Stimulus Dependence of Interocular Suppression

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Abstract

Suppression is assessed using a variety of methods with different stimuli that vary in color, contrast, size, and luminance. We hypothesized that stimulus variation may yield different spatial extents of suppression. Here, to evaluate the role of stimulus characteristics, we measured the suppression zone using a binocular rivalry paradigm in normal observers by systematically varying the parameters of dichoptic Difference of Gaussian stimuli. The stimuli consist of a constantly visible horizontal reference seen by one eye while two vertical suppressors were presented to the other eye. With a keypress, the suppressors appeared for 1 second, to induce a robust transient suppression zone in the middle part of the reference. Subjects adjusted the width between the suppressors to determine the zone. The zone decreased significantly with increasing spatial frequency and lower contrast. The horizontal zone was larger than the vertical zone by a factor of 1.4. The zone was smaller with negative contrast stimuli compared to positive contrast polarity but independent of eye dominance, luminance and colored filters. We then fit a model to determine the optimal parametric definition of the suppression zone and found that the zone consists of two parts: a stimulus-dependent and a fixed non-stimulus dependent zone.

Introduction

Binocular rivalry is a visual phenomenon where one experiences the alternating perception of dissimilar images shown to the two eyes. Dissimilar images can result from interocular differences in luminance, contrast, motion, form, colors, and orientation, for example. Dissimilar images do not allow fusion, and lead to visual confusion. In order to remove this confusion, each eye will alternately suppress the other eye to exert dominance during binocular rivalry[1]. However, under normal viewing conditions, where the two images are usually similar, observers will fuse the images into a single, unitary percept. Following Wheatstone's invention of the stereoscope in 1836, researchers have generated a wide variety of artificial situations to explore how binocular vision responds to dramatically different monocular stimuli during rivalry. A common finding is that perception fluctuates between two states with a relatively slow and patchwork alternation of the monocular images[2]. The fluctuation between the two percepts is predominantly based on stimulus strength. When one percept is dominant, the other percept is suppressed and not seen.

Apart from individuals with normal binocular vision, interocular suppression is more commonly associated with observers with abnormal binocular vision, such as amblyopia or strabismus. These individuals develop suppression in childhood as a result of a prolonged blurry image, visual confusion, or diplopia. Von Noorden described suppression as an active central inhibition of disparate and confusing images originating from the retina of the deviated eye in the presence of binocular vision from two eyes[3]. Many studies have supported his definition where suppression is needed to resolve conflicting percept[4] or to avoid diplopia from mismatched interocular features. Though his description is more inclined to ocular misalignment, suppression also plays a role in facilitating the visibility of focused images; the eye with a clear image will suppress the eye with the blurry image[5].

It is still debated if the suppression during binocular rivalry has the same mechanism as amblyopia since amblyopes have limited binocular function[6–10]. Since inhibition is one of the proposed mechanisms underlying the deficiencies in amblyopia[11], this interocular inhibition may actually originate from binocular rivalry at the very early stage. In individuals with good binocular vision, both eyes have roughly equal reciprocal strength of inhibition. In the case of amblyopia, the amblyopic eye has a weaker inhibitory strength compared to the non-amblyopic eye[12–14]. However, under balanced conditions between the two eyes, such as contrast balancing or lower luminance in the fellow eye, amblyopes also experience alternating suppression, similar to binocular rivalry of normal observers[15,16].

Amblyopia is a visual disorder that arises from binocular mismatch (unequal refractive error, presence of ocular misalignment, or sensory-deprivation) during a critical period of visual development and it affects about 3-5% of the global population[17–20]. Clinically, amblyopia is diagnosed based on findings of a deficit in visual acuity and stereo acuity after the correction of refractive error with no other ocular pathologies. The amblyopic eye also develops suppression, a pathological scotoma in the visual space of one eye when both eyes are open. Different types of amblyopia have different suppression patterns; within strabismic amblyopia, exotropia has suppression in the temporal hemiretina, while esotropia tends to have a more localized area nasal to the fovea[21]. Anisometropic amblyopia is believed to have a weaker suppression[22].

The earliest study to map the spatial extent of suppression was carried out by Von Graefe in 1896 and followed by Travers using a haploscope system[23]. The interest in characterizing the suppression scotoma according to its etiologies has been further continued in several studies with different stimuli[8,9,22,24–28]. Generally, the suppression area and its depth are associated with the severity of amblyopia. As a result of that, the assessment of suppression plays a crucial role in diagnosis, treatment, and prognosis for amblyopia and strabismus.

In clinical settings, suppression is assessed with the Worth-4-Dot test, Bagolini lens, Sbisa Bar and synoptophore. It is challenging for clinicians to compare the result obtained from one test to the other given that each test is designed with different stimulus parameters and dichoptic presentation[29,30]. For example, the W4D test, which uses anaglyph colors, is performed in two different lighting conditions: normal room illumination and in the dark. Also, the two different colors used may introduce some form of binocular dissociation[31]. On the other hand, the Bagolini test uses striated lenses placed in front of the eyes and an observer will perceive orthogonal high spatial frequency stimulus (thin streak of light). To assess the depth of suppression, the luminance in the fellow eye is decreased by using the Sbisa bar or Neutral Density filters. One recent study found that the variations of the striation on the Bagolini lens (coarse versus laser-cut) would even affect the perceived length of the light streaks[32]. Another clinical instrument, the synoptophore can identify the suppression zone by comparing the angle between the two tubes, while adjusting the background luminance can estimate its depth. The synoptophore testing slides are designed with various object sizes, line thicknesses, colors, and features. On account of these limitations, the results are often variable and hard to compare with different sets of slides.

Meanwhile in the literature of binocular rivalry, different sets of stimuli used in laboratory experiments have shown significant variability. Lei & Schor (1994) found that the size of suppression during binocular rivalry changes with the contrast and spatial frequency of the stimuli[33]. The dominant eye is able to suppress the non-dominant eye longer during the occurrence of binocular rivalry[34,35]. What about the spatial extent? Will contrast polarity also affect the suppression zone? These various factors have not been systematically explored in a single study.

The literature above has shown significant variability not only between the stimuli used to study binocular rivalry and clinical assessment of amblyopia, but also within the clinical tests themselves. We posit that these variabilities may affect the nature of the suppression scotoma, causing a change in its size according to the stimulus used. Therefore, here we investigate how stimulus parameters affect the assessment of suppression in a comprehensive series of studies. Since suppression in amblyopia may vary according to its etiologies, severity, visual acuity, and other factors, in order to have better control, we instigated suppression in observers with good binocular vision by using orthogonal Difference of Gaussian bars in different conditions (spatial frequency, contrast, contrast polarity, eye dominance, luminance, and colored filters). After a series of experiments, we confirmed that the suppression zone is not fixed. We found that it varies with some, but not all of these stimuli parameters.

To measure the spread of suppression, we adopted the dichoptic stimuli from Lei & Schor (1994), comprising a constantly visible horizontal DoG (reference) seen by one eye with two vertical DoGs (suppressors) that are intermittently presented to the other eye (Fig 1). The DoG stimulus has a center white portion surrounded by darker grey areas on both sides. With a keypress, the suppressors appeared for 1 second, to induce a robust transient suppression zone in the middle part of the reference. Subjects adjusted the width between the suppressors to determine the maximum separation that still produced suppression, delimiting the borders of the suppression zone[36]. We measured the zone in an extensive series of experiments, varying spatial frequency (0.888 to 11.54cpd), contrast (12.5-100%), dominant vs. non-dominant eye, stimulus orientation (horizontal vs vertical dimension), contrast polarity (different combinations of the reference and suppressors with positive and negative contrast polarity), colored filters (matched vs. dichoptic), and ND filters (1 and 2 log units). A total of eleven subjects volunteered for the different sub-experiments.

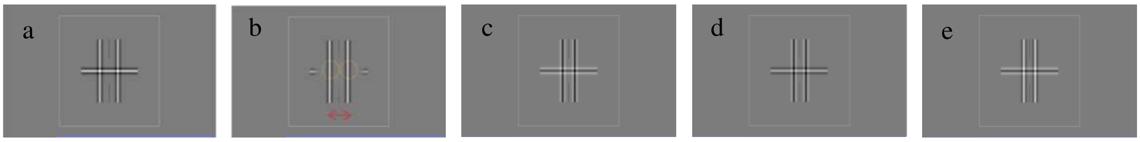

Figure 1: Stimuli used in the experiment. (a) The horizontal reference bar was presented continuously to one eye. The two vertical suppressors were presented briefly to the other eye. The DoG bars had a white center surrounded by a darker grey region on both sides. A white square outline served as the binocular fusion lock. Two fine vertical black lines pointing towards the center part of the reference served as a fixation guide. (b)The area of perceived suppression upon vertical suppressor appearance is outlined by the yellow circles. Subjects adjusted the separation of the vertical bars to the widest setting that still suppressed the horizontal segment between them. The distance between the center of the two suppressors is termed as the suppressio zone, (red arrow). (c-e) These figures illustrate the different combinations of contrast polarity: (c) black-black, (d) white-black, and (e) black-white. The first color in the combination refers to the center of the horizontal reference followed by the vertical suppressors.

