An anisotropy of orientation-tuned suppression that matches the anisotropy of typical natural scenes

Edward A. Essock
Department of Psychological and Brain Sciences, University of Louisville, Louisville, KY, USA

Andrew M. Haun
Department of Psychological and Brain Sciences, University of Louisville, Louisville, KY, USA

Yeon Jin Kim
Department of Psychological and Brain Sciences, University of Louisville, Louisville, KY, USA

Broadband oriented-noise masks were used to assess the orientation properties of spatial-context suppression in ‘general’ viewing conditions (i.e., a fixated, large field of ‘naturalistic’ noise). Suppression was orientation-tuned with a Gaussian shape and bandwidth of 40° that was consistent across test orientation (0°, 45°, 90°, and 135°). Strength of suppression was highly anisotropic following a “horizontal effect” pattern (strongest suppression at horizontal and least suppression at oblique test orientations). Next, the time course of anisotropic masking was investigated by varying stimulus onset asynchrony (SOA). A standard “oblique effect” anisotropy is observed at long SOAs but becomes a “horizontal effect” when a noise mask is present within approximately 50 ms of the test onset. The orientation-tuned masking appears to result from an anisotropic gain-control mechanism that pools the weighted responses to the broadband mask, resulting in a changeover from oblique effect to horizontal effect. In addition, the relative magnitude of suppression at the orientations tested corresponds to the relative magnitudes of the content of typical natural scenes at the same orientations. We suggest that this anisotropic suppression may serve to equalize the visual system’s response across orientation when viewing typical natural scenes, ‘discounting’ the anisotropy of typical natural scene content.

Keywords: contrast gain control, contrast normalization, horizontal effect, natural scenes, 1/f noise, oblique effect, surround suppression, SOA, masking


Introduction

It is now evident that cortical neurons do not function simply as independent, parallel linear filters of the spatio-temporal stimulus image (e.g., reviewed in Carandini, 2004; Shapley, 2000; Wilson & Wilkinson, 2004). Neuronal output has been shown to be altered by the activity of other neurons tuned to other orientations and/or spatial frequencies (e.g., Blakemore & Tobin, 1972; Bonds, 1989; DeAngelis, Freeman, & Ohzawa, 1994; DeAngelis, Robson, Ohzawa, & Freeman, 1992; Heeger, 1992; Heeger, Simoncelli, & Movshon, 1996). Thus, the response of a given neuron to a specific stimulus will be altered considerably when that stimulus is in a scene with many stimulus components present as compared to when the stimulus is viewed in isolation.

These nonlinear interactions between different cortical neurons tuned to different spatial frequencies and orientations are typically viewed as types of contrast adaptation, masking, or suppression (see Rust & Movshon, 2005 for a review), perhaps serving to optimize neural responses based on the contrasts of other components in the scene being viewed. At least some of these mechanisms can profitably be modeled as a divisive contrast gain control, or contrast normalization, process (Carandini, Heeger, & Movshon, 1997; Geisler & Albrecht, 1992; Heeger, 1992; Schwartz & Simoncelli, 2001; Wilson &Humanski, 1993). We have recently suggested (Essock, DeFord, Hansen, & Sinai, 2003; Hansen & Essock, 2004, 2005, 2006; Hansen, Essock, Zheng, & DeFord, 2003) that within the orientation dimension this suppression might be expected to be greater at certain dimension values due to the greater number of neurons tuned to those orientations. Specifically, there is evidence that in several species there are fewer neurons tuned to oblique orientations than horizontal or vertical orientations (De Valois, Yund, & Hepler, 1982; Kennedy, Martin, Orban, & Whitteridge, 1985; Maffei & Campbell, 1970; Mansfield, 1974; Mansfield & Ronner, 1978; Zemon, Gutowskif, & Horton, 1983), and more recently, it has become apparent that there are also relatively more neurons tuned to horizontal than vertical (Li, Peterson, & Freeman, 2003; see also figures in Chapman & Bonhoeffer, 1998; Chapman, Stryker, & Bonhoeffer, 1996; Coppola, White, Fitzpatrick, & Purves, 1998; Mansfield, 1974; Mansfield & Ronner, 1978; Tiao
oblique effect to a horizontal effect. Effect to determine the timeframe within which a broad-
measured the time course of this broadband suppression horizontal test orientation. In the second experiment, we weakest at oblique orientations and strongest at the suppression is indeed orientation-tuned and that it is profile, assess its shape, and compare its tuning properties was varied in order to measure its orientation tuning was always made up of a range of content (usually a2 0
and vertical gratings better than oblique gratings (e.g., Campbell, Kulikowski, & Levinson, 1966; Mitchell, Freeman, & Westheimer, 1967). However, when tested with broadband patterns (e.g., natural scenes) instead of narrowband stimuli (e.g., an isolated grating), humans see oblique content best, vertical next best, and horizontal worst (Essock et al., 2003; Hansen & Essock, 2004, 2005, 2006; Hansen et al., 2003). We have suggested that if a type of suppression is orientation-tuned (i.e., it draws from only neighboring orientations rather than all orientations equally) this “horizontal effect” would be predicted on the basis of the neural numerical bias, the responses pooled in a contrast normal-
weight) be greatest for stimulus content near horizontal orientation (see Figure 1A). Thus each noise pattern was band that were the mirror images about the test’s
construction together random-phase sine gratings across 7 octaves in 0.25 octave steps from 0.2 to 25.6 cpd (1 to 128 cycles per 512 pixels) in a 5° orientation band (1° steps). Also summed were the (random-phase) sine waves in a 5° band that were the mirror images about the test’s orientation (see Figure 1A). Thus each noise pattern was constructed as a pair of 5°-wide orientation bands centered ±5°, 15°, 25°, 35°, or 45° from the test grating orientation (shown in Figure 1). All components had equal amplitude, equivalent to a ‘naturalistic’ 1/f² slope in the Fourier domain (Field & Brady, 1997). The 20 mask patterns were

Methods

General

Contrast sensitivity was measured for an 8-cpd sine grating (Gaussian windowed to 1.6° width at half-height) at each of four orientations (0°, 45°, 90°, and 135° clockwise from vertical), presented foveally. A fairly high spatial frequency was selected in order to test conditions where a significant oblique effect is typically obtained (e.g., Camisa, Blake, & Lema, 1977; Campbell et al., 1966; Essock & Lehmkuehle, 1982; Mitchell et al., 1967). The test grating was added to a noise mask and presented by Vision Research Graphics (VRG) software. Stimuli were displayed on a monochrome (white P104) Image Systems M21LMAX CRT monitor using VRG’s monochrome mode and linearization to greater than 212 levels of luminance (via a VRG grayscale expander; Pelli & Zhang, 1991). Mean luminance of the display was 36 cd/m², resolution was set to 800 by 600 pixels, and refresh rate was 200 Hz.

