

The origin of the oblique effect examined with pattern adaptation and masking

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The decreased visibility of obliquely oriented patterns as compared to horizontal or vertical ones is termed the *oblique effect*. The origin of the oblique effect in the chain of visual processing was examined by comparing the potency of oblique adapting gratings to the potency of horizontal ones. Oblique gratings (which were less visible but of equal physical contrast) were as powerful or more powerful than horizontal gratings as adapting stimuli. Obliquely oriented stimuli also produced a slightly stronger tilt aftereffect than stimuli near the cardinal axes. These results suggest that the diminished neural representation of oblique stimuli arises in the human cortex, rather than from impairments of sensitivity or resolution in the initial geniculo-cortical projection.

Keywords: oblique effect, orientation tuning, spatial vision, tilt aftereffect, masking, pattern adaptation, meridional anisotropy

Introduction

Performance on a large number of visual tasks is superior when the stimuli are oriented vertically or horizontally compared to when they are obliquely oriented. This effect was first noted in 1861 by Ernst Mach (Mach, 1861) and has subsequently been shown to also exist in children and in numerous animal species (Appelle, 1972). Oblique contours also need greater contrast to become visible. The reduced effectiveness of oblique contours compared to horizontal or vertical ones is referred to as the *oblique effect*. Although many studies have documented the existence of an oblique effect for both detection and discrimination tasks, its origin remains largely a mystery. In the 1960's two groups of researchers showed that the oblique effect was present for laser interference fringes projected directly onto the retina (Campbell, Kulikowski, & Levinson, 1966; Mitchell, Freeman, & Westheimer, 1967). Because this technique bypasses the optical blurring of the eye and diffraction by the pupil, these experiments implied a retinal or higher level origin for the effect. In 1970, Maffei and Campbell (Maffei & Campbell, 1970) showed that the oblique effect could be observed in the cortical evoked potential, but could not be observed in the electroretinogram, implying that the oblique effect arises somewhere between the site of origin of the electroretinogram and the cortical evoked potential. Consistent with this, fMRI measurements have demonstrated an oblique effect in the summed neural signal over human V1 (Furmanski & Engel, 2000).

In this paper, psychophysical observations were used together with existing knowledge of the physiology of visual cortex to further localize the origin of the oblique effect. It is well established that orientation-specific pattern adaptation first occurs in the visual cortex (Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979; Ohzawa, Sclar, & Freeman, 1982; Shou, Li, Zhou, & Hu, 1996). Although previous data suggested that simultaneous masking occurs later than the desensitizing effects of pattern adaptation (Carandini, Heeger, & Movshon, 1997), recent masking experiments in V1 suggest that masking is first produced in the LGN and is bolstered by synaptic depression at the thalamocortical synapse (Freeman, Durand, Kiper, & Carandini, 2002).

Our experiments were designed to test whether the decreased visual effectiveness of oblique patterns develops prior to, or subsequent to, the site of pattern adaptation and masking in human cortex. If the visual effectiveness of an oblique grating's neural signal is decreased prior to the site of adaptation or masking, then an oblique grating should be less powerful as an adapting or masking stimulus than a horizontal one (which is oriented along a cardinal axis). However, if the visual effectiveness of oblique gratings is not degraded until after the site of adaptation or masking, then an oblique adapting or masking grating should be just as powerful as a horizontal one. This framework assumes that the suprathreshold oblique adapting (and masking) gratings undergo a decrease in visual effectiveness at some stage of visual processing. This assumption is supported by contrast matching experiments (St. John, Timney, Armstrong, & Szpak, 1987) that showed that the absolute magnitude of

the oblique effect for a high spatial frequency grating (20 c/deg) does not decline with increasing contrast.

Our hypothesis was tested by comparing the potency of full contrast 45° oblique and horizontal adapting and masking gratings in order to raise the contrast needed to detect an intermediately oriented test pattern. The test grating that was set to contrast threshold was always oriented 22.5° counterclockwise from horizontal. This angle was chosen so that the 45° oblique and horizontal adapting and masking gratings were always equal in angular separation from the test grating. The first two experiments revealed that the oblique grating was not less powerful than the horizontal one in raising the contrast threshold of the intermediately oriented test grating. In fact, the oblique grating was slightly more powerful than the horizontal.

