

# Interocular ND filter suppression: Eccentricity and luminance polarity effects

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The depth and extent of interocular suppression were measured in binocularly normal observers who unilaterally adapted to neutral density (ND) filters (0, 1.5, 2, and 3 ND). Suppression was measured by dichoptically matching sectors of a ring presented to the adapted eye to a fixed contrast contiguous ring presented to the non-adapted eye. Other rings of alternating polarity were viewed binocularly. Rings were defined by luminance (L), luminance with added dynamic binary luminance noise (LM), and contrast modulating the same noise (CM). Interocular suppression depth increased with increasing ND, nearing significance ( $p = 0.058$ ) for 1.5 ND. For L and LM stimuli, suppression depth across eccentricity ( $\pm 12^\circ$  visual field) differed for luminance increment (white) versus luminance decrement (black) stimuli, potentially confounding eccentricity results. Suppression for increment-only (white) luminance stimuli was steeper centrally and extended across the visual field, but was deeper for L than for LM stimuli. Suppression for decrement-only (black) luminance stimuli revealed only central suppression. Suppression was deeper with CM than LM stimuli, suggesting that CM stimuli are extracted in areas receiving predominantly binocular input which may be more sensitive to binocular disruption. Increment (white) luminance stimuli demonstrate deeper interocular suppression in the periphery than decrement (black) stimuli, so they are more sensitive to changes in peripheral suppression. Asymmetry of suppression in the periphery for opposite polarity luminance stimuli may be due to interocular receptive field size mismatch as a result of dark adaptation separately affecting ON and OFF pathways. Clinically, measurement of suppression with CM stimuli may provide the best information about post-combination binocularity.

## Introduction

Interocular suppression occurs when left and right eyes receive incongruous images that cannot be fused. To prevent confusion (where two different objects are perceived at the same location) or diplopia (where one object is perceived at two different locations), one image is cortically suppressed (Sengpiel, Blakemore, Kind, & Harrad, 1994). Interocular suppression is present in amblyopia (e.g., Black, Thompson, Maehara, & Hess, 2011; Chima, Formankiewicz, & Waugh, 2016; Irvine, 1948; Li et al., 2013; Mehdorn, 1989; Sireteanu & Fronius, 1981; Travers, 1938). It is also present in observers with normal binocular vision, when binocularly viewing stimuli in the presence of unilateral blur (Chima, Formankiewicz, & Waugh, 2015; Pardhan & Gilchrist, 1990; Pianta & Kalloniatis, 1998; Simpson, 1991) or when a neutral density (ND) filter is placed before one eye (Baker, Meese, Mansouri, & Hess, 2007; Li et al., 2012; Li et al., 2013; Zhang, Bobier, Thompson, & Hess, 2011; Zhou, Jia, Huang, & Hess, 2013). Current models of both normal and abnormal binocular vision suggest that binocular performance reflects a balance between suppression and excitation between eyes (Baker, Meese, & Hess, 2008; Ding, Klein, & Levi, 2013a; Ding, Klein, & Levi, 2013b). Previously we found that interocular suppression in amblyopes was luminance-polarity dependent, with luminance increments (or white stimuli) being suppressed more strongly than luminance decrements (or black stimuli) (Chima et al., 2016). A polarity dependence was not noted for interocular suppression generated with unilateral blur, which was broad, extending across the central  $24^\circ$  field (Chima et al., 2015).

Amblyopic deficits in binocular spatial vision have been mimicked in normal observers using monocular ND filters under binocular viewing conditions. Aspects

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of amblyopic binocular visual function successfully mimicked are reduced stereoacuity (Lovasik & Szymkiw, 1985), reduced binocular summation for contrast detection (Baker et al., 2007; Pardhan, Gilchrist, Douthwaite, & Yap, 1990), reduced binocular summation for contrast discrimination (Baker et al., 2008), predominance of one eye's input during binocular rivalry (de Belsunce & Sireteanu, 1991; Leonards & Sireteanu, 1993), reduced binocular summation for visual evoked potential amplitude (Heravian-Shandiz, Douthwaite, & Jenkins, 1991; Pardhan et al., 1990), shift in habitual sensory eye dominance (Zhang et al., 2011), and imbalance for binocular phase combination (Zhou et al., 2013). ND filters have also been used to rebalance binocular vision in binocular phase combination tasks in amblyopes (Ding & Levi, 2014; Zhou et al., 2013), and, clinically, suppression in amblyopes is quantified by attenuating luminance of the non-amblyopic eye with progressively denser ND or red filters until a stimulus is perceived by the amblyopic eye (Kehrein, Kohnen, & Fronius, 2016; Mallett, 1988; Piano & Newsham, 2015; Rowe, 2012; von Noorden & Campos, 2002). ND filters placed before one eye in normal vision have been shown to mimic the dichoptic global motion performance of amblyopes (Li et al., 2013) and to better demonstrate ocular dominance shifts, such as those found in anisometropic and strabismic amblyopia, than do interocular blur differences (Liu et al., 2002).

Previous work shows that patterns of suppression across the visual field differ in microstrabismic and anisometropic amblyopes, who show central suppression, compared to strabismic amblyopes, who show central and hemispheric suppression (Babu, Clavagnier, Bobier, Thompson, & Hess, 2013; Babu, Clavagnier, Bobier, Thompson, & Hess, 2017; Campos, 1982; Chima et al., 2016; Gottlob, Charlier, & Reinecke, 1992; Hallden, 1982; Herzau, 1980; Jampolsky, Flom, Weymouth, & Moses, 1955; Joesse, Simonsz, van Minderhout, de Jong, Noordzij, & Mulder, 1997; Joesse, Simonsz, van Minderhout, Mulder, & de Jong, 1999; Li et al., 2017; Mehdorn, 1989; Pratt-Johnson & Tillson, 1983; Sireteanu & Fronius, 1981; Sireteanu, Fronius, & Singer, 1981; Travers, 1938). Interocular suppression depth measured for increment (white) luminance stimuli was measured as greater than that for decrement (black) luminance stimuli in strabismic participants (Chima et al., 2016). Suppression in these participants when presented with increment and decrement contrast-modulated (CM) noise stimuli (for which mean luminance did not change) was not different, although it was greater than for luminance-modulated noise (LM) stimuli (Chima et al., 2015; Chima et al., 2016). These findings indicate that differences in visual sensitivity to increments or decrements of luminance at different adaptation levels or differences in local luminance adaptation and

their consequences might affect depth of suppression measures.

In normal central vision, increased visual sensitivity to decrements over increments in luminance results in improved psychophysical thresholds, including Gaussian blob detection and discrimination, first-order motion detection, second-order motion with dark or light elements, second-order motion detection with dark or light luminance contamination, Gestalt grouping, symmetric perception of spatial sine-wave gratings (Lu & Sperling, 2012), square patch luminance discrimination (Whittle, 1986), patch detection under low luminance adaption (Blackwell, 1946), peripheral ( $7^\circ$  from fixation) detection thresholds (Patel & Jones, 1968), and detection of circular targets against a flickering background (Wolfson & Graham, 2001).

In Experiment 1, suppression was mapped across the central  $24^\circ$  visual field after monocular ND filter adaptation in binocularly normal participants. The same suprathreshold dichoptic matching task of (Chima et al. 2015, 2016) and the same luminance (L), luminance-modulated noise (LM), and contrast-modulated noise (CM) stimuli were used. In Experiment 2, we disentangled the effects of stimulus polarity from those of eccentricity on interocular suppression. The results are discussed in light of previous results on amblyopic suppression (Babu et al., 2013; Chima et al., 2016).

## Methods

### Participants

Four binocularly normal non-presbyopic participants (three male and one female) took part in Experiment 1. One was an author (ASC) and the others were naïve to the nature and purpose of the experiments. Participant SM had no previous experience with psychophysical experiments, whereas participants CP and SP were well practiced, as they had contributed to the results of a previous experiment with monocular blur (Chima et al., 2015). Four participants (two male and two female) took part in Experiment 2, including two additional naïve but trained participants (RW and TK), in addition to ASC and SP. Participants in both experiments were 18 to 32 years of age. They had 6/5 or better corrected visual acuity in each eye; stereoacuity of 30 arcsec or better, as measured with the Dutch Organization for Applied Scientific Research (TNO) stereo test (Lameris Ootech, Ede, The Netherlands); and no suppression measured clinically with either the Worth 4 Dot test (Luneau Ophthalmologie, Pont-de-l'Arche, France) or Bagolini striated lenses (Sbisa, Florence, Italy). All six participants were right-eye dominant as determined with the sighting dominance test (Fink, 1938). Informed

consent was obtained from all participants prior to data collection. The Anglia Ruskin University Faculty of Science and Engineering Research Ethics Committee approved the conduct of the research, ensuring that it complied with the tenets of the Declaration of Helsinki.

