicit an excitatory response for some cells, an inhibitory one for others, or there may be no effect.

To obtain a , m , and θ parameters from the raw data, response mean and variance statistics are calculated for each test phase. Parameters are obtained by fitting the data with Equation 1. Data fitting is accomplished by minimizing the χ^2 statistic using `fminsearch` in MATLAB, which implements the Nelder–Mead method (Nelder and Mead, 1965). For this fit, the amplitude a is constrained to be positive, and θ is between 0 and 360° . Confidence intervals for each parameter are obtained by a Monte Carlo simulation. Each data set is resampled and refitted. The refitted parameters are used to estimate confidence intervals. Details of this procedure have been provided previously [Efron, 1982; Press and Numerical Recipes Software (Firm), 1993]. Briefly, for each interocular phase tuning function, we measure the responses to 12 different test phases. A random data set is drawn from the original responses, and this is repeated to obtain 10,000 different data sets. For each data set, we estimate parameters of the function given in Equation 1. These parameters are used to compute the 95% confidence interval, which is then used to determine whether a parameter changes between different experimental conditions.

Binocular energy model. The binocular energy model consists of three processing stages as illustrated in Figure 8A. The first stage consists of

monocular simple cells with oriented Gabor-like receptive fields. Monocular simple cells from left and right eyes converge to create binocular disparity selective simple cells. The preferred disparity of binocular simple cells depends on differences in preferred spatial phase between left and right eye receptive fields. These binocular simple cells converge to create complex cells following the original hierarchy notion of visual processing and the motion energy model (Hubel and Wiesel, 1959, 1962; Adelson and Bergen, 1985; Ohzawa, 1998). For simplicity, we make a few assumptions. First, neurons do not exhibit a position disparity component. Second, disparity selectivity is in a direction orthogonal to the preferred orientation of the neuron, so receptive fields are collapsed into one dimension by projecting onto this orthogonal axis. Finally, since we do not vary disparity as a function of time in our experiments, the temporal component of the model is omitted. Analytically, the response of monocular simple cells can be described by the following equations:

$$R_{L1} = f\left(\sum_x H_{L1}(x) s_L(x) + r\right) \quad (2)$$

$$R_{L2} = f\left(\sum_x H_{L2}(x) s_L(x) + r\right) \quad (3)$$

$$R_{R1} = f\left(\sum_x H_{R1}(x) s_R(x) + r\right) \quad (4)$$

$$R_{R2} = f\left(\sum_x H_{R2}(x) s_R(x) + r\right), \quad (5)$$

where x is the spatial coordinate orthogonal to the preferred orientation of the cell, $s_L(x)$ and $s_R(x)$ denotes the stimulus intensity at spatial coordinate x in the left and right eyes, respectively, r is the spontaneous response, and f is the neuronal half-rectified static nonlinear function for monocular simple cells defined as follows:

$$f(x) = \begin{cases} 0, & x < 0 \\ x, & x \geq 0 \end{cases}, \quad (6)$$

and the linear kernels are defined as follows:

$$H_{L1}(x) = e^{\frac{x^2}{2\sigma^2}} \cos(\omega x) \quad (7)$$

$$H_{L2}(x) = e^{\frac{x^2}{2\sigma^2}} \cos\left(\omega x + \frac{\pi}{2}\right) \quad (8)$$

$$H_{L3}(x) = e^{\frac{x^2}{2\sigma^2}} \cos(\omega x + \pi) \quad (9)$$

$$H_{L4}(x) = e^{\frac{x^2}{2\sigma^2}} \cos\left(\omega x + \frac{3\pi}{2}\right) \quad (10)$$

$$H_{R1}(x) = e^{\frac{x^2}{2\sigma^2}} \cos(\omega x + \varphi) \quad (11)$$

$$H_{R2}(x) = e^{\frac{x^2}{2\sigma^2}} \cos\left(\omega x + \frac{\pi}{2} + \varphi\right) \quad (12)$$

$$H_{R3}(x) = e^{\frac{x^2}{2\sigma^2}} \cos(\omega x + \pi + \varphi) \quad (13)$$

$$H_{R4}(x) = e^{\frac{x^2}{2\sigma^2}} \cos\left(\omega x + \frac{3\pi}{2} + \varphi\right), \quad (14)$$

where σ represents the receptive field size, ω is the preferred spatial frequency, and φ is a phase that represents the interocular phase preference of downstream disparity selective neurons. The half-rectification component described by f is introduced to account for the response to anticorrelated stimuli (Read et al., 2002).

The response of binocular simple cells can be constructed by summing output from monocular simple cells that respond to left and right eyes and by application of a static expansive nonlinear function. This response is described by the following equations:

$$R_{bs1} = g(R_{L1} + R_{R1}) \quad (15)$$

$$R_{bs2} = g(R_{L2} + R_{R2}) \quad (16)$$

$$R_{bs3} = g(R_{L3} + R_{R3}) \quad (17)$$

$$R_{bs4} = g(R_{L4} + R_{R4}), \quad (18)$$

where the function

$$g(x) = x^2 \quad (19)$$

is the static squaring output nonlinear function. These binocular simple cells prefer the same interocular phase of φ and spatial phases of $0, \pi/2, \pi$, and $3\pi/2$, respectively. Finally, we construct the binocular complex cell by summing the binocular simple cells that prefer various spatial phases as follows:

$$R_{bc} = R_{bs1} + R_{bs2} + R_{bs3} + R_{bs4}. \quad (20)$$

To simulate the response of these neurons after contrast adaptation, we assume cortical neurons behave similarly to data reported in previous studies and that a response reduction translates to a decrease in neuronal gain (Ohzawa et al., 1982, 1985; Albrecht et al., 1984). For simplicity, we assume that the spontaneous response r is 0. Under these assumptions, the response to simple cells after adaptation is given by the following:

$$R'_{L1} = \alpha \cdot f\left(\sum_x H_{L1}(x)s(x)\right) \quad (21)$$

$$R'_{L2} = \alpha \cdot f\left(\sum_x H_{L2}(x)s(x)\right) \quad (22)$$

$$R'_{R1} = \alpha \cdot f\left(\sum_x H_{R1}(x)s(x)\right) \quad (23)$$

$$R'_{R2} = \alpha \cdot f\left(\sum_x H_{R2}(x)s(x)\right) \quad (24)$$

$$R'_{bs1} = \beta \cdot g(R'_{L1} + R'_{R1}) \quad (25)$$

$$R'_{bs2} = \beta \cdot g(R'_{L2} + R'_{R2}) \quad (26)$$

$$R'_{bs3} = \beta \cdot g(R'_{L3} + R'_{R3}) \quad (27)$$

$$R'_{bs4} = \beta \cdot g(R'_{L4} + R'_{R4}), \quad (28)$$

and parameters α and β denote gain attenuation after adaptation. After adaptation at optimal, intermediate, and null phases, the α and β parameters are assumed to be as follows: $\alpha_{\text{null}} = 0.55$, $\beta_{\text{null}} = 1$, $\alpha_{\text{intermediate}} = 0.55$, $\beta_{\text{intermediate}} = 0.75$, $\alpha_{\text{optimal}} = 0.55$, and $\beta_{\text{optimal}} = 0.55$, where α is independent of the interocular phase, and β is smallest at the optimal and largest at the null phase. An illustration of this model and response simulations are shown in Figure 8. Figure 8A shows a diagram of the binocular energy model. For simulation, we use $\omega = 1$, $\sigma = 2$, and $\varphi = \pi/2$.

Figure 1. Binocular interocular phase stimulation. **A**, Sinusoidal gratings presented to left and right eyes at varying relative phases cause retinal disparities equivalent to near and far distances. **B**, Ideal responses of three neurons across all interocular phases. These cells are selective for far, near, and fixation planes as denoted by the labels. Gratings under the abscissa represent the different interocular phase values of the dichoptic drifting grating stimulus. **C**, Adaptation paradigm. The adapting gratings are present for an initial 60 s adaptation period followed by a sequence of randomized test conditions. Each test condition consists of a 2 s presentation of test gratings and a 4 s top-up period during which the adapting grating is presented. **D**, Relevant parameters in the phase tuning curve are illustrated. Amplitude and offset are the a and m parameters, respectively, of the truncated sine function (see Materials and Methods) (Eq. 1). Optimal phase is defined as that which elicits a maximal response.

Figure 8B illustrates receptive fields of the left and right monocular simple cells as described by H_{L1} and H_{L2} . Figure 8C illustrates the response of binocular simple cells before and after adaptation, respectively. For this simulation, the response values are generated by computation of the response with stimuli described by the following:

$$s_L(x) = \sin(\omega x + t) \quad (29)$$

$$s_R(x) = \sin(\omega x + t + \varphi). \quad (30)$$

The response as a function of t is computed as t varies between 0 and 360° . This response traces out a sinusoidal function. Figure 8C is a plot of the amplitude of the response sinusoid as a function of φ . Additionally for this figure, the response is shifted vertically to an offset of 0 to emphasize changes in amplitude after adaptation.

Results

To study the effects of adaptation on disparity coding properties of binocular neurons in the primary visual cortex, we used dichoptically presented drifting sinusoidal grating stimuli. Neurons that are tuned for disparity respond selectively to different interocular phases of gratings presented to the left and right eyes (Freeman and Robson, 1982; Ohzawa and Freeman, 1986a,b; Freeman and Ohzawa, 1990; Ohzawa et al., 1996, 1997a,b; Anzai et al., 1997). This stimulation paradigm is illustrated in Figure 1. Figure 1A illustrates projections of a grating positioned in three depth planes onto the left and right retinas. In this projection, left

and right images exhibit spatial phase differences of positive, zero, and negative for near, fixation, and far planes, respectively. Neurons preferring these depth planes have interocular phase tuning functions as depicted in Figure 1*B*. Using this paradigm, dichoptic gratings at different interocular phases appear on different depth planes, so interocular phase is equivalent to binocular disparity. Since we do not know exact eye position, we measure relative interocular phase. Absolute disparity corresponding to this interocular phase can be computed from the spatial frequency of the stimulus grating and the fixation point of the cat.

We measured interocular phase tuning curves for each cell before and after adaptation to a given phase using the paradigm illustrated in Figure 1*C* as described in Materials and Methods. Optimal phase, offset, and amplitude parameters of these phase tuning functions are obtained by fitting the data with a truncated sine function. This process is described in Materials and Methods, and the parameters are illustrated in Figure 1*D* and considered in Equation 1. Together, we studied 51 neurons (30 complex and 21 simple) in the cat's striate cortex. To ensure that neurons recover completely from each adaptation procedure, we measured tuning curves for a random subset of nine cells after an arbitrary 15 min of recovery from adaptation. This period was chosen based on previous adaptation studies (Movshon and Lennie, 1979; Dragoi et al., 2000). During the recovery period, the cat views a blank screen at mean luminance. Recovery data for three representative examples of these nine neurons are shown in Figure 2. The solid, dashed, and dotted lines denote the control, adapted, and recovery interocular phase tuning curves, respectively. For the three representative cells (Fig. 2) and for all of the nine tested neurons, the recovery tuning functions are closely similar to those of the control condition. We conclude that a time period of 15 min is adequate for recovery from adaptation. For the remainder of our sample, a recovery period of at least 15 min is used following each adaptation procedure.