Prolonged viewing of a grating makes a subsequently viewed grating of similar orientation appear to be tilted away from the adapting grating, a phenomenon referred to as the tilt aftereffect (Howard, 1982). A third experiment examined the tilt aftereffect for a 22.5° oriented test stimulus. Consistent with the first two experiments, it was found that an oblique adapting grating did not produce a smaller tilt aftereffect than a horizontal adapting grating. Indeed, the oblique adapting gratings tended to be slightly more powerful than the horizontal ones. These results are discussed within the framework of a model that proposes skewed orientation tuning curves for tilted orientations (Figure 1). The skewing for cells, or neural channels, maximally sensitive to a tilted orientation (like our 22.5° test stimuli) preserves sensitivity to oblique contours, while making the channel insensitive to stimuli tilted an equal angular distance toward the horizontal axis.

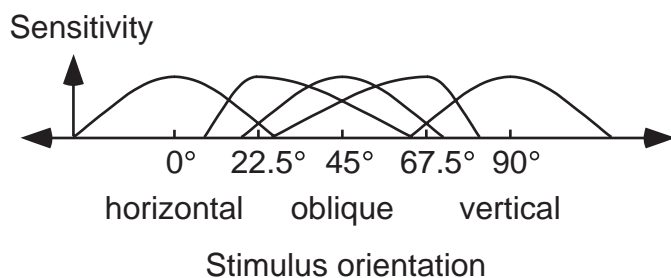


Figure 1. Asymmetric tuning curve model. This model proposes asymmetric orientation tuning curves for cortical cells (or neural channels) that are most sensitive to tilted orientations, such as our 22.5° test grating. The skewing preserves sensitivity to oblique contours, while making the channel insensitive to stimuli tilted an equal angular distance toward the horizontal axis.

Methods

Observers

Experiments were conducted on four naïve subjects with normal vision (JS, RS, JJ, and RB). The authors MM, a protanopic subject with normal acuity, and DM, a deuteranomalous subject with normal acuity, also served as subjects.

Apparatus

Stimuli were produced by a two channel 633 nm laser interferometer (He & MacLeod, 1996). This technique allows high contrast sinusoidal fringes to be projected directly onto the subject's retina, without contrast losses caused by optical aberrations or diffraction.

Stimuli

The sinusoidal gratings had a mean troland value of 1706 td (or a radiant flux of 2.87 nW/deg²) and were shown within a 3° circular field on a dark background. Preliminary experiments were conducted on each subject to confirm the existence of an oblique effect.

Procedure

Experiment 1: Adaptation

The contrast threshold for a 10 c/deg test grating oriented 22.5° counterclockwise from horizontal was measured after adaptation to either a 10 c/deg horizontal grating or, in separate sessions, after adaptation to a 10 c/deg oblique grating oriented 45° counterclockwise from horizontal (all gratings were 15 c/deg for observer DM). The subject viewed a full contrast adapting pattern for 5 seconds. After a 250 ms zero contrast interval a 250 ms test interval was presented. The observer was instructed to respond "yes" only when he could detect a grating and resolve its orientation during the test period. The "yes" or "no" response initiated the next trial, with the Log of the test grating's Michelson contrast varying under control of an up-down staircase procedure. Sessions for the two adaptation conditions were randomly interleaved. The threshold contrast was estimated as the 50% "yes" contrast on a cumulative Gaussian psychometric function fit to the data from a minimum of 200 trials per condition. During the entire experiment, subjects tracked a fixation point that moved in a small circle centered within the stimulus. The tracking eye movements traversed multiple grating cycles during each presentation to prevent retinal afterimages. In a preliminary session, the baseline contrast threshold for the test grating was measured using a zero contrast adapting grating.