A QUEST procedure was used to estimate the 75% contrast threshold point in a successive 2AFC paradigm. After a training session, each subject completed the six sessions of the experiment. Each session consisted of one QUEST run of 60 trials at each of the six (Experiment 1) or eight (Experiment 2) conditions of the experiment at each of four test orientations (i.e., 24 (6 × 4) total runs per session in Experiment 1 and 32 (8 × 4) runs per session in Experiment 2). For all data reported, the geometric mean of the six threshold estimates for each condition was calculated and taken as an observer’s threshold. Test order was counterbalanced across sessions. Three different random-phase spectra were created with each being used for two of the six sessions.

Four subjects participated in the first experiment, including two naive to the purpose of the experiment and two of the authors. In an additional control condition (see below) 11 subjects were used (the original four and seven more, six of whom were naive subjects). Three subjects participated in the second experiment, including two naive to the purpose of the experiment and one of the authors (who also participated in the first experiment). Subjects wore any needed correction and all had normal resolution acuity at all meridia. Subjects provided informed consent as approved by the university’s IRB.

Experiment 1

The mask patterns used in the first experiment were constructed in the spatial domain (using Matlab 7.0) by summing together random-phase sine gratings across 7 octaves in 0.25 octave steps from 0.2 to 25.6 cpd (1 to 128 cycles per 512 pixels) in a 5° orientation band (1° steps). Also summed were the (random-phase) sine waves in a 5° band that were the mirror images about the test’s orientation (see Figure 1A). Thus each noise pattern was constructed as a pair of 5°-wide orientation bands centered ±5°, 15°, 25°, 35°, or 45° from the test grating orientation (shown in Figure 1). All components had equal amplitude, equivalent to a ‘naturalistic’ 1/f² slope in the Fourier domain (Field & Brady, 1997). The 20 mask patterns were
then normalized to the group’s maximum deviation from the mean (positive or negative), ensuring that all patterns had the same mean and similar RMS contrast (a range of 0.09 to 0.13, overall mean 0.11), as well as identically scaled amplitude spectra. The process was repeated to produce three sets of imagery with different random-phase spectra. Images were cropped to circles with the circle’s edge ramped to the mean luminance over 8 pixels (leaving a 496-pixel diameter pattern at full contrast). The 5°-diameter stimuli were viewed in a darkened room from 2.58 m through a 5.2° circular aperture in front of the monitor. The 2AFC intervals were 500-ms intervals separated by a 240-ms ISI. In an auxiliary experiment (see below), identical stimuli were created, except a different random-phase spectrum was created on each trial.

Experiment 2

Methods from the second experiment were essentially equivalent to those of Experiment 1, differing only in the following ways. The stimuli were created via an inverse Fourier transform of constructed 1/f amplitude spectra...
with randomized phase, which was then multiplied by a rectangular (i.e., ’ideal’) bandpass filter (see Essock et al., 2003 or Hansen & Essock, 2006 for more details). The spatial frequency band used was four octaves, ranging from 1 to 16 cpd, and the orientation bandwidth was $15^\circ$ (see Figure 1B), similar to the first step of the orientation probe masks of Experiment 1 (which was also $15^\circ$ across but with a central $5^\circ$ gap). These stimuli were made smaller (384 pixels) to meet constraints imposed by the very brief stimulus presentations but were viewed from 1.92 m to result in the same angular size ($5^\circ$) as in Experiment 1.

The mask and target were presented with varying SOA, for 50 ms (10 video frames) each. SOA, defined as the mask onset time minus the target onset time, was varied across 9 values: $-400$, $-200$, $-100$, $-50$, 0 (simultaneous presentation), $+50$, $+100$, $+200$, and $+400$ ms. One of the test intervals contained both the mask and the test target and the other interval contained only the mask. Trial duration was determined by SOA (as shown in Figure 1C) and the ISI was 500 ms.

Results

Experiment 1: Orientation tuning of broadband suppression

Contrast threshold in each condition for the four subjects was averaged and is shown in Figure 2A. When the sine-wave test grating was presented alone (no-mask baseline condition) all four subjects demonstrated an oblique effect in contrast sensitivity (Figure 2B). Thresholds were significantly lower for the $0^\circ$ and $90^\circ$ gratings than for the $45^\circ$ and $135^\circ$ gratings ($t(3) = 5.433$, $p = 0.01$) and did not differ within the $0^\circ$ and $90^\circ$ or the $45^\circ$ and $135^\circ$ pairs ($p > 0.05$). The magnitude of the average oblique effect (cardinal–oblique threshold difference) was $0.15$ log units, typical for a static 8-cpd grating (e.g., see Essock & Lehmkuhle, 1982).

