# The tilt aftereffect and adaptation-induced changes in orientation tuning in visual cortex

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### Abstract

The tilt aftereffect (TAE) is a visual illusion in which prolonged adaptation to an oriented stimulus causes shifts in the perceptions of subsequent stimuli. Historically, the TAE has been attributed to response suppression of neurons tuned to the adapting orientation. Recent physiological studies of neurons in primary visual cortex (V1) have identified two effects of adaptation: a response suppression at the adapting orientation as well as a shift in the preferred orientations of neurons away from the adapting orientation. Here we construct a population coding model in V1 that includes both factors, and show that both are necessary for quantitatively explaining the TAE. The model suggests that the orientation shifts counteract the response suppression to keep the perceptual errors in orientation small after adaptation.

## Introduction

The tilt aftereffect (TAE) is a striking visual illusion in which prolonged adaptation to an oriented visual stimulus causes subsequent stimuli to appear rotated away from the adapting orientation (Gibson and Radner 1937; He and MacLeod 2001; Magnussen and Johnsen 1986; Mitchell and Muir 1976). Explaining this and other aftereffects in terms of neural mechanisms has been an important outstanding problem. Historically, a popular explanation of the TAE has been a hypothesized relative suppression of neurons tuned to the adapting orientation (Clifford et al. 2000; Coltheart 1971; Sutherland 1961; Wainwright 1999). Recent physiological studies have confirmed that adaptation leads to suppression of neural responses near the adapting orientation. These experiments have also identified an additional effect of adaptation: the preferred orientations of neurons repulsively shift away from the adapting orientation (Dragoi et al. 2001; Dragoi et al. 2000). Here we construct a population coding model that includes both factors, and show that the repulsive shifts of preferred orientations are necessary for quantitatively explaining the TAE. According to the model, the TAE is indeed caused by the relative suppression of neural responses. However, it is substantially weakened by the preferred orientation shifts. We suggest that the visual system uses the repulsive shifts of preferred orientations to reduce the perceptual error in orientation that could be induced by neural response suppression.

Quantitative measurements of the TAE are schematically summarized in the graph of Figure 1a, which depicts the difference between the perceived and true orientation of a test stimulus as a function of the difference between the test and adapting orientations. According to this graph, the perceived orientation is similar to the true orientation, but rotated away from the adapting orientation by up to 4 degrees (Clifford et al. 2000; Gibson and Radner 1937; Magnussen and Johnsen 1986; Mitchell and Muir 1976). That is, the adapting orientation "repels" the perceived orientation. Neurons in the primary visual cortex (V1) respond selectively to the orientation of a stimulus (Hubel and Wiesel 1962). Orientation selectivity is generally characterized by a tuning curve depicting the firing rate of a neuron as a function of stimulus angle. Two major changes in tuning curves of V1 neurons are observed after adaptation, particularly when the adapting orientation is close to a cell's preferred orientation (Dragoi et al. 2000)(Figure 1b). First, the amplitude of the tuning curve on the flank near the adapting orientation depresses after adaptation; this is often accompanied by an increase in response amplitude on the opposite or far flank. Second, the location of the peak response, or preferred orientation of the cell, shifts away from the adapting orientation, so that the effect is "repulsive". The amount of the shift depends on the difference between the preferred and the adapting orientations, and can be up to 9 degrees (Dragoi et al. 2000)(Figure 1b).

To show that the adaptation-induced changes of the tuning curves of V1 neurons are quantitatively consistent with the TAE, we mathematically analyze a population coding model. Similar to previous models (Clifford et al. 2000; Gilbert and Wiesel 1990; Pouget et al. 2000; Vogels 1990; Wainwright 1999), our model assumes that the population response profile of V1 neurons to a stimulus determines its perceived orientation. The analysis unveils a quantitative relationship between adaptation-induced changes of the perceived orientations and those of the tuning curves<u>: The amplitude</u> suppression of the tuning curves near the adapting orientation is positively correlated with the sum of the repulsive shifts of perceived orientations and the preferred orientations of neurons. We use this quantitative relationship to check the consistency between the psychophysical and physiological data. From the measured amount of the TAE and the shift of the preferred orientations, we predict the response suppression of the tuning curves near the adapting orientation is then compared with the observed response suppression. The results confirm that the TAE is quantitatively consistent with the measured changes of tuning curves of V1 neurons under adaptation.

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The relationship further illustrates that, for a given response suppression, the repulsive shift of the preferred orientation reduces the amount of the TAE, and hence the perception error.

## Methods

#### **Experimental data**

In this paper we use data from physiological and psychophysical experiments documented previously. Here we briefly describe these experiments. In the physiological experiments (Dragoi et al. 2000), the orientation tuning curves of neurons in V1 of anesthetized cats were measured by presenting high contrast square wave drifting gratings at 16 orientations (equally spaced at 22.5 degrees), and recording the spike trains. The gratings had a spatial frequency of 0.5 cycle/degree, and temporal frequency of 1 Hz. Before adaptation, each orientation was presented for 10 trials, with each trial lasting 2.5 seconds. Neuron spike rates were averaged over trials for each orientation. Adaptation was induced by presenting a drifting grating at the adapting orientation for 2 minutes. After adaptation, each of the 16 orientations was presented for 112 trials, with each trial lasting 2.5 seconds, preceded by a 5 second presentation of the adapting orientation in order to maintain the effects of adaptation.

In the psychophysical experiments that measured the TAE (Clifford et al. 2003; Clifford et al. 2000), human subjects were presented with <u>contrast reversing</u>, <u>stationary</u> sinusoidal gratings with spatial frequency 1 cycle/degree and temporal frequency 1 Hz. The TAE was measured using adapting stimuli at 6 orientations of equal spacing of 15 degrees. Each adapting stimulus was presented for 1 minute. After adaptation, the perceived vertical orientation was measured using test stimuli with orientations progressively closer to the subjects' judgment of vertical orientation. Each testing stimulus lasted 400 msec followed by a 5 second presentation of the adapting stimulus to maintain the effects of adaptation. The test stimuli were presented for 60 trials. The difference between the true and perceived vertical orientation was the TAE.

#### The model

The central feature of our model is the rate function, which is a compact description of the tuning curves of the neuronal population. Our goal is to show how the activity of the neuron population, as defined by the rate function, changes as a result of the response suppression and orientation shift of tuning curves. We describe three different procedures for calculating through the rate function the relationship between the changes of the tuning curves and those of population responses, and illustrate our results in detail with one method, the winner-take-all method. We then show that the other two methods, the population vector method and the maximum likelihood method, lead to similar results.