## Equipment

A MacBook Pro (Apple, Inc., Cupertino, CA) running MATLAB (MathWorks, Natick, MA) with Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) was used to generate stimuli. Stimuli were presented on eMagin DualPro head-mounted OLED displays (Dual Pro Z800; eMagin Corp., Hopewell Junction, NY) via a Matrox DualHead2Go adapter (Matrox Graphics, Inc., Quebec, Canada). One screen for each eye allowed for dichoptic presentation of stimuli. Each screen had a resolution of  $800 \times 600$  pixels, refresh rate of 60 Hz, mean luminance of  $45 \text{ cd/m}^2$ , and an effective viewing distance of 80 cm. The eMagin displays for each eye were linearized and equalized for luminance using a ColorCAL II Colorimeter (Cambridge Research Systems, Rochester, UK).

Neutral density filters (Wratten 2 No. 96; Eastman Kodak Company, Rochester, NY) were used to provide interocular differences in retinal illuminance. These filters reduce luminance energies of all visible wavelengths equally, although the stimuli used in this study were constructed from gray levels only. The no-filter condition provided a screen mean luminance of  $45 \text{ cd/m}^2$  which, assuming a pupil diameter of 5.5 mm (Watson & Yellott, 2012), converts to a retinal illuminance of approximately 247 Td·s. The three filter strengths used were 1.5, 2, and 3 ND, which attenuated the mean luminance by  $32\times$  (to  $1.42 \text{ cd/m}^2$ , or approximately 10.1 Td·s assuming a pupil diameter of 7.11 mm),  $100\times$  (to  $0.45 \text{ cd/m}^2$ , or approximately 3.34 Td·s assuming a pupil diameter of 7.42 mm), and  $1000\times$  (to  $0.045 \text{ cd/m}^2$ , or approximately 0.350 Td·s assuming a pupil diameter of 7.76 mm), as confirmed with the colorimeter. Results of pilot experiments showed that a 1.5-ND filter was the least dense filter, resulting in consistent measurable suppression. The filters were cut, placed into photographic slide mounts, and affixed to the left goggle screen, such that the whole of the left eye display was attenuated. Right and left eye displays were positioned very close to the eyes, so that the nose effectively blocked any luminance from one eye from reaching the other, preventing cross-talk.

## Stimuli

Examples of the luminance, luminance-modulated noise, and contrast-modulated noise stimuli employed are provided in Figures 1A–F. Stimuli consist of four

concentric rings of alternating polarity, such that the high-modulation rings (e.g., central rings) differ from the background mean modulation by the same magnitude as the low-modulation rings (e.g., outermost rings). Images presented to the left eye (Figure 1, left) were binocularly combined with those presented to the right eye (Figure 1, right) to give one fused cyclopean image subtending  $24^\circ$  of the central circular visual field. In Experiment 2, stimuli were tested both in this pattern and in the inverted polarity pattern.

Although larger foveal and peripheral spatial summation areas have been found for CM compared to LM stimuli (Sukumar & Waugh, 2007), in a previous control experiment (Chima et al., 2015) it was found that the sector sizes chosen here—the same for L (Figures 1A, 1B), LM (Figures 1C, 1D), and CM (Figures 1E, 1F) stimuli—do not influence suppression outcomes. Four concentric rings were split into eight sectors (a total of 32 sectors), denoted by black lines in Figure 2 (blue lines denoting orientations). The outer edges of the rings (the central ring being a circle) were  $\pm 1.30^\circ$ ,  $2.90^\circ$ ,  $5.95^\circ$ , and  $12.00^\circ$  from center.

As LM and CM stimuli are defined by luminance or contrast modulations of noise, rings and adjustable sectors were quantified in terms of their modulation. The following equation (Schofield & Georgeson, 1999) describes how L, LM, and CM stimuli were constructed:

$$I(x, y) = I_0 [1 + nN(x, y) + lL(x, y) + mnM(x, y)N(x, y)] \quad (1)$$

where  $I(x, y)$  is the luminance at position  $(x, y)$  and  $I_0$  is mean luminance;  $n$  is noise contrast;  $N(x, y)$  is the value of binary noise (+1 or -1) at position  $(x, y)$ ;  $l$  is the (luminance) modulation of L and LM rings; and  $m$  is the (contrast) modulation of CM rings.  $L(x, y)$  and  $M(x, y)$  take the values of -1, +1, or 0, representing the basic pattern used to generate all stimulus types: bright (+1) and dark (-1) concentric rings on a background (0).

In the following experiments, L stimuli were created using

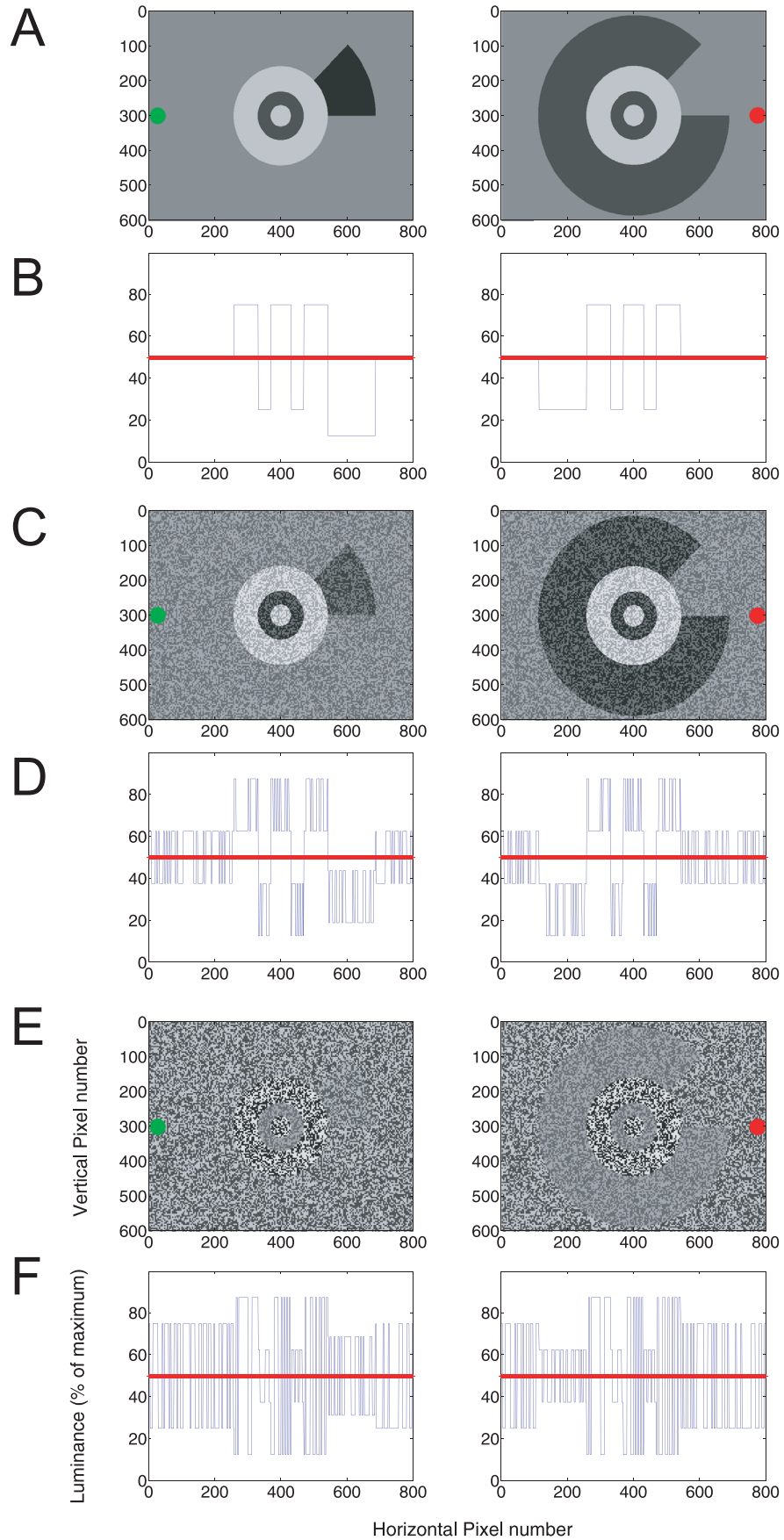
$$I(x, y) = I_0 [1 + lL(x, y)] \quad (2)$$

For L stimuli,  $l$  takes values between 0 and 1.

LM stimuli were created using

$$I(x, y) = I_0 [1 + nN(x, y) + lL(x, y)] \quad (3)$$

The modulation of the binary noise  $N(x, y)$  is  $n = 0.25$ , which is added to the luminance profile  $lL(x, y)$ , and  $l$  takes values between 0 and 0.75 (limited by noise amplitude). For example, when  $l = 0.5$ , bright rings have a range of 62.5% to 87.5% of maximum





←

Figure 1. Examples of L (A), LM (C), and CM (E) stimuli. B, D, and F show luminance profiles (excluding blindspot markers) taken 1 pixel above the horizontal midline, where the red line is mean luminance. Left and right columns show views to left and right eyes, respectively. For CM stimuli (E, F), average luminance of the stimuli remained constant at the mean luminance, but the *contrast* of the high and low modulation CM rings and the adjustable sector changed. Thus, the difference between each ring is a modulation of contrast rather than a modulation of luminance. A, C, and E show green and red blindspot markers for right and left eyes, respectively. All horizontal axes show horizontal pixel numbers (as in F). A, C, and E share the same ordinate axis scale, as do B, D, and F.