Contrast threshold for the test grating in the presence of the mask, however, showed highest thresholds at horizontal, rather than at oblique orientations (Figure 2A). At the mask closest to the test, contrast threshold was greatest for the horizontal test grating ($1.02$ log contrast), least for the oblique orientations (an average of $1.13$), and roughly intermediate for vertical ($1.12$): a highly significant change in the anisotropy that was obtained when no mask is present ($F(3,9) = 99.161$, $p < 0.001$). The magnitude of this horizontal effect anisotropy is fairly small, likely due to the narrow orientation bandwidth and low local contrast of these masks (cf. Experiment 2, which used masks of higher local contrast and larger orientation bandwidth, and see also Discussion section, below). To illustrate the consistency of the effect, seven additional

Figure 2. (A) Average data for the four observers. Mean contrast threshold for the 8-cpd sine-wave test grating shown at each of the four test orientations ($0^\circ$, $45^\circ$, $90^\circ$, and $135^\circ$). Data are shown for the grating superimposed on the mask probe at each of the five mask locations tested (i.e., the 5° noise masks centered ±5°, 15°, 25°, 35°, or 45° from the test grating’s orientation). (B) Mean data for the grating alone (the no-mask baseline condition) are shown on the left. Individual baseline data show a consistent oblique effect across individuals. (C) To evaluate the generality of the effect, thresholds were measured for 11 subjects with the masks located at the ±5° position (see text). Each subject shows highest threshold at the horizontal test orientation. The group mean is shown at lower right. For (A), ±1 standard error of the group mean is shown; for (B) and (C), ±1 standard error of the mean of 6 replications is shown. Error bars in all subsequent figures (except Figures 3A and 6) also indicate ±1 standard error of the mean.
subjects (11 total) were tested for the first mask position (noise bands centered at ±5°) and results are shown in Figure 2C individually for the 11 subjects. In every case (11 of 11) threshold at horizontal is highest and thresholds at obliques are low (the opposite of the typical (unmasked) ‘oblique effect’ anisotropy). That is, although small in these conditions, the horizontal effect anisotropy is consistent and highly significant (horizontal threshold versus mean oblique threshold, correlated t-test \( t_{(10)} = 7.717, p < 0.001 \)).

To show the orientation tuning of the suppression, threshold elevation (masked threshold divided by baseline threshold) is plotted in Figure 3A as a function of mask-to-target orientation difference.\(^1\) The magnitude of the suppression (termed ‘suppression factor’ after Petrov, Carandini, & McKee, 2005) is seen to be clearly orientation-tuned and has a bandwidth (full width at half-height) of about 40° for all test orientations. Comparison of fall-off of the suppression factor across orientation shows that two differences are apparent in these profiles at the different test orientations. First, there is a stark difference in masking between oblique and cardinal orientations. For example, by 45° from the test orientation, elevation is slight for the oblique test orientations (factors of 1.3 and 1.4) whereas clear suppression for the 0° and 90° targets still remains at 45° away (factors of 2.1 and 2.4 for vertical and horizontal, respectively). The second difference is that horizontal and vertical threshold elevations are more different from each other closer to the peak of the tuning function (i.e., the 5° point) and this difference diminishes away from the peak (e.g., the 35° point). The profile of the tuning curves is essentially Gaussian, and best-fit Gaussians were used to provide the curves plotted in Figures 3A and 3B.

Two further conditions were run. First, to verify that suppression is symmetrical (as assumed above), we tested masking to both sides of the peak separately by using a single 5° mask (Figure 3B). Bandwidth was also approximately 40° in this condition (see Discussion section).

Figure 3. (A) Suppression factor (masked threshold divided by baseline threshold) for each of the four test orientations is plotted as a function of mask/target orientation difference to allow a direct comparison of their shape. Error bars indicate the mean of the individual subjects’ standard errors (calculated for ratios of measurements, as indicated in the text). Note that at the peaks of the curves, a horizontal effect is apparent with greatest suppression for horizontal targets, next most at vertical, and least at obliques at these nearby mask orientations. Across other mask orientations, the four curves are very similar, primarily differing in terms of a greater upward shift of both horizontal and vertical curves indicating less suppression overall at oblique orientations. Horizontal (red squares), vertical (blue circles), 45° oblique (magenta up-triangles), and 135° (teal down-triangles) are plotted as a function of mask orientation. (B) A control condition shows that the suppression tuning curves are symmetrical about the target orientation. Here the mask consisted of only one of the two 5° masks shown in Figure 1. Best-fitting Gaussian function has the same bandwidth as those in (A).

subjects (11 total) were tested for the first mask position (noise bands centered at ±5°) and results are shown in Figure 2C individually for the 11 subjects. In every case (11 of 11) threshold at horizontal is highest and thresholds at obliques are low (the opposite of the typical (unmasked) ‘oblique effect’ anisotropy). That is, although small in these conditions, the horizontal effect anisotropy is consistent and highly significant (horizontal threshold versus mean oblique threshold, correlated t-test \( t_{(10)} = 7.717, p < 0.001 \)).

To show the orientation tuning of the suppression, threshold elevation (masked threshold divided by baseline threshold) is plotted in Figure 3A as a function of mask-to-target orientation difference.\(^1\) The magnitude of the suppression (termed ‘suppression factor’ after Petrov, Carandini, & McKee, 2005) is seen to be clearly orientation-tuned and has a bandwidth (full width at half-height) of about 40° for all test orientations. Comparison of fall-off of the suppression factor across orientation shows that two differences are apparent in these profiles at the different test orientations. First, there is a stark difference in masking between oblique and cardinal orientations. For example, by 45° from the test orientation, elevation is slight for the oblique test orientations (factors of 1.3 and 1.4) whereas clear suppression for the 0° and 90° targets still remains at 45° away (factors of 2.1 and 2.4 for vertical and horizontal, respectively). The second difference is that horizontal and vertical threshold elevations are more different from each other closer to the peak of the tuning function (i.e., the 5° point) and this difference diminishes away from the peak (e.g., the 35° point). The profile of the tuning curves is essentially Gaussian, and best-fit Gaussians were used to provide the curves plotted in Figures 3A and 3B.

Two further conditions were run. First, to verify that suppression is symmetrical (as assumed above), we tested masking to both sides of the peak separately by using a single 5° mask (Figure 3B). Bandwidth was also approximately 40° in this condition (see Discussion section).