#### Results

Orientation perception is commonly presumed to arise from the population responses of V1 neurons to oriented stimuli (Clifford et al. 2000; Gilbert and Wiesel 1990; Pouget et al. 2000; Vogels 1990; Wainwright 1999). From this point of view, it is easy to see how adaptation-induced changes of the tuning curves of V1 neurons lead to errors in orientation perception, since such changes alter the population response profiles of V1 neurons. Thus, the neural basis of the TAE is simple to grasp qualitatively. However, it is not obvious that the specific changes of tuning curves observed in the physiological experiments (Dragoi et al. 2000) are quantitatively compatible with the TAE. The experiments show that the preferred orientations of neurons shift away from the

adapting orientation; moreover, maximum firing rates are reduced especially for neurons with preferred orientations near the adapting orientation. Do these changes lead to shifts of the perceived orientation away from the adapting orientation, as in the TAE? Moreover, are the amounts of change of tuning curves consistent with the magnitude of perception shifts in the TAE? We address these questions by mathematically analyzing the relationship between the changes of tuning curves and those of orientation perception in a population coding model.

To do this, two issues about population coding models must be addressed. The first issue concerns the diversity of orientation tuning properties of V1 neurons. Tuning curves of V1 neurons, even for those with the same preferred orientations, may have quite different widths and maximum rates (Hubel and Wiesel 1962). Such diversity makes our mathematical analysis difficult. We overcome this difficulty by replacing all neurons of the same preferred orientation with a single "representative neuron". The tuning curve of this single neuron is the average of those of the neurons with the same preferred orientation. Thus, in our population coding model, there is one neuron for each preferred orientation. Before adaptation, the tuning curves of all neurons have the same Gaussian shape. Each neuron is labeled with its preferred orientation in the unadapted state. After adaptation, the tuning curves remain Gaussian; however, the preferred orientations may shift from the neuron labels. Moreover, the amplitudes and the widths of the tuning curves may change as well.

The second issue concerns how the rest of the brain "reads out" orientation from V1 neuron responses. This is not a settled matter in population coding models in general (Pouget et al. 2000). Among many possible proposals, three methods are commonly used in the literature: the winner-take-all, the population vector, and the maximum likelihood methods. In the winner-take-all method, the perceived orientation is set to the label of the neuron that fires maximally to the stimulus. In the population vector method

(Georgopoulos et al. 1982; Gilbert and Wiesel 1990; Vogels 1990), each neuron contributes a two-dimensional vector with orientation equal to twice of its label and length equal to its firing rate; summation of these vectors results in a population vector, whose orientation is taken as twice of the perceived orientation. In the maximum likelihood method (Paradiso 1988; Pouget et al. 2000), each perceived orientation is associated with a predetermined template of population responses. These templates are compared to the population response to a stimulus, and the one that best matches determines the perceived orientation. In our analysis of the neural basis of the TAE, we use all three methods, and show that they lead to similar results. The winner-take-all method is the simplest, and is amenable to mathematical analysis; we therefore explain our results mostly in terms of this readout method. The results from the other two methods are presented later and compared.

We first define symbols and functions that are useful for our analysis. Each neuron in the population has a label, which is its preferred orientation  $\psi$  in the unadapted state. It should be emphasized that  $\psi$  is an invariant label. After adaptation, the label of each neuron remains the same as before adaptation, even though its preferred orientation may change substantially. The *rate function*  $F(\psi, \phi)$  is defined as the firing rate of neuron  $\psi$  to a stimulus with orientation  $\phi$ . Note that the two Greek letters are mnemonic. Since the orientation of the stimulus is a "physical" quantity, it is denoted by the letter  $\phi$  ("phi"). The label of a neuron is a "psychic" quantity, so it is denoted by the letter  $\psi$  ("psi"). When considered as a function of the stimulus orientation  $\phi$  only, F is the tuning curve of the neuron with label  $\psi$ . When considered as a function of the neuron label  $\psi$  only, F is the population response to a stimulus with orientation  $\phi$ . Therefore the rate function F is a complete description of both population responses and tuning curves. The rate function can be visualized with a threedimensional graph of firing rate versus neuron label and stimulus orientation (Figure 2). Two curves on the surface of the rate function are convenient to define. The first is the *perception line*  $\psi_p(\phi)$ , which marks the perceived orientation of stimulus  $\phi$ . In the winner-take-all method,  $\psi_p(\phi)$  is computed by maximizing the rate function  $F(\psi, \phi)$  with respect to the neuron label  $\psi$  for fixed stimulus orientation  $\phi$ . The second is the *neuron line*  $\phi_n(\psi)$ , which marks the preferred orientation of neuron  $\psi$ , and is the maximum of the rate function  $F(\psi, \phi)$  with respect to the stimulus orientation  $\phi$  for fixed neuron label  $\psi$ . Before adaptation,  $\phi_n(\psi)$  is equal to  $\psi$ , but it may shift after adaptation.

Figure 2 illustrates the relationship between the rate function (left) and the neuron and perception lines (right) in various situations. Both population responses (blue) and tuning curves (red) are shown in the left graphs. The maxima of the blue curves in the left graph define the perception line, which is plotted on the right in blue as a graph of  $\psi_p(\phi)$  versus  $\phi$ . The maxima of the red curves in the left graph define the neuron line, which is plotted on the right as a graph of  $\psi_p(\phi)$  versus  $\phi$ .

Figure 2a shows the rate function before adaptation, which looks like a ridge that is diagonally oriented in the  $\psi - \phi$  plane (Figure 2a, left). The perception and neuron lines coincide exactly at the top of the ridge, which means that perceived orientations are the same as true orientations. When the lines are plotted in two dimensions, they both lie along the diagonal (Figure 2a, right).

The rest of Figure 2 illustrates the rate function after adaptation. According to experimental data from neural recordings in V1, tuning curves adapt in two ways. First, the preferred orientations of the tuning curves shift. Second, the amplitudes of the tuning curves are suppressed for neurons with labels close to the adapting orientation (Dragoi et al. 2000). It is helpful to first examine the hypothetical cases of each change happening in isolation (Figures 2b and 2c). Then we will proceed to the realistic case of both changes happening simultaneously (Figure 2d). Without loss of generality, it will be assumed that the adapting stimulus is oriented at 0 degrees.