Results

Experiment 1

A) Effect of Spatial Frequency (n=8)

We found that higher spatial frequency stimuli yielded a smaller suppression zone. Figure 2 shows the mean across all subjects with congruent white center stimuli at 100% contrast. As spatial frequency increases, the zone decreases significantly ($p<0.001$). When the spatial frequency increased by 1 log unit, the zone decreased by approximately 0.83 log unit (steepness of line) when fitted with linear regression OLS on log-log coordinates. The gray lines in Figure 2 show the corresponding size of one, two, and three full cycles of the DoG. The size of a full cycle is calculated from the spatial frequency of the DoG. For example, a DoG of 0.888 cpd will have a center width of 29.64 arcmins and spans an area of 67.57 arc minutes for a full cycle. We found that the mean zone across all subjects was close to 2 cycles of the DoG for low spatial frequencies but closer to 3 cycles at high spatial frequencies.

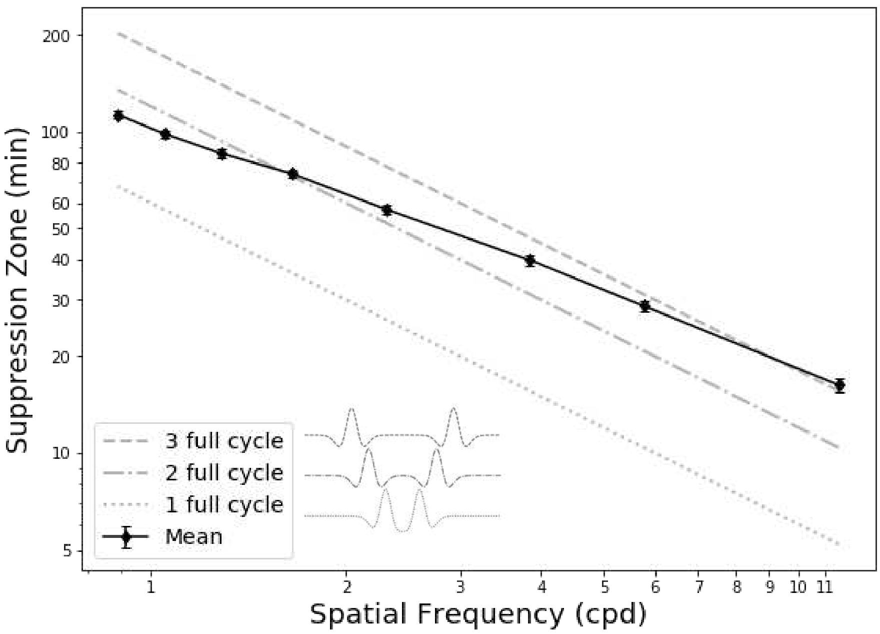

Figure 2: Suppression zone as a function of spatial frequency. The solid black line is the mean values across all eight subjects. The other lines represent the size of the single, double, or triple full cycle of the DoG stimuli. The mean values are almost two full cycles of the DoG at low spatial frequencies but three full cycles at higher frequencies. The vertical error bar represents the standard error. The lower left panel illustrates the separation between the center to center of the two DoG at one, two, or three full cycles.

B) Effect of Contrast (n=8)

From Experiment 1A, we found that the zone reduced as spatial frequency increased. With lower stimulus contrast, the mean also decreased significantly ($p<0.001$). Figure 3 plots the mean result across all subjects at different contrast levels. From the OLS fit, we found that for a log unit reduction of contrast, the zone decreased by 0.168 log unit in minutes. The reduction follows a similar pattern across all spatial frequencies, as shown by the downward vertical shift. All of the subjects except S07 had a similar downward shift of the slope when the stimuli were presented at lower contrast.

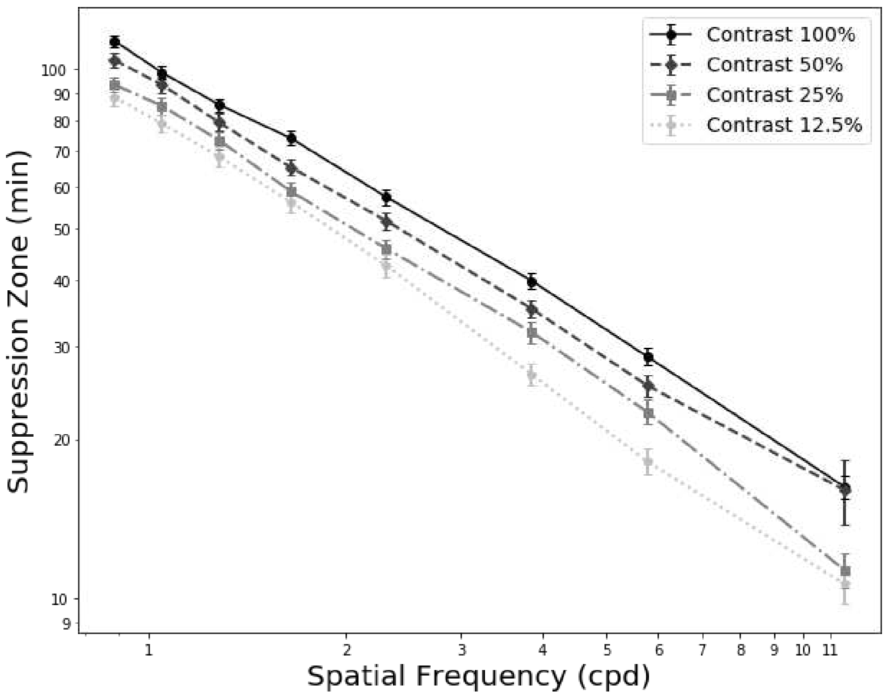

Figure 3: The reduction of suppression zone as a function of contrast (n=8). The solid black line (contrast 100%) is similar to the results obtained from Experiment 1A. This line is shifted downward with lower contrast. The vertical error bars represent the standard error.

C) Effect of Eye Dominance (n=8)

When we presented the suppressors to either of the eyes, the suppression zone did not significantly differ based on the suppressor eye when averaged across subjects (p=0.81). This suggests that the size is similar in normal subjects irrespective of eye dominance. We also analyzed the effect of ocular dominance at different contrasts and confirmed that the zone is not affected by ocular dominance. The spread of the suppression zone was independent of eye dominance across all contrast levels and spatial frequencies.

We fitted the results in Experiment 1 with an Ordinary Least Square (OLS) linear model to predict the suppression zone based on the different parameters: spatial frequency, contrast, and eye dominance. The model was well fitted with a significant regression equation $F(3, 2796) = 2929$ ($p<0.001$) with an R^2 value of 0.759 (Adj. R^2=0.758). The predicted log10 (Zone, in arcminutes) is equal to 2.024 - 0.830 * log10 (Spatial Frequency, in cycles per degree) + 0.1678 * log10 (Contrast, Weber proportion) + 0.0016 (Dominant Eye). Eye Dominance was coded as 1 to indicate the right eye was dominant (or 0 for left eye). Out of the three parameters, only spatial frequency and contrast were significant predictors of the spatial extent of suppression.

Experiment 2

A) Horizontal versus Vertical Dimension (n=8)

To investigate the effect of different dimensions and spatial frequency, we fitted the result with a similar OLS model. This model was well-fitted with an equation $F(2, 877) = 1654$ ($p<0.001$) with an R^2 value of 0.790 (Adj. R^2=0.790). The intercept coefficient for the vertical dimension was -0.1384 when compared to the horizontal dimension. We found an asymmetric pattern in the suppression zone: the horizontal dimension was larger than the vertical dimension. This effect manifested across all subjects (n=8) and is shown in Figure 4. Out of the eight observers, 7 observers had a horizontal to the vertical ratio in the range of 1.21 to 1.84. The mean ratio across all subjects at all spatial frequencies was 1.41 ± 0.26 (standard deviation). In other words, the horizontal dimension (width) was about 1.4 times larger than the vertical (height). Therefore, the area of suppression is elliptical in shape and not circular.

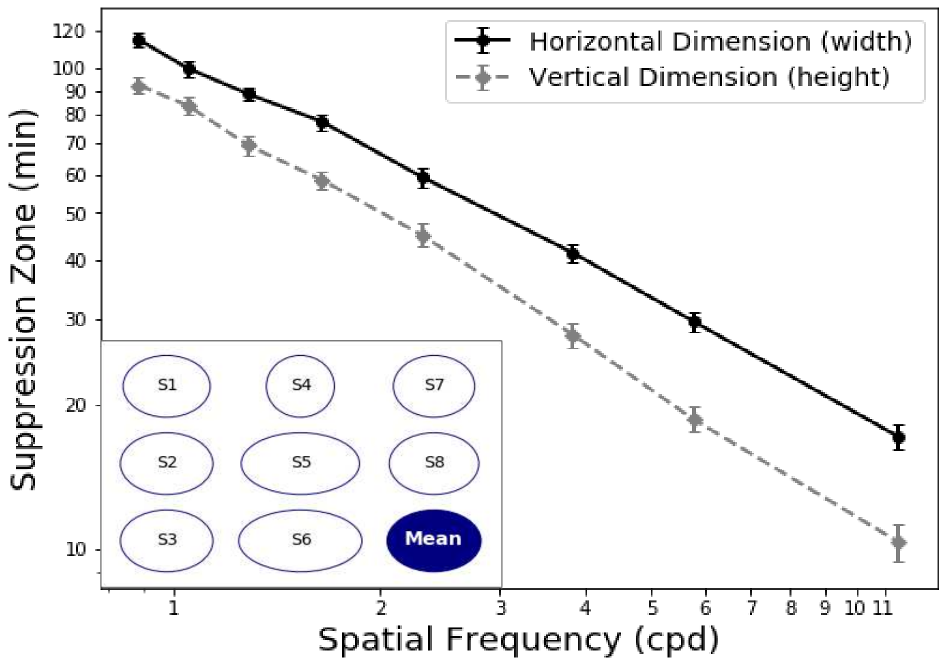

Figure 4: This plot shows that the ratio between the zones for the two dimensions, horizontal and vertical is consistent across all spatial frequencies. The horizontal size was larger by approximately 1.4x than the vertical zone, suggesting that the suppression zone is elliptical in shape. The schematic on the lower left shows the ratio of horizontal to vertical zone for each subject. The mean area of suppression is elliptical in shape (dark blue). Standard errors are shown on the vertical bars.