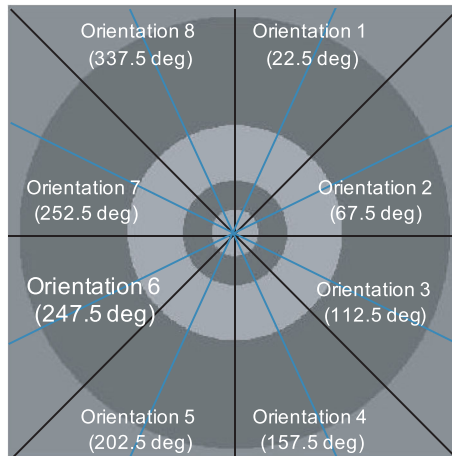


Figure 2. Schematic representation of the L stimuli. Black lines delineate sectors, and blue lines show orientations (see Analysis section for explanation). These lines did not appear on the actual stimulus.

screen luminance and 12.5% to 37.5% for dark rings (Figures 1D, 1E).

For CM stimuli the equation is

$$I(x, y) = I_0 [1 + nN(x, y) + mM(x, y)N(x, y)] \quad (4)$$

For these stimuli,  $n = 0.50$ , and  $m$  takes values between 0 and 1. For example, when  $m = 0.5$ , luminance ranges between 12.5% and 87.5% of maximum screen luminance for the high-contrast rings and 37.5% to 62.5% of maximum for the low-contrast rings.

All stimuli had the same alternating concentric ring pattern (see Figures 1 and 2), defined either by a luminance change,  $IL(x, y)$ , for L and LM stimuli or by a contrast change,  $mM(x, y)$ , for CM stimuli. For noisy (LM and CM) stimuli, the noise check size was  $4 \times 4$  pixels with an angular subtense of 10 arcmin at 80 cm (equivalent viewing distance), clearly resolvable for all of our participants at all eccentricities tested (Anderson & Thibos, 1999; Ludvig, 1941; Millodot, Johnson, Lamont, & Leibowitz, 1975; Rovamo, Virsu, & Näsänen, 1978).

Ten different images of stimuli were created using randomly generated binocularly correlated noise after each participant response, with noise set to zero for L stimuli. Presenting the 10 images in random order every

two temporal frames created dynamic noise stimuli; each frame was presented for 33.3 ms. Smith and Ledgeway (1997) demonstrated the importance of using dynamic noise when investigating contrast-defined motion perception when local stochastic biases in static noise produce luminance artifacts in second-order stimuli. Further details of stimulus generation and calibration checks are provided in Chima et al. (2015, 2016).

## Procedure

Prior to the experiments, which were performed in a dark room, each participant binocularly viewed a video on the head-mounted displays for at least 20 minutes with the ND filter to be used in the experiment. This was considered adequate based on findings by MacMillan, Gray, and Heron (2007), who used similar displays and test field matches. Any additional effects of continuing adaptation after 20 minutes during the experiment would be spread across sectors and conditions conducted in counterbalanced order, with the mean taken across four runs. If a run required no filter, a shorter adaptation period took place. Participant pupil size was not controlled, and the effects of the ND filter may have varied among participants; however, the effects are likely to have been similar for each participant across the three stimulus types (L, LM, and CM).

Suppression was measured using an interocular modulation matching task, the same as in previous studies (Chima et al., 2015; Chima et al., 2016). For all rings other than the one being tested, the same pattern was shown to both eyes (Figure 1A). For the tested ring, this pattern was presented to the non-filtered right eye, except for the sector to be tested (Figure 1A, right). The tested sector only was presented to the filtered left eye (Figure 1A, left).

The modulation ( $l$  or  $m$  from Equations 2 to 4) of the tested sector presented to the filtered left eye was adjusted to obtain a perceptual match with the contiguous ring presented to the right eye, allowing the point of subjective equality (PSE) to be quantified. Responses were gathered using a two-alternative forced-choice paradigm combined with a one-down, one-up staircase, and the participant indicated whether

a modulation increase or decrease of the sector was required to match the contiguous ring. The staircase started randomly from either halfway between a physical modulation match and maximum adjustable modulation or halfway between a modulation match and minimum adjustable modulation. An audio cue indicated when six reversals were complete to finish that staircase and to start the next on a new sector. Sectors were presented in systematic and counterbalanced order to distribute practice, residual ND filter adaptation, and fatigue effects. Four experimental runs were conducted for each condition. The no-filter condition was the baseline measurement of suppression for each participant, as some did not have a completely balanced interocular match due to sensory eye dominance.

In Experiment 1, each of 32 different sectors across the central circular 24° visual field was tested. Filter levels tested were 0 ND (no filter), 1.5 ND, 2 ND, and 3 ND. Perceptual matches were made initially starting with the sector on the most peripheral ring to the right of the vertical. When PSE was reached here (as detailed above), the second sector clockwise (i.e., skipping one sector) was measured. When four sectors on this peripheral ring were completed in this fashion, the same orientations were measured in the same order in the next eccentricity closer to fixation. After continuing in this fashion to the central ring, a break was enforced while maintaining the level of adaptation. The remaining sectors were then measured outward from the center in an anticlockwise fashion. The next run for a particular condition was performed in the reverse order on a different day, starting from the center and having a half-way break after the peripheral ring. Each of these orders was performed twice for each condition. As much as possible, multiple conditions with the same filter level were completed on the same day to avoid repeated adaptation to different luminance levels. For example, if participants were adapted to 2-ND normal (i.e., not polarity-inverted L and LM), then CM stimuli were measured in one session. In two of a total of four repeats of the same condition, stimulus type order would be reversed.

In Experiment 2, 16 horizontal sectors for orientations 2 and 3 (right horizontal sectors) and orientations 6 and 7 (left horizontal sectors) were tested on L and LM stimuli (see Figure 2). Testing was carried out for the standard stimulus map and for a reversed (or opposite-polarity) stimulus map (white or high-contrast rings became black or low-contrast rings, and vice versa). No-filter and 2-ND filter conditions only were tested, and sectors were tested to ensure that right–left visual field order was counterbalanced. Four runs of each sector contributed to the means presented. Two participants (SP and AC) additionally completed reverse-polarity CM stimulus maps.

A number of control experiments were conducted to estimate stimulus visibility used in these experiments by measuring discrimination thresholds for sectors of different type, polarity, and filter adaptation viewing level, which may have differed and resulted in different suppression depth measures. For these visibility estimates, participants monocularly viewed the same concentric ring stimuli. On each trial, participants indicated whether the sector to be discriminated was at orientation 1 or was directly opposite at orientation 5 (see Figure 2). This two-alternative forced-choice procedure was combined with a three-down, one-up staircase to converge on discrimination threshold responses.

Participants practised with each stimulus type before experimental data were collected, ensuring that the standard deviation of the staircase generated was stable (within 15% of the mean). Throughout testing, participants were advised to maintain steady fixation on the center of the stimulus. If their gaze wandered, brightly colored blindspot markers became visible, and the participant was instructed to re-fixate before responding.

## Analysis

For each sector for each condition, the mean point of subjective equality was measured and averaged across four experimental runs. PSE values were normalized across stimulus types to calculate suppression depth using the following equation:

$$S_{norm} = \frac{(M_{match} - M_{baseline})}{M_{baseline}} \quad (5)$$

where  $S_{norm}$  is the normalized depth of suppression,  $M_{match}$  is the PSE modulation, and  $M_{baseline}$  is the baseline modulation of 0.50. Depth of suppression was expressed as  $-1$  to  $1$ , where  $1$  was the maximum level of suppression (modulation of sector in filtered eye required to be increased to maximum in the filter eye to perceptually match that of the contiguous ring),  $0$  was an interocular match (modulation of sector and contiguous ring perceived as the same in each eye), and  $-1$  was the maximum binocular facilitation (modulation in filtered eye required to be reduced to minimum to perceptually match that of the contiguous ring). Note that luminance could not exceed  $2 \times I_0$  for the LM stimuli, so  $M_{match}$  could not take values above  $0.75$ . Because  $M_{baseline} = 0.5$ , this means that  $S_{norm}$  could not exceed  $0.5$  (from Equation 5). This limit does not apply to the L and CM stimuli, where luminances stay within screen luminance range for  $M_{match}$  up to  $1$ ; thus, the upper limit is  $S_{norm} = 1$ .