Experiment 2: Masking

The contrast threshold for a 10 c/deg test grating oriented 22.5° counterclockwise from horizontal was measured in the presence of either a simultaneously presented 10 c/deg horizontal or, in separate sessions, a 45° masking grating (all gratings were 30 c/deg for observer DM). The masking grating had a Michelson contrast of 0.60 for observers RS and JS, and 0.40 for observer MM. A lower masking contrast was necessary for subject MM to prevent detection of a difference frequency grating (see next paragraph). 250 ms intervals of the full contrast masking grating alone and the masking grating plus test grating were presented with a 500 ms inter-stimulus interval. The observer adjusted the contrast of the test grating until he could just see the test grating, and resolve its orientation, during the mask plus test interval. The subject's response initiated the next trial. Sessions for the two masking conditions were randomly interleaved. There was no fixation point present, but the observer was instructed to view the center of the test field. With the high spatial frequency used, the uncertainty of fixation from presentation to presentation was large enough to ensure that there was no retinal afterimage of the masking grating. In a preliminary session, the baseline contrast threshold for the test grating was measured using a zero contrast masking grating.

Simultaneously presented gratings of the same spatial frequency and different orientation, such as those used in this experiment, can produce moiré patterns, gratings with a spatial frequency given by the vector difference between the components, through visual system nonlinearity (MacLeod, Williams, & Makous, 1992). The difference frequency gratings produced by the two masking conditions had the same spatial frequency, but their orientations differed by 22.5°. Our observers reported that the difference frequency grating was not subjectively apparent at the contrast levels used in this experiment, and it has been previously shown that the contrast of a difference frequency grating is very low when one of the component gratings is at contrast threshold (Willis, Smallman, & Harris, 2000). Despite this, we thought it appropriate to increase the spatial frequency of the two masking gratings by 0.8 c/deg ($1/\cos(22.5^\circ)$). This slightly increased the spatial frequency of the difference frequency gratings for both conditions, and ensured that they were the same orientation.

Experiment 3: Tilt Aftereffect

Prior to this experiment, a fine black comparison line was placed across a 1.3° diameter test field and oriented roughly perpendicular to a 15 c/deg test grating oriented 22.5° counterclockwise from vertical. The tilt aftereffect produced by 15 c/deg adapting gratings oriented 15° clockwise and 15° counterclockwise from the test grating were measured in separate sessions. The subject viewed a full contrast adapting pattern for 5 seconds. After a 250

ms zero contrast interval, a 250 ms full contrast test grating was presented. The observer reported the tilt direction of the test grating with respect to the perpendicularly oriented comparison line. The response initiated the next trial, with the test grating orientation varying in 0.5° steps under control of an up-down staircase procedure. The adaptation data for each subject was gathered in two sessions. In the first session, the trials were conducted in four blocks, in ABBA order. In the second session, the trials were blocked in BAAB order. Subjects completed a total of 200 trials per adaptation condition. The adaptation-affected test grating orientation was estimated as the 50% "clockwise" tilt response on a cumulative Gaussian psychometric function fit to the data. A preliminary condition using a zero contrast adapting grating provided a measurement of the test angle that was judged as perpendicular to the comparison line. Tilt aftereffect magnitude for each condition was computed as the angular difference between the adaptation-affected orientation and the baseline orientation setting.

All observers completed initial runs of each condition with the comparison line oriented 22.5° counterclockwise from vertical. After each subject's performance stabilized, the comparison line was rotated 90° and the experiment was conducted as described above. This procedure ensured that each subject was practiced at the perpendicularity setting task, but had no previous exposure to high contrast adapting or test stimuli at the orientations used for the experiment.

The tilt aftereffect has previously been measured using scaling, parallel setting, dot alignment, and discrimination of angle size techniques (Howard, 1982). In these methods, the physical location of the comparison stimulus must be placed far enough away from the adapting/test location to ensure that the adaptation affects only the orientation of the test stimulus, leaving the comparison stimulus unaffected. Our novel technique for measurement of the tilt aftereffect used a perpendicular comparison line. This avoided the problem described above by allowing the adapting, test, and comparison stimuli to be presented in one spatial location. Two findings support the use of this technique: judgments of perpendicularity can be made with precision (Wheeler Onley & Volkman, 1958) and the perceived orientation of the comparison line is unaffected by the adapting grating, which differs in orientation by 75°.

Results

In preliminary experiments, the contrast threshold of a 10 cycles/degree of visual angle (c/deg) sinusoidal laser interference fringe was measured as a function of orientation (the spatial frequency was 15 c/deg for observer DM). The presence of an oblique effect in the subjects participating in subsequent experiments was

verified, with subjects RS, JS, MM, and DM showing 0.31, 0.31, 0.26, and 0.23 Log unit differences in contrast threshold between horizontal and 45° oblique gratings.