<u>B) Effect of Contrast Polarity (n=6)</u>

We also tested the stimuli at 100% contrast with four different combinations of contrast polarity: White-White, Black-Black, Black-White, and White-Black. We fitted the data in another OLS model because the original model only includes White-White stimuli. We included 2 independent parameters in this model: spatial frequency and contrast polarity (4 categorical). The model was well-fitted with an equation $F(4, 1275) = 836.2$ ($p<0.001$) with an R^2 value of 0.724 (Adj. R^2=0.723). In relation to Black-Black stimuli, the difference in intercept coefficients were 0.0096, 0.0538, and 0.0513 for Black-White, White-Black, and White-White, respectively. Thus, the two negative contrast polarity stimuli were significantly different from the two positive contrast polarity, White-White ($p<0.001$) and White-Black (p=0.001). With a black center reference, the zone was slightly smaller than the white center reference. This result suggests that the contrast polarity of the reference may determine the spread of suppression.

<u>Experiment 3</u>

<u>A) Effect of Colored Filters (n=6)</u>

We fitted a mixed linear regression model for Experiment 3 and included 6 categorical levels: Baseline (no filter), binocular 1ND, binocular 2ND, binocular red, binocular green, and dichoptic red-green. Compared to the isoluminant 1ND filter, the zone was not statistically significant with a red filter (p=0.712), green filter (p=0.503), and red-green filter (p=0.250), suggesting that colors do not affect the suppression zone. With dichoptic chromatic filters (red-green), the data were near significance (p=0.063). When we compared matched chromatic (binocular red or green) to dichoptic chromatic filters (red-green), four out of the six subjects had individual $p<0.023$ suggesting individual variability (three subjects had larger suppression size while one had a smaller size).

B) Effect of Luminance (n=6)

From the model, we do not find any significant difference in the zone as a function of luminance ($p>0.05$). The suppression zone remained robust and is independent of the luminance level despite a reduction of 2 log units.

Discussion

In a series of experiments, we determined that the spatial extent of suppression depends on the properties of the stimuli used to instigate rivalrous suppression. Of all the factors, the spatial frequency of the stimuli affects the size the most. Our finding agrees with other studies, in which finer stimuli had a smaller suppression area compared to coarse stimuli[33,37] and the range of suppression is not scale invariant. Even though the size of suppression varies from subject to subject, the changes as a function of spatial frequency were consistent across all subjects. Although we used the same set of spatial frequencies as Lei & Schor, our results for the overall suppression zone were smaller, especially at lower spatial frequencies. There are several possible reasons for the discrepancy, one of which may be the different response methods used. They used a forced-choice Method of Limits while we used a Method of Adjustment which has been reported to yield smaller estimates because of the nature of the underlying decision process[38]. Another possible reason is vergence control. Compared to their experiment which was performed using a haploscope system, our experiment was performed with passive glasses, which allow a more naturalistic vergence demand.

We found that the area of suppression reduced with lower contrast. Similarly, low contrast orthogonal gratings have been found to fuse more easily into plaid patterns, whereas those with higher contrast tend to be rivalrous[39,40]. Our data agree with the general finding that rivalry is less pronounced at lower contrast. Since rivalry is more pronounced with higher contrast, it has been commonly associated with the parvocellular pathway[41,42]. However, stimuli with higher spatial frequencies are fused more easily than lower spatial frequencies, implying the involvement of magnocellular pathway[43]. We found no difference in contrast-dependence of low-vs-high spatial frequencies, suggesting both pathways maybe involved[44].

Can the effects observed be as a result of contrast energy differences? To test this, we determined the contrast energy for each stimulus, by integrating the squared local contrast over the entire DoG and expressed the suppression zone as a function of contrast energy. Based on Figure 5, any contrast energy level could yield multiple suppression zones. Contrast energy alone could not account for the zone we observed; residual effects of spatial frequency remained. In addition to contrast and spatial frequency, spatial frequency and size also covary with this stimulus; the size of the DoG stimulus is inversely proportional to its spatial frequency. Future work with modified stimuli is needed to decouple the effects of contrast, spatial frequency, size, and the physical contrast (the contrast hitting the retina, which is reduced at high spatial frequencies due to the optics of the eye as defined by the modulation transfer function).

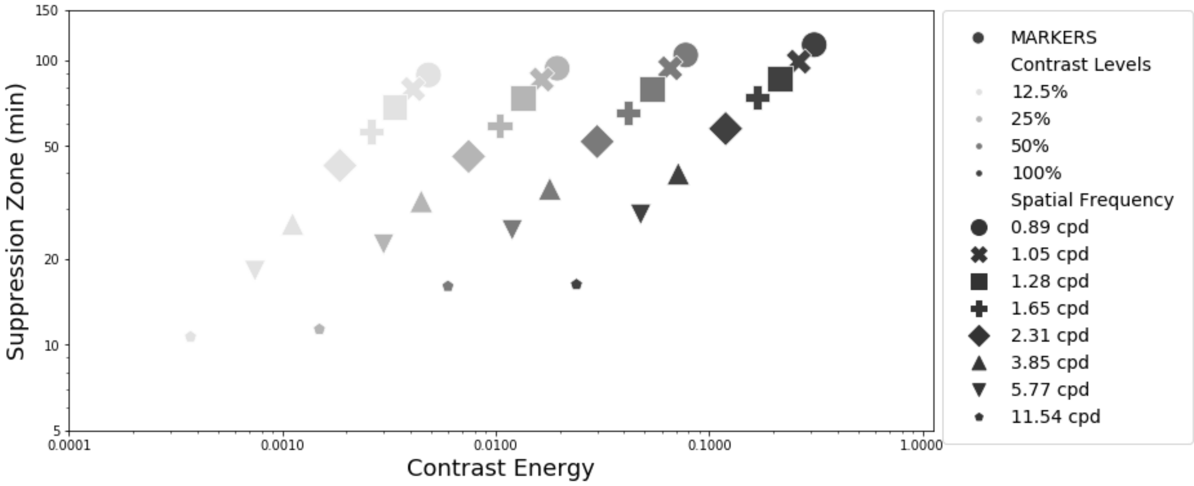

Figure 5: This plot illustrates how suppression zones change as a function of contrast energy. Different shapes of the markers indicate different spatial frequencies while the grayscale shades indicate the contrast level. Any contrast energy level could result in multiple suppression zones.

Many aspects of binocular vision and vergence are more extensive in the horizontal meridian. For example, Panum's fusional area and range of fusional vergence is larger in the horizontal than the vertical dimension. Similarly, we found that the suppression area is not circular but elliptical in shape, with a horizontal dimension larger than vertical across all spatial frequencies, in agreement with the result found by Kaufman[36]. Another study which used similar orthogonal stimuli found that normalized suppression time is longer in the horizontal dimension than vertical[45]. In contrast to Lei & Schor, we did not find that the suppression zone was vertically elongated at low spatial frequencies and horizontally elongated at high spatial frequencies.

What could have contributed to the anisotropy of the suppression zone? Kaufman proposed vergence error, while Lei & Schor argued that if there is vergence error, the suppression area would be a constant value corresponding to the amount of individual vergence error. Vergence error would also lead to double vision. To avoid this, our stimulus had an outer binocular fusion lock and two vertical fixation lines pointing towards the middle region of the reference. None of our subjects reported double vision or difficulty fusing the stimuli. Additionally, our setup allows a more natural vergence and accommodation than a haploscope system. While the effect of vergence should be minimal due to the use of a long horizontal reference bar, to precisely study the relationship between vergence control and the spread of suppression as proposed by Kaufman, recording the binocular eye position is needed. In addition to the vergence system, there are a multitude of horizontal versus vertical anisotropies in the visual pathway, including cone density and ganglion cell distribution[46,47] that may contribute to the elliptical suppression zone.

Any additional feature close to the suppression area may affect the outcome[45]. With that in mind, we set the width of the reference to be equal to the height of the suppressors while in Lei & Schor, the reference was longer than the suppressors. To investigate if the sharp edges of the suppressors would increase saliency and affect the outcome, we conducted a control experiment with different vertical suppressor heights (from 1.67 to 16.7°) while the length of reference was fixed at 8.5°. Three subjects (S1, S2, & S4) participated in this experiment and we found that the size of the suppression zone was independent of the suppressor length (Repeated measure ANOVA, $F(9,18) = 0.60$, $p = 0.78$).

We found that the suppression area is slightly smaller with negative polarity stimuli than with positive contrast polarity. One explanation would be the suppression mechanism is present in two different pathways: the ON and OFF pathway. The ON pathway processes light increments (positive contrast), while the OFF pathway is selective for decrements (negative contrast). The receptive fields of the ON cells were found to be larger by 20% than the OFF cells[48]; therefore, may possibly be the explanation behind our result.

