Orthogonal adaptation improves orientation discrimination

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Abstract

We investigated the effect of adaptation on orientation discrimination using two experienced observers, then replicated the main effects using a total of 50 naïve subjects. Orientation discrimination around vertical improved after adaptation to either horizontal or vertical gratings, but was impaired by adaptation at 7.5 or 15° from vertical. Improvement was greatest when adapter and test were orthogonal. We show that the results can be understood in terms of a functional model of adaptation in cortical vision. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Orientation discrimination; Adaptation; Tilt aftereffect; Computational model; Spatial vision

1. Introduction

The functional benefits of light adaptation by photoreceptor cells in the retina are well established, enabling our visual systems to operate in a vast range of conditions from near darkness to bright sunlight (Barlow, 1969). However, evidence of a functional role for cortical adaptation is equivocal. Some studies have reported enhancements in contrast discrimination after adaptation (Abbonizio, Langley, & Clifford, 1998; Greenlee & Heitger, 1988), but others have not (Maatanen & Koenderink, 1991; Ross, Speed, & Morgan, 1993; Foley & Chen, 1997). Motion adaptation has been found to improve differential sensitivity to speed (Clifford & Langley, 1996; Bex, Bedingham, & Hammett, 1999; Clifford & Wenderoth, 1999) and direction-of-motion (Phinney, Bowd, & Patterson, 1997), but evidence for functional benefits of adaptation to contrast and spatial image properties remains inconclusive. Barlow, Macleod, and van Meeteren (1976) failed to find improvements in the detection of changes in contrast, spatial frequency or orientation following adaptation. Subsequently, adaptation has been found to have little or no effect on spatial frequency discrimination around the adapting frequency (Regan & Beverley, 1983; Greenlee & Thomas, 1992), while reducing orientation discrimination thresholds by approximately 25% for discriminations around the adapting orientation (Regan & Beverley, 1985).

In this study, we sought to relate the effects of adaptation on judgements of relative orientation, as assessed by orientation discrimination thresholds, to biases in the perception of absolute orientation following adaptation. Prolonged exposure to an oriented pattern affects the perceived orientation of a subsequently observed pattern, a phenomenon known as the tilt aftereffect (TAE) (Fig. 1A). For adapting orientations between 0 and 50°, a vertical test appears to be repelled away from the adapter in orientation, the 'direct' effect (Gibson & Radner, 1937), with the strongest effect occurring between 10 and 20°. For larger angles, there is a smaller attraction effect, the 'indirect' effect, such that a vertical test appears rotated towards the adapter. The strongest attraction effect is observed between 75 and 80° (Wenderoth & Johnstone, 1987), and occurs robustly when the display includes relatively large adapting gratings or long adapting and test lines (Gibson & Radner, 1937; Morant & Harris, 1965; Muir & Over, 1970; Mitchell & Muir, 1976). Gibson and Radner explained the TAE in terms of the visual system's

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tendency towards the 'norms' of spatial orientation: horizontal and vertical. However, TAEs to horizontally or vertically oriented adapting stimuli (Kohler & Wallach, 1944) cannot be explained in this way. Indeed, the similarity of the angular dependence of the TAE for vertical and oblique test stimuli (Mitchell & Muir, 1976) suggests that the effect is better understood in terms of relative rather than absolute or normative orientations.

The existence of the repulsive (direct) TAE shows that prolonged exposure increases mean differences in perceived orientation around the adapting orientation (Fig. 1b,c). This increase corresponds to the positive slope of the fitted angular tuning function for the TAE around 0° (Fig. 1a). While the indirect TAE can be thought of as attraction to the adapting orientation, it can equally well be considered as repulsion from a virtual axis perpendicular in orientation to the adapter (van der Zwan & Wenderoth, 1995; Wenderoth, 1997). Attraction to an adapter remote in orientation effectively increases mean differences in perceived orientation around the orthogonal to the adapter. This increase again corresponds to a positive slope of the TAE tuning curve, this time around 90° (Fig. 1a).

If successful discrimination on any given trial requires a certain difference in 'perceived' orientation, then this suggests that a smaller 'physical' difference in orientation should be necessary to reach perceptual discrimination threshold. On this basis, one would expect to find analogues to the direct and indirect TAEs in terms of post-adaptation orientation discrimination (Fig. 1d). Specifically, thresholds would be expected to decrease around and perpendicular to the adapting orientation. However, the direct TAE is consistently larger than the indirect TAE (Wenderoth & Johnstone, 1988). If the mean difference in perceived orientation between two stimuli were all that determined their discriminability, then adaptation should decrease thresholds around the adapting orientation more than around the orthogonal.