Figure 3. (A) Suppression factor (masked threshold divided by baseline threshold) for each of the four test orientations is plotted as a function of mask/target orientation difference to allow a direct comparison of their shape. Error bars indicate the mean of the individual subjects’ standard errors (calculated for ratios of measurements, as indicated in the text). Note that at the peaks of the curves, a horizontal effect is apparent with greatest suppression for horizontal targets, next most at vertical, and least at obliques at these nearby mask orientations. Across other mask orientations, the four curves are very similar, primarily differing in terms of a greater upward shift of both horizontal and vertical curves indicating less suppression overall at oblique orientations. Horizontal (red squares), vertical (blue circles), 45° oblique (magenta up-triangles), and 135° (teal down-triangles) are plotted as a function of mask orientation. (B) A control condition shows that the suppression tuning curves are symmetrical about the target orientation. Here the mask consisted of only one of the two 5° masks shown in Figure 1. Best-fitting Gaussian function has the same bandwidth as those in (A).

Figure 4. Whether the monitor was upright (blue symbols) or tilted 45° (magenta symbols), a horizontal effect was obtained for orientation with respect to retinal orientation (rather than with respect to orientation on the monitor raster). All four subjects show a comparable horizontal effect in the two conditions. Stimulus duration was 50 ms in this condition.
Second, to verify that the anisotropy of thresholds reported here is not due to potential anisotropic properties of the CRT raster (see Klein, Hu, & Carney, 1996), additional subjects were tested with the monitor upright or tilted 45°, and the “tilted” and “upright” monitor thresholds were compared (see also Essock et al., 2003, for a similar control). As shown in Figure 4, the same horizontal effect (defined with respect to retinal coordinates) was obtained in both monitor positions.

**Experiment 2: Time course of broadband anisotropic suppression**

Contrast thresholds for the 8-cpd test in the presence of the broadband noise mask (15° orientation band) as a function of test/mask SOA is shown in Figure 5 (left column) for the three subjects and their mean. All subjects demonstrated a typical oblique effect in contrast sensitivity when no mask was present (Figure 5, right) and the

![Figure 5](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932855/)

Figure 5. **Left:** Contrast thresholds for an 8-cpd grating presented at varying SOAs with a broadband mask. A horizontal effect is apparent at 0 ms and +50 ms SOAs. At much longer SOAs an oblique effect can be seen. **Right:** Baseline thresholds for the same gratings with no accompanying mask stimulus.
oblique effect averaged 0.37 log units across subjects. As to be expected, an oblique effect was also obtained when the test and mask were widely separated in time (e.g., SOA of ±400 ms). However, when the test and mask are close together in time, masking is pronounced, with horizontal test thresholds becoming highest, and vertical thresholds becoming lowest (e.g., for the 0-ms SOA condition, thresholds were -1.22, -1.01, -0.87, and -1.03, for V, 45°, H, and 135°, respectively, indicating that horizontal thresholds were higher than oblique thresholds by 0.15 log units). Thus, even a brief coincident broadband mask (0 or ±50 ms SOAs) results in a shift in the anisotropy from a 0.37 log unit oblique effect to a 0.15 log unit horizontal effect—a net change of more than 0.5 log units between horizontal and the obliques (and a significantly different anisotropy: $F_{(3,16)} = 18.336, p < 0.001$). Plotted in terms of suppression factor (masked/unmasked threshold) across SOA (Figure 6) it is apparent that threshold elevation begins within -200 ms (i.e., mask preceding test), grows rapidly, and is much greater for horizontal than oblique, with vertical intermediate in a typical “horizontal effect” pattern.

The suppression is asymmetric, with the horizontal effect (and proportionally, suppression in general) larger for backward masking (positive SOA) conditions (e.g., +50 ms compared to -50 ms). Such a result is predictable if these results are viewed as a combination of the temporal response of neurons to a stimulus flash (i.e., a right-skewed response: e.g., Albrecht, Geisler, Frazor, & Crane, 2002) and a rapid temporal onset of a dynamic gain-control signal (e.g., Bonds, 1991; Geisler & Albrecht, 1992; Snippe, Poot, & van Hateren, 2004). Based on such reports, we model sensitivity to a masked stimulus as resulting from a fast exponential gain-control component and a skewed, “1½ Gaussian”, temporal response to the test (see Appendix A). By fitting such curves to the threshold data, the temporal parameters underlying the response suppression can be inferred (as detailed in Appendix A). The anisotropy of the suppression associated with the broadband masks is seen to occur primarily in the response of the dynamic gain control to the mask (shown in Figure 7A), with the suppression at horizontal having the greatest magnitude (i.e., the steepest rise) and a proportionally faster decline, and the other orientations being fairly similar (but with vertical slightly lower). The response purely associated with the test grating (i.e., without the masking suppression applied) is shown for the four different orientations in Figure 7B. These curves show that for a particular (suprathreshold) contrast, the response to horizontal and vertical test gratings is quite similar and that both are higher than the response to oblique test gratings (i.e., the oblique effect of contrast sensitivity is apparent). When this response to the test grating (Figure 7B) is suppressed through divisive gain control by the anisotropic response to the mask stimulus (Figure 7A), the horizontal response is the smallest, as shown in Figure 8 (e.g., compare the dashed lines, representing response during the 0-ms SOA condition, across test orientations).

Since the horizontal effect is greatest at the simultaneous SOA, the process that generates this anisotropy must be tightly linked to the presence of the broadband mask, as each stimulus had a duration of only 50 ms. Furthermore, as noted above, the absolute threshold level for gratings presented immediately before the noise mask (+50 ms SOA) is much higher than that for gratings presented immediately after the noise (−50 ms SOA); thresholds for the +50 ms gratings at vertical, oblique, and horizontal were, respectively, 1.37, 1.52, and 1.90 times greater than thresholds for the −50 ms gratings. From this asymmetry we can conclude that suppression has a rapid onset, with significant magnitude by 50 ms (see Bonds, 1991; Geisler & Albrecht, 1992; Wilson & Humanski, 1993; and also Figure 7) and also that the response to the test flash is asymmetric. Thus, as

![Figure 6. Suppression factor (masked threshold divided by baseline threshold) is plotted as a function of SOA. Error bars as in Figure 3A. Smooth lines are best fits from the model detailed in Appendix A. The horizontal/vertical difference at small SOAs is caused by an anisotropic weighting factor (w) of the dynamic gain-control term, which emphasizes horizontal over vertical. At larger SOAs, elevation at horizontal and vertical orientations becomes more similar, as the static $A_H$ parameter (anisotropic i.e., oblique effect pattern) weight of the semisaturation constant) comes to dominate w. Color coding is the same as in Figure 3; red: horizontal, blue: vertical, magenta and teal: 45° and 135°, respectively.](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932855/ on 11/12/2018)
detailed in Appendix A, the time course of the broadband masking is anisotropic (following a horizontal effect) in magnitude.