With higher levels of ND filter, suppression was sometimes too deep to measure, especially for central sectors (all four participants with 3 ND for CM stimuli, and two of four participants with L and LM stimuli). If the staircase reached the maximum measurable normalized suppression value,  $S_{norm}$  was set to the maximum value for further analysis. Statistical analyses were conducted with and without all three ND suppression values.

For Experiment 1, data were analyzed using a repeated-measures analysis of variance (ANOVA) with within-group factors of stimulus type (L, LM, and CM), ND strength (0, 1.5, 2, and 3 ND), sector orientation (eight levels of orientation shown by blue lines in Figure 2), and sector eccentricity (four levels of eccentricity: 1.30°, 2.90°, 5.95°, and 12.00°). In Experiment 2, analysis was the same except there were two levels of ND strength (0 and 2 ND), two levels of stimulus polarity (increment and decrement), two levels of sector orientation (left, orientations 6 and 7; right, orientations 2 and 3), and four levels of eccentricity (as per Experiment 1). All ANOVA results were adjusted using the conservative Greenhouse–Geisser correction for violation of sphericity and independence of errors.

## Results

### Experiment 1: Interocular suppression of L, LM, and CM stimuli

Suppression depth for each sector, ND level, and stimulus type was averaged across four participants and provided as finely graded color maps (Figure 3). In the figure, maximum suppression with a normalized value of 1 is indicated by a red sector, a balanced interocular match is indicated by a yellow sector, and facilitation is indicated by a green sector. A physically veridical interocular match for which the inputs from the two eyes were balanced at physical mid-points has a value of 0 and is indicated by a yellow sector.

#### Depth of suppression with increasing interocular retinal illuminance difference

Interocular filter suppression depth increased significantly with filter density,  $F(1.51, 4.53) = 47.30$ ,  $p = 0.001$ , such that sectors changed from an interocular match (yellow) or mild facilitation (light green) to mild suppression (orange) and deep suppression (red) with increasing ND filter (Figure 3). Figure 4A shows average suppression depth plotted against ND filter strength. Interocular filter suppression nears statistical significance with the 1.5-ND filter and is highly significant for 2 ND and 3ND. Increases

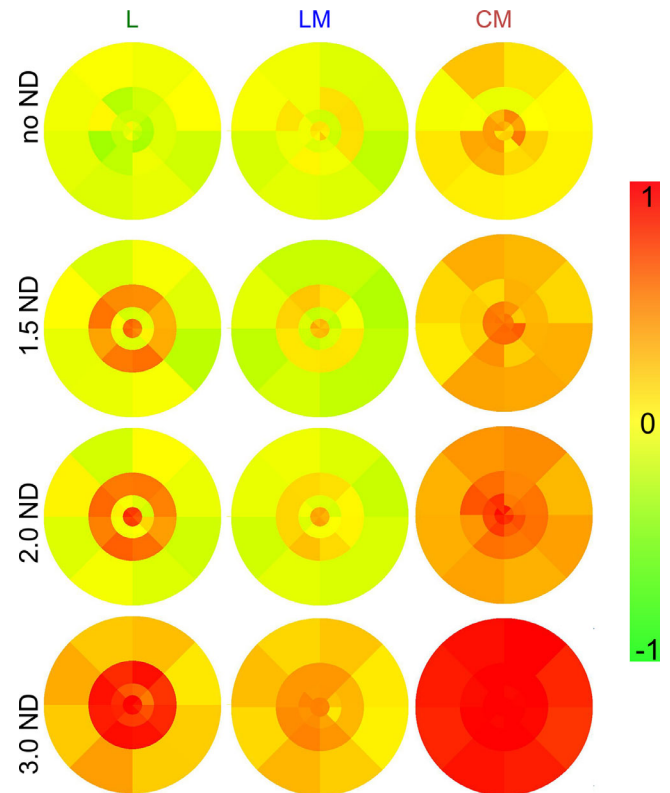


Figure 3. Color-coded suppression maps averaged across four participants from Experiment 1 for each level of ND (0, 1.5, 2, and 3 ND) for each stimulus type (L, LM, and CM). Each sector is represented by a color denoting the depth of suppression on a scale where green represents facilitation (normalized value of  $-1$ ) and yellow represents an interocular match (normalized value of 0).

in suppression depth with filter density, however, depended on the type of stimulus used to measure it,  $F(2.69, 8.08) = 9.65$ ,  $p = 0.005$ . In Figure 4B, the 0-ND filter suppression value for each stimulus type is subtracted from the value at each ND level to show the change in suppression depth relative to the 0-ND condition. Linear functions are fit to 0- to 2-ND sections of the data. For 3 ND, interocular modulation matches could not always be achieved within the available physical range, in which case contributing values were set to the maximum modulation for that stimulus type. A repeated-measures ANOVA performed on slopes (Figure 4B) for all participants across the three stimulus types (L, LM, and CM) revealed a significant main effect of stimulus,  $F(1.86, 5.57) = 13.77$ ,  $p = 0.007$ . Tests of simple effects show that the slopes were steeper for L stimuli than for LM stimuli,  $F(1, 3) = 31.89$ ,  $p = 0.011$ , and were also steeper for CM stimuli than for LM stimuli,  $F(1, 3) = 15.70$ ,  $p = 0.029$ .

The overall effect of orientation (see Figure 2) approached significance,  $F(2.81, 8.43) = 4.019$ ,

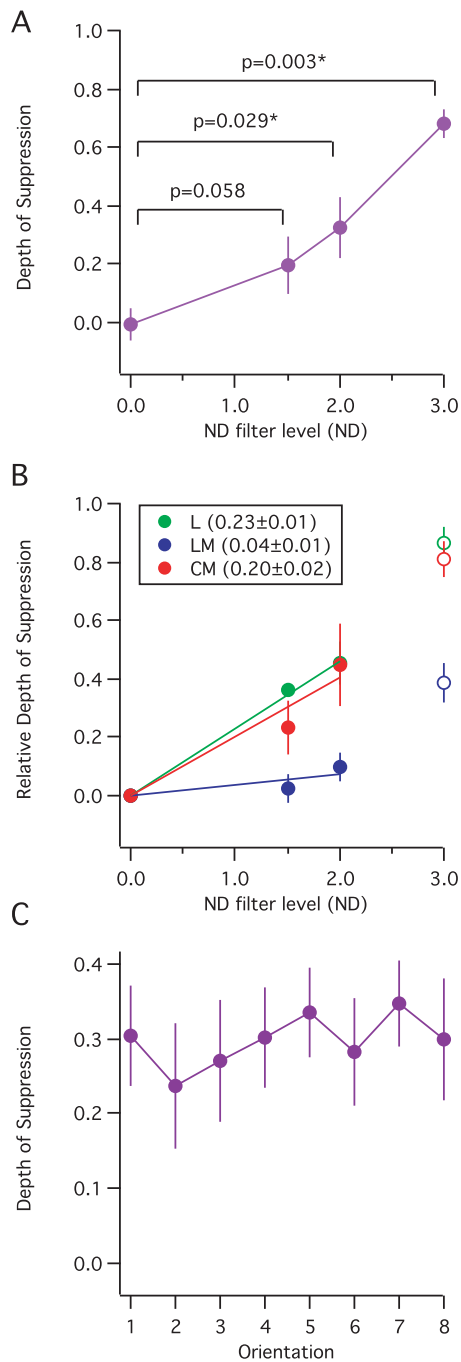


Figure 4. (A) Suppression depth averaged across all sectors, ND strengths, participants, and stimulus type. (B) Relative suppression depth (relative to 0 ND) averaged across all sectors for L (green), LM (blue), and CM (red) stimuli. The legend includes linear slope estimates. Data for 3 ND are shown as open circles, but means include maximum modulation values if perceptual matches could not be achieved. (C) Suppression depth averaged across all sectors, ND strengths, stimulus types, and participants for orientations 1 to 8. Error bars show  $\pm 1$  SE except for the zero point in B, which has zero variance.

$p = 0.0502$ , and is shown in Figure 4C. A Tukey pairwise post hoc analysis revealed that orientation 2 (right visual field near horizontal midline) differed from orientation 5 ( $p = 0.013$ ; left visual field near horizontal midline) and 7 ( $p = 0.004$ ; left lower visual field). There were no higher order interactions of orientation with filter strength, eccentricity, or stimulus type. The orientation effect (left vs. right visual field) was re-examined in Experiment 2.

#### Extent of suppression with increasing interocular retinal illuminance difference

There was a significant effect of eccentricity on suppression measures,  $F(1.42, 4.27) = 8.53$ ,  $p = 0.036$ , but the eccentricity effect was dependent on stimulus type,  $F(1.77, 5.30) = 14.59$ ,  $p = 0.008$ , so in Figure 5 data are collapsed across orientation to investigate eccentricity effects for different stimulus types at different ND filter levels. Maximum physical measurable values are represented by black dashed lines in Figure 5, and it can be seen that for the 3-ND filter condition, depth of suppression for the central sectors often reached maximum. A repeated-measures ANOVA was therefore performed excluding all 3-ND data; however, the results provided the same main effects and interactions as those just described.