The two previous studies exploring the effect of adaptation on orientation discrimination were based on a very small number of subjects. The threshold reduction reported by Regan and Beverley (1985) was based on the data of only two subjects, and discrimination thresholds were only tested within $\pm 35°$ of the adapting orientation. Barlow et al. (1976) used only one subject. They compared the effect of adaptation to a grating parallel to the test stimulus with the effect of orthogonal adaptation, presumably under the assumption that orthogonal adaptation would have no beneficial effect, rather than measuring baseline thresholds in an unadapted condition.

In this study, we investigate the effect of adaptation at a range of orientations on discrimination around the vertical using two experienced observers. We then replicate the main effects using a total of 50 subjects naïve to the purposes of the study.
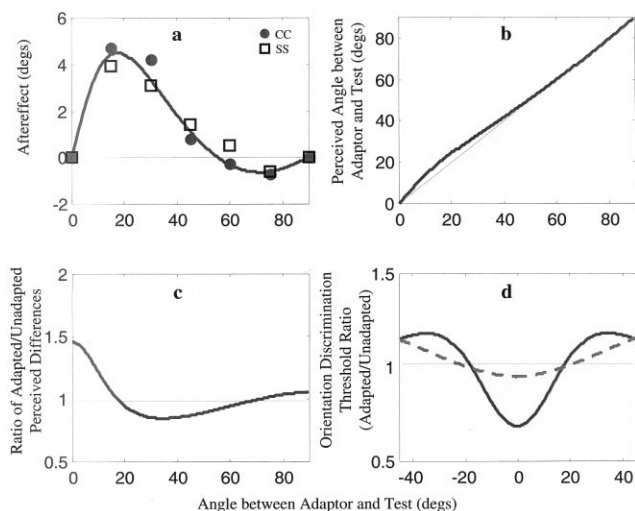

Fig. 1. (a) Angular tuning function of the tilt aftereffect. Data for two observers are redrawn from Clifford, Smith & Wenderoth (2000a). The bold curve is a fit derived from the model of Clifford et al. (2000b). (b) The effect of adaptation on the perceived angle between adapter and test, calculated by adding the angle between adapter and test to the fitted angular tuning function of the tilt aftereffect in (a). (c) The effect of adaptation on mean differences in perceived orientation, calculated as the slope of the graph in (b). Bold lines represent the adapted state, feint the unadapted. (d) Graph from (c) replotted for comparison with Fig. 3a,b. Solid line, adapting orientations around the test orientation (vertical); dashed line, adapting orientations around the orthogonal.

2. Methods

Adapting and test gratings had a spatial frequency of 1.5 cpd (6.0 cpd for C.W.G.C.), and were presented at 80% contrast in two 6.5° (3.3° for C.W.G.C.) diameter circular apertures at a mean eccentricity of 5.4° (2.7° for C.W.G.C.) to the left and right of a central fixation spot. The adapting gratings appeared for 1 min before the first trial, and for 5 s before every subsequent trial, counter-phasing at 0.83 Hz. The test stimuli appeared at a random spatial phase for 100 ms, preceded for 50 ms by a uniform dark field. Subjects viewed the screen from a distance of 57 cm (114 cm for C.W.G.C.), and were required to make a 2AFC judgement as to which of two spatially separated test gratings oriented at $\pm \theta°$ to the vertical appeared to be tilted more clockwise (Fig. 2). The orientation of the test gratings was determined by the method of constant stimuli. For the naïve subjects, each condition consisted of ten trials at each of 22 stimulus levels at 0.2° intervals, while for the experienced observers each condition consisted of eight trials at each of 14 stimulus levels, again at 0.2° intervals. A logistic function was fitted to the data, and the difference between its 50 and 75% points was taken as an estimate of the discrimination threshold.
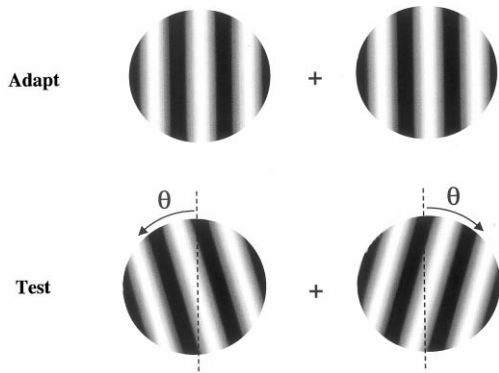
Fig. 2. Schematic diagram of the adaptation and test phases of the experimental protocol. In the adaptation phase, parallel grating stimuli appear in circular windows to the left and right of a central fixation marker. In the test phase, these same windows contain gratings oriented at $\pm\theta°$ to the vertical. Subjects are required to indicate which of the test stimuli appears to be oriented more clockwise.
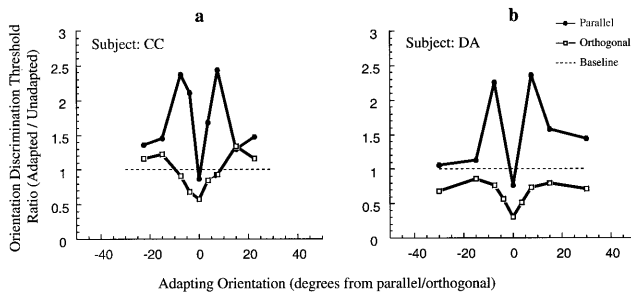