Discussion

The horizontal effect of gain control

The present results show that the effect of a large broadband mask on sensitivity to a grating is anisotropic. Specifically, this broadband suppression is orientation-tuned with equal bandwidth at different test orientations but with different strengths—the suppression is greatest at horizontal, least at oblique, with an intermediate amount at vertical (Figures 3A and 6). This finding of anisotropic suppression is readily fit into prevailing models of contrast gain control and is parsimonious with the evidence of an anisotropic distribution of neural units (see Introduction section). It also fits well with the previous reports that oblique content is most salient in natural or natural-like images and horizontal content is least salient (Essock et al., 2003; Hansen & Essock, 2004, 2005, 2006; Hansen et al., 2003). The present data show that the typical oblique effect is obtained for simple, unmasked stimuli (i.e., in a spectrally isolated context, or in a context of very few components; see Essock et al., 2003; Hansen & Essock, 2006), but when viewed in the context of other stimuli (i.e., a broadband mask), the greater suppression at horizontal (and secondly at vertical) suppresses the visibility of horizontal and vertical content below that of oblique content.

Figure 7. (A) Magnitude of gain-control response as a function of time (as derived by the model [Appendix A]) is plotted for each of the four testing orientations. Curves are composites of two exponential functions as described in Appendix A. The suppression is highly anisotropic; much stronger at horizontal than at the other orientations and slightly weaker at vertical than at oblique test orientations. The primary anisotropic factor is the weighting parameter \( w \), though the decay constant \( p \) is also greatest at horizontal (i.e., the horizontal gain-control decays most rapidly). (B) Best-fit functions reflecting the response to the 50-ms grating itself (without the gain-control factor applied), shown for each of the orientations of the test grating (see Appendix A). Plots reflect differential responsiveness to a fixed-contrast suprathreshold test grating and show a clear oblique effect (greater response at horizontal and vertical).

Figure 8. Modeled response functions during SOA masking conditions are shown for the four test orientations separately in each of the four panels. The response to the masked test grating at the four tested orientations (comparing across the four panels) reflects the combination of two different anisotropies: one essentially static component \( (A_M) \) unrelated to SOA, and one \( (w) \) associated closely with the presence of the mask (shown in Figure 6A). As in Figure 6B, these are responses calculated to reflect output to a fixed contrast of suprathreshold input. For negative SOAs (dashed lines), responses are suppressed throughout the timeframe due to the slow decay of the mask’s gain control. For positive SOAs (solid lines), note the sharp ‘scalloped’ appearance due to the rapid onset of response suppression.
In general, current models of contrast gain control, both physiological and psychophysical (e.g., Foley, 1994; Heeger, 1992; Holmes & Meese, 2004; Wilson & Humanski, 1993), suggest that the detecting mechanism’s response is divided by the sum of a semisaturation constant and a summed normalization pool consisting of the responses of numerous filters that are driven by the various components of the stimulus image. Specific models differ as to the properties of this normalization pool (including whether there are multiple sources/pools and the occurrence of facilitation) but a basic framework (as advanced by Foley, 1994) has been put in place for conceptualizing these contextual modifications to contrast sensitivity. The present results verify our earlier conjecture (e.g., Hansen et al., 2003) that the normalization pool is tuned in orientation, and that when viewing a large broadband pattern as used here, the response of the gain-control system across orientation is anisotropic in a horizontal-effect pattern. A model presented in Appendix A suggests that the anisotropic suppression observed here stems from:

1. a static factor that serves to alter the semisaturation constant and works against the oblique effect bias that is built into the semisaturation constant, and
2. a dynamic factor that increases the strength and speed of suppression at horizontal relative to the other orientations (seen in Figure 7A).

The anisotropic suppression that we observe here could come from any of several sources. That is, modulation of a cortical detecting mechanism’s output by the stimulus context may be viewed generally (e.g., as a single pool; Carandini, 2004) or in detail (i.e., as a set of similar, but quantitatively distinct mechanisms; Meese, Summers, Holmes, & Wallis, 2007; Rust & Movshon, 2005). Perhaps the primary distinction in the present literature is between overlay (“cross orientation”) and surround suppression, and it appears that the anisotropy that we observe here could have its basis in either or both of these processes. Petrov et al. (2005) have delineated psychophysically in humans some of the properties of these two different types of masking, and our stimuli would appear suited to drive both. The mechanism that is consistently found to be strongly orientation-tuned (about 40° width-at-half-height), surround suppression, is reported to be absent at 0° eccentricity, but quite strong by 1° eccentricity (Petrov et al., 2005; Snowden & Hammett, 1998; Xing & Heeger, 2000). Our 5° backgrounds and 1.6° (at half-height) tests are large enough to partially fall outside of the surround-suppression-free region and thus may drive, at least to some extent, such a mechanism. The second mechanism, overlay suppression, is strong throughout the central 5° and would clearly be driven by our test conditions (Petrov et al., 2005). Although Petrov et al. suggest that this overlap suppression mechanism is only broadly orientation-selective (~90° at half-height), even a broadly tuned anisotropic mechanism would deliver more suppression at certain test orientations than at others, so it is not surprising that a strong horizontal effect was observed. For all of these reasons, we conclude that overlay suppression as well as surround suppression appear to play a role in the current test conditions, and that either or both could be the source of the horizontal effect of anisotropic suppression in these general-viewing conditions. Indeed, the two differences apparent in the orientation tuning of the suppression at different test orientations (Figure 3A) match the orientation tuning of the two suppression mechanisms:

1. The difference shown across the full 90° (±45°) range of orientations seen in comparing horizontal and vertical tuning curves to oblique tuning curves matches well with the tuning of overlay suppression;
2. the difference between the suppression tuning curves for horizontal and vertical test orientations reflects a more narrowly tuned process like surround suppression.