With colored filters, the area of suppression is similar to achromatic stimuli of equivalent luminance. With dichoptic red-green filters, we did not find any significant difference. However, when analyzed individually, we found individual variability. This implied that the effect of color rivalry is not universal across subjects, but could be affected by individual fusional vergence. It is worth noting that these subjects have normal binocular vision and vergence range. In the case of individuals with intermittent exotropia with weak fusional vergence, color rivalry could inadvertently dissociate binocularity and facilitate suppression. In the literature, color difference induces stronger rivalry and reduces fusion because of inhibitory mechanisms from chromatic-sensitive neurons in the visual cortex[49,50]. Besides the colored filters, we also found that suppression size is independent of luminance and eye dominance. Clinically, suppression is detected more frequently when the Worth-4-Dot test is performed in the dark than room lighting. Thus, differences seen with the W4D tested in darkness are likely due to lack of peripheral fusion and possibly an increase in stimulus contrast against a dark background.

While some literature has suggested that different suppression mechanisms are involved between observers with normal binocular vision and amblyopia, under balanced conditions between the two eyes, such as contrast balancing or lower luminance in the fellow eye, amblyopes do experience alternating suppression, similarly to binocular rivalry[10,16]. These two types of suppression show similar traits. For example, they are both scale dependent in observers with normal binocular vision[51] or amblyopia[52]. There is also evidence that the suppression from imbalanced binocular inhibition is also spatial frequency-dependent in observers with amblyopia[53,54]. Transient suppression or binocular rivalry is thought to reflect competition between monocular neurons within the primary visual cortex[55]. It is quite possible that constant suppression arises from transient suppression, but deepens with time and spreads into higher cortical areas. Constant suppression of the amblyopic eye with cessation of binocular rivalry is a major obstacle to regain binocular vision and stereopsis.

The two parts of the suppression zone: stimulus-dependent and non-stimulus-dependent

If suppression were based solely on stimulus characteristics, parsimony would dictate that the suppression zone should be directly proportional to the stimulus size--in fact, this is what Lei and Schor found: a suppression zone of exactly three cycles of the DoG across all spatial frequencies. Instead, we found that the suppression zone was not strictly proportional to the stimuli, having a smaller proportion at lower spatial frequencies.

To account for the discrepancy, we fit each subject’s data with a log-transformed linear model of the form log (Suppression Zone)=log (p*(B*2.28) + delta), where p is a subject-dependent proportion of cycles of the DoG spatial frequency (B=central lobe width and B*2.28 is one cycle, as specified in Equations 1-4), and delta is a subject-dependent offset that is common across spatial frequencies. The “p" term can be understood as the suppression zone relative to the size of the stimulus. We fit this model using PyMC3[56], which uses Markov chain Monte Carlo to determine optimal parameters for generic statistical models with minimal assumptions. Although PyMC3 incorporates Bayesian principles, we used flat (uninformative) priors. The model fit the individual data well, as shown by the 95% confidence intervals in Figure 6 (shaded blue regions), resulting from chains of length 2000. Figure 7 shows the two model parameters for each subject: the individual's baseline proportion of the stimulus size and the common fixed zone. The stimulus-dependent component, p, is 1.5-2.5 (cycles), and is likely affected by the observer's criterion during the task: some subjects may be more conservative while others may be more lenient. The model's constant term ranges between 5 and 15 arc minutes for all subjects except S3.

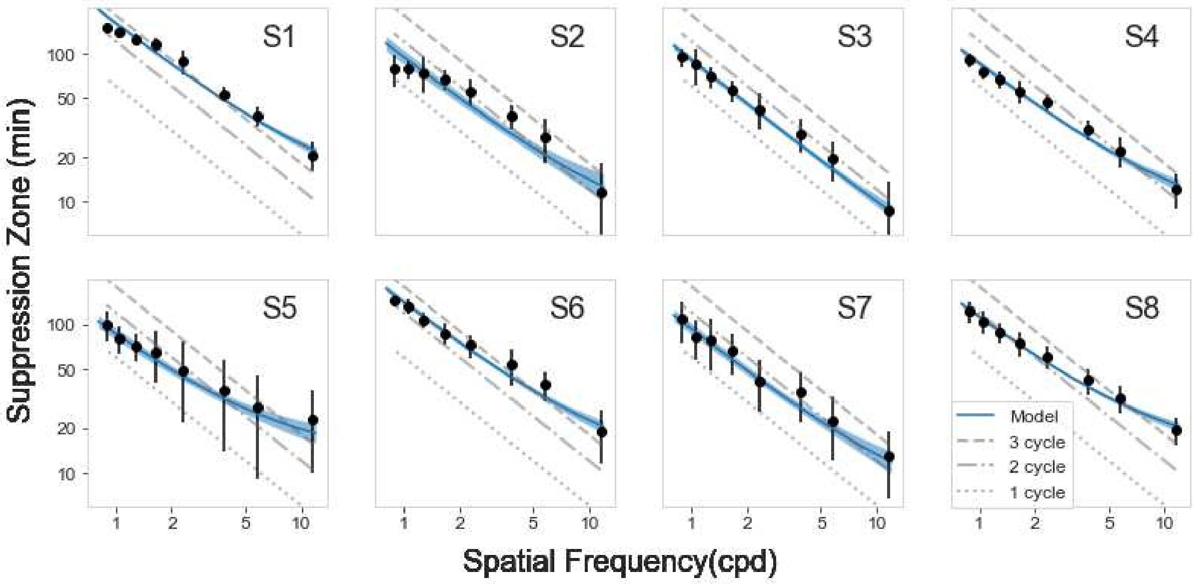

Figure 6: The model predicts the individual results well, indicated by the shaded blue region, indicating 95% credible intervals from the fits. Different dashed lines indicate the multiplication of the number of full cycles (in cpd).

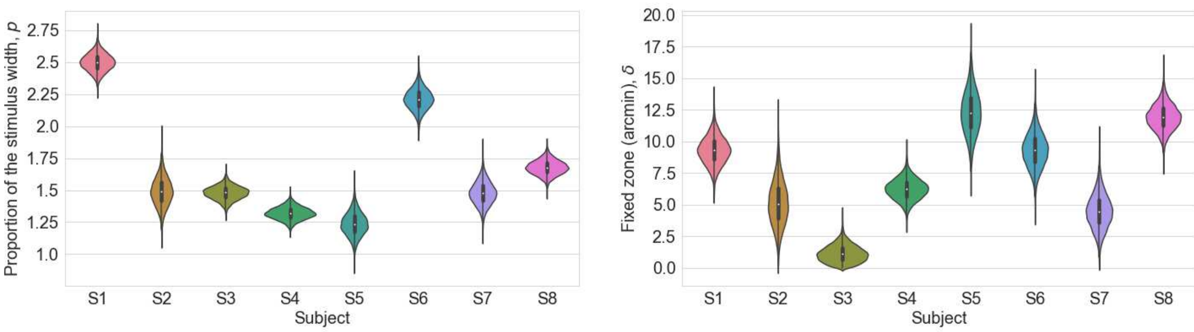

Figure 7: In the model, the parameter estimates for the proportion of stimulus width is between 1.25 and 2.5 cycles (left panel). The constant term delta is 5-12.5 arc minutes for most subjects (right panel).

For example, for subject S1, the suppression zone was 2.5 cycles of the DoG, with a fixed zone of ~10 arc minutes, meaning their zone was ~2.5 cycles at low spatial frequencies and more than 3 cycles at the highest spatial frequencies. Interestingly, one of Lei and Schor's three subjects did show a pattern like this. This static zone can also be understood as the gap between the two suppressors, when the innermost edges of the DoGs are lined up to equivalent points on their envelope at each spatial frequency, as illustrated in Figure 8 (right panel). This suggests the contribution of two elements to the spatial extent of suppression, as shown schematically in Figure 8 (left panel): a stimulus-dependent component that scales with the stimulus size that spreads from the locus of dissimilarity (dark blue circles, emanating from the intersection point of suppressors and reference) and a non-stimulus-dependent component (cyan region, centered at fixation). This fixed zone may be related to Panum's Fusional Area at the fovea. Coincidentally, with a finer stimulus, Kaufman reported that the strongest suppression occurred when the gap between the suppressors was 14 arc minutes[36].