Fig. 3. Orientation threshold elevation as a function of adapting orientation for (a) subject C.W.G.C., (b) subject D.H.A. Adapting orientation is plotted relative to (●) the vertical and (□) the horizontal. All tests were around vertical. Elevation values less than 1 correspond to improvements in orientation discrimination following adaptation.

3. Results

Fig. 3 shows orientation discrimination threshold elevation for the experienced observers as a function of the orientation of the adapting stimulus. Threshold elevation was calculated as the ratio of adapted to unadapted discrimination thresholds. Unadapted discrimination thresholds ranged from 0.23 to 0.34° for subject C.W.G.C., and from 0.24 to 0.39° for D.H.A. For near-parallel orientations, the threshold elevation plots have a similar form to that reported by Regan and Beverley (1985), who found that orientation discrimination thresholds were decreased around the adapting orientation, but increased for angles of 10–20° between adapter and test. Our data show minima at adapting orientations parallel and perpendicular to the test. Discrimination thresholds at these minima are lower than the unadapted level, showing that adaptation has improved performance, with the lowest thresholds in the orthogonal adaptation condition.

To establish the generality of these improvements, we measured orientation discrimination thresholds following adaptation in a group of naïve subjects. Forty naïve subjects were tested first without adaptation, then again with adaptation. Ten each of these adapted to gratings oriented vertically (0°), horizontally (90°), at 7.5, or at 15°. The other ten naïve subjects were tested twice without adaptation to control for the effect of practice. Subjects were randomly assigned to conditions prior to the first test. After the first test, subjects with orientation discrimination thresholds greater than 2° were excluded from further participation. This led to the exclusion of a total of six subjects.

All thresholds were measured around the vertical. Fig. 4 plots the orientation threshold from the second trial against the initial unadapted threshold for each subject. The best-fit lines through the origin have slopes of 0.66 for the parallel adaptation condition and 0.58 for orthogonal adaptation, compared with 1.01 for the unadapted, corresponding to reductions in discrimination thresholds of 34 and 43%, respectively. For adaptation at 7.5 and 15°, the slopes were 1.41 and 1.17, corresponding to increases of 41 and 17%, respectively. The significance of the reductions in discrimination thresholds for each adaptation condition was established by comparing the residuals of the separate adapted and unadapted line-fits with the residuals from fitting a single line to all 20 data points (Dobson, 1991). Parallel and orthogonal adaptation both reduced discrimination thresholds significantly, while 7.5° adaptation produced a significant increase (parallel, $F_{(1,18)} = 4.89$, $P < 0.05$; orthogonal, $F_{(1,18)} = 9.79$, $P < 0.01$; 7.5°, $F_{(1,18)} = 5.36$, $P < 0.05$; 15°, $F_{(1,18)} = 1.16$, $P > 0.1$ n/s).

Threshold elevations from the naïve and experienced observers on the 0, 7.5, 15 and 90° conditions are compared in Fig. 5. In all cases, the same qualitative trend is evident. Orientation discrimination thresholds are reduced most after orthogonal adaptation, and to a lesser extent after parallel adaptation. Thresholds are elevated most after 7.5° adaptation, and to a lesser extent after 15° adaptation.