Investigating the eccentricity main effect, for all stimulus types suppression was deepest centrally,  $F(1, 3) = 12.49$ ,  $p = 0.039$ , found by comparing the central sector to all peripheral sectors with planned comparisons. Testing simple effects of eccentricity for L and LM stimuli only, suppression differed significantly for alternate (opposite polarity) rings,  $F(1,3) = 14.85$ ,  $p = 0.031$ , such that incremental (white stimuli) showed deeper suppression than decremental (black) stimuli. This gave a bull's-eye appearance to the suppression maps shown in Figure 3 and the zigzag patterns in Figures 5A and B (absent for CM stimuli in Figure 5C). To highlight these differences, Figure 6 shows data averaged for 1.5- and 2-ND filters for each stimulus type, as they differed significantly only in suppression depth,  $F(1,3) = 24.94$ ,  $p = 0.015$ , and not in suppression pattern and therefore are not subject to any ceiling effects (like the 3-ND results).

Figure 6 highlights the eccentricity effects of suppression but also illustrates that for L and LM stimuli only suppression depth depended on the polarity of the luminance target. As described in the paragraph above, suppression measured for incremental L and LM (or white) sectors was significantly deeper than that measured for decremental L and LM (or black) sectors,  $F(1,3) = 14.85$ ,  $p = 0.031$ . This polarity effect makes it difficult to view true eccentricity effects for luminance-based stimuli. To disentangle polarity from eccentricity effects, Experiment 2 was conducted.



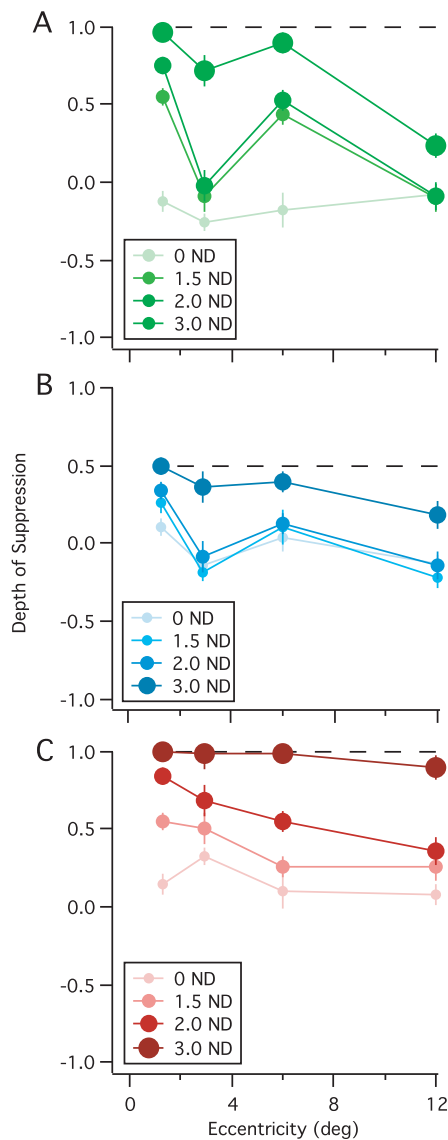


Figure 5. Depth of suppression averaged across all participants and orientations for each ND level and for each stimulus type. Black dashed lines show ceiling suppression values for each stimulus type: (A) L, (B) LM, and (C) CM. Error bars show  $\pm 1$  SE across participants.

#### Effect of adding noise on ND filter suppression depth measured with luminance-defined stimuli

The effects of adding dynamic binary noise to the luminance stimulus on suppression measures were assessed by comparing results for L versus LM stimuli only. Patterns of L and LM suppression were similar, although deeper suppression was measured for L stimuli than for LM stimuli,  $F(1, 3) = 23.11$ ,  $p = 0.017$ . The significant interaction between filter level and stimulus type as shown in Figure 4B highlights that suppression depth increased at a greater rate per ND level for L stimuli (slope =  $0.23 \pm 0.01$ ) than for LM stimuli (slope =  $0.04 \pm 0.01$ ), which, as mentioned

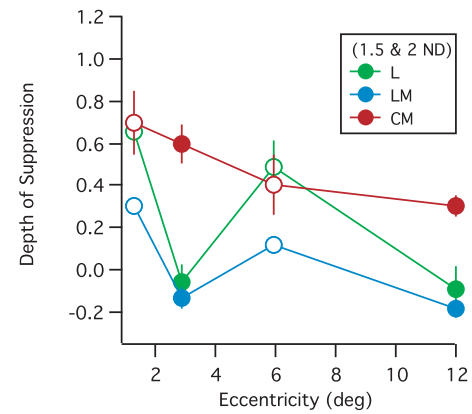


Figure 6. Suppression depth averaged across participants, orientations, and 1.5 and 2 ND for each eccentricity. Separate curves show different stimulus types. Closed symbols, decremental sectors; open symbols, increment symbols. Error bars show  $\pm 1$  SE between ND levels.

above, did reach statistical significance,  $F(1, 3) = 31.89$ ,  $p = 0.011$ . Figures 5 and 6 show that the polarity effect was shared but was less notable for LM stimuli than for L stimuli.

#### Suppression of luminance- versus contrast-modulated noise stimuli

A repeated-measures ANOVA on LM versus CM data only revealed that suppression was deeper for CM stimuli than LM stimuli at all ND levels and at all eccentricities (comparing blue and red traces in Figure 6),  $F(1,3) = 108.03$ ,  $p = 0.002$ . However, there was a significant interaction between suppression depth and ND filter level for these two stimulus types,  $F(1.99, 5.97) = 12.26$ ,  $p = 0.008$ , reflected by the significantly steeper CM slope value ( $0.20 \pm 0.02$ ) than LM slope value ( $0.04 \pm 0.01$ ) in Figure 4B,  $F(1, 3) = 15.70$ ,  $p = 0.029$ .

#### Control Experiment 1.1: The effect of noise amplitude on suppression depth measures

Differences in measured CM and LM suppression depth could be attributed to the different noise amplitudes used (0.50 and 0.25, respectively). These different levels were chosen to increase the measurable modulation ranges for measurements of suppression. Could the stronger suppression depths measured for the CM stimuli be due to the weaker visibility of these stimuli? In this control experiment, noise amplitude ( $n$  in Equation 1) was equated for LM and CM stimuli at 0.375. At this noise amplitude for the 0-ND condition, stimuli were as equally visible (dotted line in Figure 7) as the noise amplitudes used in the main experiment (LM,  $n = 0.25$ ; CM,  $n = 0.50$ ). Suppression measures were

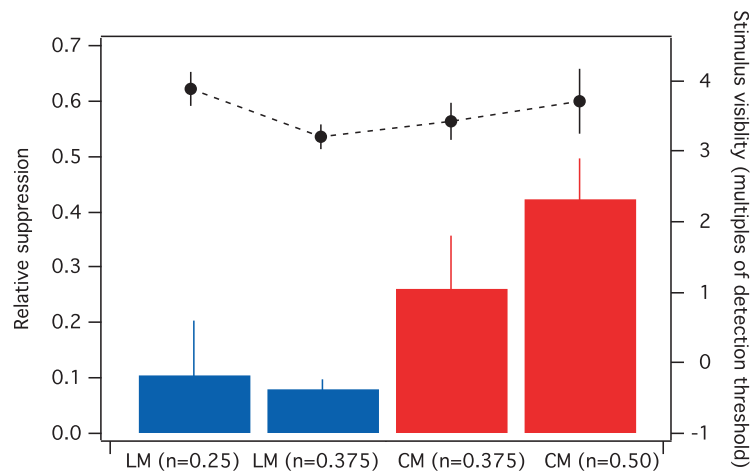


Figure 7. Relative suppression (left ordinate axis) calculated as the difference between no-filter and 2-ND conditions when all sectors were averaged. Colored bars show LM (blue) and CM (red) with different noise amplitudes. The black line shows stimulus visibility defined as multiples of detection threshold (right ordinate axis). Error bars represent  $SE$ .