In Figure 2b, the preferred orientations shift after adaptation, with no change in tuning curve amplitudes. In the rate function on the left, the preferred orientations are the maxima of the red curves. The neuron line (preferred orientation  $\phi$  versus neuron label  $\psi$ ) is plotted on the right (red). It is shifted away from the diagonal. The shift vanishes at 0 and 90 degrees, and is maximal at an intermediate orientation. Similar shifts are observed experimentally in V1 neurons after adaptation (Dragoi et al. 2000). Because the height of the ridge is constant, the maxima of the blue curves lie along the same line as the maxima of the red curves. Consequently the perception line (blue) coincides with the neuron line; both are identically shifted away from the diagonal. The shift in the neuron line is repulsive ( $\phi_n(\psi) > \psi$ ), while the shift in the perception line is attractive ( $\psi_p(\phi) < \phi$ ).

In Figure 2c, the tuning curve amplitudes are suppressed for neurons tuned near the adapting orientation, causing the ridge of the rate function to be depressed near the origin. But there is no shift in preferred orientations, so the neuron line lies along the diagonal, as in the unadapted state of Figure 2a. Because of the lowered ridge height, the maxima of the blue curves shift away from the diagonal. As shown on the right, the perception line shifts repulsively ( $\psi_p(\phi) > \phi$ ). In other words, suppression alone can induce repulsive shifts of perception. Indeed, this was the mechanism of the TAE in previous models (Clifford et al. 2000; Coltheart 1971; Sutherland 1961; Wainwright 1999).

To summarize, Figure 2c shows that suppression of tuning curve amplitudes produces a repulsive shift in the perceived orientation, as observed in the TAE. Figure 2b shows that a repulsive shift of preferred orientations leads to an attractive shift in the perceived orientation, contrary to the observed TAE. In other words, suppression and repulsive shift of tuning curves have antagonistic effects on the perceived orientation

Figure 2d illustrates the effect of combining both suppression and shift, which corresponds to what is observed experimentally in V1. The neuron and perception lines both shift repulsively. To produce the same perceptual shift as in Figure 2c, a stronger suppression of the ridge near the origin is necessary to produce the repulsive shift of the preferred orientation (compare to the rate function of Figure 2c). The stronger amplitude suppression counteracts the weakening effect of the repulsive shift of the preferred orientation on the TAE.

In Figures 2b, the neuron and perception lines coincided exactly, and there was no change in the tuning curve amplitudes. In Figures 2c and 2d, there was a separation between the neuron and perception lines, and the tuning curve amplitudes were suppressed near the origin. Figure 3 presents a graphical "proof" that separation between the neuron and perception lines is necessarily accompanied by suppression of tuning curve amplitudes. Consider a path that travels from the red neuron line (point 1) to the blue perception line (point 2) back to the red neuron line (point 3). We will prove that the rate function is larger at point 1 than at point 3. The vertical path from 1 to 2 travels along the  $\phi$  direction, and therefore traces out the tuning curve of some neuron, which is graphed to the right of the box. Because 1 is on the neuron line, it corresponds to the maximum of the tuning curve. Therefore the rate function at 1 is larger than at 2. The horizontal path from 2 to 3 travels along the  $\psi$  direction, and therefore traces out the population response for some orientation, which is graphed above the box. Because 2 is on the perception line, it corresponds to the maximum of the population response. Therefore the rate function is larger at 2 than at 3. It follows that the rate function at 1 is larger than at 3. This downhill path can be continued, alternating between the neuron

and perception lines, proving that tuning curve amplitudes are suppressed near the origin.

The arguments of Figure 3 can be made quantitative. The general idea is to specify the neuron and perception lines, and then derive the amount of amplitude suppression that is required. This calculation can be done by modeling the rate function as

$$F(\psi,\phi) = A(\psi) \exp\left(-\frac{(\phi - \phi_n(\psi))^2}{2\sigma(\psi)^2}\right).$$
(1.1)

Here the tuning curve of neuron  $\psi$  is Gaussian with amplitude  $A(\psi)$ , width  $\sigma(\psi)$ , and preferred orientation  $\phi_n(\psi)$ . The functions  $\phi_n(\psi)$  and  $\sigma(\psi)$  are determined by neural data, while the perception line  $\psi_p(\phi)$  is determined by TAE data. From Eq. (1.1) it follows that (see Appendix for derivation):

$$A(\psi) = \exp\left(\int_{0}^{\psi} d\psi' \frac{\left(\phi_n(\psi') - \psi_p^{-1}(\psi')\right)}{\sigma(\psi')^2} \left(\frac{d\phi_n(\psi')}{d\psi'} - \frac{\left(\phi_n(\psi') - \psi_p^{-1}(\psi')\right)}{\sigma(\psi')}\frac{d\sigma(\psi')}{d\psi'}\right)\right) (1.2)$$

Here  $\psi_p^{-1}(\cdot)$  is the inverse function of the perception line. The formula allows the possibility that the widths of tuning curves vary for different neurons. The adapting orientation is at 0. This formula was used to construct Figure 2. It will also be used in the remainder of this paper, which will quantitatively compare this "predicted" amplitude from the model with the tuning curve amplitudes measured experimentally in <u>V1 neurons</u>.

<u>To further simplify Eq. (1.2), two approximations are helpful.</u> First, the tuning curves of different neurons are assumed to have the same width, <u>though this width may</u> <u>change after adaptation</u>. Second, the neuron and perception lines are approximated as

piecewise linear. The approximate lines coincide with the original neuron and perception lines at the origin or 0 degrees (the adapting orientation), at 90 degrees (orthogonal to the adapting orientation), and at locations of maximal shifts, respectively. These approximations allow us to explicitly express the amplitude of the tuning curves as a function of five parameters: the width parameter  $\sigma$  of the tuning curves; the location  $\Phi$  and magnitude  $\delta$  of the maximum repulsive shift of the perceived orientations; and the location  $\Psi$  and magnitude  $\Delta$  of the maximum repulsive shift of the preferred orientations (see Appendix for details). The amplitude  $A(\psi)$  of the tuning curve for neuron  $\psi$  near the adapting orientation at 0 is approximately given by the following expression:

$$A(\psi) \approx \exp\left(\left(\frac{\Delta}{\Psi} + \frac{\delta}{\Phi}\right)\frac{\psi^2}{2\sigma^2}\right).$$
 (1.3)

This formula succinctly summarizes how the amplitude of the tuning curves depends on the shifts of the perception and the preferred orientation. As the neuron label  $\psi$  goes further away from the adapting orientation at 0, the amplitude grows exponentially; the rate of the growth is proportional to the sum of the repulsive shifts of the perceived and the preferred orientations, and is inversely proportional to the width of the tuning curves. The rise of the amplitude is more pronounced for large  $\Delta$  compared to the case of  $\Delta = 0$ (i.e. no shift of preferred orientation), as illustrated in Figure 2d and 2c.