4. Discussion

4.1. Relating post-adaptation orientation discrimination to the tilt aftereffect and post-adaptation contrast detection

In Section 1, we argued that, if the discriminability of two stimuli is limited by the mean difference in their perceived orientation, one would expect to find analogues to the direct and indirect TAEs in terms of post-adaptation orientation discrimination. Given that the direct TAE is consistently larger than the indirect

TAE (Wenderoth & Johnstone, 1988), adaptation should decrease thresholds around the adapting orientation more than around the orthogonal. This is the opposite of what we found experimentally, suggesting that the mean difference in perceived orientation is not the sole determinant of orientation discrimination.

What else might be affecting orientation discrimination? Physiological evidence of response adaptation from single-cell studies suggests that prolonged exposure decreases the signal-to-noise ratio of neurons responding to the adapting stimulus (Maffei, Fiorentini, & Bisti, 1973). Psychophysically, this is reflected in increased contrast detection thresholds around the adapting orientation (Gilinsky, 1968; Blakemore & Nachmias, 1971; Regan & Beverley, 1985). When adaptation and test phases stimulate the same orientation-tuned neurons, as when adapter and test are parallel or near-parallel, the decreased signal-to-noise ratio will tend to impair subsequent discrimination performance by increasing variability in perceived orientation, moderating the effect of increased mean differences. However, when adapting and test stimuli excite groups of neurons tuned to different orientations, as for orthogonal or near-orthogonal adapting and test orientations,
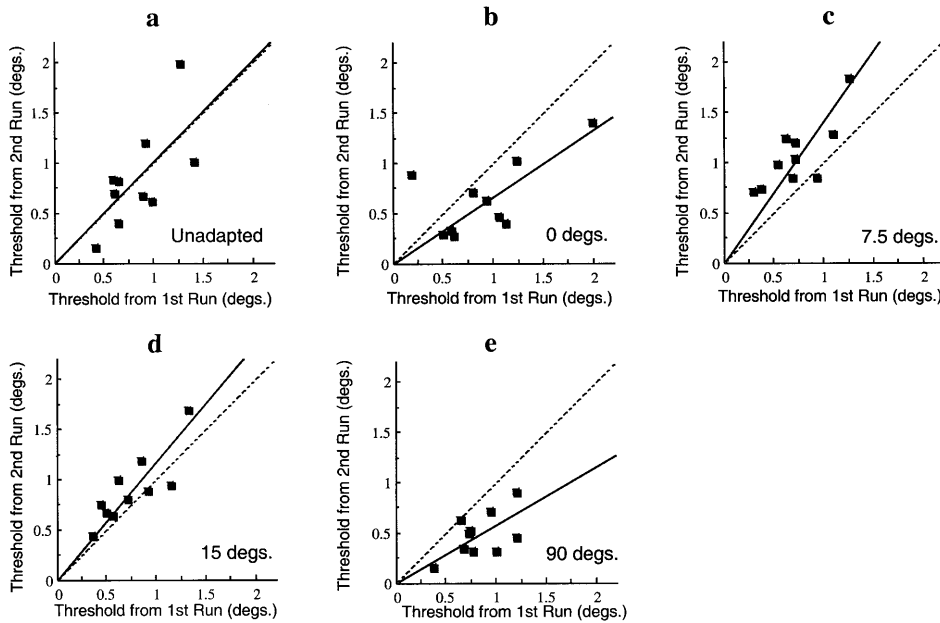

Fig. 4. Scatter plots of pairs of orientation discrimination thresholds around the vertical for 50 naïve subjects. Each point represents the data from one subject. For all naïve subjects, the first threshold was measured without adaptation. The second threshold was measured without adaptation, to control for the effect of practice (a), or after adaptation to a vertical grating (b), a grating oriented at 7.5° to the vertical (c), a 15° grating (d), or after adaptation to a horizontal grating (e). The solid lines are the best fits through the origin of the data. The line of no effect is shown (dashed) for comparison.
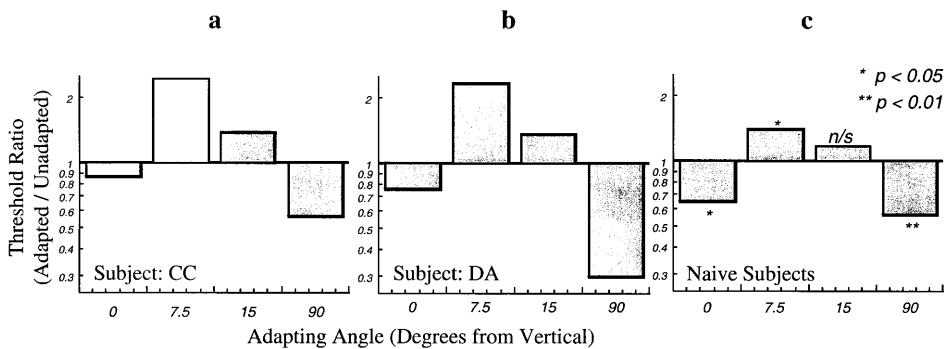