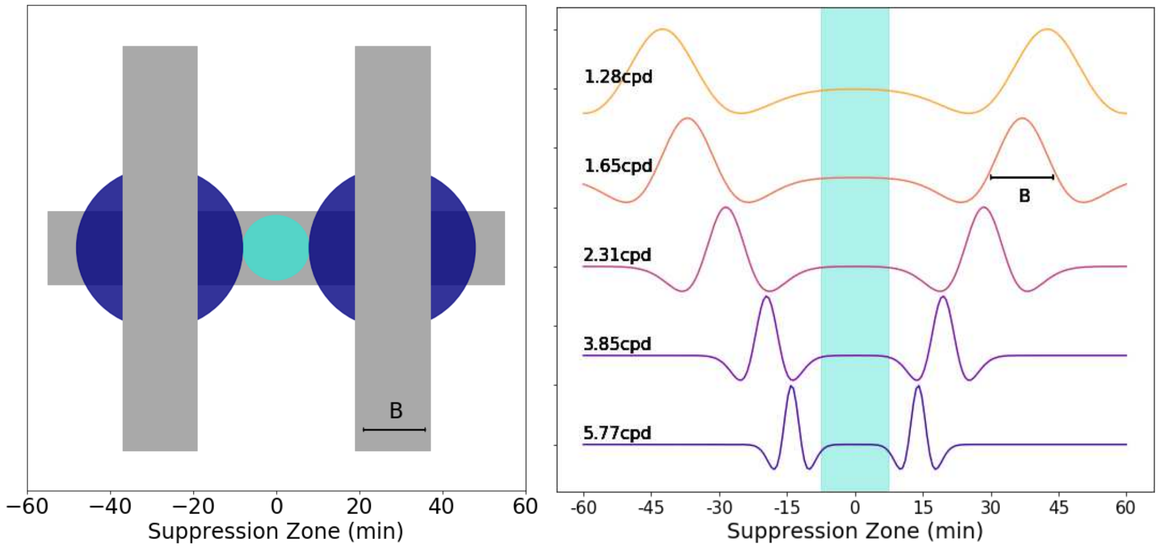

Figure 8: (Left panel) Illustration of the postulated suppression zone. The two vertical bars represent the suppressors while the horizontal bar represents the reference. Surrounding the suppressor, the area in dark blue represents the area of suppression which is stimulus-dependent. In between the dark blue areas, the cyan patch corresponds to the non-stimulus dependent component (edge-to-edge separation, ES), where subjects were asked to fixate during the experiment. (Right panel) Illustration of the edge-to-edge separation at different spatial frequencies. The ES is scale invariant, as indicated in the shaded cyan region. We only include a few spatial frequencies for illustration purposes. B is the width of the center part of the DoG.

In summary, we found that the spatial extent of suppression is not fixed, but changes with stimulus parameters (spatial frequency, contrast, and contrast polarity). In addition, our model predicted a fixed suppression zone which is non-stimulus dependent, with size approximately ~10 arc minutes. Interocular suppression is known to originate subsequent to the retina, and in the higher levels of the visual processing hierarchy that are tuned to increasingly abstract visual features, likely contributing to its dynamic, stimulus-dependent characteristics. These findings set a lower limit on the generality of suppression size measurement, and may help to understand how to compare across the myriad apparatuses and stimuli used in different clinical tools and studies.

Methods:

Participants: We recruited a total of 11 subjects with normal binocular vision. All had good visual acuity except for two subjects (S8 & S9) whose glasses were not fully corrected for distance but had good near acuity. Subjects were either emmetropes or wore their normal correction during the experiment. Eight of the subjects were male, and three were female (Mean age=31.9±10.91year old). Subject S5, a presbyope wore additional plus lenses corrected for 1 meter. Below are the data for all the subjects. Three of the subjects (S1, S3 & S5) are the authors of this paper, while the other subjects were naïve observers. These data were collected from two different sets of experiments; Experiment 1 and 2 were done together, while Experiment 3 was done later with additional subjects. Some of the subjects from Experiment 1 and 2 participated in Experiment 3, as shown in Table 1. Two subjects (S2 and S4) were assigned to participate in a control experiment (see Discussion) rather than Experiment 2B. Written informed consent was obtained from all participants before the experiment, and the experimental procedures were approved by the Institutional Review Board of the University of Houston. All experimental procedures were performed in accordance with this protocol.

Subject ID	Age (year)	Visual Acuity	Stereo Acuity (arc seconds)	Ocular Dominance @ 1m	Experiment
S1	30	OD: 20/20 OS: 20/20	40	Left	1, 2 & 3
S2	25	OD: 20/16 OS: 20/17	30	Right	1, 2 & 3 except condition 2B
S3	46	OD: 20/16 OS: 20/24	40	Right	1, 2
S4	24	OD: 20/18 OS: 20/17	30	Left	1 & 2 except condition 2B
S5	58	OD: 20/18 OS: 20/15	20	Left	1, 2
S6	30	OD: 20/21 OS: 20/31	40	Right	1, 2
S7	23	OD: 20/19 OS: 20/12	30	Right	1, 2 & 3
S8	24	OD: 20/14 OS: 20/57	30	Right	1, 2
S9	34	OD: 20/50 OS:20/20	32	Left	3
S10	32	OD: 20/20 OS:20/20	25	Left	3
S11	25	OD: 20/20 OS:20/20	40	Right	3

Table 1: Clinical data for each subject.

Preliminary assessment: We measured visual acuity using the computer-based FrACT 3.10.5 acuity test[57] and stereo acuity with the Randot Stereo Test. Motor eye dominance was performed using the hole-in-card method to determine ocular dominance. We tested eye dominance at 6 meters and also 1 meter, which is the distance from the display screen to the observer during the experiment. Proper demonstrations and explanations were given to ensure participants understood the task.

Set-up: We used a PROPixx DLP LED Projector (VPixx Technologies Inc) to rear-project the stimuli on a large projection screen. Subjects sat 1.03m away from the screen. Each pixel on the screen subtended one arc minute. The screen resolution was 1920 x 1080 pixels and subtended a total angle of 32 x 18 °. The projector has a linear contrast response (gamma), confirmed with a Konica Minolta LS-160 photometer. A circular polarizer, which temporally switched between the left and right eye images at 120Hz, was used to present the stimuli dichoptically. Subjects used a chinrest and performed the task with passive 3D glasses along with their optical correction. The luminance on the projector screen was approximately 320 cd/m^2 and reduced to 145 cd/m^2 with the polarized glasses. During the experiment, the room was completely dark except for the projector.

Stimulus: To provide robust interocular suppression while allowing parametric modulation of low-level stimulus parameters we adapted the stimuli used by Lei & Schor (1994)[33]. The original stimulus is from Kaufman, 1963 where rivalrous images were presented to either eye[36]. One eye will see two vertical lines while the other sees a horizontal line. Because of the disparate images, at the intersection between the lines, an area of suppression occurs. When all lines are presented simultaneously, the suppression scotoma alternates between the two eyes. To manipulate which stimuli are suppressed, the horizontal line ("reference") can be kept constant, such that the temporal onset of the vertical lines ("suppressors") will induce suppression of the horizontal line.

The stimuli were drawn with Psychopy software[58] and based on Difference of Gaussians.

$$\mathrm{DoG}\ (\mathrm{x}) = 3^{\left(\frac{-\mathrm{x}^2}{\sigma^2}\right)} - 2^{\left(\frac{-\mathrm{x}^2}{2.25\sigma^2}\right)} \tag{1}$$

$$\sigma = \frac{\mathrm{B}}{1.75} \tag{2}$$

The DoG appeared as a white center bar flanked by darker bars on each side. The stimuli have a bandwidth of 1.75 octaves. B is the width of the center peak of the DoG to be drawn in pixels:

$$B\ (\mathrm{degree}) = \mathrm{Width\ (pix\ or\ min)} \times \frac{2.28}{60} \tag{3}$$

The dominant spatial frequency of each stimulus is calculated based on this formula:

$$\mathrm{Spatial\ Frequency\ (cpd)} = \frac{1}{(2.28 \times \mathrm{B})} \tag{4}$$

The single horizontal bar (width=8.5º) served as a reference bar. It was continuously visible while two vertical bars (height=8.5º) served as suppressors, appearing symmetrically to the left and right of the center of the screen for a duration of 1 second. Each time the subject pressed a key, the onset of the suppressors induced robust transient interocular suppression at the intersection with the reference. This suppression usually lasted less than a second. During the suppression period, each suppressor induced a circular zone of suppression at the intersection (as outlined by the yellow dotted line in Figure 1b). The distance between the suppressors indicated the diameter of the suppression zone: the sum of a radius from each of the two suppressors. As a result, the inner part of the reference bar was suppressed and disappeared, as depicted in Figure 1b. Two vertical fixation lines were drawn to indicate the fixation area and participants were instructed to keep their fixation between these two lines during the experiment. An outer square (15 x 15º) served as a binocular fusion lock. The task was to align the suppressors by turning a knob (Method of Adjustment) so that the middle part of the reference bar just barely disappeared. The position of the suppressors was randomly assigned at the beginning of each trial with a maximum of 200 arc minutes separation.

Subjects were instructed to adjust the position of the suppressors inward from the outermost position to find the widest spacing that reliably abolished the entire intervening portion of the reference line. After three consecutive onsets to ensure robust suppression, subjects pressed a key to save the distance between the suppressors and advance to the next condition. To control for contrast adaptation to the horizontal reference bar, after each trial, a grey background appeared. Subjects were free to move their eyes freely between trials but instructed to fixate at the fixation area when the suppressors appeared. The distance between the center of the suppressors is termed as the suppression zone in arc minutes. The zone is equal to the diameter of the transient suppression scotoma.

Experimental Conditions

Experiment 1 and Experiment 2 were performed in the same sessions (with a random sequence), while Experiment 3 was performed later. Within the experimental blocks corresponding to each experiment, the order of the conditions was randomized. Each experiment was repeated five times, yielding five measurements for each condition.

Experiment 1

(A) Effect of Spatial Frequency

We varied the spatial frequencies of the stimuli congruently (both suppressors and reference were always presented with similar spatial frequency). The spatial frequencies tested were 0.888, 1.049, 1.282, 1.649, 2.308, 3.847, 5.77 and 11.54 cpd. The contrast of the stimuli was fixed at 100% Weber contrast.