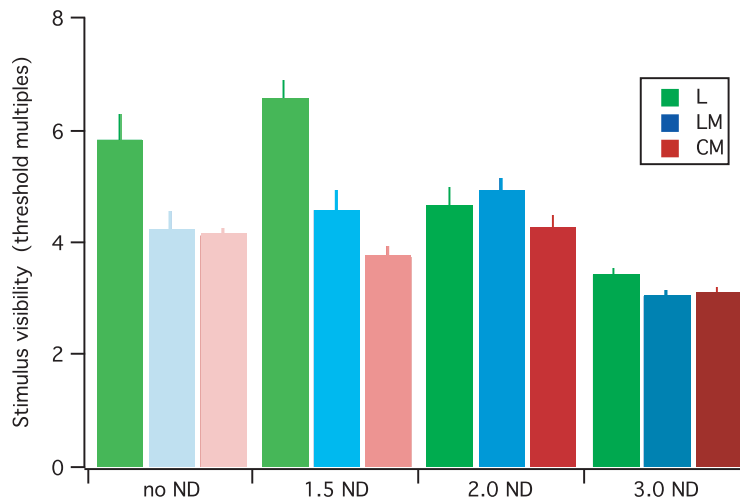


Figure 8. Stimulus visibility (multiples of detections thresholds) for central modulation increment sectors of stimuli used in the main experiment for each stimulus type (L, green; LM, blue; CM, red) and each level of ND. Results are for two participants who took part in Experiment 1. Error bars show  $+1 SE$ .

also checked for central increment stimuli using 0.375 noise amplitude for 0 and 2 ND for two participants (ASC and SP). Results are provided in Figure 7. For LM stimuli, increasing noise amplitude (from 0.25 to 0.375) decreased visibility ( $3.9 \times \pm 0.2$  to  $3.2 \times \pm 0.2$ ) but gave suppression depths similar to those of the main experiment ( $0.10 \pm 0.10$  and  $0.08 \pm 0.02$  for 0.25 and 0.375 noise amplitudes, respectively). For CM stimuli (red bars of Figure 7), visibility was slightly reduced when noise amplitude was reduced from 0.50 to 0.375 ( $3.7 \times \pm 0.5$  to  $3.4 \times \pm 0.3$ ), which was expected as CM stimuli noise supports the stimulus. Concurrently, suppression was reduced from  $0.42 \pm 0.07$  to  $0.26 \pm 0.09$ . Thus, despite equating noise amplitude and

visibility for both stimulus types, suppression was found to be significantly deeper for CM stimuli compared to LM stimuli ( $0.26 \pm 0.09$  vs.  $0.08 \pm 0.02$ ). Thus, the difference in suppression depth between LM and CM stimuli was not due to noise amplitude differences.

#### **Control Experiment 1.2: The effect of ND filter strength on stimulus visibility**

For all stimulus types, monocular detection thresholds were measured after adaptation to each ND filter level. Results are shown in Figure 8 for L, LM, and CM central increment stimuli averaged for two participants (ASC and SP). The visibility of L stimuli

was greater than the visibility of LM stimuli for the 0- and 1.5-ND conditions. For higher ND filters, the deleterious effect that dynamic noise has on detection of luminance-defined stimuli was reduced. Changes in stimulus visibility did not vary systematically with suppression depth measured at different ND filter levels. Thus, it is not likely that the depth of suppression was due to differences in stimulus visibility caused by adaptation to different ND strengths across stimulus type.

## Experiment 2: Suppression of incremental and decremental modulation stimuli

In Experiment 1, different depths of suppression were measured for increment and decrement luminance stimuli, making it difficult to see suppression patterns due to eccentricity for L and LM stimuli. In Experiment 2, we sought to disentangle luminance polarity from eccentricity effects on interocular filter suppression. We were also able to test again the orientation effect by our use of sectors near the horizontal midline in the right versus left visual field.

### Luminance and luminance-modulated noise stimuli polarity differences

Figure 9 shows suppression means for the 2-ND filter for L (Figure 9A) and LM (Figure 9B) increment and decrement stimuli averaged across four participants. In Experiment 1, we found a strong eccentricity effect; however, the central sectors for L and LM stimuli were always luminance increments. In Experiment 2, we grouped the data into luminance increments and luminance decrements to separately examine eccentricity effects. Comparisons of suppression depth and eccentricity patterns between L and LM increments and decrements are provided in Figures 9A and 9B. A significant eccentricity effect was found when L and LM decremental stimuli were combined for the 2-ND filter condition,  $F(1.58, 4.74) = 7.95$ ,  $p = 0.033$ , although there was also a significant stimulus type by eccentricity interaction, which revealed a steeper eccentricity effect for L stimuli than for LM stimuli,  $F(1.57, 4.70) = 7.30$ ,  $p = 0.039$ . Planned comparisons carried out on decremental (black) L stimuli found that suppression was significant only for the central sectors,  $F(1,3) = 10.23$ ,  $p = 0.049$ , whereas the peripheral sectors showed no significant suppression,  $F(1,3) = 0.75$ ,  $p = 0.450$ . Suppression for central LM decrements was lower and did not reach statistical significance,  $F(1,3) = 7.43$ ,  $p = 0.072$ .

As in Experiment 1, there was a small but statistically significant orientation effect,  $F(1,3) = 16.18$ ,  $p = 0.028$ , without any significant higher order interactions found with stimulus type, polarity, ND, or eccentricity.

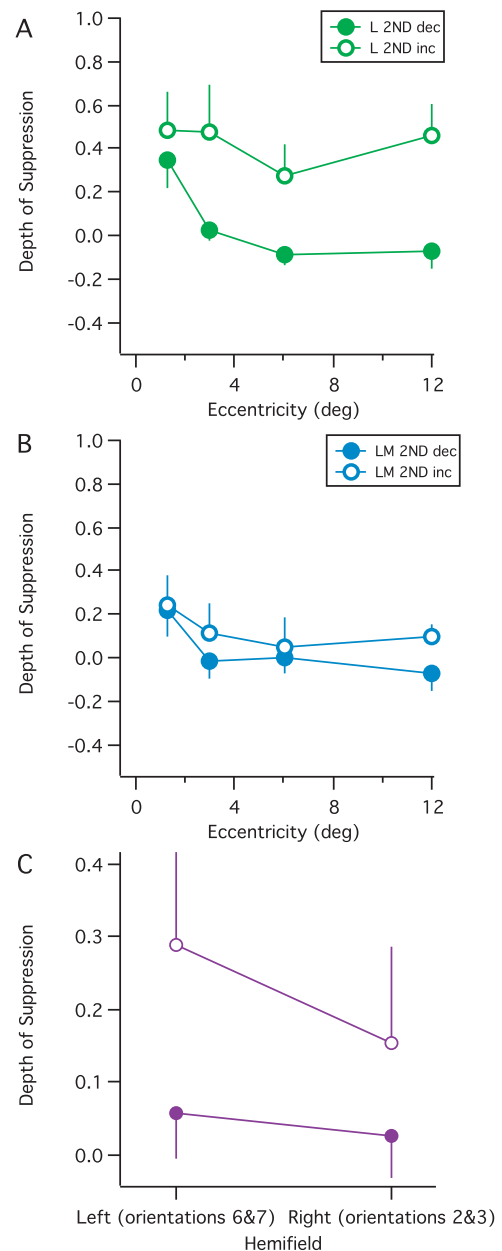


Figure 9. (A) Suppression across eccentricity for L increments (open symbols) and for L decrements (closed symbols), with 2-ND filter before one eye. (B) Same as A, but for LM stimuli. (C) Data averaged across all sectors in left versus right hemifields for increments and decrements (2-ND only). Error bars show  $+1 SE$  for increment stimuli and  $-1 SE$  for decrement stimuli.

This finding suggests that suppression is slightly stronger on the left than the right visual field in our right-eye-dominant participants.

### Increment and decrement differences with luminance- and contrast-modulated stimuli

Figures 10A and 10B show interocular suppression maps across stimulus type (L, LM, and CM) for

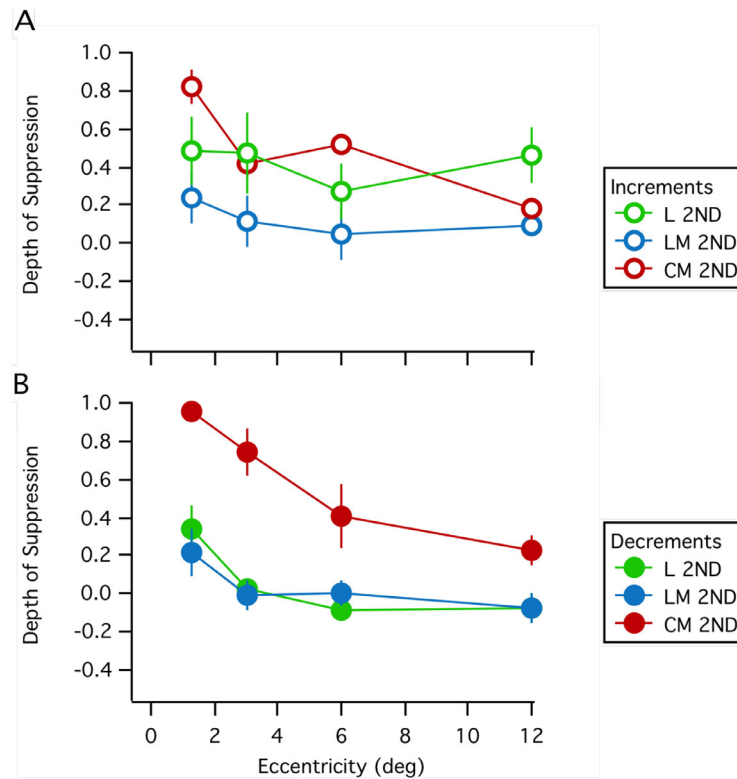


Figure 10. Suppression across eccentricity for L (A), LM (B), and CM (C) increments (open symbols) and decrements (closed symbols), respectively. All represented conditions were performed with a 2-ND filter. Error bars show  $\pm 1$  SE.

incremental (white) and decremental (black) L and LM stimuli and incremental (high-contrast) and decremental (low-contrast) CM stimuli, respectively. Two participants contributed to this full set of results. As found in Experiment 1, suppression was found to be deeper for CM than for LM stimuli,  $F(1,1) = 802.87$ ,  $p = 0.022$ . No significant differences in suppression depth were found between CM incremental and decremental stimuli,  $F(1,1) = 0.36$ ,  $p = 0.66$ , even for central sectors,  $F(1,1) = 1.25$ ,  $p = 0.46$ . Suppression for CM stimuli was, therefore, the same whether matching contrast was greater or smaller than mean noise contrast.