Equation (1.2) is used to quantitatively check the consistency between psychophysical data on the TAE and adaptation-induced changes of the neuron tuning curves. Fitting with fourth order polynomials, we determine the perception line  $\psi_p(\phi)$ from the psychophysical data on the TAE (Clifford et al. 2000)(Figure 4a), and the neuron line  $\phi_n(\psi)$  from the physiological data (Dragoi et al. 2000) (Figure 4b). The fitting assumes that there are no shifts of the preferred orientations for neurons at 0 degree (the adapting orientation) and 90 degrees. In the physiological experiments, adaptation also changes the width of the tuning curves as evident from the changes of the orientation selectivity indices (OSIs) (Dragoi et al. 2000). We convert the data on the OSIs to that on the width parameters assuming a linear relationship between the OSIs and the width parameter (Swindale 1998). The relationship is determined by two points: the width parameter is zero when OSI is 1, and the averaged half width of tuning curves before adaptation is 30 degrees (Watkins and Berkley 1974). We fit the converted data on the width parameters with a straight line (Figure 4c).

Using the experimentally determined perception and neuron lines and tuning width parameters, we calculate the amplitude of the tuning curves using Equation (1.2). The calculated amplitude curve is plotted in Figure 5, left (red curve). We compare this curve with physiological data on the amplitude changes of the tuning curves, which are calculated by taking the ratios of the observed maximum firing rates of neurons after and before adaptation (the green circles with error bars in Fig. 5). (These data are derived from neurons studied by (Dragoi et al. 2000), but are presented in this form for the first time. The spontaneous firing rates are subtracted before calculating the ratios). The overall scaling of the amplitude curve is not determined in the theory; we therefore scaled the curve to best match the experimental data. The comparison is in rough quantitative agreement. (The mean square root difference between the data (the green circles) and corresponding values on the theory curve (MSRD) is 0.08. Mathematically,  $MSRD = \sqrt{\sum_{i=1,N} (d_i - p_i)^2 / N}$ , where  $d_i$  is the *i*-th data point,  $p_i$  is the predicted value, and N is the number of the data points.)

To see if the observed changes of the tuning curves, in particular whether the shifts in preferred orientation, are essential for agreement between the theory and the data, we calculated the amplitude curve using the perception line from the psychophysical data but assuming no shifts of the preferred orientations. The results are plotted in Figure 5, right (dotted red line). The comparison (MSRD 0.14) is clearly not as good as that with the preferred orientation shifts.

These results do not depend on either the exact shapes of the perception and the neuron lines, or the variations of the tuning width. This is evident from the results that use the formula assuming piecewise linear approximations of the perception and neuron lines, and a constant width for the tuning curves (the formula is given in Equation (1.13) and (1.14) in Appendix). The case with the repulsive shifts is plotted in Figure 5, left (magenta curve), and that without is plotted in Figure 5, right (dotted magenta line). The results with the approximations closely resemble those without. Parameters for the piecewise linear approximations are as follows: the maximum perceived orientation shift is 4 degrees when the testing and adapting angles are 15 degrees apart (Clifford et al. 2000); the maximum preferred orientation shift is 10 degrees when the neuron label and the adapting angle is 25 degrees apart; and the half width of the tuning curves is 30 degrees (Watkins and Berkley 1974).

We conclude from these comparisons that the observed changes of the neuron tuning curves after adaptation are quantitatively consistent with the TAE measured psychophysically. Moreover, the repulsive shifts of the preferred orientations are especially important for a better quantitative explanation of the TAE.

So far we have presented results using the winner-take-all method for reading out perceived orientations from the population responses. Similar results are obtained using two other readout methods: the population vector and the maximum likelihood.

In the population vector method, the perceived orientation of a stimulus is constructed from the responses of all neurons. Each neuron is assigned a vector, with the length proportional to the neuron's firing rate, and the angle with the horizontal axis equal to twice of the neuron label (the preferred orientation before adaptation). Summation of the vectors gives a population vector, whose angle is assigned as twice of the perceived orientation. Mathematically, the perceived orientation of stimulus  $\phi$  is expressed according to the following formula:

$$\psi_{p}(\phi) = \frac{1}{2} \arctan \left( \frac{\int\limits_{\phi=90}^{\phi=90} d\psi \sin(2\psi) F(\psi, \phi)}{\int\limits_{\phi=90}^{\phi=90} d\psi \cos(2\psi) F(\psi, \phi)} \right) \qquad (1.4)$$

This readout method is more complicated than the winner-take-all method, and it is not straightforward to describe closed-form mathematical expressions for the amplitude function  $A(\psi)$ . Nevertheless, we can approximately compute this function by following an optimization procedure.

This is done by parameterization of the amplitude function. For each parameter set, a unique amplitude function is determined. Using the amplitude function, the rate function is constructed from the tuning curves, and is used to calculate the perceived orientations of all stimuli. The shifts of the perceived orientations relative to the true stimulus orientations are then compared with the psychophysical data. We search the parameter space until the best comparison is reached. Some parameters can lead to multi-peaked population profiles for some stimuli, for which the population vector method breaks down (Pouget et al. 2000); we therefore exclude such parameters in the search.

Mathematically, the above procedure can be expressed as follows. We parameterize  $A(\psi)$  with Chebyshev polynomials (Press et al. 1988) up to the fifth order, as below:

$$A(\psi) = 1 + \sum_{k=1}^{5} a_k \left( \cos\left(k \arccos\left(\frac{\psi - 45}{45}\right)\right) - \cos(180k) \right) \quad . \tag{1.5}$$

Here  $a_k, k = 1,...,5$  are the parameters. For each set of parameters, the perception line  $\psi_p(\phi, \{a_k\})$  is calculated through Equations (1.5), (1.1), and (1.4). We search the parameter space to minimize the following error function:

$$E(\{a_k\}) = \int_{0}^{90} d\phi (\psi_p(\phi, \{a_k\}) - \psi_{p, observed}(\phi))^2 + R(\{a_k\}).$$
(1.6)

Here  $R(\{a_k\})$  is the regularization factor. This factor is introduced to restrict the solution in parameter space so that no multiple peaks are allowed in the population profiles for any stimulus orientation, since the population vector method breaks down for multi-peaked population profiles. The factor *R* is 0 if the population profiles for all stimuli are one-peaked; otherwise, *R* is assigned a large number so that the error is large. The exact value of this large number does not affect the results (in our calculations, the value of the number is 15). Minimization of the error function leads to an amplitude function that produces a perception line as close as possible to the one determined by the psychophysical experiments, with the constraints that the population activity profiles for all stimuli are one-peaked. We use Powell's Method (Press et al. 1988) for minimizing the error function.