(B) Effect of Contrast

Four different congruent contrasts were used (100%, 50%, 25%, and 12.5% Weber contrast) to investigate the effect of contrast at all spatial frequencies. The contrast is defined as [(peak luminance of the center DoG - luminance of grey background)/ mean luminance].

(C) Effect of Eye Dominance

The vertical suppressors were randomized between the two eyes (dominant and non-dominant) to study the effect of eye dominance. Experiments 1A, B, and C were randomized and grouped as a block (8 spatial frequencies x 4 contrasts x 2 eyes= 64 trials per block).

Experiment 2

(A) Horizontal versus Vertical Orientation

We rotated the stimuli 90° to study the vertical dimension of suppression. The constant reference was oriented along the vertical meridian while the double suppressors appeared parallel to the horizontal meridian. The height of the area of suppression was the vertical space between the double horizontal suppressors. Each block consists of 8 spatial frequencies at 100% contrast.

(B) Effect of Contrast Polarity

We tested four different combinations of contrast polarity: white-white (both reference and suppressors have a white center), black-black (both have a black center), white-black (reference with white center while suppressors have a black center) and black-white stimuli (reference has black center while suppressors have a white center). We tested the different combinations with all eight spatial frequencies at 100% contrast (8 spatial frequencies x 4 contrast polarity = 32 trials per block).

Experiment 3

(A) Effect of Color Filters

We tested the same stimuli with colored filters at 0.888, 2.308, and 5.77 cpd (100% contrast). Subjects wore the colored filters on top of the polarized glasses. In the matched chromatic filter condition, the color of the filters (red or green) were the same in both eyes while in dichoptic chromatic filters (commonly used for anaglyph), the red filter was placed in front of the right eye while the green filter was placed in front of the left eye. By adding the colored filters, the average luminance reduced from 145cd/m^2 to 15 cd/m^2 (approximately 1 log unit reduction) for both colors. To isolate the effect of chromaticity, the result with red and green filters were compared to a 1ND filter (15 cd/m^2). The colored filters were cardboard consumer anaglyph filters. The subjects adapted to the filters for three minutes before each experiment.

(B) Effect of Luminance

We performed the same experiment with 1ND (15 cd/m^2) and 2ND (1.5 cd/m^2) filters. The ND filters were placed on a holder and positioned in front of the subjects. Subjects adapted for three minutes prior to the experiment.

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Author Contribution
W.H.L., S.B.S and D.R.C. designed the study. W.H.L. conducted the experiments. W.H.L. and D.R.C analyzed the data. W.H.L., S.B.S and D.R.C wrote the paper.

Additional Information
Competing Interests: The authors declare that they have no competing interests.

Figures

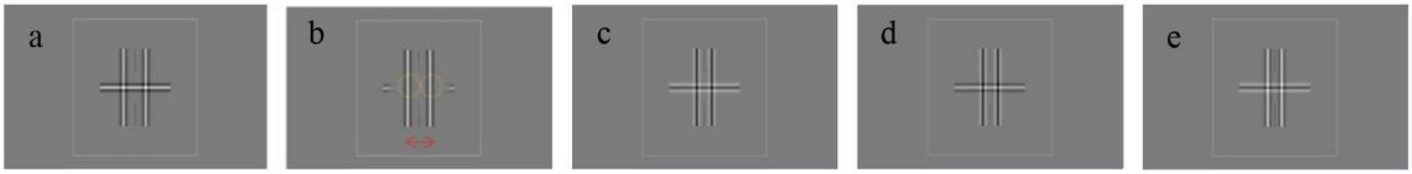

Figure 1

Stimuli used in the experiment. (a) The horizontal reference bar was presented continuously to one eye. The two vertical suppressors were presented briefly to the other eye. The DoG bars had a white center surrounded by a darker grey region on both sides. A white square outline served as the binocular fusion lock. Two fine vertical black lines pointing towards the center part of the reference served as a fixation guide. (b)The area of perceived suppression upon vertical suppressor appearance is outlined by the yellow circles. Subjects adjusted the separation of the vertical bars to the widest setting that still suppressed the horizontal segment between them. The distance between the center of the two suppressors is termed as the suppressio zone, (red arrow). (c-e) These figures illustrate the different combinations of contrast polarity: (c) black-black, (d) white-black, and (e) black-white. The first color in the combination refers to the center of the horizontal reference followed by the vertical suppressors.

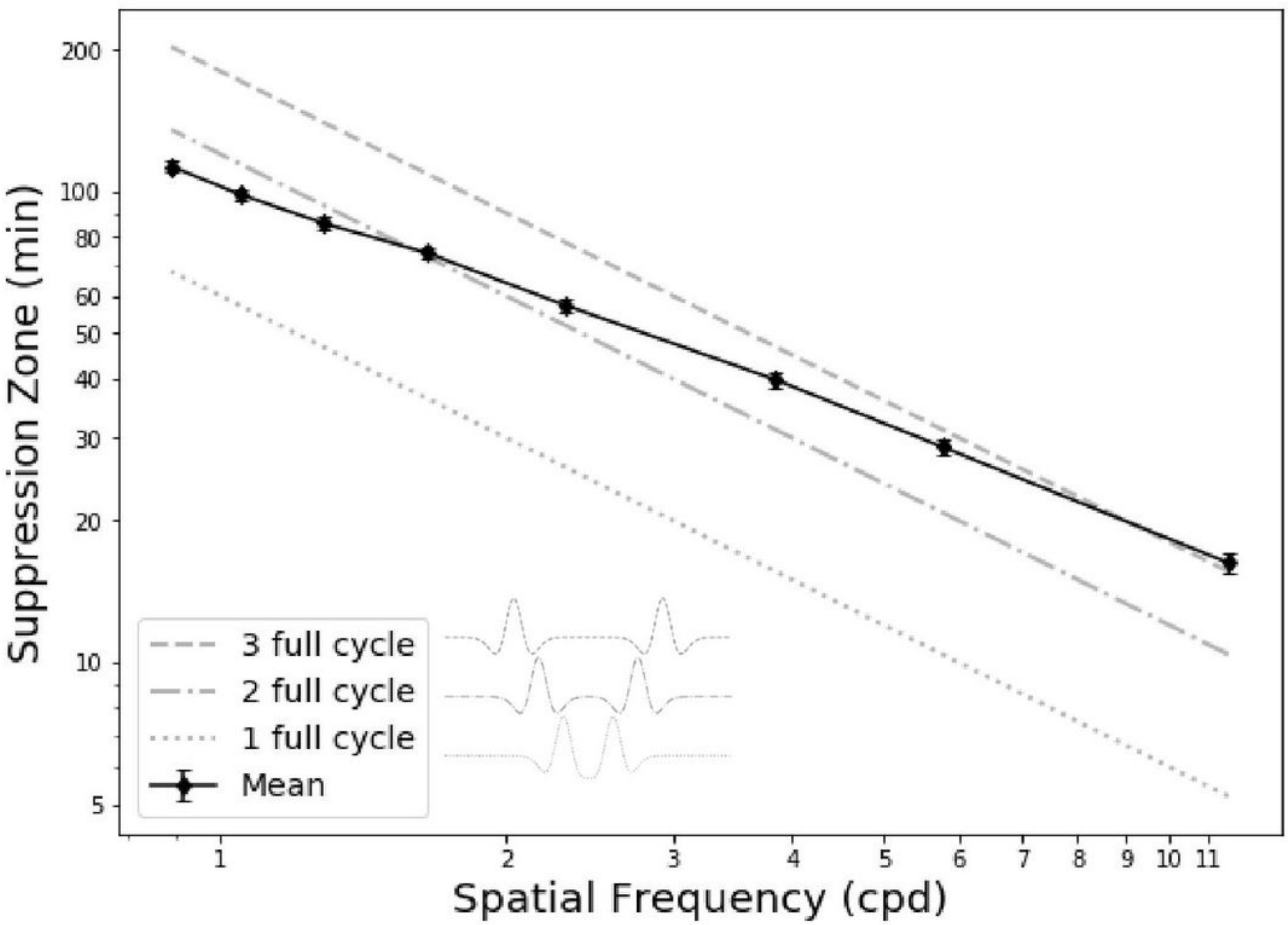

Figure 2

Suppression zone as a function of spatial frequency. The solid black line is the mean values across all eight subjects. The other lines represent the size of the single, double, or triple full cycle of the DoG stimuli. The mean values are almost two full cycles of the DoG at low spatial frequencies but three full cycles at higher frequencies. The vertical error bar represents the standard error. The lower left panel illustrates the separation between the center to center of the two DoG at one, two, or three full cycles.