Perhaps, the two anisotropies revealed in the model presented in Appendix A imply that the orientation difference (H > V) in the speed and strength of the gain-control response to the mask, w (Figure 7A) results from surround suppression, and that the orientation difference (H = V > Oblique) in the shift of the response curves associated with the semisaturation constant (AMK) results from overlay suppression.

Finally, we note the similarity between the observation that the horizontal effect strongly affects the perceptual salience of broadband patterns and the suggestions that the suppressive field appears to provide a modulatory effect on attention (e.g., Carandini, 2004; Petrov & McKee, 2006). Consistent with the notion of context suppression modulating attention, we have suggested that the horizontal effect serves to make objects stand out in natural scenes by relatively suppressing typical backgrounds (Hansen & Essock, 2004, and see below). Evidence that this horizontal effect of perceptual salience stems from orientation- and also spatial-frequency-tuned suppression (i.e., that the “suppressive field” is local in the frequency domain as well as in space) comes from a perceptual illusion that enhances perceptual salience at edges in the frequency domain (see Essock, Hansen, & Haun, 2007).

Tuned suppression of orientation channels

The bandwidth of these channels inferred from broadband noise masking is about 40° (full width at half-height) matching well with prior estimates of bandwidth estimated from masking studies that used a simple sine-wave mask (i.e., consisting of a single orientation and single spatial frequency, rather than a more complex stimulus;
Blake & Holopigian, 1985; Campbell & Kulikowski, 1966; Phillips & Wilson, 1984). Blake and Holopigian found that when the test paradigm allowed “off-channel looking” bandwidth was 36° and was 48° when off-channel looking was precluded. As the present task prevented off-channel looking, the present bandwidths of 40° are a little narrow relative to bandwidth from the corresponding condition of Blake and Holopigian, perhaps owing to the greater number of components in the present masks contributing more to the gain-control pool, and thereby serving to narrow the detecting channels. Some simple grating masking studies find oblique channels to be about 20% broader than horizontal or vertical channels (Blake & Holopigian, 1985; Campbell & Kulikowski, 1966; Harvey & Doan, 1990) as do certain neurophysiological studies (e.g., Li et al., 2003). However, one simple-grating masking study (Phillips & Wilson, 1984) does not find an anisotropy. Similarly, with the present study’s broadband masks, no tuning anisotropy was detected, indicating that the gain-control pool has an equal extent along the orientation dimension at cardinal and 45°-oblique orientations. It is worth noting that if the gain pool for horizontally tuned channels was narrower than the pools at other orientations, this would tend to nullify the anisotropy of the pooled response associated with the numerical bias of oriented filters (reducing or eliminating the horizontal effect seen with broadband images). However, the present data show equal-bandwidth gain-control pooling, ensuring that the pool associated with a more numerically represented orientation gets more input and hence stronger suppression. This is also consistent with the finding that broadening the orientation bandwidth of a stimulus and/or mask increases the magnitude of the horizontal effect (e.g., Hansen & Essock, 2006).

With a suprathreshold matching paradigm, Hansen and Essock (2006) have shown that a horizontal effect is obtained with stimuli with narrow orientation bandwidth (but broad spatial frequency bandwidth) similar to our masks used here. Thus, it is unlikely that the high horizontal thresholds reported here could be explained as the result of a greater response to horizontal ‘pedestals’ (thereby causing larger increment thresholds to be obtained). This possibility was tested directly by measuring Tvc functions of several subjects for 8-cpd gratings at the four orientations used in the experiments reported here. The results (Figure 9) show that while grating detection (i.e., detection on very low contrast pedestals) is better at cardinal than oblique orientations, detection of contrast increments is nearly identical for the four orientations across the higher pedestal contrast levels (i.e., the curves overlap at all but lowest contrasts). That is, despite the fact that the cardinal population response should certainly be larger for these stimuli, an anisotropy is not obtained, supporting our assertion that the anisotropy of masking that we report here is due to a broadband gain adjustment and is not a transducer effect.2

Figure 9. Tvc (threshold versus contrast) functions for the gratings used in Experiment 1. The oblique effect is present at and near the detection threshold, but the functions converge at higher contrasts indicating that the overall response gain is equivalent for the different test orientations in the absence of a broadband gain pool input. Despite better sensitivity at cardinal orientations, there is not an inversion of the anisotropy at higher contrasts: the overall response gain is equivalent for different test orientations in the absence of an active anisotropic gain control.

Implications for natural scene coding

An ecological account of the horizontal effect observed for the perceived salience of above-threshold broadband patterns has been proposed (Essock et al., 2003; Hansen & Essock, 2004, 2005). It was suggested that anisotropic suppression (horizontal > vertical > oblique) in the form of a divisive contrast gain-control mechanism with local pooling (i.e., local in the Fourier plane) would have the effect of “discounting” the most prevalent content in a typical scene (i.e., horizontal and vertical). Thus, objects of other spectral distributions would be relatively enhanced compared to the ‘discounted’ background of typical scenes. Indeed, when we measure the average bias in the Fourier spectrum of a large sample of natural scenes (the set of natural-scene images analyzed in Hansen & Essock, 2005), it averages 7% more horizontal than vertical content (amplitude), 12% more vertical than oblique, and 20% more horizontal than oblique—a pattern strikingly similar to the pattern of orientation biases in log threshold elevation obtained in the present study (with the more-natural stimulus conditions of Experiment 1): for the ±5° masks, about 11% more horizontal than vertical suppression, 15% more vertical than oblique, and 28% more horizontal than oblique. That is, suppression was in an H:V:Ob ratio of 1.0:0.93:0.80, closely matching the scene content ratio (1.0:0.93:0.83) in a typical sample of natural scenes. Secondly, this anisotropic pattern of
suppression would allow for efficient coding of natural scenes by “whitening” the typical anisotropy in natural scenes (Atick & Redlich, 1992; Barlow, 1959, 2001). Having the magnitude of suppression at a given orientation proportional to the prevalence of content at that orientation in typical natural scenes would have the effect of equalizing the responses of the visual system across all orientations when viewing typical natural scenes. Finally, an orientation-tuned suppressive mechanism would serve to enhance “edges” in the orientation dimension, making boundaries between oriented textures more salient. Strong “bands” of illusory enhancement do indeed occur at such boundaries between oriented textures more salient. Strong orientation-tuned suppressive mechanism would serve to enhance “edges” in the orientation dimension, making boundaries between oriented textures more salient. Strong orientation-tuned suppressive mechanism would serve to enhance “edges” in the orientation dimension, making boundaries between oriented textures more salient.