In previous work in which dichoptic grating presentation was used, we used an index to indicate the degree of phase-specific interaction. This binocular interaction index (BII) is defined as the amplitude of the phase tuning curve divided by the offset. Using BII, nearly all simple cells and approximately one-half of complex cells exhibited some degree of phase tuning (Ohzawa and Freeman, 1986a,b; Chino et al., 1994; Smith et al., 1997). The same index applied to monkey primary visual cortex suggests a slightly lower level of phase selectivity (Smith et al., 1997). For the present work, we have chosen a different criterion. We use one-way ANOVA to determine whether responses vary for different stimulus conditions. Responses for every repetition of each nonadapted stimulus condition are considered as a group. Each neuron is considered to be selective for interocular phase if the mean response values in every group are not equal ($p < 0.05$). The current criterion is different from BII in that it is independent of the interocular phase tuning function offset parameter. Instead, phase selectivity is determined by amplitude and noise level. Using this criterion, all 21 simple and 25 of 30 complex cells recorded exhibit phase-specific binocular interaction. This is generally consistent with previous results but a greater proportion of complex cells are considered phase specific with the current criteria (Ohzawa and Freeman, 1986a).

Adaptation has different consequences at optimal and null depths

To determine whether adaptation has differential effects at different interocular phases, we compare phase tuning curves after

Figure 2. Control, adapted, and recovery data for three representative neurons. The solid blue and dotted green lines denote nonadapted control and recovery conditions, respectively. The dashed red lines show data after adaptation. The unfilled red arrows denote the interocular phases of the adapting gratings. The vertical bars denote ± 1 SE.

adaptation to optimal and null phases. We first measure the nonadapted interocular tuning curve and then the tuning curve after adaptation to optimal phase. This procedure is repeated for the null phase. Each tuning curve is measured using many repetitions and results are statistically analyzed as described in Materials and Methods. Changes in turning curve offsets and amplitudes are examined following adaptation. In general, adaptation at the optimal phase substantially reduces subsequent tuning curve amplitude and offset. At the null phase, it reduces the offset while leaving the amplitude minimally affected.

Figure 3 illustrates interocular phase tuning curves before (solid blue) and after adaptation to optimal (dotted green) and null (dashed red) phases for six representative neurons. Results depicted in Figure 3*A–C* are simple cells, and those in Figure 3*D–F* are complex cells. The lines denote the best truncated sine fits to the data (see Materials and Methods), and the bars denote 1 SE. The green and red arrows denote the approximate optimal and null adaptation phases, respectively. Neurons in Figure 3*B–D* show no change in tuning curve amplitude from adaptation at the

null phase. The cells in Figure 3, *A* and *E*, show small attenuations in amplitude due to adaptation at the null phase. In contrast, all neurons exhibit substantial attenuation in tuning curve amplitudes caused by adaptation at the optimal phase. The neurons in Figure 3, *C* and *D*, show a reduction in response offset after adaptation to the null phase, whereas this effect is less for cells in Figure 3, *A* and *E*, and negligible for that in Figure 3*B*. For adaptation at optimal phases, all illustrated neurons exhibit clear reductions in response offset. Data in Figure 3*F* are from one of the five complex cells that are not selective for interocular phase. Adaptation reduces subsequent responses for these cells as shown in Figure 3*F*, but this reduction is most pronounced at interocular phases near that of the adaptation stimulus. These representative neurons illustrate that adaptation at the optimal interocular phase substantially suppresses subsequent responses. In contrast, adaptation at null phases has minimal effects on the strength of the disparity-related responses.

The differences in effects of adaptation at optimal and null interocular phases are clear for most neurons in our population. To further examine these effects, we fit all interocular phase tuning curves for each neuron in our population with a truncated sine function as described in Materials and Methods. Amplitude and offset parameters of the function are used in subsequent comparisons as depicted in Figure 1*D*. Figure 4*A* shows data for comparisons of the interocular phase tuning curve amplitudes between adapted and nonadapted conditions for a population of 28 neurons. The red triangles denote the condition in which adaptation is applied at null interocular phases. The green circles represent optimal interocular phase adaptation. Some neurons were adapted twice, at both the null phase and at the optimal phase (with recovery in-between adaptation), and thus are represented by two points. The filled and unfilled symbols denote simple and complex cells, respectively. For adaptation at the null interocular phase (red triangles), there is minimal change in amplitude as indicated by the close proximity of the symbols to the $Y = X$ line. This comparison shows that adapted amplitude is $\sim 0.87 \pm 0.15$ times that of the nonadapted amplitude. This small attenuation in amplitude may be attributed to a decrease in input to cortical neurons due to limited contrast adaptation in LGN neurons (Ohzawa et al., 1982, 1985; Duong and Freeman, 2007). Similarly, most green circles lie below the $Y = X$ line, indicating that adaptation at the optimal interocular phase (green circles) substantially reduces the amplitude of the interocular phase tuning curve. This comparison shows that the adapted amplitude is $\sim 0.37 \pm 0.12$ times that of the nonadapted condition. These effects are similar for both simple (filled) and complex (unfilled) cells.

Offset values of the interocular phase tuning curves before and after adaptation are examined in Figure 4*B*. Most data points lie below the $Y = X$ line, indicating that adaptation decreases the offset of the interocular phase tuning curves. However, adaptation at optimal phases (green circles) shows more pronounced effects than those at null (red triangles). For this data set, slopes

Figure 3. Adaptation data for six representative neurons. The solid blue, dashed red, and dotted green lines denote interocular phase tuning curves for the nonadapted, adapted at null phase, and adapted at optimal phase conditions, respectively. The red and green arrows denote null and optimal phases, respectively. *A*, *B*, and *C* are simple cells, and *D*, *E*, and *F* are complex cells. Error bars denote ± 1 SE.

for optimal and null conditions are 0.47 ± 0.10 and 0.62 ± 0.07 , respectively.