In Figure 5, left, we show the result (black curve) obtained using the experimentally determined curves for the shifts of the preferred and perceived orientations as well as the width parameters (Figure 4). The result is quite similar to that of the winner-take-all method (red curve in Figure 5), and again compares well with the experimental data (MSRD 0.07). We also calculated the amplitude function without repulsive shifts of the preferred orientations and changes of the tuning width, which is shown in Figure 5, right (dotted black curve). The comparison with the data (MSRD 0.16) is less compelling than that with the preferred orientation shifts.

The results using the maximum likelihood method (the blue curve in Figure 5, left, with repulsive shifts of the preferred orientations, MSRD 0.08; and the dotted blue curve in Figure 5, right, without, MSRD 0.17) are also quite similar to those of the winner-take-all method. In the maximum likelihood method, the perceived orientation of a stimulus  $\phi$  is determined by fitting the population profile with preset templates, which are the population profiles before adaptation. Each perceived orientation has a corresponding template. The template corresponding to a perceived orientation  $\phi$  is a Gaussian function centered at  $\phi$  with the width parameter  $\sigma$ . The fitting procedure minimizes the integral of the square error between the template and the population profile through scaling the maximum of a template. The label of the best-matched template is assigned as the perceived orientation. To calculate the amplitude function  $A(\psi)$ , we follow a numerical optimization procedure similar to that for the population vector average method. A regularization factor is also similarly introduced, since the maximum likelihood method is valid only for one-peaked population profiles just like the vector average model.

The above results demonstrate that the TAE is consistent with adaptation-induced changes of the tuning curves of V1 neurons. The observed repulsive shifts of the preferred orientations after adaptation are especially important for better quantitative agreement. We can show this in another way: from the adaptation-induced changes of the tuning curves, we predict the TAE and compare to the psychophysical data. Specifically, we construct the rate function through Equation (1.1) with the amplitude function  $\underline{A(\psi)}$ , the preferred orientations  $\phi_n(\psi)$ , and the width parameters  $\sigma(\psi)$ . From the rate function we obtain the population response profile for a given stimulus orientation, and determine the perceived orientation using a population coding method (winner-take-all, population vector, or maximum likelihood). The difference between the perceived and true orientations of the stimulus is the predicted TAE. We use the amplitude function shown in the left graph of Figure 5 (solid red curve for winner-take-

all, solid black curve for population vector, or solid blue curve for maximum likelihood). The width parameters are given in the curve plotted in Figure 4c. We first calculate the TAE *with the repulsive shifts of the preferred orientations*, given in the curve of Figure 4b. The results are plotted in Figure 6, where the solid red, black, and blue curves are from winner-take-all, population vector, and maximum likelihood coding methods, respectively. The predicted TAE agrees with the data (green circles, same as in Figure 4a) quite well (the mean square root difference between the data and predictions are 0.36, 0.50, and 0.44, respectively). We then calculate the TAE *with no shifts of the preferred orientations*. The results are plotted in Figure 6, where the dotted red, black, and blue lines are from winner-take-all, population vector, and maximum likelihood, respectively. The predicted TAE does not agree with the data as well (the mean square root differences are 7.09, 2.00, and 2.90, respectively). Without the repulsive shifts of the preferred orientations, the predicted TAE is much larger than observed.

# Discussion

Our results demonstrate that the observed magnitude of the TAE is consistent with the amount of suppression and preferred orientation shift observed in V1 neurons. These two types of tuning curve changes have antagonistic effects on the TAE. The functional significance of this antagonism is unclear. One possibility is that relative suppression is an inevitable "design constraint" on neural circuitry, and that the shift in preferred orientations has evolved to counter its effects. It is unlikely that our conclusion depends on the exact details of how the rest of the brain reads out the orientation information from the population responses of V1 neurons. This is evident from the agreement among the results using three different readout methods.

Past models of the TAE have relied only on the relative suppression of neural responses (Clifford et al. 2000; Coltheart 1971 ; Dong 1996; Sutherland 1961; Wainwright 1999). Our calculations indicate that these models are incomplete, because they cannot reconcile quantitatively the amount of relative suppression with the magnitude of the TAE. To produce the observed magnitude of the perception shift, theses models need less suppression than observed experimentally (Figure 5, right); on the other hand, with the observed amount of suppression, the model predicts too much perceptual shift. Our model includes not only the suppression but also the repulsive shift of the preferred orientations, and indicates that these two changes of the tuning curves together lead to a quantitatively consistent model of the TAE. Such consistency suggests that the psychophysical phenomenon of TAE can be explained by the properties of V1 neurons.

In this paper we have focused on the effects of prolonged adaptation (on the order of minutes). Recent physiological experiments have studied the effects of brief adaptation (less than 1 sec) (Chung et al. 2002; Dragoi et al. 2002; Felsen et al. 2002; Muller et al. 1999). These experiments demonstrate that a brief adaptation can also cause the tuning curves to suppress relatively and shift repulsively, similar to that during prolonged adaptation. However, the TAE is weak, if any, for brief adaptation (Magnussen and Johnsen 1986). A possibility is that in this case the repulsive shift cancels the shift of perception that can arise from the relative suppression, resulting in a weak TAE. This hypothesis can be quantitatively tested in the same way as in this paper by comparing the observed amount of suppression to that calculated with the observed shifts of the preferred orientations alone.

Previously, while simulating the tilt illusion, a psychophysical phenomenon related to the TAE, Gilbert and Wiesel (1990) observed the opposing effects of amplitude suppression and repulsive shifts of preferred orientations on orientation 20

perception. Our mathematical analysis goes beyond this qualitative observation, and unveils a quantitative relationship between the suppression and the shifts of perception and preferred orientations. Such relationships enable us to check the consistency between psychophysical and physiological data. The relationship is also useful as a caution against an over-simplified conclusion that the directions of shifts in the tuning curves and the perceived orientations are always opposite (Teich and Qian 2003; Yao and Dan 2001). As our analysis shows, the relative directions depend on the change of the amplitudes of the tuning curves. Inferring perception from tuning curves must be done through a careful analysis of the firing rate function constructed from the tuning curves.