Conclusions

There are, of course, many types of cortical suppression and gain control (e.g., see Figure 1 in Rust & Movshon, 2005). The relationship between various types of suppression as well as that shown in the present paradigm is yet to be established. The present suppression presumably reflects the activity of a variety of suppressive mechanisms. What is clear is that the net effect of stimulation by broadband content, such as when viewing a natural scene, is rapid, orientation-tuned suppression that serves to relatively enhance sensitivity to oblique content compared to horizontal, and less so, vertical stimuli. For the reasons stated above, we suggest that this anisotropic suppression serves an ecological role in viewing and processing natural scenes: a normalization, by an intrinsic neural bias, that mirrors the anisotropy present in natural scenes and serves to compensate for the anisotropy in typical natural scenes by equalizing or whitening the visual system’s response across different orientations.

Appendix A

The SOA threshold data from Experiment 2 were modeled as a conventional Naka–Rushton formulation of dynamic contrast gain control, followed by a threshold applied to the total response output. Separate weights were allowed for each test orientation to fit the anisotropic thresholds and their changeover from an oblique effect to a horizontal effect.

The response \( R \) to the target grating as a function of time from grating onset \( t \) was defined as a ‘1½ Gaussian’ as per Albrecht et al., 2002 (also Frazor, Albrecht, Geisler, & Crane, 2004):

\[
R_{on} = e^{-\left(\frac{t}{\sigma_1}\right)^2}, t \leq \mu \\
R_{off} = ae^{-\left(\frac{t}{\sigma_1}\right)^2} + (1-a)e^{-\left(\frac{t}{\sigma_2}\right)^2}, t > \mu.
\]

The full response function was therefore defined as

\[
R = [R_{on} R_{off}],
\]

where \( \mu \) is the peak response latency for the grating response (fixed at 70 ms; cf. Müller, Metha, Krauskopf, & Lennie, 2001) and \( \sigma_1 \) and \( \sigma_2 \) serve as time constants for the Gaussian components; \( a \) defines the partial contribution of each component to the offset side of the response, but since it invariably reduced to zero when the model was fit to our data, it was fixed at that value.

We assumed that the gain-control response to the mask \( M \) was tightly linked with the onset and offset of the masking stimulus (i.e., ‘fast’ gain control, cf. Albrecht et al., 2002; Bonds, 1991; Geisler & Albrecht, 1992). Time \( s \) corresponded to SOA, defined as in the Methods section as mask onset minus grating onset (i.e., mask preceding grating is negative SOA, while mask following grating is positive SOA). The onset function operated for a duration of 50 ms and was defined as an exponential function:

\[
M_{onset}(t, s) = w\left(1 - e^{-\frac{t}{\tau_{on}}}\right), 0 \leq t - s \leq 50,
\]

where \( w \) is the magnitude of the gain-control signal and \( \tau_{on} \) is the onset time constant. As our data included no information about processes faster than 50 ms, we could not allow \( \tau_{on} \) to vary, and so it was fixed at a constant value of 100 ms, similar to values inferred by Snippe et al. (2004).

Two alternative decay functions, an exponential offset and a power offset, were used to model the data; neither worked out to provide, on average, a superior fit than the other, so only the results from the exponential offset are included here. The exponential decay of the gain-control response \( M_{offset} \) was defined as

\[
M_{offset}(t, s) = M_{onset}(50, 0) \times e^{-\left(\tau_{off} \times (t - s - 50)\right)}, t - s > 50,
\]

where \( \tau_{off} \) determined the rate of exponential decay. The full masking function, \( M \), was therefore defined as

\[
M(t, s) = [M_{onset} M_{offset}].
\]

These functions were combined in a form to emulate the components of the typical Naka–Rushton type of contrast response function (see, e.g., Foley, 1994; Holmes &
Meese, 2004), which intrinsically incorporates a dynamic gain-control component:

$$R(t, s)_{out} = \frac{cR(t)}{(AMK_0 + M(t, s))}, \quad AM = 0 = 1.$$  \hspace{1cm} (A6)

Here $c$ is the contrast of the target grating, and $AMK_0$ is the static contrast gain, or semisaturation constant, of the mechanism and $M(t, s)$ is the dynamic gain-control component. $R(t)$, from Equation A1, windows the response to contrast, $c$, in time. Detection, or sensitivity, was presumed to be mediated by summation of the final output $R(t, s)_{out}$ over time (i.e., during one 2IFC interval):

$$R(s) = \sum_t R(t, s)_{out}$$  \hspace{1cm} (A7)

so that when $R(s)$ equals the observer’s response criterion $R_c$, $c$ equals contrast threshold. We can simplify matters by making $R_c = 1$, so that $R_c/c = S(s)$, where $S$ is the sensitivity of the mechanism detecting the target stimulus. So, to find the sensitivity of the mechanism at each SOA $s$, we compute

$$S(s) = \frac{1}{c} \sum_t R(t, s)_{out} = \sum_t \left( \frac{R(t)}{(AMK_0 + M(t, s))} \right),$$  \hspace{1cm} (A8)

which can be inverted for a fit to our threshold data.