Some neurons were separately adapted at both the optimal interocular phase and the null interocular phase. Amplitude and offset values following adaptation to optimal (y -axis) and null (x -axis) phases are given, respectively, in Figure 4, *C* and *D*, for 7 simple cells and 13 complex cells. For both amplitude and offset, most data points lie below the unity line, indicating that the effect of adaptation is more pronounced for the optimal compared with the null cases. Best fit lines through these data points have slopes of 0.34 ± 0.12 and 0.73 ± 0.14 for Figure 4, *C* and *D*, respectively. In Figure 4*C*, if the data for simple cells were closer to the $Y = X$ line than those for complex cells, it would indicate that adaptation at the optimal interocular phase would have a more prominent effect on complex compared to simple cells. Although this would be consistent with some previous work (Albrecht et al., 1984; Ohzawa et al., 1985), it does not appear to be the case in the present data. Together, these data demonstrate that adaptation at the optimal phase substantially reduces response rates by diminishing both amplitude and offset of the interocular phase tuning curves. However, adaptation at the null phase reduces the offset of the interocular phase tuning curve but the amplitude is left relatively unchanged. Coding for disparity is captured by the tuning curve amplitude and not the offset (Ohzawa and Freeman, 1986a,b; Ohzawa et al., 1990, 1996, 1997a,b; Smith et al., 1997; Ohzawa, 1998). Therefore, adaptation at the null phase slightly reduces response rate and decreases tuning curve offset but does not change disparity coding characteristics since amplitude is left mainly unchanged.

Adaptation at an intermediate binocular disparity changes binocular depth selectivity

To determine whether adaptation changes the disparity selectivity of neurons, we compare interocular phase preference of neurons before and after adaptation to phases that are intermediate

Figure 4. Adaptation data at optimal and null interocular phases for a population of neurons. **A**, Comparison of interocular phase tuning curve amplitudes before and after adaptation. The green circles and red triangles denote adaptation to the optimal and null phases, respectively. The dashed green and red lines denote corresponding best fits, and the slopes for these lines are 0.87 ± 0.15 and 0.37 ± 0.12 , respectively. **B**, Comparison of the interocular phase tuning curve offset before and after adaptation. The dashed green and red lines denote corresponding best fits, and the slopes for these lines are 0.47 ± 0.10 and 0.62 ± 0.07 , respectively. **C**, Comparison of the interocular phase tuning curve amplitudes for adaptation at the optimal and null phases. The best fit line (dashed) has a slope of 0.34 ± 0.12 . **D**, Comparison of interocular phase tuning curve offsets for adaptation at optimal and null phases. The best fit line (dashed) has a slope of 0.73 ± 0.14 . For all plots, the filled and unfilled symbols denote simple and complex neurons, respectively, and the solid lines denote the $Y = X$ line. Units for all axes are in spikes/second.

between optimal and null. Data from these tests are shown in Figure 5A–C for three representative neurons. The solid blue and dashed red vertical lines denote preferred phase before and after adaptation, respectively. The gray traces depict fits to 30 different Monte Carlo simulations. In the three cases illustrated in A–C, adaptation changes the preferred phase by 132.4, 12.6, and -13.5° , respectively. To examine this effect over a population of neurons, we compare optimal phases before and after adaptation. Changes due to adaptation are emphasized by first translating every tuning curve so that the optimal nonadapted phase is 0. After this translation, the optimal and null phases correspond to 0 and 180° , respectively. Figure 6A shows optimal phase after adaptation as a function of the adaptation point. We omit adaptation data where the adapting phases are between 30 and 330° . This is because adaptation at phases near 0 causes substantial reduction in response, and parameters cannot be reliably estimated. Error bars along the y-axis represent 68.3% confidence intervals around estimated optimal phases after adaptation. Error bars along the x-axis represent the same confidence intervals for the nonadapted case. Red denotes neurons for which the non-adapted and adapted interocular phase tuning preferences are different ($p < 0.05$). Significance testing is performed by calculation of phase parameter confidence intervals generated from Monte Carlo simulations using interocular phase tuning data before and after adaptation. Details of this procedure are de-

Figure 5. Interocular phase tuning curve changes due to adaptation for three representative neurons. The solid blue lines denote fits to nonadapted responses, and the dashed red lines represent fits to adapted responses. The gray traces show fits to 30 different Monte Carlo simulations drawn from the original data set. The red arrows denote interocular phase values used for adaptation. The neurons in **A**, **B**, and **C** are simple cell, complex cell, and complex cell, respectively. The solid blue and dashed red vertical lines denote optimal phases for the non-adapted and adapted conditions, respectively. The shifts in phase for neurons in **A**, **B**, and **C** are 132.4, 12.6, and -13.5° , respectively. Error bars denote ± 1 SE.

scribed in Materials and Methods. The unfilled black arrows denote neurons shown in Figure 5, and the dashed curved line represents a best sine function fit through all data points. Shown in Figure 6B are the mean phase shifts as a function of the adaptation point for 12 different ranges. Error bars represent 1 SE. Variability is pronounced for adapting phases near 0° (or 360°) as expected due to low response rates.

The population data shown in Figure 6 indicate that adaptation points below or above 180° have negative or positive shifts, respectively, in optimal phase. To further quantify this result, we have partitioned the data points into two groups: those with adaptation points $<150^\circ$ or $>210^\circ$. Data points within 30° of 180° are omitted since they show little or no shift in peak due to adaptation. These two groups contain 7 and 12 data points, respectively. The average and SEM of shift in phase due to adaptation for these groups are -17.48 ± 5.90 and 19.07 ± 12.12 , respectively, and these values are significantly different (t test; $p < 0.05$). These data imply that adaptation shifts the optimal or null phases away from or toward the adapting point, respectively.