Adaptation Experiment

The threshold elevation of a 22.5° test grating was measured after adaptation to a horizontal grating and after adaptation to a 45° grating. If the decreased visual effectiveness of oblique patterns is produced prior to the site of adaptation, then the horizontal adapter should be less powerful in elevating the contrast threshold of the intermediately oriented test than the horizontal adapter. Experiments were performed on four observers. The threshold elevations produced by both adapting gratings for each subject are shown in Figure 2. The gray areas denote the SEM of the baseline condition for each subject. The data are displayed in Log units (base 10) of threshold elevation from this baseline value. Error bars = +/- SEM. The oblique adapter was not less powerful than the horizontal adapter. In spite of its reduced visibility, the oblique adapter produced more threshold elevation of the 22.5° test than the horizontal adapter.

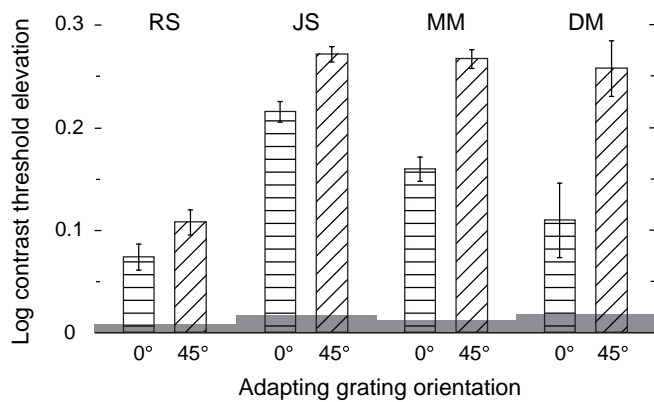


Figure 2. Pattern Adaptation. The threshold elevation for a test grating oriented 22.5° counterclockwise from horizontal was measured after adaptation to a horizontal grating and after adaptation to a 45° grating. If the decreased visual effectiveness of oblique patterns is produced prior to the site of adaptation, then the horizontal adapter should be less powerful in producing a threshold elevation of the intermediately oriented test than the horizontal adapter. This figure shows the threshold elevations produced by both adapting gratings for four subjects. The oblique adapter was not less powerful than the horizontal adapter. In spite of its reduced visibility, the oblique adapter produced slightly more threshold elevation of the 22.5° test than the horizontal adapter.

In a control experiment, we confirmed that the amount of threshold elevation produced by a 45° adapting grating on a 45° test was not significantly different from the amount of threshold elevation produced by a 0° adapting grating on a 0° test (Figure 3).

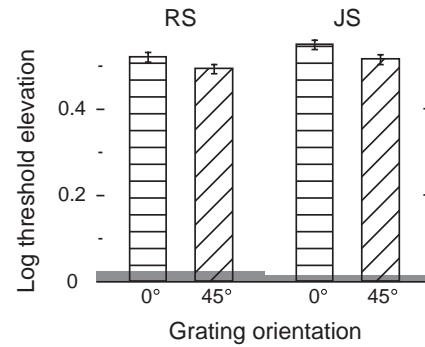


Figure 3. Adaptation control experiment. The threshold elevation produced by adapting to a grating of the same orientation as the test was measured for horizontal and oblique orientations. The amount of threshold elevation produced by a 45° adapting grating on a 45° test was not significantly different from the amount of threshold elevation produced by a 0° adapting grating on a 0° test for the two subjects.