This formulation requires two static gain-control parameters, $AM$ and $K_0$, fulfilling the role of the familiar semisaturation constant, which is often characterized as the offset (i.e., lateral shift) of such a mechanism. $AM$ is equal to 1 when no mask is present and is a free parameter modifying the constant $K_0$ when a mask is present. $K_0$ then is the absolute semisaturation constant in the absence of masking conditions and is responsible for the oblique effect seen in the baseline condition (i.e., larger weights for obliques). Therefore, $AM$ can be viewed as representing a change in the static gain of the detecting mechanism during masking conditions, something like an “adaptation” factor (accounting for the upward shift of the thresholds at long SOAs relative to baseline in this test paradigm).

The output $S$, as described above, is inverted for a direct comparison with our contrast threshold data (separately for each test orientation). Best-fitting outputs were derived for all three subjects and for the average data, through a downhill simplex algorithm varying 6 parameters ($\sigma_1$, $\sigma_2$, $w$, $\tau_{off}$, $AM$, and $K_0$), with a seventh parameter, $\tau_{on}$, fixed at 100 ms as described above.

Two gain-control parameters are found to be anisotropic and cause the suppression to vary across orientation: $w$ and $AM$. However, whereas $AM$ is anisotropic with horizontal and vertical equivalent (and different than obliques), $w$ was found to be greatest at horizontal and least at vertical. Being tied to the dynamic gain-control component, $w$ only affects sensitivity when $M$ and $R$ overlap, which is why the appearance of the horizontal effect is seen only at small SOAs, $AM$ weights horizontal and vertical equally, to some extent ‘undoing’ the oblique effect of the semisaturation constant $K_0$ during broadband masking conditions. The combined effect of $w$ and $AM$ is heavily biased toward horizontal.

**Fit of the model**

Goodness of fit was assessed by the “reduced chi-square” metric, $r\chi^2$, and was found to be near 1.0 suggesting a moderately good fit for the degrees of freedom used. As detailed below, the fit of the model was found to be significantly better than corresponding isotropic models and was also better than other simpler models with fewer parameters.

The reduced chi-square metric compares the error in a model’s fit of a data set to the number of free parameters in the model and the number of data points fit. The difference between model and data is taken and divided by the measurement error for each data point, summed across all points, and then divided by the number of fitted points ($N$) minus the number of parameters ($p$): $r\chi^2 = \frac{\sum \left[ \frac{(model(x) - data(x))^2}{\sigma(x)} \right]}{N - p}$  \hspace{1cm} (A9)

The model presented here originally varied seven parameters at each orientation (28 total). However, since three ($\sigma_1$, $\sigma_2$, and $m$) parameters did not vary consistently with orientation, the model that was fit to the data had four parameters ($AM$, $w$, $K$, and $\tau_{off}$) that were allowed to vary with orientation and three were held constant, yielding 19 parameters (or 4.75 per orientation). This model provided an average $r\chi^2$ of 1.11 (1.57, 1.23, and 0.53 for our 3 subjects).

To test whether the model’s anisotropy improves the fit over an isotropic model, this result (1.11) was compared to a fit of the seven-parameter model to the data from Experiment 3 averaged across orientation. The average $r\chi^2$ value was 3.70 (3.83, 2.84, and 4.44, respectively for the three observers), clearly higher despite having far fewer varying parameters. To consider a simpler gain mechanism, the fit of the model was also compared to Gaussian functions, fit separately for each orientation (with four parameters for each orientation: peak amplitude, variance (duration of the function), temporal position (function mean), and vertical offset). This function yielded a poor fit to the data with much larger ($r\chi^2$) values. Here the mean $r\chi^2$ was 3.98 (6.19, 4.08, and 1.67, for the three subjects, respectively).
The nature of the errors of the model’s fit suggests that the model might be improved in the future by adding a more complex temporal response to the mask. Specifically, the underestimate of the negative-SOA tails and the overestimate of the positive-SOA tails suggest the action of a long-lasting suppressive component (i.e., a decay process with a rather large time constant) rather than the static $A_M$ included here. However, such additional complexities cannot be addressed by the present experiments.

**Acknowledgments**

This work was supported by grant #N00014-03-1-0224 from the Office of Naval Research and a graduate fellowship from the Kentucky Space Grant Consortium, NASA-EPSCoR.

Commercial relationships: none.

Corresponding author: Edward A. Essock.

Email: essock@louisville.edu.

Address: Department of Psychological and Brain Sciences, University of Louisville, Louisville, KY 40292, USA.

**Footnotes**

1. Since suppression ratios ($y$) were calculated from two independent values (i.e., $y = x_1 / x_2$), with accompanying errors $s_1$, $s_2$, the errors given for the ratios ($s_y$) are propagated from $s_1$ and $s_2$. Thus, $s_y$ can be calculated in terms of the Gaussian error propagation (Lo, 2005) such that $s_y^2 = (\bar{\Delta}y/\bar{\Delta}x_1)^2s_1^2 + (\bar{\Delta}y/\bar{\Delta}x_2)^2s_2^2$, where $\bar{\Delta}y/\bar{\Delta}x_1 = 1/x_2$ and $\bar{\Delta}y/\bar{\Delta}x_2 = -x_1/x_2^2$. Standard errors were calculated in this fashion for each individual’s suppression ratios. In the plots of suppression factor (Figures 3A and 6), these were averaged across subjects and plotted.

2. Furthermore, the threshold elevations seen in these experiments are far larger than would be expected from a pedestal effect. That is, the contrast within these broadband masks, which should be expected to directly stimulate the detecting mechanism, constitutes less than 10% of the total pattern contrast, equivalent to a masking grating of relatively low contrast. (In Figure 9 thresholds at the right end of the TVC data are for a masking grating at 50% contrast and are comparable in magnitude to the peak elevated thresholds in Experiment 1.)

**References**


primary visual cortex. *Journal of Neuroscience, 16*, 6443–6453. [PubMed] [Article]