Fig. 5. Comparison of the effects of adaptation on orientation discrimination for (a) subject C.W.G.C., (b) subject D.H.A. and (c) the naïve observers. All three graphs show the same trends: (i) a reduction in post-adaptation discrimination thresholds for orthogonal adaptation; (ii) a smaller reduction for parallel adaptation; (iii) a small increase in thresholds after adaptation to a 15° grating; (iv) a larger increase after adaptation to a grating oriented at 7.5° to the vertical. The data for C.W.G.C. and D.H.A. are redrawn from Fig. 3a,b with averaging over the ± 7.5 and ± 15° conditions. The data for the naïve observers are the ratios of the slopes of the best-fit lines in Fig. 4b–e to the slope of the best-fit line in the control condition shown in Fig. 4a.
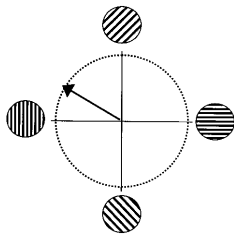
Fig. 6. Double-angle representation of orientation used by the model, in which horizontal and vertical are opposites. A population vector is formed from the responses of orientation-tuned model neurons. The direction of the population vector represents the model's prediction of perceived orientation. The length of the vector corresponds to the response magnitude.
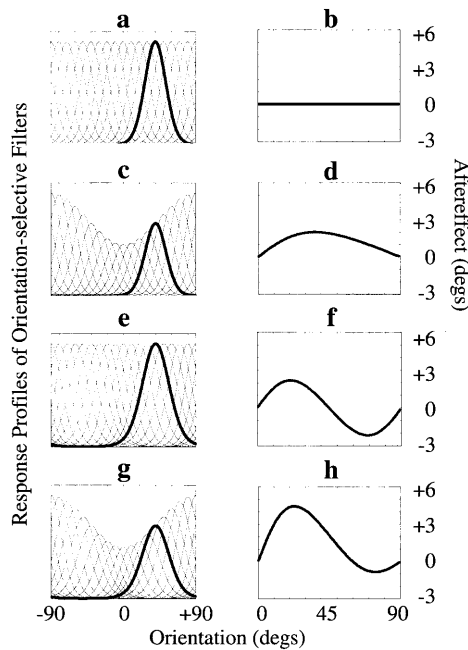

Fig. 7. (a) The responses of 18 orientation-selective filters peaking 10° apart. The tuning curve of the filter peaking at +40° is shown in bold for illustrative purposes. In the unadapted state, the filters have equal peak responses and a full-width at half-height of 30°, which produces veridical estimates at all orientations (b). To simulate the effects of an oriented adapting stimulus, we adjust the filter responses in two ways. First, we inhibit the responses of filters tuned to nearby orientations (c). This shifts the population response away from the adapting orientation (d). Second, we increase the orientation band-width of filters with preferred tunings away from the adapting orientation (e). This produces direct and indirect effects of similar magnitude (f). In combination (g), inhibition around the adapting orientation and broadening away from the adapting axis produce an angular tuning function of the form observed psychophysically (h).

decreases in the signal-to-noise ratio of neurons responding to the adapting stimulus should not affect discrimination. Thus, the difference in discrimination performance around adapting and orthogonal orientations predicted on the basis of mean differences in perceived orientation should be reduced or even reversed by the effect of decreased signal-to-noise ratio,

and hence increased response variability, around the adapting orientation.