Masking Experiment

The threshold elevation of a 22.5° test grating was measured in the presence of a simultaneously presented horizontal masking grating and a 45° masking grating. Experiments were performed on the same four observers. The threshold elevations produced by both masking gratings for each subject are shown in Figure 4. The gray areas denote the SEM of the baseline condition for each subject. The data are displayed in Log units (base 10) of

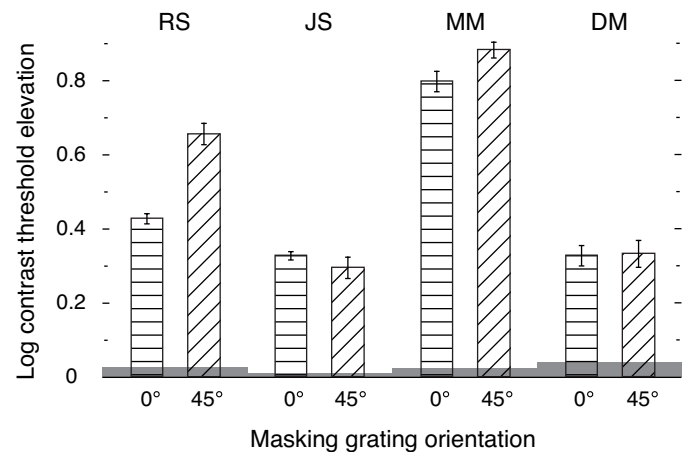


Figure 4. Masking. The threshold elevation for a test grating oriented 22.5° counterclockwise from horizontal was measured in the presence of a simultaneously presented horizontal masking grating or a 45° masking grating. This figure shows the threshold elevations produced by both masking gratings for four subjects. For RS and MM, the oblique adapter produced slightly more threshold elevation of the 22.5° test than the horizontal masking grating. The oblique masking grating was not significantly less powerful than the horizontal one for JS and DM.

threshold elevation from this baseline value. Error bars = \pm SEM. For subjects RS and MM, the oblique adapter produced slightly more threshold elevation of the 22.5° test than the horizontal masking grating. The oblique masking grating was not significantly less powerful than the horizontal one for JS or DM.

Tilt Aftereffect Experiment

Measurements were made of the tilt aftereffect produced on a tilted test (roughly 22.5° degrees counterclockwise from vertical) by adapting gratings rotated either 15° more obliquely, or 15° more vertically, than the test. The results are shown in Figure 5. The errors of the tilt aftereffect magnitudes were calculated as the square root of the sum of the squares of the pre- and post-adaptation angle estimate errors. The 95% CI was calculated using a bootstrapping procedure. For comparison with the other data sets, the error estimate was converted to SEM by dividing by 1.96. Error bars = \pm SEM. The gray areas denote the SEM of the baseline condition for each subject. The magnitude of the tilt aftereffect was larger with the more oblique adapting grating than with the more vertical adapting grating for three or four subjects tested. However, the difference in tilt aftereffect magnitude for the two adapting conditions was only statistically significant for observer DM.

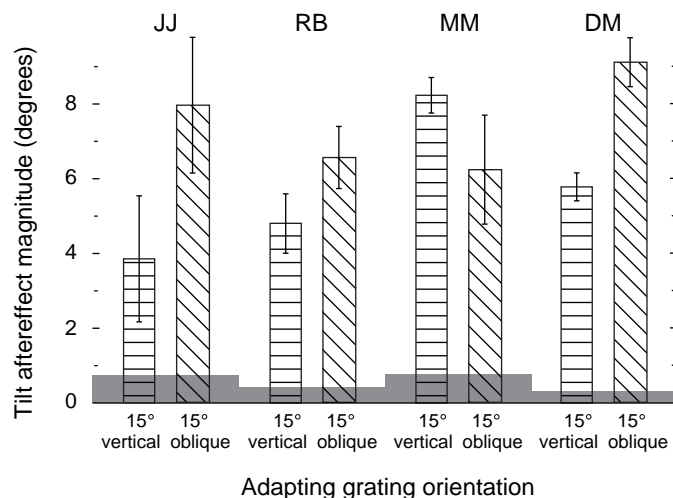


Figure 5. Tilt aftereffect. The tilt aftereffect was measured for four subjects. The test stimulus was a grating oriented roughly 22.5° degrees counterclockwise from vertical. Adapting gratings were oriented either 15° more obliquely, or 15° more vertically, than the test stimulus. The tilt aftereffect was larger with the more oblique adapting grating than with the more vertical adapting grating for three of the four subjects. The difference in tilt aftereffect magnitude for the two adapting conditions was only statistically significant for observer DM.