Figure 6. Adapted tuning curve peak versus adaptation point for a population of neurons. **A** shows the effects of adaptation on the preferred interocular phase for adaptation points $> 30^\circ$ away from the nonadapted preferred phase. Red represents data points demonstrating a statistically significant shift ($p < 0.05$), and black denotes data points with statistically insignificant shifts. Error bars denote a 68.3% confidence interval around the estimated phases. The open arrows in the first and third quadrants point to data for neurons in Figure 5. The dashed black curve denotes a best fit sine function through all data points. Data points near 0 have been omitted because adaptation at these phases generally results in weak responses, and the optimal phase cannot be determined reliably. **B** shows the mean phase shift in degrees as a function of the adaptation point for 12 adaptation point ranges from 0 to 360° . Error bars denote ± 1 SE.

Our data demonstrate two major results. First, adaptation at the optimal phase substantially reduces subsequent tuning curve amplitude and offset. At the null phase, adaptation reduces the offset while leaving amplitude virtually unchanged. Second, for interocular phase values that are intermediate between optimal and null phase values, adaptation causes a shift in peak. The adapted preferred interocular phase is shifted away from that in the nonadapted case. These findings are summarized in the idealized curves of Figure 7A–C. In **A**, three interocular tuning curves are shown. The solid blue line denotes the original non-adapted interocular tuning curve. The effect of adaptation at the optimal interocular phase (dotted green) substantially reduces both the amplitude and the offset of the tuning curve. Adaptation to the null phase (dashed red) only marginally reduces the offset of the tuning curve and leaves the amplitude relatively unchanged as shown in Figure 7A. The nonadapted condition is shown again in Figure 7B (solid blue). Also shown are conditions of adaptation to phases within 180° above (dotted green) or below (dashed red) optimal interocular phase values. These conditions produce changes in optimal phase values that are increased or decreased relative to the nonadapted case, respectively. Figure 7C illustrates a change in peak following adaptation relative to the adapting point as given by the solid curve. If adaptation had no effect on the optimal interocular phase, then the solid curve should lie on the unity line (dashed). However, adaptation generally shifts the peak away from the adapting point. When the optimal phase

Figure 7. Diagram summarizing the effects of adaptation on interocular phase tuning curves. **A**, Adaptation to optimal (dotted) and null (dashed) phases. **B**, Adaptation to phases within 180° above (dotted cyan) or below (dashed magenta) optimal. **C**, Comparison of the interocular phase preference before and after adaptation relative to the adapting point. The dashed line is $Y = X$. The solid black curve denotes the preferred phase before and after adaptation.

before adaptation is less than that of the adapting point, the optimal phase is decreased. Similarly, when optimal phase before adaptation is greater than the adapting point, adaptation increases the optimal phase. This is illustrated in Figure 7C by the observation that the solid line lies below the $y = x$ unity line for points between -180 and 0° , and above it for points between 0 and 180° .

Predictions from the binocular energy model

The adaptation findings reported here are relevant to the standard binocular energy model. To examine this, we compare our adaptation results to predictions of a toy hierarchical binocular energy model as illustrated in Figure 8A. This model consists of three processing stages. In the first stage, LGN afferents converge to monocular simple cells creating receptive fields that are selective for stimulus orientation. Monocular simple cells that respond to left or right eye stimulation converge to create binocular simple cells. Spatial phase differences between left and right mon-

Figure 8. Binocular energy model. **A**, Simple schematic of a variant of the energy model. LGN neurons generate orientation selective monocular simple cells. These monocular simple cells (MS) converge to create binocular simple cells (BS). Binocular simple cells at different phase disparities converge to create binocular complex cells (BC). **B** shows the spatial receptive fields of left monocular (solid) and right monocular (dashed) neurons. The phase preferences for these neurons are 90° apart. **C** shows response predictions of the binocular energy model as a function of interocular phase for a binocular simple cell. Black denotes nonadapted response. Red, blue, and green denote adaptation at the null, intermediate, and optimal phases, respectively. The amplitudes for these response functions are 1.3, 0.39, 0.30, and 0.22, respectively. Details of this simulation are given in Materials and Methods. **D** illustrates effects of adaptation on the population response to stimuli near the adapting phase. The solid blue lines denote response before adaptation, and the dotted green lines denote response after adaptation. The vertical lines illustrate peaks of the population response curves. The unfilled red and black arrows denote adapting and stimulating phases, respectively.

ocular receptive fields determine disparity preference of the resulting binocular simple cell. Binocular complex cells are generated from convergence of spatially out-of-phase binocular simple cells. Additional details of this model have been described in previous studies (Ohzawa et al., 1990; Ohzawa, 1998; Read and Cumming, 2003). In addition, we describe the quantitative stages of the model along with our simulation results for simple cells in Materials and Methods. Here, we compare the predictions of the model against our data with respect to adaptation at the optimal, null, and intermediate phases.

First, we examine the binocular energy model with respect to adaptation at the optimal and null phases. Since the first cortical stage in the model consists of monocular simple cells (Fig. 8A, MS) that are susceptible to visual adaptation (Movshon and Lennie, 1979; Ohzawa et al., 1982, 1985; Albrecht et al., 1984; Müller et al., 1999; Dragoi et al., 2000, 2001; Read and Cumming, 2003), the effects of adaptation at this stage are not dependent on interocular phase, but they are robust (Movshon and Lennie, 1979; Ohzawa et al., 1982, 1985; Albrecht et al., 1984; Müller et al., 1999; Dragoi et al., 2000, 2001). Because these monocular simple cells show substantial adaptation that does not depend on interocular phase, their responses should be greatly reduced after adaptation to the null phase. A reduction in responses of the monocular simple cells, which represent the first processing stage in the