We briefly note some general constraints on the source of the suppression. Suppression in V1 neurons could be due to changes within the cortex itself, or to changes in the inputs to the cortex. The latter type of change, though no doubt present, does not seem to be important for the psychological and physiological experiments considered in this paper. Adaptation is induced with a drifting grating, which tends to activate all LGN neurons equally over time, since they are at most weakly tuned to orientation(Hubel and Wiesel 1961). Therefore, any adaptation of thalamocortical input is expected to be unspecific for orientation. Thus, the locus of orientation-specific adaptation is likely to be the cortex. One plausible scenario involves adaptation of the excitatory connections between neurons tuned to the adapting orientation, which would cause the responses of these neurons to be suppressed (Dong 1996; Felsen et al. 2002; Teich and Qian 2003). Quantitative support in favor of this idea comes from independent studies of the effects of recurrent excitation. Recurrent excitation is estimated to amplify cortical responses by a factor of about two or three (Ferster et al. 1996). Therefore, weakening of recurrent excitation by adaptation would be expected to reduce the amplitudes of tuning curves by up to this factor, which is in rough quantitative accord with the tuning curve suppression depicted in Figure 5. Another

possible source of adaptation within the cortex is reduction in spiking of neurons due to activation of long-lasting hyperpolarizing currents after prolonged spiking activity (Carandini and Ferster 1997; Sanchez-Vives et al. 2000).

We have shown that the TAE is consistent with the physiological data obtained from anesthetized cat V1 neurons. Two caveats should be observed. First, the psychophysics of the TAE is based on human experiments. However, we do not expect this to be a big problem, since V1 is quite similar across mammalian species and it is probable that human V1 neurons behave similarly to cat V1 neurons under adaptation. It might be possible to test the TAE and measure V1 neuron responses in the same animal. Quantitative consistency of the psychophysical and physiological data in such experiments should provide a stronger ground for concluding that the TAE arises from the properties of V1 neurons. Second, our model relies on a simple assumption - the unadapted tuning curves of the neurons are the same, and the adaptation induced changes of the tuning curves depends only on the distance between the labels of the neurons and the adapting orientation. This assumption, which is also the basis of most of the previous models of the TAE (Clifford et al. 2000; Coltheart 1971; Sutherland 1961; Wainwright 1999), enables us to derive in compact forms the quantitative relationship between the changes of the tuning curves and the TAE. In reality, the tuning curves have a wide range of shapes, and adaptation-induced changes of these curves also depend on the locations of neurons relative to the orientation map (Dragoi et al. 2001). Our model does not account for the observed diversity of neuron properties. It remains to be seen how inclusion of this diversity, which inevitably requires large scale simulations of the visual cortex, might modify our results.

Besides the TAE, there are other adaptation induced aftereffects such as the motion aftereffect (Huk et al. 2001) and the spatial frequency aftereffect (Humanski and Wilson 1993). Population coding models similar to the one in this paper can also be

useful for quantitatively checking the consistency between psychophysical and physiological data in these aftereffects. A recent study of motion adaptation in MT neurons in anesthetized monkeys demonstrates an attractive shift in the direction tuning of these neurons, towards the adapting direction (Kohn and Movshon 2004 ; 2003). Whether or not such an attractive shift in direction tuning generalizes to other kinds of adaptation, such as orientation adaptation, in visual cortical areas remains to be examined. However, these findings raise the issue of the perceptual locus of adaptation induced changes, in particular whether specific visual areas are privileged sites for specific percepts and whether there are different mechanisms and consequences of pattern adaptation in different cortical areas. A more complete description of neuronal responses and the consequences of pattern adaptation in different areas of visual cortex will be required to resolve these issues.

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# Appendix

In the following, we describe the procedures for calculating  $A(\psi)$  with the winner-takeall method. For convenience, we let the adapting orientation be at 0, and discuss only the case of  $\psi > 0$  (the case for  $\psi < 0$  is similar). The overall scaling of  $A(\psi)$  is not determined from the calculations. Here we simply set A(0) = 1.

In the winner-take-all method, the label of the neuron that fires the most in the population equals the perceived orientation. The population response curve to a

stimulus  $\phi$  is given by  $F(\psi, \phi)$  with  $\phi$  held constant. The peak location of this curve is given by setting to zero the partial derivative of the rate function with respect to the neuron label, i.e.

$$0 = \frac{\partial F(\psi, \phi)}{\partial \psi}$$

$$= \frac{dA(\psi)}{d\psi} \exp\left[-\frac{(\phi - \phi_n(\psi))^2}{2\sigma(\psi)^2}\right] +$$

$$A(\psi) \exp\left[-\frac{(\phi - \phi_n(\psi))^2}{2\sigma(\psi)^2}\right] \cdot$$

$$\left[\frac{\phi - \phi_n(\psi)}{\sigma(\psi)^2} \frac{d\phi_n(\psi)}{d\psi} + \frac{(\phi - \phi_n(\psi))^2}{\sigma(\psi)^3} \frac{d\sigma(\psi)}{d\psi}\right].$$
(1.7)

Here we used Equation (1.1) for the rate function  $F(\psi, \phi)$ . Re-arranging terms in above equation, we find

$$\frac{dA(\psi)}{d\psi} = A(\psi)\frac{\phi_n(\psi) - \phi}{\sigma(\psi)^2} \left[\frac{d\phi_n(\psi)}{d\psi} - \frac{\phi_n(\psi) - \phi}{\sigma(\psi)}\frac{d\sigma(\psi)}{d\psi}\right].$$
(1.8)

Solving the above equation for  $\psi$ , we obtain the perceived orientation of stimulus  $\phi$ . In other words, the solution of the above equation is given by  $\psi = \psi_p(\phi)$ . An equivalent expression of the solution is  $\phi = \psi_p^{-1}(\psi)$ , where  $\psi_p^{-1}$  is the inverse function of the perception line  $\psi_p(\phi)$ . Therefore, the above equation can also be written as

$$\frac{dA(\psi)}{d\psi} = A(\psi) \frac{\phi_n(\psi) - \psi_p^{-1}(\psi)}{\sigma(\psi)^2} \left[ \frac{d\phi_n(\psi)}{d\psi} - \frac{\phi_n(\psi) - \psi_p^{-1}(\psi)}{\sigma(\psi)} \frac{d\sigma(\psi)}{d\psi} \right].$$
(1.9)

This equation gives the relationship among the amplitude function  $A(\psi)$ , the perception  $\lim \psi_p(\phi)$ , the neuron  $\lim \phi_n(\psi)$ , and the width parameter  $\sigma(\psi)$ . Notice that the changes of the amplitudes of the tuning curves, depicted by the derivative on the left

hand side of the above equation, cannot be arbitrary. Noting that

$$\frac{1}{A(\psi)} \frac{dA(\psi)}{d\psi} = \frac{d\ln A(\psi)}{d\psi}, \text{ we solve the above differential equation to find}$$
$$A(\psi) = \exp\left(\int_{0}^{\psi} d\psi' \frac{\left(\phi_{n}(\psi') - \psi_{p}^{-1}(\psi')\right)}{\sigma(\psi')^{2}} \left(\frac{d\phi_{n}(\psi')}{d\psi'} - \frac{\left(\phi_{n}(\psi') - \psi_{p}^{-1}(\psi')\right)}{\sigma(\psi')} \frac{d\sigma(\psi')}{d\psi'}\right)\right) (1.10)$$

Numerically integrating the above equation gives the amplitude function  $A(\psi)$  with given neuron and perception lines, as well as the tuning width parameters.