4.2. Computational modelling of post-adaptation orientation discrimination

We have recently proposed a model suggesting that the tilt aftereffect and its spatial analogue, the tilt illusion, result from self-calibration and decorrelation (Barlow & Foldiak, 1989) among the responses of populations of orientation-selective neurons in visual cortex (Clifford, Wenderoth, & Spehar, 2000b). The model employs a double-angle representation in which horizontal and vertical are opposites (Fig. 6), so that 180° in model space corresponds to 90° in tilt (Gilbert & Wiesel, 1990; Vogels, 1990). Each model neuron acts as a 'labelled line', representing its preferred orientation. The response of the model neuronal population is the vector sum of the individual neuronal responses.

To compute the vector sum, each model neuron contributes a vector in the direction representing its preferred orientation with a length proportional to its response. In its unadapted state, the model produces veridical estimates at all orientations (Fig. 7a,b). To simulate the effects of an oriented adapting stimulus, we adjust the neuronal responses in two ways. First, we inhibit the responses of neurons tuned to nearby orientations. This shifts the population response away from the inducing orientation (Fig. 7c,d) in the manner originally proposed by Sutherland (1961). Second, we increase the orientation bandwidth of neurons with preferred tunings away from the inducing orientation. For example, if the inducer is vertical, bandwidth will be broadened most for neurons tuned to oblique orientations (Fig. 7e,f). The broadly tuned profile of inhibition among our model neurons resembles that observed in V1 neurons in the presence of an oriented inducing stimulus surrounding the receptive field (Blakemore & Tobin, 1972). Under similar conditions, changes in the orientation bandwidth of V1 cells have also been reported (Gilbert & Wiesel, 1990). In combination, inhibition around and broadening away from the inducing orientation produce an angular tuning function of the form observed psychophysically (Fig. 7g,h).

We have shown previously that the model can be applied to the domains of orientation, motion and colour to account for the angular tuning functions of aftereffects in those visual modalities (Clifford et al., 2000b). If we assume that detection of an oriented stimulus is limited by the sensitivity of the unit most responsive to that orientation, then the model can also predict the effect of adaptation on contrast detection threshold (see Fig. 8a). Detection thresholds are elevated most around the adapting orientation and unaffected at distant orientations (Gilinsky, 1968; Blakemore & Nachmias, 1971; Regan & Beverley,

1985). Here, we show that the model can be extended to account for the effect of adaptation on orientation discrimination by assuming that discrimination performance depends on two factors. Discrimination between a pair of stimuli is assumed to depend not only upon the mean difference in their perceived orientation, but also on the magnitude of the population response they elicit. The greater the magnitude of the response to a given stimulus, the lower the variability in its perceived orientation. The consequences of these assumptions for the predictions of the model are illustrated in Fig. 8.

The effect of adaptation to a stimulus oriented at 0° on the gains and orientation bandwidths of the model neurons is illustrated in Fig. 8a. The effect of adaptation on perceived differences in orientation is shown in Fig. 8b. Perceived differences in orientation are increased around and orthogonal to the adapting orientation. The increase is larger around the adapting orientation than orthogonal to it, consistent with the relative magnitudes of the direct and indirect tilt aftereffects. However, adaptation markedly reduces the magnitude of the population response to stimuli around the adapting orientation, while leaving the response magnitude around the orthogonal orientation almost unchanged (Fig. 8c). Decreases in response magnitude around the adapting orientation tend to offset the improvements in discrimination performance that would be predicted solely on the basis of increases in mean perceived orientation differences, resulting in smaller reductions in orientation discrimination thresholds around the adapting orientation than or-

thogonal to it (Fig. 8d). The functions plotted in Fig. 8d are the product of those in Fig. 8b,c, and they capture certain essential features of the data. First, discrimination thresholds are lowest orthogonal to the adapting orientation. Second, discrimination performance also improves parallel to the adapting orientation. Third, discrimination performance is maximally impaired for orientations around 10° away from the adapting orientation.

4.3. Comparison with existing data on post-adaptation orientation discrimination and other computational models of tilt adaptation

Our results on the effect of adaptation on orientation discrimination around the adapting orientation are in qualitative agreement with those of Regan and Beverley (1985). They found that orientation discrimination thresholds were decreased by approximately 25% around the adapting orientation, but increased by up to 50–60% for angles of 10–20° between adapter and test. Interestingly, in vernier acuity tasks, angles of 10–20° between mask and target stimuli have also been shown to produce maximal elevation of thresholds, although without reductions for parallel mask and target (Waugh, Levi, & Carney, 1993; Levi & Waugh, 1996; Mussap & Levi, 1997). The results from the naïve subjects tested here were very similar to those of Regan and Beverley (1985): parallel adaptation decreased thresholds by 34%, while adaptation at 7.5° raised them by 41%. The two experienced observers both showed the same trend, although improvements for parallel adaptation were smaller while increases in threshold for 7.5° adaptation were larger.