model, should cause a large decrease in offset and amplitude of the response of subsequent binocular neurons. Contrary to the model, we do not observe a large reduction in response amplitude after adaptation to the null phase. This is apparent in Figure 4A in which the red data points lie near the line $y = 0.86x$, which means that the adapted response amplitude is 86% of that for the non-adapted condition. However, as described in Materials and Methods and illustrated in Figure 8C, the energy model predicts that the adapted amplitude is $\sim 30\%$ of the nonadapted amplitude. Furthermore, we observe a large decrease in tuning curve amplitude after adaptation to the optimal phase. This decrease of $\sim 70\%$ is approximately twice that for adaptation to the null phase. These observations are illustrated in Figure 4, A and C. The binocular energy model with the addition of neural fatigue only predicts $\sim 25\%$ more reduction for adaptation at the optimal compared with the null phase. This is demonstrated by Figure 8C and in Materials and Methods. These results illustrate a clear discrepancy between the energy model prediction and our experimental data.

There is also a problem with the binocular energy model with respect to adaptation at an intermediate phase. As demonstrated in Figures 5 and 6, disparity selective neurons exhibit a lateral shift in tuning after adaptation to gratings at intermediate interocular phases. This property cannot be explained by a standard feedforward binocular energy model. As illustrated in Figure 8C, a simple addition of neural fatigue at various stages in the binocular energy model would create suppression after adaptation, but this would be uniform across all test phases. We conclude, therefore, that simple modifications (e.g., by adding neural fatigue) to the binocular energy model do not account for the data presented here.

Discussion

Selectivity of neurons in the primary visual cortex changes that following adaptation to specific visual stimuli. This property has been demonstrated for various parameters of visual stimuli including orientation, spatial frequency, direction of motion, and spatial position (Movshon and Lennie, 1979; Marlin et al., 1988, 1991, 1993; Saul and Cynader, 1989a,b; Müller et al., 1999; Dragoi et al., 2000, 2001). In the current study, we show that adaptation effects are also exhibited in the binocular disparity domain. Changes in neuronal disparity selectivity caused by adaptation have important consequences regarding the coding of stereoscopic depth. First, a change in disparity selectivity with adaptation as we have demonstrated is not consistent with the widely accepted hierarchical binocular energy model and suggests that recurrent corticocortical connectivity may play a substantial role in shaping disparity selectivity in primary visual cortex. Second, this neurophysiological phenomenon may affect various perceptual adaptation findings on contrast detection and depth discrimination. Third, short-term reversible adaptation in disparity may serve as a first step for long-term disparity plasticity and perceptual disparity learning processes. Finally, the changes in preferred disparity that accompany adaptation may yield advantages in the neuronal coding of stereoscopic depth. In particular, this process may conserve energy by optimally coding depth information with a sparse discharge rate (Attwell and Laughlin, 2001; Lennie, 2003).

The binocular energy model is currently accepted as a standard by which the primary visual cortex encodes and processes depth information. This elegant model consists of three processing stages: the first level is that of monocular simple cells; the second, binocular simple cells; and the third is binocular complex

cells. Minor adjustments and extensions of this model have been put forward to quantitatively explain some of the observed behavior of binocular neurons in the primary visual cortex (Read et al., 2002; Read and Cumming, 2003, 2004). However, these extensions maintain a serial processing paradigm.

The binocular energy model cannot explain several properties demonstrated by our experimental data. First, adaptation at a null phase has virtually no effect on the subsequent disparity-related response. Second, adaptation at the optimal phase reduces response substantially more than that at the null phase. Finally, adaptation at an intermediate phase changes the optimal phase value. The first two properties can be explained with a minor modification to the energy model. The modification is that binocular simple cells with different degrees of phase selectivity are created directly from LGN input, instead of from monocular simple neurons. In this case, the binocular energy model can be altered by removal of the monocular simple cell stage such that all cortical neurons would exhibit some degree of interocular phase selectivity. This revision is consistent with our current data and previous observations regarding relative interocular phase selectivity of cortical neurons. We note that almost no simple cells are entirely monocular when dichoptic tests are used (Freeman and Robson, 1982; Ohzawa and Freeman, 1986a,b). In a revised model, adaptation at the null phase would suppress subsequent responses, but only to the extent that adaptation suppresses LGN neurons. Adaptation at the null phase would only minimally affect responses from LGN neurons (Ohzawa et al., 1985; Duong and Freeman, 2007), which are not selective for binocular disparity. Adaptation at the optimal interocular phases, however, would still show substantial reductions in response levels. This model revision would explain the data we show here in Figures 3 and 4. However, an additional mechanism is still required to account for the third property (i.e., preferred phase changes following adaptation to an intermediate phase as illustrated in Figures 5 and 6). It is possible that a dendritic or recurrent model of disparity computation can account for our adaptation data (Archie and Mel, 2000). A more plausible explanation may be that this disparity-specific adaptation arises from a combination of intracortical tonic hyperpolarization processes (Sanchez-Vives et al., 2000a,b), suppression, and plasticity at corticocortical synapses (Ferster and Lindström, 1985; Stratford et al., 1996; Chung et al., 2002).