Discussion

At least four relatively low level physiological models have been proposed to explain the oblique effect. Two of them, which suggest a more robust neural representation for cardinal than for oblique orientations, can be classified as "gain" models. The first suggests that there are more cells (Mansfield, 1974; Orban, Vandebussche, & Vogels, 1984), or more cortical area (Coppola, White, Fitzpatrick, & Purves, 1998), devoted to horizontal and vertical orientations than to obliques. If this were the case, then oblique adapting and masking gratings would be expected to produce a weaker effect on the intermediately oriented test pattern, by virtue of their diminished neural representation at the cortical site where masks or pre-exposed patterns modify contrast sensitivity. The finding that oblique adapting and masking gratings are not less powerful than horizontal ones provides evidence against this explanation. Measurements of orientation discrimination in the presence of varying amounts of orientation noise also argue against a gain-based explanation (Heeley, Buchanan-Smith, Cromwell, & Wright, 1997). In a variation on the gain-based model, Dragoi et al. (Dragoi, Sharma, & Sur, 2000; Dragoi, Turcu, & Sur, 2001) suggested that a greater cortical area devoted to cardinal orientations makes their responses more stable, or resistant to modification by adaptation to other orientations. In contrast, obliquely tuned cells, which are more likely to be surrounded by cells with different orientation preference, would be more susceptible to adaptation. This model does not explain our finding that a test grating oriented at 22.5° is affected more by adaptation to a 45° grating than by adaptation to a horizontal grating.

The second model proposes that cortical cells tuned to horizontal and vertical orientations are more sensitive than cells tuned to obliques. This explanation accounts for the detection oblique effect, but is not easily reconciled with the observation that angled lines are perceived as tilted toward the nearest oblique (Lennie, 1971). It also cannot account for experiments that demonstrate the persistence of an oblique effect for vernier acuity when the horizontal and oblique lines are made equally detectable or discriminable (Saarinen & Levi, 1995). Versions of this scenario, where the orientation-dependent variation in sensitivity arises before the site of pattern adaptation and masking, predict that horizontal stimuli should be more powerful as adapting and masking stimuli than equal contrast obliques. This prediction is contrary to our results.

A third explanation of the oblique effect posits narrower tuning curves for horizontal and vertically tuned cells than for obliques (Andrews, 1967). This would account for the orientation-discrimination oblique effect because cells tuned to horizontal and vertical orientations would have steeper tuning curves, making them more

sensitive to changes in orientation. The gradually sloping tuning curves for obliques would render them less sensitive to changes in orientation (Regan & Beverley, 1985). Depending on the quantitative parameters of the model, the orientation of minimum angular discrimination performance would not necessarily be 45° (Regan & Price, 1986). If one imagines that detection is governed by a "winner takes all" process, then the narrowness of the tuning curves (with equal peak sensitivity) should have no effect on the contrast needed to detect a grating. However, if detection is governed by a weighted sum of units stimulated by the test grating, then wider tuning curves for obliques should give them an advantage for detection. This is because more cells tuned to nearby orientations would be stimulated when the test was obliquely oriented. Such a reverse oblique effect for detection has not been observed. (A reverse oblique effect has, however, been shown for two tasks that require the extraction of form from random dot patterns (Regan & Regan, 2002; Wilson, Loffler, Wilkinson, & Thistlethwaite, 2001)). Orientation tuning measurements in primate (De Valois, Yund, & Hepler, 1982) and cat (Dragoi et al., 2000) do not reveal a variation in tuning curve width with orientation. In our experiment the test was always oriented at 22.5° . The extent to which the two adapting or masking stimuli elevated the threshold would depend on their strength within the neural channel used for detecting 22.5° orientations. By this logic, different tuning curve widths for horizontal and oblique orientations should have no effect on their adapting or masking efficacy on the 22.5° test. Therefore, this model is also unable to account for our findings.

A fourth model proposes that obliquely tuned units contain more intrinsic neural noise than horizontally or vertically tuned units. However, noise-titrated orientation acuity experiments (Heeley et al., 1997) have demonstrated that differences in noise between cardinal and obliquely tuned units cannot be the cause of the oblique effect.