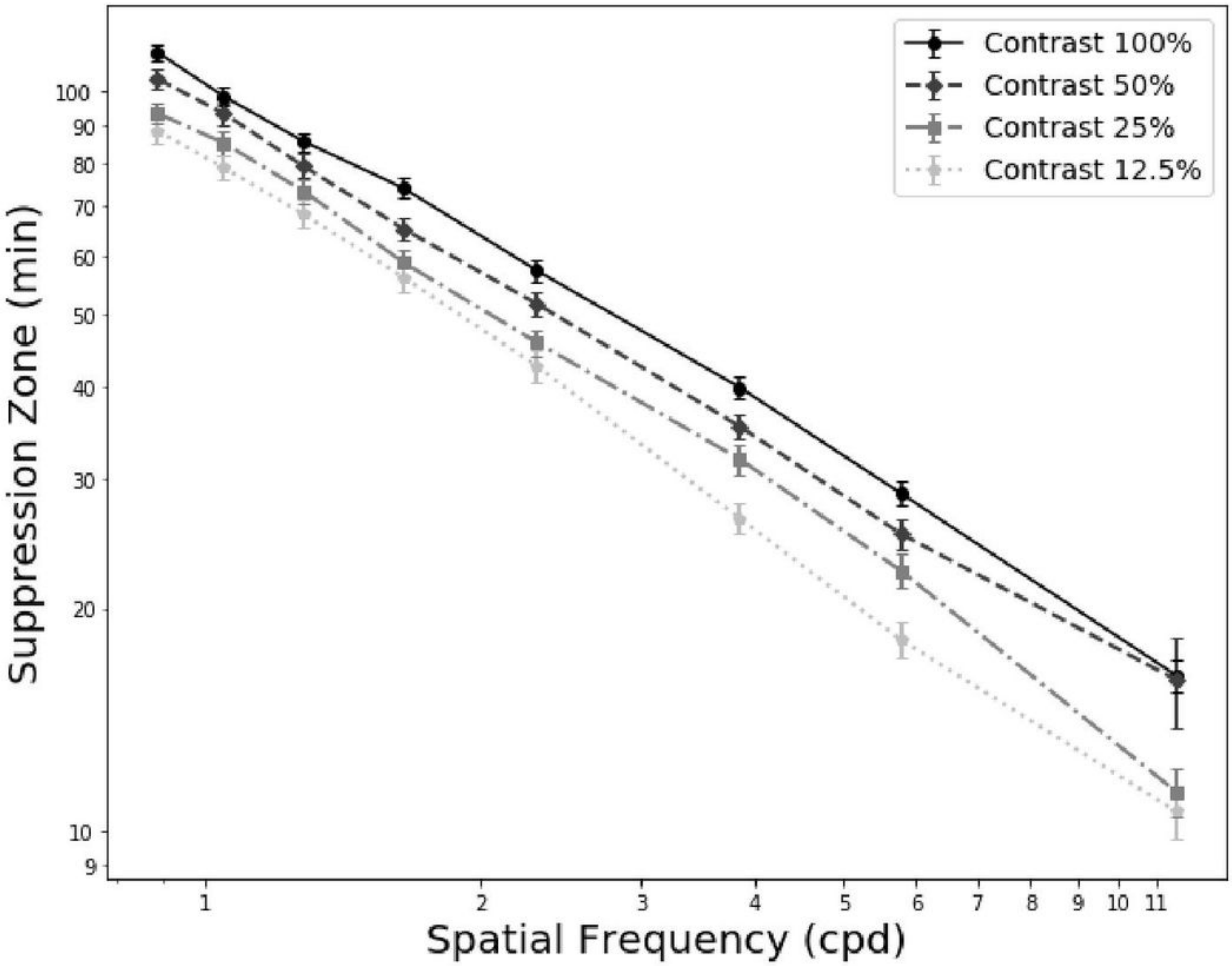

Figure 3

The reduction of suppression zone as a function of contrast (n=8). The solid black line (contrast 100%) is similar to the results obtained from Experiment 1A. This line is shifted downward with lower contrast. The vertical error bars represent the standard error.

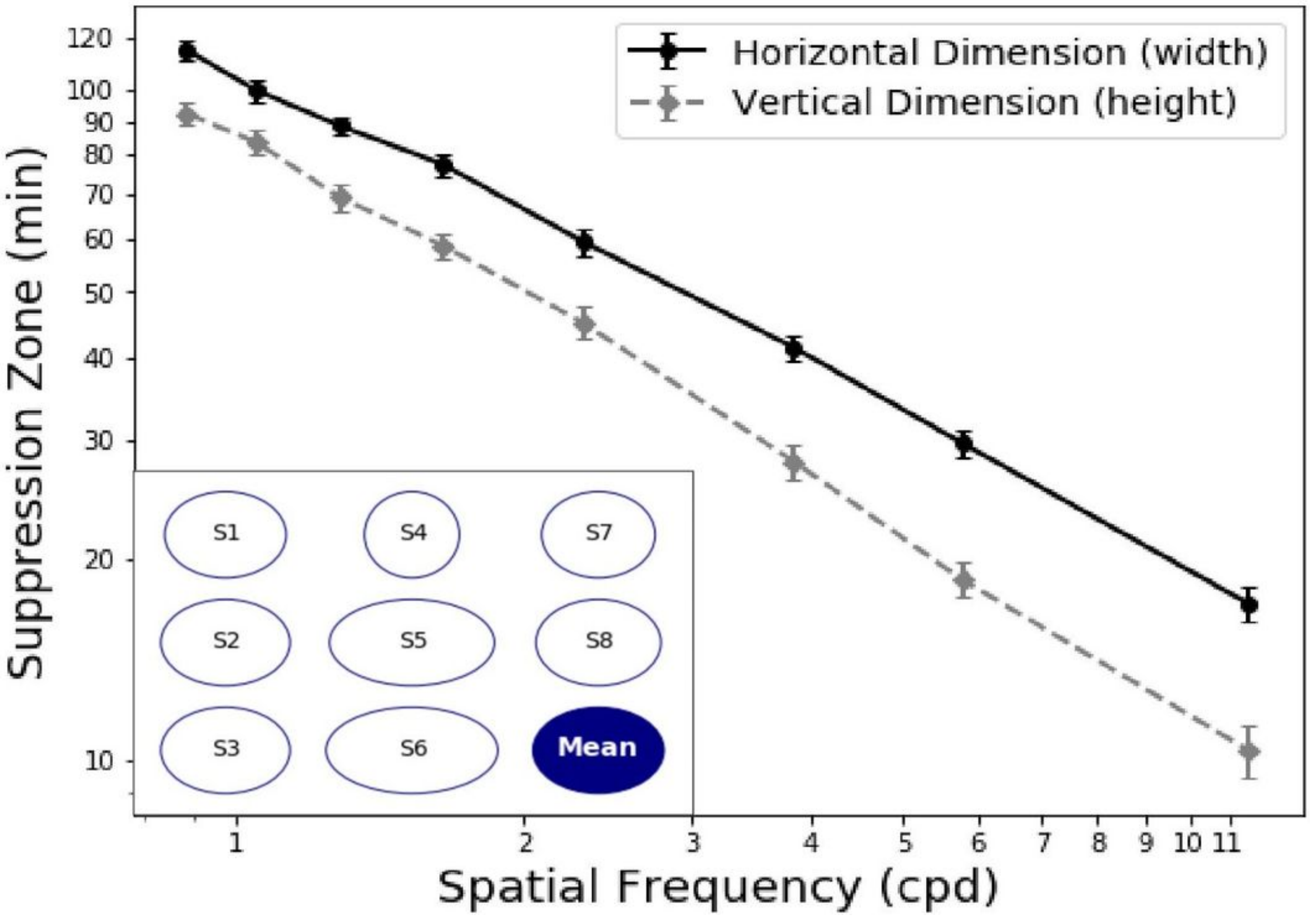

Figure 4

This plot shows that the ratio between the zones for the two dimensions, horizontal and vertical is consistent across all spatial frequencies. The horizontal size was larger by approximately 1.4x than the vertical zone, suggesting that the suppression zone is elliptical in shape. The schematic on the lower left shows the ratio of horizontal to vertical zone for each subject. The mean area of suppression is elliptical in shape (dark blue). Standard errors are shown on the vertical bars.

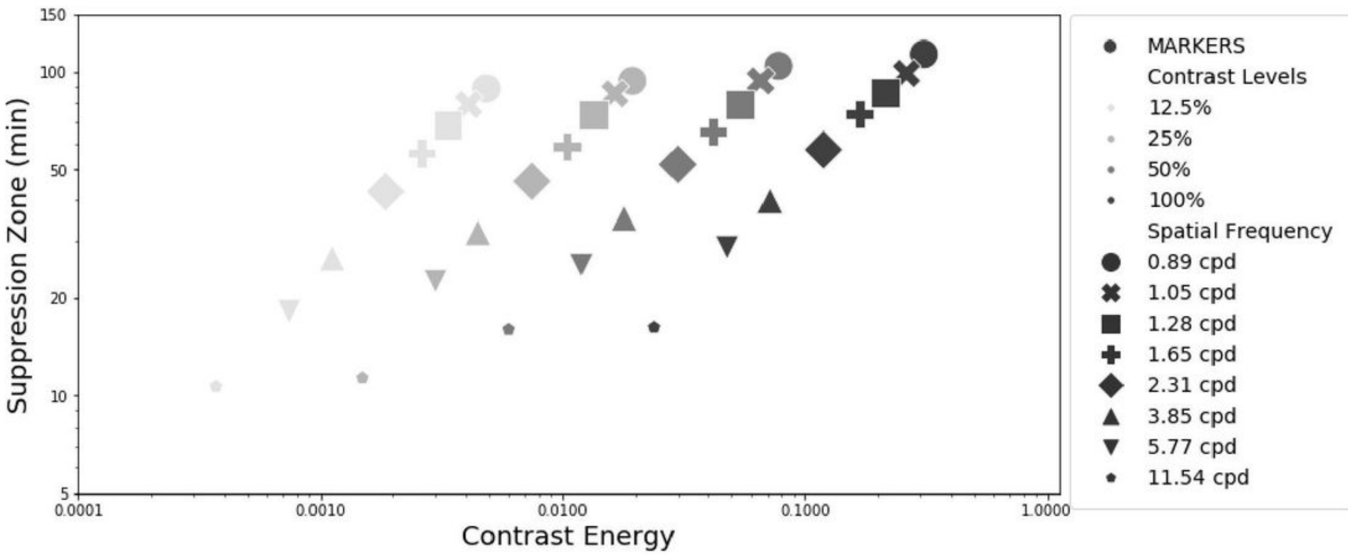

Figure 5

This plot illustrates how suppression zones change as a function of contrast energy. Different shapes of the markers indicate different spatial frequencies while the grayscale shades indicate the contrast level. Any contrast energy level could result in multiple suppression zones.