For the adapted state, we can explicitly evaluate Equation (1.10) with piecewiselinear approximations to the neuron and the perception lines and assuming that the tuning width parameter is a constant  $\sigma$ . The neuron line is approximated with two straight lines determined by three pairs of neuron label and the preferred orientation:  $(0,0), (\Psi, \Psi + \Delta), (90,90)$ , where  $\Psi$  is the label of the neuron that shows the maximum preferred orientation shift  $\Delta$ . This gives the following expression for the approximated neuron line:

$$\phi_n(\psi) = \begin{cases} k_1 \psi, & \text{for } 0 < \psi < \Psi, \\ 90 + k_2 (90 - \psi), & \text{for } \Psi < \psi < 90. \end{cases}$$
(1.11)

Here  $k_1 = \frac{\Psi + \Delta}{\Psi}$  and  $k_2 = \frac{\Psi + \Delta - 90}{\Psi - 90}$  are the slopes of the two lines. Similarly, the

perception line is approximated with two straight lines determined by three pairs of the stimulus orientation and the perceived orientation:  $(0,0), (\Phi, \Phi + \delta), (90,90)$ , where  $\Phi$  is the orientation of the stimulus that shows the maximum perception shift  $\delta$ . The inverse function of the approximated perception lines is given by the following equation:

$$\psi_p^{-1}(\psi) = \begin{cases} k_3 \psi, & \text{for } 0 < \psi < \Phi + \delta, \\ 90 + k_4 (90 - \psi), & \text{for } \Phi + \delta < \psi < 90. \end{cases}$$
(1.12)

Here  $k3 = \frac{\Phi}{\Phi + \delta}$  and  $k_4 = \frac{\Phi - 90}{\Phi + \delta - 90}$  are the slopes of the two lines of the inverse

function. Plugging in Equations (1.11) and (1.12) into Equation (1.10) yields the following expression for the amplitude modulation:

Case 1:  $\Psi \leq \Phi + \delta$ . In this case, we have

$$A(\psi) = \begin{cases} \exp\left(\frac{a\psi^2}{2\sigma^2}\right), & \text{for } 0 < \psi < \Psi, \\ \exp\left(\frac{b\psi^2 + c\psi + d}{2\sigma^2}\right), & \text{for } \Psi \le \psi < \Phi + \delta, \\ \exp\left(\frac{f\psi^2 + g\psi + h}{2\sigma^2}\right), & \text{for } \Phi + \delta < \psi \le 90. \end{cases}$$
(1.13)

Here the constants are given by

$$a = k_1 (k_1 - k_3), b = k_2 (k_2 - k_3), c = 180k_2 (1 - k_2), d = 90^2 (1 - k_2)^2 + k_3 (k_2 - k_1) \Psi^2,$$
  

$$f = k_2 (k_2 - k_4), g = 180k_2 (k_4 - k_2), \text{ and}$$
  

$$h = k_3 (k_2 - k_1) \Psi^2 + k_2 (k_4 - k_3) (\Phi + \delta)^2 + 90^2 (1 - k_2)^2 + 180k_2 (1 - k_4) (\Phi + \delta).$$

Case 2:  $\Phi + \delta < \Psi$ . In this case, we have

$$A(\psi) = \begin{cases} \exp\left(\frac{a\psi^2}{2\sigma^2}\right), & \text{for } 0 < \psi < \Phi + \delta, \\ \exp\left(\frac{u\psi^2 + v\psi + w}{2\sigma^2}\right), & \text{for } \Phi + \delta \le \psi < \Psi, \\ \exp\left(\frac{f\psi^2 + g\psi + s}{2\sigma^2}\right), & \text{for } \Psi < \psi \le 90. \end{cases}$$
(1.14)

Here the constants are given by

•

$$u = k_1 (k_1 - k_4), v = -180k_1 (1 - k_4), w = k_1 (k_4 - k_3) (\Phi + \delta)^2 + 180k_1 (1 - k_4) (\Phi + \delta), \text{ and}$$
  
$$s = k_1 (k_4 - k_3) (\Phi + \delta)^2 + k_4 (k_2 - k_1) \Psi^2 + 90^2 (1 - k_2)^2 + 180 (1 - k_4) (k_1 (\Phi + \delta) + (k_2 - k_1) \Psi)$$

As can be seen from Equations (1.13) and (1.14), piecewise-linear approximations of the neuron and the perception lines result in a piecewise-Gaussian surface for the rate function. Away from the adapting orientation at 0, the amplitude function increases exponentially with the square of the distance of the neuron label from the adapting orientation. The rate factor of this exponential can be expressed as follows when the shifts of the perceptions and preferred orientations are small compared to  $\Phi$  and  $\Psi$ , respectively:

$$\frac{a}{2\sigma^2} \approx \frac{1}{2\sigma^2} \left( \frac{\Delta}{\Psi} + \frac{\delta}{\Phi} \right).$$
(1.15)

The above equation shows that larger repulsive shifts of perception and repulsive shifts of the preferred orientation add up to cause a faster rise of the amplitudes of the tuning curves away from the adapting orientation.

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# **Figure Captions**

Fig. 1. Summary of psychophysical and physiological data related to the effects of orientation adaptation. (a) Prolonged adaptation to a tilted grating on the left causes the vertical test grating on the right to appear rotated away from the orientation of the adaptor (Gibson and Radner 1937; He and MacLeod 2001; Magnussen and Johnsen 1986; Mitchell and Muir 1976). The curve on the right schematically summarizes the difference between the perceived orientation and the true orientation of the stimulus as a function of the difference between the true and adapting orientations. (b) Prolonged adaptation to a grating causes repulsive shifts of the preferred orientations of neurons in V1 (Dragoi et al. 2000). On the left, the tuning curves of two neurons are shown. For each neuron, the gray curve represents the tuning curve of a neuron before adaptation. The black curve is the tuning curve after adaptation. The adapting orientation is represented by the gray vertical line. The preferred orientation shifts repulsively away from the adapting orientation (horizontal arrows). The amplitude of the tuning curve also changes. For the neuron with preferred orientation close to the adapting orientation, the amplitude depresses (left vertical arrow). For the neuron with preferred orientation far from the adapting orientation, the amplitude may increase (right vertical arrow). On the right, the curve schematically summarizes the difference between the preferred orientation after adaptation and the preferred orientation before adaptation as a function of distance between the preferred and adapting orientations.