### Control Experiment 2.1: The effect of polarity on stimulus visibility

It is possible that differences found in suppression depth might reflect different stimulus visibilities for different polarities at different eccentricities. Detection thresholds after adaptation to the 2-ND filter, like that used to generate the suppression results of Figure 10, were measured for all stimulus types and polarities, centrally and peripherally. Detection threshold results are shown in Figure 11 expressed in visibility units with respect to the stimuli used in Experiment 2. Sectors were more visible (in multiples of threshold detection

units) for L stimuli than for LM and CM stimuli, but were similar for incremental and decremental stimuli both centrally and peripherally. There was a significant main effect of stimulus type,  $F(2,2) = 54.86$ ,  $p = 0.018$ , and no significant main effects of eccentricity or polarity were found with a repeated-measures ANOVA. This pattern of stimulus visibility was unlike that found for suppression depth measures, so it cannot account for them; that is, differences in visibility cannot explain differences in suppression measures noted between incremental and decremental L stimuli in the periphery or between differences between central and peripheral suppression of CM stimuli.

## Discussion

The depth and extent of interocular suppression using monocular ND filters for various stimulus types (L, LM, and CM) and for incremental and decremental modulations were characterized in this study. Suppression deepens as interocular retinal illuminance differs between the eyes. As for interocular blur suppression (Chima et al., 2015) and amblyopic suppression (Chima et al., 2016), adding dynamic noise to L stimuli to create LM stimuli reduces interocular



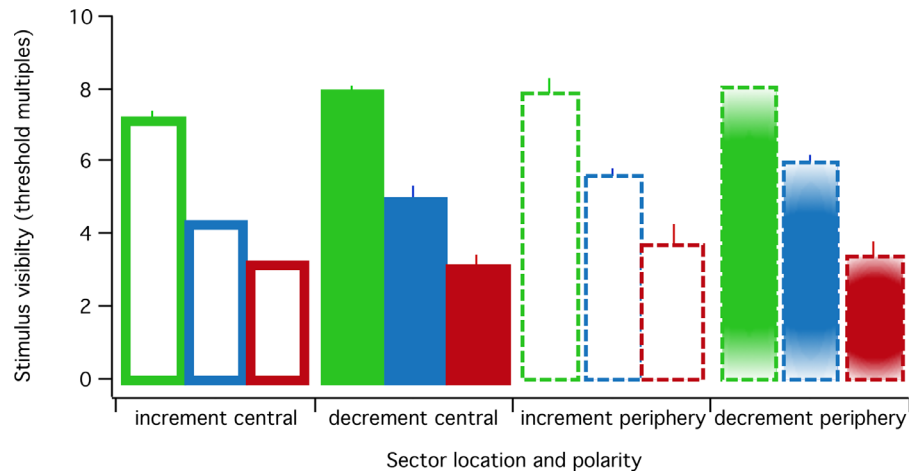


Figure 11. Stimulus visibilities (i.e., multiples above detection threshold with 2 ND) for central and peripheral sectors for incremental or decremental stimuli. Results are for participants who took part in Experiment 2. L (noiseless) sectors are shown in green, LM sectors are shown in blue, and CM sectors are shown in red. Error bars show +1 SE.

suppression. Interocular suppression of CM stimuli using similar dynamic noise is also deeper than for LM stimuli in all cases (blur, ND filter, and amblyopia). Unlike the effects of increasing interocular dioptric blur, which produced deepening but broadly flat suppression across the central 24° (Chima et al., 2015), increasing interocular filter strength led to different patterns of suppression, depending on stimulus type and modulation polarity used to measure it. Suppression for incremental and decremental CM stimuli was similar, being deepest centrally and extending over a broader area than L/LM decrement (black) suppression, which was only central. For L and LM incremental (white) stimuli there was also broader, less centralized suppression. Polarity-dependent luminance suppression is a key finding of this study. This result is compatible with greater dark adaptation effects on ON versus OFF pathways leading to a mismatch in receptive field sizes between eyes for luminance increment (white) stimuli that cannot be binocularly combined.

A small but statistically significant orientation effect was also found in Experiments 1 and 2 (Figures 4C and 9C), such that sectors in the left visual field were suppressed slightly more than sectors in the right visual field (near the horizontal midline), regardless of stimulus type or polarity, ND filter strength, or eccentricity. This finding may be a result of all participants in this study being right eye dominant. Fahle (1987) also reported increased inhibition to binocular rivalry stimuli presented to the left versus the right visual field in normal binocular participants. In that study, right eye/left eye dominance duration ratios were 1.1 centrally and almost 2.0 at 33° in the right versus left visual field. Fahle suggested that this finding was due to temporal field over nasal field dominance and the fact that most humans are right-eye

dominant. Hemifield suppression has also been reported previously in strabismic amblyopia (Chima et al., 2016; Sireteanu & Fronius, 1981), where, in general, when stimuli are aligned with the strabismic eye in esotropia stronger suppression is measured in the temporal hemifield.

### Does visual sensitivity itself regulate interocular suppression during unequal adaptation?

Cone density reduces steeply from the foveola and asymptotes at approximately 1.4° eccentricity, coinciding with an increase in rod density from a rod-free foveola (e.g., Curcio, Sloan, Kalina, & Hendrickson, 1990). Visual sensitivity at lower mesopic luminances (1.5 to 3 ND with natural pupils providing ~10.1 to 0.35 Td·s retinal illuminance) becomes more dependent on rods than cones (Watson & Yellott, 2012). In our experiments, suppression measured for the central sectors (outer edge at 1.3°) would have been predominantly cone driven. With increasing filter strength, sensitivity of the filtered eye would have decreased centrally, encouraging central suppression and loss of stimulus polarity effects, both of which are observed at 3 ND. Our control data show that, with increasing filter strength and adaptation, sensitivity to discriminating the target sector in the filtered eye decreased, particularly for 3 ND (see Figure 8). However, sensitivity was highest for L stimuli and lowest for CM stimuli, whereas suppression depths for L and CM stimuli were similar. Suppression depths for LM stimuli were shallowest, even though sensitivity for LM stimuli was higher than for CM stimuli. There is a mismatch in estimated target visibility (based on

monocular discrimination thresholds) and measured interocular suppression depth.

Reduced cone sensitivity but enhanced rod sensitivity in more peripheral sectors also cannot explain greater peripheral suppression of L and LM incremental stimuli but not decremental stimuli. Our data show that monocular sensitivities to discriminating the target sector within the ring for incremental and decremental stimuli are similar (see [Figure 11](#)), but interocular suppression depths measured for these stimuli combined dichoptically in the periphery differed. Incremental L stimuli were suppressed more strongly. Thus, although sensitivity differences between eyes may partially influence suppression depth measures, our results show that other factors, such as the ability to combine information across different field sizes between eyes, are important.

### Luminance increment and decrement sensitivity differences do not explain differences in suppression

Outside the central sectors, there were significant differences in suppression measured for incremental and decremental luminance stimuli ([Figure 9A](#)). Incremental (or white) luminance stimuli were suppressed more than decremental stimuli out to  $\pm 12^\circ$  in the visual field, with the difference becoming greater the more peripherally suppression is measured. Why might this be? There are well-known differences in visual sensitivity to luminance increments (white) and decrements (black), with greater sensitivity reported for decremental stimuli (for a review, see [Westheimer, 2007](#)). Differences have been reported psychophysically in normal vision (e.g., [Lu & Sperling, 2012](#); [Whittle, 1986](#)) and electrophysiologically (e.g., [Komban et al., 2014](#); [Kremkow et al., 2014](#); [Xing, Yeh, & Shapley, 2010](#); [Zemon, Gordon, & Welch, 1988](#)). Relevant to the current study, decrement luminance discrimination thresholds from medium gray background levels of  $-50\%$  (the same as the decremental luminance surrounding rings) are much smaller than for luminance increments ([Whittle, 1986](#)). Potentially, as sectors were made darker than the surrounding rings, they could have become more discriminable, resulting in lower measures of suppression than were measured for incremental luminance (white) rings. However, this property is not able to explain the current experimental findings, as the reported difference in discriminability between incremental and decremental stimuli was largest at high adaptation levels, becoming small at dim (but still photopic) light levels ([Whittle, 1986](#)). Differences in suppression depths measured in our experiments for incremental versus decremental luminance stimuli became larger with dimmer (moving to mesopic) adaptation levels (from no filter to 2 ND).