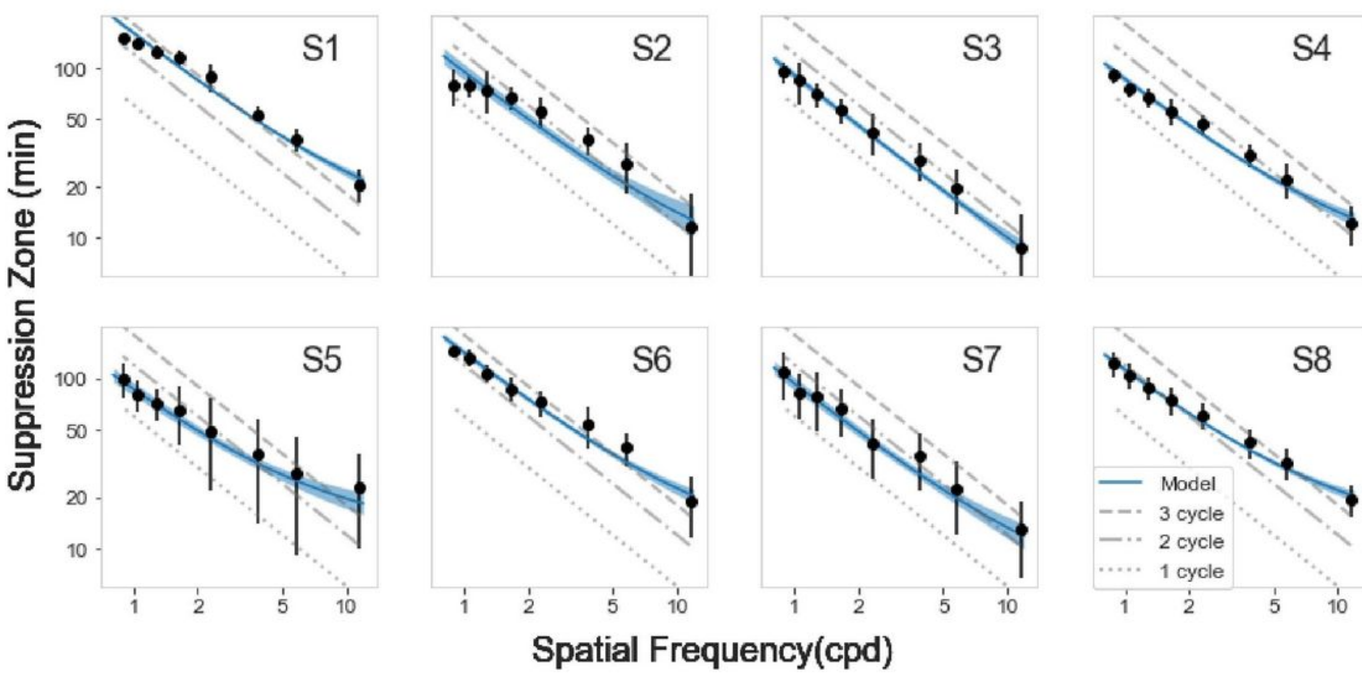

Figure 6

The model predicts the individual results well, indicated by the shaded blue region, indicating 95% credible intervals from the fits. Different dashed lines indicate the multiplication of the number of full cycles (in cpd).

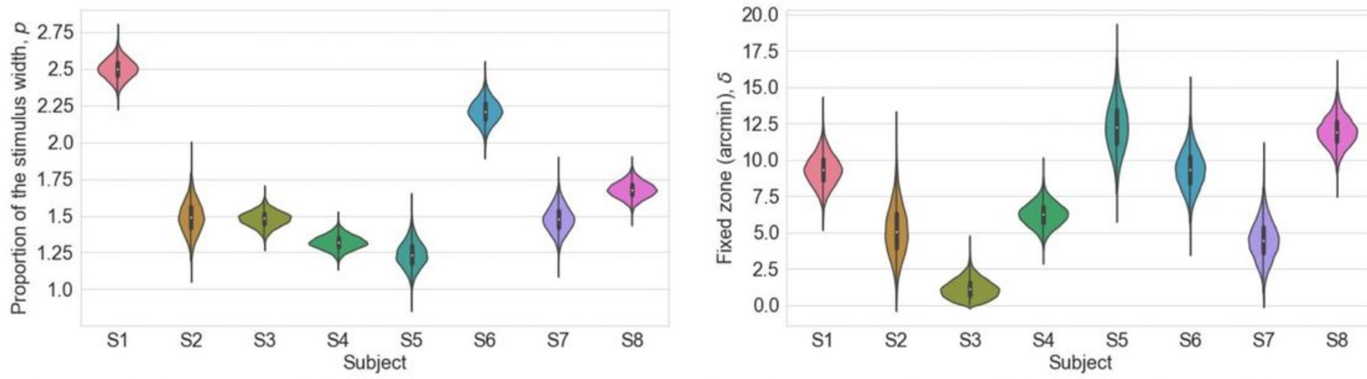

Figure 7

In the model, the parameter estimates for the proportion of stimulus width is between 1.25 and 2.5 cycles (left panel). The constant term delta is 5-12.5 arc minutes for most subjects (right panel).

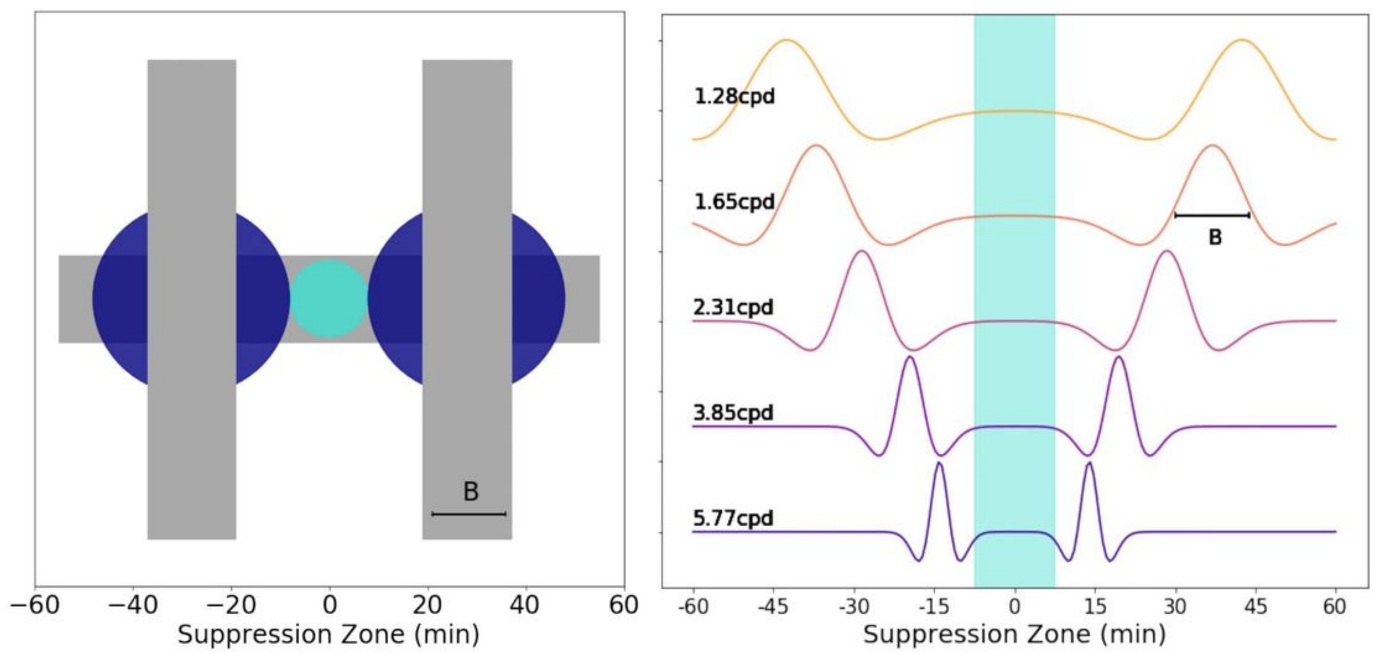

Figure 8

(Left panel) Illustration of the postulated suppression zone. The two vertical bars represent the suppressors while the horizontal bar represents the reference. Surrounding the suppressor, the area in dark blue represents the area of suppression which is stimulus-dependent. In between the dark blue areas, the cyan patch corresponds to the non-stimulus dependent component (edge-to-edge separation, ES), where subjects were asked to fixate during the experiment. (Right panel) Illustration of the edge-to-edge separation at different spatial frequencies. The ES is scale invariant, as indicated in the shaded cyan region. We only include a few spatial frequencies for illustration purposes. B is the width of the center part of the DoG.