**Fig. 2.** Relationship between changes of tuning curves and shifts of perception. Left column: plots of the rate functions. Each point on the surface of a rate function represents the firing rate of a neuron at one stimulus orientation. Here  $\psi$  is the neuron label, and  $\phi$  is the stimulus orientation. Only the part of the rate functions for  $0 < \psi < 90$  and  $0 < \phi < 90$  is shown. The adapting orientation is at 0. The red lines are

tuning curves, and the blue lines are the population response curves. The red and blue dots indicate maxima of the tuning and population response curves, respectively. Right column: plots of the lines of the perceived orientations (blue) and the preferred orientations (red). The lines correspond to the rate function on the left in the following way: the red line represents the locations of the peaks of the tuning curves, and the blue line represents the locations of the peaks of the population response curves. The magenta lines indicate that the red and blue lines coincide. Only the parts for  $0 < \psi < 90$  are shown. (a) Before adaptation. The tuning curves all have the same Gaussian shape, and the preferred orientations are the same as the neuron labels. Peaks of tuning curves and population curves coincide. There is no shift of perception. (b) Preferred orientations shift repulsively (i.e. they are further away from the adapting orientation compared to their values in the unadapted state), while the amplitudes remain uniform. The peaks of tuning curves and population curves still coincide. The perceived orientations shift attractively, contrary to the TAE. (c) The preferred orientations do not shift, but the amplitudes suppress near the adapting orientation. Peaks of tuning curves and population curves no longer coincide. The perceived orientations shift repulsively, as in the TAE. (d) The preferred orientations shift repulsively, and the amplitudes suppress near the adapting orientation. The suppression is much stronger than in (c). This is needed to produce the same amount of repulsive shift of the perceived orientations as in (c).

Fig. 3. <u>Graphic "proof" that repulsive shift of preferred and perceived orientations is</u> <u>necessarily accompanied by suppression of tuning curve amplitudes.</u> In the box, the red line indicates the preferred orientation for the neuron with label  $\psi$ , and is termed *the neuron line*; the blue line indicates the perceived orientation for the stimulus at orientation  $\phi$ , and is termed *the perception line*. <u>Consider a path that travels from the</u> red neuron line (point 1) to the blue perception line (point 2) back to the red neuron line (point 3). We show that firing rate is larger at point 1 than at point 3. The vertical path from 1 to 2 travels along the  $\phi$  direction, and therefore traces out the tuning curve of some neuron, which is graphed to the right of the box. Because 1 is on the neuron line, it corresponds to the maximum of the tuning curve. Therefore the firing rate at 1 is larger than at 2. The horizontal path from 2 to 3 travels along the  $\psi$  direction, and therefore traces out the population response for some orientation, which is graphed above the box. Because 2 is on the perception line, it corresponds to the maximum of the firing rate is larger at 2 than at 3. It follows that the firing rate at 1 is larger than at 3. This downhill path can be continued, alternating between the neuron and perception lines, proving that tuning curve amplitudes are suppressed near the origin. This suppression is large if the distance of the path is long, or equivalently, the repulsive shifts of the preferred orientations and the perceived orientations are large. Narrow tuning curves or population response curves have a similar effect.

**Fig. 4.** Least-squares fits of experimental psychophysical and physiological data. (a) The amount of repulsive shift of the perceived orientation is plotted against the difference between the testing orientation and the adapting orientation. The gray dots are the psychophysical experimental data taken from (Clifford et al. 2000). The black curve is the least square fit of the data to a polynomial of the form  $\phi(90-\phi)a(1+b\phi)(1+c\phi)$ . The fitting parameters are

a = 0.0061, b = -0.011, c = -0.017. (b) The amount of repulsive shift of the preferred orientation is plotted against the difference between the neuron label and the adapting orientation. The gray dots are taken from the physiological experimental data of (Dragoi et al. 2000). The black curve is the least square fit of the data to the same polynomial

form as in (a), with the parameters a = 0.011, b = -0.0086, c = -0.0085. (c) The tuning width parameter is plotted against the difference between the neuron label and the adapting orientation. The gray dots are adapted from the orientation tuning index data of (Dragoi et al. 2000). The black line is a least squares fit of the data to a line of the form  $a + b\psi$ , with the parameters a = 27, b = -0.34.

Fig. 5. Consistency of model results with physiological and psychophysical data on adaptation. From the physiological data, we calculate the ratio of the amplitudes of the tuning curves after and before adaptation, after subtraction of the spontaneous firing rates (adapted from (Dragoi et al. 2000). The green circles are obtained by averaging these ratios within 15 degree bins, and the error bars are the standard errors of the mean. The curves are the theoretical calculations of the ratio as a function of the difference between the neuron label (i.e. preferred orientation before adaptation) and the adaptation orientation. Theoretical curves are scaled to minimize the square error relative to the data. Curves are color-coded to indicate the population coding methods used: winner-take-all (red and magenta), population vector (black), and maximum likelihood (blue). (Left) The solid curves on the left are calculated with repulsive shifts of both perceived and preferred orientations, as in Figure 2d. Except the magenta curve, all curves are calculated using the results shown in Figure 4 for shifts of the perceived and preferred orientations, as well as the changes of the tuning width. The magenta curve is calculated using the piecewise linear approximations to the shifts, and a constant tuning width. (Right) The dotted curves on the right are calculated with the shifts of the perceived orientations, but without the repulsive shifts of the preferred orientations, as in the model of Figure 2c. The curves on the left are more consistent with the physiological data than those on the right. For the amount of the TAE measured in psychophysical experiments, the repulsive shifts of preferred orientations

are necessary for better explaining the observed amount of relative suppression of the tuning curves.

**Fig. 6.** Prediction of the TAE with adaptation-induced changes of tuning curves. The perceived orientation of a stimulus is calculated by obtaining population response profile from the rate function constructed using the adaptation-induced changes of tuning curves. The difference between the perceived and true orientations is the TAE. We use the amplitudes of the tuning curves as given in the left graph of Figure 5 (the red, black, or blue curves for winner-take-all, population vector, or maximum likelihood coding methods, respectively). The width parameters are given in the curve of Figure 4c. Results with the repulsive shifts of the preferred orientations, as given in the curve of Figure 4b, are plotted as the solid curves. Results with no shifts of the preferred orientations are plotted as the dotted curves. Red, black, or blue indicates that the population coding method use is winner-take-all, population vector, or maximum likelihood, respectively. The green circles are the psychophysical data, same as in Figure 4a.



Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.



Fig. 5.



Fig. 6.