In addition, discrimination data for our incremental and decremental stimuli show little difference in discriminability centrally or peripherally when viewed monocularly by the eye adapted to the ND filters ([Figure 11](#)).

### What about a mismatch in receptive field size between eyes during adaptation that is different for ON and OFF pathways?

With dark adaptation, electrophysiological estimates of receptive field center size increase in cat retinal ganglion cells ([Barlow, Fitzhugh, & Kuffler, 1957](#); [Peichl & Wässle, 1983](#)) and cat lateral geniculate nucleus cells ([Kaplan, Marcus, & So, 1979](#); [Virsu, Lee, & Creutzfeldt, 1977](#)). Psychophysical estimates of perceptive field size also increase with dark adaptation in humans ([Ransom-Hogg & Spillmann, 1980](#)). The inability of the binocular visual system to fuse inputs from larger with smaller receptive fields in the adapted filter eye and non-adapted (no filter) eye, respectively, may be key to explaining interocular suppression. This is analogous to strabismic suppression. [Sengpiel et al. \(2006\)](#) suggested that strabismic suppression is deeper centrally due to the lack of binocular convergence of small foveal receptive fields, an explanation also put forth by [Sireteanu and Fronius \(1981\)](#), whereas the larger receptive fields in the periphery of the two eyes are more likely to be fusible. Differences in receptive field size could also explain why suppression is measured at the eccentric point corresponding to the non-amblyopic eye fovea in strabistics ([Chima et al., 2016](#)).

Dark adaptation affects temporal tuning properties of ON and OFF retinal ganglion cells in mice differently ([Pandarinath, Victor, & Nirenberg, 2010](#)), so it is plausible that spatial tuning properties are also differently affected. One possibility is that with dark adaptation, receptive field centers of the OFF pathway (that process decremental luminance stimuli) change very little in size, resulting in essentially normal binocular combination in the periphery ([Figure 9](#)). Receptive fields of the ON pathway (that process incremental luminance stimuli) might increase in size more with dark adaptation and no longer be optimally combined with the smaller receptive fields from the non-adapted eye ([Figure 9](#)). Such an explanation would seem compatible with the psychophysical finding that there are fewer discriminable steps available to decremental than incremental luminance pathways ([Whittle, 1986](#)), resulting in a lower range of available receptive field sizes.

Differences in the effects of dark adaptation on ON and OFF pathways are likely to originate at the retinal level ([Kuffler, 1953](#); [Werblin, 1974](#)). An OFF pathway bias may be mediated more by rods than cones

(in our experiments, outside the central  $1.3^\circ$ ) in the mesopic range tested. In support of this possibility, Cao, Zele, and Pokorny (2007) reported that, when observers adapted to lower luminance levels, quicker reaction times were found for luminance decrements than increments when rods were isolated, but no polarity difference was found when rods and cones were targeted simultaneously. Different adaptation characteristics have also been found for increments and decrements within the chromatic domain (Chichilinsky & Wandell, 1996; Walraven, 1977).

Amblyopia has also been reported to affect the ON pathway more than the OFF pathway (Pons, Jin, Mazade, Dul, Zaidi, & Alonso, 2019). Sustained optical blur during development was suggested to weaken ON cortical pathways more than OFF pathways, a response imbalance proposed to remain in adults even after best optical correction. Previous results on interocular suppression in adult strabismic but not microstrabismic participants (with best optical correction) do also demonstrate increased suppression of incremental luminance, over decremental luminance stimuli (Chima et al., 2016).

Differential luminance polarity adaptation should not occur with CM stimuli, as there is no change in overall mean luminance across the stimulus, so the lack of measured polarity suppression difference for CM stimuli may be expected. For contrast-modulated textures of densely packed elements, similar lateral inhibition was measured irrespective of stimulus decremental or incremental contrast centers or surrounds (Sato, Motoyoshi, & Sato, 2016; Solomon, Sperling, & Chubb, 1993). Combined with the results of the present study, it may be suggested that ON/OFF processing asymmetries are limited to luminance-defined stimuli.

### Effect of dynamic noise on first-order luminance-defined stimuli

Interocular suppression is shallower for LM noise stimuli than for L stimuli without added noise, although the spread of suppression is similar across the visual field, and differences in suppression between incremental and decremental stimuli are still present but reduced. Dynamic noise may introduce temporal transients, which clinically have been found to break down suppression in amblyopia (Scheiman and Wick, 2008), so this may contribute to shallower suppression measures for LM stimuli than for L stimuli. In addition, if internal noise is greater in the adapted eye (Bennett, Sekuler, & Ozin, 1999; Nagaraja, 1964), then adding the same stimulus noise to both eyes would result in less of a difference in sensitivity between them for LM stimuli than for L stimuli (see Figure 8), resulting in lower measures of interocular suppression. The addition

of correlated luminance noise reduces binocular detectability of both increments and decrements by similar amounts (Cohn, Leong, & Lasley, 1981), so differences in receptive field size that might occur between eyes due to adaptation differences between ON and OFF pathways as described in the section above should still apply.

### Suppression of LM compared to CM dynamic noise stimuli

As has been found previously for interocular blur suppression (Chima et al., 2015), microstrabismic and strabismic suppression (Chima et al., 2016), depth of interocular suppression is greater and more extensive across the visual field for CM stimuli than LM stimuli during unequal luminance adaptation. The effects of increasing interocular differences in blur, ND filter, and amblyopia are also steeper. No differences have been found in suppression depth for CM decremental versus incremental stimuli at any filter or adaptation level (neither are there any consistent physical shifts in mean luminance). Eccentricity maps show a similar pattern of suppression for CM stimuli to L and LM decremental stimuli, less similar to L and LM incremental stimuli.

Deeper suppression for CM stimuli than LM stimuli may be caused by differences in cortical processing mechanisms for the two stimulus types. Specifically, disrupted binocularity interferes more with the efficient combination of CM stimuli than LM stimuli, and CM stimuli are more sensitive to change due to binocular disruption, indicating that they are inherently processed by predominantly binocular mechanisms (Chima et al., 2015; Chima et al., 2016; Skerswetat, Formankiewicz, & Waugh, 2016). The dynamic noise in the current experiments was interocularly correlated; however, whether or not the noise was correlated may not have affected outcomes (Georgeson & Schofield, 2016; Zhou, Georgeson, & Hess, 2014; Zhou, Liu, Zhou, & Hess, 2014). The lack of need for carrier correlation between eyes in these studies of dichoptic phase perception and grating binocular summation suggests that CM envelope extraction occurs after binocular combination. Thus, CM stimulus extraction is likely served by mechanisms receiving binocular input that is different from LM stimuli (Allard & Faubert, 2007; Baker & Mareschal, 2001; Chima et al., 2015; Chima et al., 2016; Hairol & Waugh, 2010; Mareschal & Baker, 1998; Schofield & Georgeson, 1999; Schofield & Georgeson, 2003; Skerswetat et al., 2016; Wong, Levi, & McGraw, 2001).

The larger area of central CM suppression compared to LM suppression found in the present study lends further support to the idea that CM envelope extraction involves cortical areas with larger receptive fields (e.g., V2) than earlier striate areas, also found in physiological studies (Foster, Gaska, Nagler, & Pollen, 1985; Gattass,

Gross, & Sandell, 1981; Gattass, Sousa, & Gross, 1988; Kennedy, Martin, Orban, & Whitteridge, 1985). Cortical representation of the fovea is also larger in V2 than V1 (Schira, Tyler, Breakspear, & Spehar, 2009), suggesting that deeper suppression is required to remove this larger area from perception, thus eliminating diplopia.

## Conclusion

Interocular suppression as a result of wearing monocular ND filters in binocularly normal observers deepens with increasing filter strength from around 1.5 ND and higher. Incremental luminance (white) targets are suppressed more strongly over more extensive retinal areas than decremental luminance (black) targets, which are suppressed only centrally. Differences may arise from different rod–cone contributions and different ON and OFF pathway responses to dark adaptation, although discriminability differences between black and white stimuli cannot be ruled out. We suggest that with adaptation a greater shift through receptive field sizes occurs for the ON pathway, so that mismatches in size between eyes cannot be combined effectively, leading to interocular suppression. A similar mechanism can also explain suppression in binocularly anomalous participants. Clinically, increment rather than decrement luminance stimuli reveal greater levels of suppression in peripheral binocular imbalance and strabismic amblyopia. CM stimuli are more sensitive to suppression than LM stimuli and are robust to stimulus polarity; therefore, they might be most helpful in assessment of mild amblyopia and in microstrabismus.

*Keywords:* interocular suppression, ND filters, polarity, luminance-modulated noise, contrast-modulated noise, increment, decrement

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