Although our observers had contrast thresholds that were 0.3 Log units higher for oblique gratings than for horizontal gratings, oblique patterns were not less effective than horizontal ones as adapting or masking stimuli. This result is problematic for the models reviewed above, but it is consistent with the prediction that the decreased visual effectiveness of oblique stimuli arises after the site of pattern adaptation and masking in cortex. To view the experimental results within this hierarchical framework, it is important to review what is known about the anatomical loci of pattern adaptation and masking.

Pre-adaptation to spatial contrast has been shown to produce a tonic hyperpolarization of cells in the cat primary visual cortex, without affecting the stimulus driven modulations of membrane potential. This hyperpolarization makes the cell less likely to reach spike threshold in response to all subsequently presented stimuli in an unselective manner (Carandini & Ferster,

1997; Sanchez-Vives, Nowak, & McCormick, 2000). Psychophysical experiments have shown that pattern adaptation produces a decrease in visibility for subsequently presented patterns that is strongest when the test pattern is the same as the adapting pattern (Blakemore & Campbell, 1969; Gilinsky, 1968). This additional selective component of pattern adaptation has also been demonstrated in cortical cells (Carandini, Movshon, & Ferster, 1998; Movshon & Lennie, 1979), suggesting that in addition to a tonic hyperpolarization, adaptation selectively alters the synaptic weights of the inputs to a cortical cell or modifies the connections between different groups of cells.

Masking has been actively used to study spatial vision for decades, but it has only been recently that detailed physiological models have been proposed to account for masking phenomena (Carandini et al., 1997; Foley, 1994; Freeman et al., 2002). A recent series of V1 physiology experiments resulted in the conclusion that the masking effect is generated partly in the LGN and is supplemented by synaptic depression at the thalamocortical synapse (Freeman et al., 2002). This proposal, that masking originates earlier in visual processing than pattern adaptation, could explain why the adaptation experiment produced a stronger pattern of asymmetry between oblique and horizontal than the masking experiment.

Older models of masking were based on the premise that units respond with a compressive nonlinearity (Legge & Foley, 1980). The addition of a masking stimulus to a test stimulus drives a given unit into the compressive range, requiring more of the test stimulus to elicit a criterion response. A key feature of such models is that the various units undergo *independent* modification of their sensitivities. Renewed interest in contrast gain control sparked a new class of models (Foley & Chen, 1997; Watson & Solomon, 1997), which normalize the linear response of each unit by a measure of stimulus energy from a large pool of neurons (Carandini & Heeger, 1994; Geisler & Albrecht, 1992; Heeger, 1992). These models suggest that masking and adaptation are the result of this nonlinear contrast gain control, or normalization, in primary visual cortex.

Based on the assumption of independent sensitivity regulation, an adapting or masking stimulus would elevate the threshold of a test grating if and only if the mask was detected by the same mechanism as the test. With the "normalization pool" scenario, the mask must affect the pooled signal that modulates sensitivity for a particular test. In either case, our results could be due to the neural representation of the oblique stimulus being slightly more powerful than the horizontal one (i.e., a reverse oblique effect) prior to the site of adaptation or masking. This would cause oblique stimuli to excite the test channel more than horizontal stimuli, and therefore result in stronger adaptation and masking.

An alternative possibility is that the strength of the oblique and horizontal stimuli is the same, but the neural channel that detects the 22.5° test is slightly more sensitive to oblique orientations than to horizontal orientations. This would require the orientation tuning curves within the 22.5° channel to be skewed such that the tail would be longer on the oblique side than on the horizontal side, making them insensitive to the major axis but still sensitive to the diagonal (Figure 1). This model would predict our unexpected result that 45° adapters and masks are more powerful than horizontal ones at raising the threshold of a 22.5° test. The 22.5° channel would contain units that have greater sensitivity to the adapting and masking gratings that are at 45° than to horizontal stimuli, causing greater adapting and masking efficacy for the oblique stimuli.