The specificity of adaptation to disparity at a single-neuron level in primary visual cortex, as we report here, may have substantial consequences for visual perception. First, the selective effect of phase tuning amplitude attenuation on neurons that prefer phases near that of the adapter, as shown in Figures 3, 4, and 7A, may have two perceptual consequences. First, elevations of contrast detection thresholds, due to adaptation to binocular gratings, may be confined to disparities near that of the adapter. This is consistent with previous behavioral studies in human subjects (Blakemore and Hague, 1972; Stevenson et al., 1992; Cormack et al., 1993). Second, adaptation may cause a perceptual aftereffect in depth in which perceived depth after adaptation is shifted away from the adapting plane, which is also consistent with previous behavioral results (Blakemore and Julesz, 1971). Furthermore, much like the orientation domain, changes in tuning peaks with adaptation, as shown in Figures 5, 6, and 7B, may serve to alleviate the artifacts of depth aftereffects (Jin et al., 2005). Finally, depth-specific adaptation at a single-neuron level, as we report here, suggests that the neural population activated by stimuli near an adapter changes following adaptation. This idea is illustrated by the diagram in Figure 8D. Position along the hori-

zontal axis indicates optimal interocular phase for a population of neurons. The solid blue curves denote the total nonadapted response to stimuli with interocular phases indicated by the open black arrows. The dotted curves (green) denote the population response to the same stimuli following adaptation to a stimulus with an interocular phase indicated by the open red arrow. The vertical lines illustrate the peaks of these responses. Clearly, the peaks are separated by a greater amount following adaptation, as illustrated by the difference between the dotted green and the solid blue vertical lines. These results therefore predict that depth discrimination sensitivity following adaptation to a fixed disparity is increased near the adapting level. This specific prediction has apparently not been tested. However, a similar result has been reported in the orientation domain (Regan and Beverley, 1985).

Finally, since contrast adaptation has the undesirable effect of elevating contrast detection threshold near the adapting level (Blakemore and Campbell, 1969b; Blakemore and Hague, 1972; Stevenson et al., 1992; Cormack et al., 1993), it is worth considering possible benefits of adaptation in visual processing. First, a reduction in response following sustained stimulation by a given pattern is desirable in that it decreases the required energy expenditure. This is due to a reduction of total spike rates (Attwell and Laughlin, 2001; Lennie, 2003). Second, non-pattern-specific adaptation due to membrane hyperpolarization provides a mechanism for decorrelation of the visual stimulus in the temporal domain (Wang et al., 2003). This allows neurons to encode a visual scene with relative efficiency. Third, changes in tuning curves due to adaptation of different stimulus dimensions may act to decorrelate the specific variables being studied. This type of phenomenon has been demonstrated in the orientation domain (Müller et al., 1999) and, in our current study, for stereoscopic disparity processing. Finally, we observe that adaptation at the null interocular phase, as depicted in Figure 3, A and B, decreases the offset of the interocular phase, but leaves the amplitude virtually unchanged. This effect decreases spike rates to conserve energy without changing the interocular phase amplitude, which represents disparity coding properties of binocular neurons. Therefore, although adaptation has some apparently undesirable effects such as elevation in contrast detection thresholds, it may serve to reduce energy expenditure by decreasing the numbers of action potentials that are needed to convey information (Attwell and Laughlin, 2001; Lennie, 2003) and by increasing the sensitivity for patterns near those of the adapter (Regan and Beverley, 1985).

References

- Adelson EH, Bergen JR (1985) Spatiotemporal energy models for the perception of motion. *J Opt Soc Am A* 2:284–299.
- Albrecht DG, Farrar SB, Hamilton DB (1984) Spatial contrast adaptation characteristics of neurones recorded in the cat's visual cortex. *J Physiol* 347:713–739.
- Anzai A, Ohzawa I, Freeman RD (1997) Neural mechanisms underlying binocular fusion and stereopsis: position vs. phase. *Proc Natl Acad Sci U S A* 94:5438–5443.
- Archie KA, Mel BW (2000) A model for intradendritic computation of binocular disparity. *Nat Neurosci* 3:54–63.
- Attwell D, Laughlin SB (2001) An energy budget for signaling in the grey matter of the brain. *J Cereb Blood Flow Metab* 21:1133–1145.
- Blakemore C, Campbell FW (1969a) Adaptation to spatial stimuli. *J Physiol* 200:11P–13P.
- Blakemore C, Campbell FW (1969b) On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J Physiol* 203:237–260.
- Blakemore C, Hague B (1972) Evidence for disparity detecting neurones in the human visual system. *J Physiol* 225:437–455.