Barlow et al. (1976) reported that there were no improvements in orientation discrimination as a result of adaptation. In that experiment, the effect of adaptation to a grating parallel to the test stimulus was compared with the effect of orthogonal adaptation, presumably under the assumption that orthogonal adaptation would have no beneficial effect. We also found that thresholds after parallel adaptation were similar to, in fact slightly higher than, those for orthogonal adaptation. However, we measured baseline thresholds in an unadapted condition, while Barlow et al. (1976) did not. When compared with the unadapted condition, our results show that rather than there being no improvement for parallel adaptation, there are in fact improvements in both the parallel and orthogonal conditions.

The model proposed in this study to account for the effects of adaptation on the perception and discrimination of orientation has a functional basis in terms of the robust and efficient coding of image information (Clifford et al., 2000b). Other functional models have been proposed to account for the existence of the repulsive
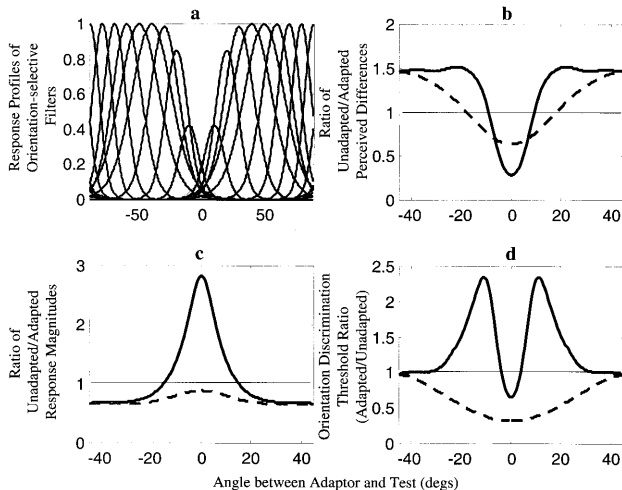

Fig. 8. (a) Response profiles of orientation-selective model neurons after adaptation. Effect of adaptation on (b) mean differences in perceived orientation, (c) magnitude of population response, and (d) orientation discrimination thresholds. The functions plotted in (d) are the product of those in (b) and (c). Bold lines, the adapted state; feint lines, the unadapted; solid lines, adapting orientations around the test orientation (vertical); dashed lines, adapting orientations around the orthogonal.

tilt aftereffect (Regan & Beverley, 1985; Wilson & Humanski, 1993; Dong, 1996; Wainwright, 1999) and the improvement in orientation discrimination after parallel adaptation (Regan & Beverley, 1985; Wainwright, 1999). However, we know of no other model capable of predicting the improvement in orientation discrimination after orthogonal adaptation reported here, let alone the relative magnitudes of the parallel and orthogonal effects.

It is important to note that the functional decomposition of the tilt aftereffect we have proposed (Clifford et al., 2000b) is distinct from the phenomenological direct/indirect distinction, although a similar decomposition has been proposed on the basis of experimental studies manipulating low-level contributions (Morant & Harris, 1965; Wenderoth & Johnstone, 1987). As illustrated in Fig. 7c,d, the effect of response inhibition, which we have previously identified with an error-correcting mechanism at the level of the neuronal population response, contributes to the magnitude of the direct but not the indirect effect. In contrast, the proposed changes in orientation bandwidth, which serve to decorrelate neuronal responses to the prevailing stimulus distribution, contribute in similar measure to the direct and indirect effects (Fig. 7e,f). A combination of these two processes predicts the correct relative magnitude: a larger direct than indirect effect (Fig. 7g,h).