A model of this sort also produces qualitative predictions that are compatible with several other experimental results. It predicts better orientation discrimination around horizontal and vertical orientations than around oblique orientations. This is because a small change in orientation would produce a greater change in response where the slopes of the tuning curves are the greatest. The skewing of intermediately tuned curves makes those cells, along with those maximally sensitive to 45°, least sensitive to changes in orientation because of their shallower tuning curves for oblique orientations. The model is also compatible with the observation that 22.5° lines are perceptually closer to 45° than 0° (Lennie, 1971). This is because cells that are most responsive to 22.5° are often excited by orientations that also stimulate more obliquely tuned cells and the similarity in these neural representations could lead to the perceptual similarity of the stimuli. Previous researchers have found greater adapting (Gilinsky & Mayo, 1971) and masking (Campbell & Kulikowski, 1966) half-widths for oblique than for horizontal and vertical stimuli: a result that would also be expected if oblique stimuli activate a wider range of orientation channels.

On the other hand, this skewed tuning curve model does not, without further assumptions, account for the decreased detectability of oblique stimuli. It is possible, as we have suggested, that the detection sensitivity losses for oblique stimuli occur at stages of visual processing subsequent to the site of pattern adaptation and masking. Alternatively, if they occur at prior stages, the effect of the asymmetry in tuning at 22.5° must be enough to outweigh them in our experiments. It should also be noted that although our experimental results cast doubt on gain- and sensitivity-based explanations of the oblique effect, they do not directly contradict them. It is possible that gain or sensitivity differences exist, but that they are overshadowed by other mechanisms in our experiments.

The validity of this model has a bearing on the still contentious issue of the role of intracortical connections,

as opposed to afferent connections from the LGN, in shaping orientation selectivity (Ringach, Bredfeldt, Shapley, & Hawken, 2002; Sompolinsky & Shapley, 1997). Assuming that the distribution of receptive field centers among a cortical unit's afferents had even or odd symmetry, it could not generate an asymmetrical tuning curve. However, intracortical connections could. To account for our results, such asymmetries must be introduced into the neural representation at or before the site of pattern adaptation and masking.

Prolonged viewing of a grating makes a subsequently viewed grating of similar orientation appear to be tilted away from the adapting grating (Howard, 1982). This effect, often referred to as the tilt aftereffect or successive tilt contrast, is thought to reflect a skewing of the distribution of activity over orientation-selective cells (Gilbert & Wiesel, 1990). It is likely that the skewing is produced by the same orientation-selective sensitivity reduction reflected in contrast threshold measures after pattern adaptation. To specifically test the model that channels tuned to tilted orientations are more sensitive to oblique than to vertical stimuli, measurements were made of the tilt aftereffect produced on a tilted test (roughly 22.5° degrees counterclockwise from vertical) by adapting gratings rotated either 15° more obliquely, or 15° more vertically, than the test. The magnitude of the tilt aftereffect was larger with the more oblique adapting grating than with the more vertical adapting grating for three or four subjects tested (Figure 5). However, the difference in tilt aftereffect magnitude for the two adapting conditions was only statistically significant for observer DM. This asymmetry in the orientation tuning of the tilt aftereffect provides some, if limited, support for the model.

Asymmetry in the orientation selectivity of cells in cat cortex has previously been demonstrated (Henry, Dreher, & Bishop, 1974; Rose & Blakemore, 1974), with one study reporting that 60% of cells in cat area 17 showed tuning asymmetries in excess of 20% (Hammond & Andrews, 1978). Unfortunately, none of these studies reported the relationship between preferred orientation and degree of asymmetry. Allison and Bonds (Allison & Bonds, 1994) demonstrated that inactivation of the infragranular layers of cat cortex with GABA broadens the orientation tuning of supragranular visual neurons. In most cells, the broadening was asymmetric, suggesting that intracortical inhibition could play a role in producing asymmetric orientation tuning curves. Asymmetries in orientation tuning have not been reported in primate cortex, but it is possible that skewing has not been seen because of a tendency to measure orientation tuning with a small number of orientations and to fit the data with symmetric functions (Swindale, 1998) or because orientation tuning is now often quantified by the circular variance of a cell's response to different orientations.

Conclusions

The results of these experiments indicate that the neural representation of obliquely oriented stimuli is not impoverished at the site of pattern adaptation or masking. The data are not compatible with explanations of the oblique effect that require more numerous, more sensitive, or more narrowly tuned neurons for horizontal and vertical orientations than for obliques. These results, as well as data from other published experiments, are compatible with a model where cortical cells tuned to tilted orientations have skewed tuning curves, with higher sensitivity for more oblique orientations than for the major axes.

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