- Blakemore C, Julesz B (1971) Stereoscopic depth aftereffect produced without monocular cues. *Science* 171:286–288.
- Carandini M, Ferster D (1997) A tonic hyperpolarization underlying contrast adaptation in cat visual cortex. *Science* 276:949–952.
- Chino YM, Smith EL 3rd, Yoshida K, Cheng H, Hamamoto J (1994) Binocular interactions in striate cortical neurons of cats reared with discordant visual inputs. *J Neurosci* 14:5050–5067.
- Chung S, Li X, Nelson SB (2002) Short-term depression at thalamocortical synapses contributes to rapid adaptation of cortical sensory responses in vivo. *Neuron* 34:437–446.
- Cormack LK, Stevenson SB, Schor CM (1993) Disparity-tuned channels of the human visual system. *Vis Neurosci* 10:585–596.
- Dragoi V, Sharma J, Sur M (2000) Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron* 28:287–298.
- Dragoi V, Rivadulla C, Sur M (2001) Foci of orientation plasticity in visual cortex. *Nature* 411:80–86.
- Duong T, Freeman RD (2007) Spatial frequency-specific contrast adaptation originates in the primary visual cortex. *J Neurophysiol* 98:187–195.
- Efron B (1982) The jackknife, the bootstrap, and other resampling plans. Philadelphia: Society for Industrial and Applied Mathematics.
- Felsen G, Shen YS, Yao H, Spor G, Li C, Dan Y (2002) Dynamic modification of cortical orientation tuning mediated by recurrent connections. *Neuron* 36:945–954.
- Ferster D, Lindström S (1985) Synaptic excitation of neurones in area 17 of the cat by intracortical axon collaterals of cortico-geniculate cells. *J Physiol* 367:233–252.
- Freeman RD, Ohzawa I (1990) On the neurophysiological organization of binocular vision. *Vision Res* 30:1661–1676.
- Freeman RD, Robson JG (1982) A new approach to the study of binocular interaction in visual cortex: normal and monocularly deprived cats. *Exp Brain Res* 48:296–300.
- Horsley V, Clarke RH (1906) The structure and functions of the cerebellum examined by a new method. *Brain* 31:45–124.
- Hubel DH, Wiesel TN (1959) Receptive fields of single neurones in the cat's striate cortex. *J Physiol* 148:574–591.
- Hubel DH, Wiesel TN (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J Physiol* 160:106–154.
- Jin DZ, Dragoi V, Sur M, Seung HS (2005) Tilt aftereffect and adaptation-induced changes in orientation tuning in visual cortex. *J Neurophysiol* 94:4038–4050.
- Lennie P (2003) The cost of cortical computation. *Curr Biol* 13:493–497.
- Marlin SG, Hasan SJ, Cynader MS (1988) Direction-selective adaptation in simple and complex cells in cat striate cortex. *J Neurophysiol* 59:1314–1330.
- Marlin SG, Douglas RM, Cynader MS (1991) Position-specific adaptation in simple cell receptive fields of the cat striate cortex. *J Neurophysiol* 66:1769–1784.
- Marlin S, Douglas R, Cynader M (1993) Position-specific adaptation in complex cell receptive fields of the cat striate cortex. *J Neurophysiol* 69:2209–2221.
- Movshon JA, Lennie P (1979) Pattern-selective adaptation in visual cortical neurones. *Nature* 278:850–852.
- Müller JR, Metha AB, Krauskopf J, Lennie P (1999) Rapid adaptation in visual cortex to the structure of images. *Science* 285:1405–1408.
- Nelder JA, Mead R (1965) A simplex method for function minimization. *Comput J* 7:308–313.
- Ohzawa I (1998) Mechanisms of stereoscopic vision: the disparity energy model. *Curr Opin Neurobiol* 8:509–515.
- Ohzawa I, Freeman RD (1986a) The binocular organization of simple cells in the cat's visual cortex. *J Neurophysiol* 56:221–242.
- Ohzawa I, Freeman RD (1986b) The binocular organization of complex cells in the cat's visual cortex. *J Neurophysiol* 56:243–259.
- Ohzawa I, Sclar G, Freeman RD (1982) Contrast gain control in the cat visual cortex. *Nature* 298:266–268.
- Ohzawa I, Sclar G, Freeman RD (1985) Contrast gain control in the cat's visual system. *J Neurophysiol* 54:651–667.
- Ohzawa I, DeAngelis GC, Freeman RD (1990) Stereoscopic depth discrimination in the visual cortex: neurons ideally suited as disparity detectors. *Science* 249:1037–1041.
- Ohzawa I, DeAngelis GC, Freeman RD (1996) Encoding of binocular disparity by simple cells in the cat's visual cortex. *J Neurophysiol* 75:1779–1805.
- Ohzawa I, DeAngelis GC, Freeman RD (1997a) The neural coding of stereoscopic depth. *Neuroreport* 8:iii–xii.
- Ohzawa I, DeAngelis GC, Freeman RD (1997b) Encoding of binocular disparity by complex cells in the cat's visual cortex. *J Neurophysiol* 77:2879–2909.
- Press WH, Numerical Recipes Software (Firm) (1993) Numerical recipes in C, Ed 2, Vol 2.0. Cambridge, UK: Cambridge UP.
- Read JC, Cumming BG (2003) Testing quantitative models of binocular disparity selectivity in primary visual cortex. *J Neurophysiol* 90:2795–2817.
- Read JC, Cumming BG (2004) Understanding the cortical specialization for horizontal disparity. *Neural Comput* 16:1983–2020.
- Read JC, Parker AJ, Cumming BG (2002) A simple model accounts for the response of disparity-tuned V1 neurons to anticorrelated images. *Vis Neurosci* 19:735–753.
- Regan D, Beverley KI (1985) Postadaptation orientation discrimination. *J Opt Soc Am A* 2:147–155.
- Sanchez-Vives MV, Nowak LG, McCormick DA (2000a) Membrane mechanisms underlying contrast adaptation in cat area 17 *in vivo*. *J Neurosci* 20:4267–4285.
- Sanchez-Vives MV, Nowak LG, McCormick DA (2000b) Cellular mechanisms of long-lasting adaptation in visual cortical neurons *in vitro*. *J Neurosci* 20:4286–4299.
- Saul AB, Cynader MS (1989a) Adaptation in single units in visual cortex: the tuning of aftereffects in the spatial domain. *Vis Neurosci* 2:593–607.
- Saul AB, Cynader MS (1989b) Adaptation in single units in visual cortex: the tuning of aftereffects in the temporal domain. *Vis Neurosci* 2:609–620.
- Skottun BC, De Valois RL, Grosof DH, Movshon JA, Albrecht DG, Bonds AB (1991) Classifying simple and complex cells on the basis of response modulation. *Vision Res* 31:1079–1086.
- Smith EL 3rd, Chino YM, Ni J, Ridder WH 3rd, Crawford ML (1997) Binocular spatial phase tuning characteristics of neurons in the macaque striate cortex. *J Neurophysiol* 78:351–365.
- Stevenson SB, Cormack LK, Schor CM, Tyler CW (1992) Disparity tuning in mechanisms of human stereopsis. *Vision Res* 32:1685–1694.
- Stratford KJ, Tarczy-Hornoch K, Martin KA, Bannister NJ, Jack JJ (1996) Excitatory synaptic inputs to spiny stellate cells in cat visual cortex. *Nature* 382:258–261.
- Wang XJ, Liu Y, Sanchez-Vives MV, McCormick DA (2003) Adaptation and temporal decorrelation by single neurons in the primary visual cortex. *J Neurophysiol* 89:3279–3293.