In terms of orientation discrimination, the proposed changes in orientation bandwidth predict improvements of similar magnitude after parallel and orthogonal adaptation (dashed line in Fig. 8d), while response inhibition tends to impair discrimination performance around the adapting orientation (compare solid and dashed lines in Fig. 8d). A combination of these two processes predicts the correct relative magnitude of improvements around the parallel and orthogonal orientations: a larger improvement orthogonal to the adapting orientation (compare Fig. 8d with Fig. 2a,b). Previous models have assumed, somewhat counter-intuitively, that the same process is responsible for elevations in contrast detection threshold and reductions in orientation discrimination threshold around the adapting orientation (Regan & Beverley, 1985; Wainwright, 1999). However, in both models, it was assumed that orientation discrimination depends only upon the mean difference in perceived orientation. No account was taken of the accompanying change in signal-to-noise ratio and the consequent increase in response variability. We have shown that, if response magnitude is taken into account, the response inhibition that impairs contrast detection also tends to impair orientation discrimination around the adapting orientation.

4.4. Implications of tilt adaptation for our understanding of the cortical coding of other sensory dimensions

We have argued previously that the mechanisms underlying orientation perception may be closely related to those in other visual modalities (Clifford et al., 2000b). From a computational perspective, the problem of extracting information from the image signal can be cast as the recovery of orientation information in various domains (Adelson & Bergen, 1991). The common phenomenology of repulsive and attractive adaptation effects in domains such as spatial orientation (Gibson & Radner, 1937) and direction-of-motion (Schrater & Simoncelli, 1998), coupled with enhancements in post-adaptation discrimination around the adapting orientation or direction-of-motion (Phinney et al., 1997), adds psychophysical weight to this theoretical observation. From a neurobiological perspective, it is known that primate primary visual cortex contains columns of orientation-selective cells (Hubel & Wiesel, 1962) while the middle temporal area (V5) contains columns of cells tuned to direction of motion (Albright, Desimone, & Gross, 1984). This columnar architecture is also found elsewhere in the visual cortex and beyond, such as in the auditory cortex (Mountcastle, 1997). Indeed, recent psychophysical studies of auditory spatial localisation have revealed not only repulsive aftereffects, but also improved localisation around the adapting location (Kashino, 1997; Kashino & Nishida, 1998). The theoretical, psychophysical and physiological parallels between visual domains and between vision and audition suggest that insight gained into the mechanisms underlying the perception of tilt could contribute significantly to our wider understanding of neural information processing.

Acknowledgements

Appendix A

We investigated the response properties of a set of 18 orientation-selective filters peaking 10° apart. The response, $f(\theta)$ of each filter as a function of orientation, θ, is defined by an equation of the form:

$$f(\theta) = \alpha \exp\{\beta[\cos(\theta - \theta_0) - 1]\} \qquad (1)$$

where α is the peak response, β controls the width of the tuning curve, and θ_0 is the peak tuning. This function is known as the circular normal distribution, a periodic function with a profile very similar to a Gaussian (Pouget, Zhang, Deneve, & Latham, 1998). In the

unadapted state, all the filters have parameter values of $\alpha = 1.0$ and the same value of β (Fig. 7a). For the simulations in Figs. 1 and 7, the unadapted value of $\beta = 5.0$, giving a full-width at half-height of just over 30°. For the simulation in Fig. 8, the unadapted value of $\beta = 15.0$, giving a full-width at half-height of just over 17°. These values were chosen to provide good fits to the data, but were not crucial to the overall form of the fitted functions. Orientation bandwidths of 17 and 30 are well within the range reported for simple cells in V1 (Watkins & Berkley, 1974).

Each filter acts as a 'labelled line', representing its preferred orientation. The response of each filter is a vector pointing in the direction representing the filter's preferred orientation with a length proportional to the filter's response. The response of the population is the vector sum of the individual filter responses, which produces veridical estimates at all orientations (Fig. 7b). Adaptation to a pattern of orientation ϕ affects the peak responses and widths of the filters as follows. The peak responses after adaptation are given by:

$$\alpha_\phi(\theta_0) = \alpha \left[1 - \lambda \exp\left(\frac{\theta_0 - \phi}{\sigma}\right)^2 \right] \quad (2)$$

and the orientation bandwidths are given by:

$$\beta_\phi(\theta_0) = \beta \{1 - \mu[1 - 2\cos(\theta_0 - \phi)]\} \quad (3)$$

where λ and σ determine the magnitude and range of response compression, respectively, and μ controls the change in bandwidth. It should be noted that, for each filter, the peak tuning, θ_0, is unaffected by adaptation. For the simulation shown in Fig. 5, $\lambda = 0.60$, $\mu = 0.92$, and $\sigma = 25°$, and for the simulation in Fig. 8, $\lambda = 0.90$, $\mu = 0.60$, and $\sigma = 15°$.

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