Author/s:
Malavita, MS;Vidyasagar, TR;McKendrick, AM

Title:
The effect of aging on the eccentricity dependency of orientation anisotropy of perceptual surround suppression

Date:
2021-01-01

Citation:
Malavita, M. S., Vidyasagar, T. R. & McKendrick, A. M. (2021). The effect of aging on the eccentricity dependency of orientation anisotropy of perceptual surround suppression. Journal of Vision, 21 (1), pp.1-12. https://doi.org/10.1167/JOV.21.1.13.

The effect of aging on the eccentricity dependency of orientation anisotropy of perceptual surround suppression

Menaka S. Malavita Department of Optometry and Vision Sciences, The University of Melbourne, Parkville, Victoria, Australia

Trichur R. Vidyasagar Department of Optometry and Vision Sciences, The University of Melbourne, Parkville, Victoria, Australia

Allison M. McKendrick Department of Optometry and Vision Sciences, The University of Melbourne, Parkville, Victoria, Australia

The features of perceptual surround suppression vary with eccentricity, such that the suppression strength is increased for horizontally oriented stimuli relative to other orientations near the fovea, but is strongest for radially oriented stimuli more peripherally. Perceptual suppression also varies with age, which has been well-studied for central fixation. However, only limited data are available regarding perceptual suppression in older adults for nonfoveal vision, and none of those studies have taken orientation biases of contrast sensitivity into account. Here, we explored the effects of older age on the eccentricity dependency of orientation biases of perceptual suppression. We found increased perceptual suppression in older adults at both 6° and 15° eccentricities relative to younger adults. A main effect of the horizontal orientation bias was found at 6° and a main effect of the radial orientation bias was found at 15° in both groups. In summary, perceptual surround suppression of contrast is stronger for older adults compared with younger adults at 6° and 15° eccentricities, but retinotopic orientation anisotropies are maintained with age. This study provides new insight into parafoveal visual perception in older adults, which may be particularly important to understand the visual experience of those who depend on nonfoveal vision owing to common age-related eye diseases.

Introduction

The strength of perceptual surround suppression of contrast increases as a function of eccentricity for both threshold and supra-threshold tasks (Petrov et al., 2005; Snowden & Hammett, 1998; Xing & Heeger, 2000). For example, in the fovea surround suppression is not observed for contrast threshold tasks, although it is present just outside foveal vision (1° eccentricity) (Petrov et al., 2005) and suppression strength increases dramatically at 10° eccentricity for supra-threshold tasks (Xing & Heeger, 2000). Older adults demonstrate increased perceptual center-surround suppression of contrast in foveal vision for supra-threshold center stimuli (Karas & McKendrick, 2009, 2011, 2012, 2015). Consistent with the observation of increased contrast suppression foveally for supra-threshold contrast tasks, Malavita et al. (2017) reported that perceptual suppression elevation in the perifoveal vision (8° eccentricity) is greater in older adults than younger adults for threshold contrast tasks (Malavita et al., 2017). Different effects seem to arise for supra-threshold processing, with Nguyen and McKendrick (2016) reporting that, at 6° eccentricity, older adults have decreased surround suppression for contrast matching tasks (Nguyen & McKendrick, 2016), despite suppression strength being increased foveally in the same individuals. A detailed understanding of parafoveal visual perception may be particularly important to understand visual experience in conditions such as macular degeneration, which leads to people partially or completely depending on their nonfoveal vision. Furthermore, the characteristics of peripheral surround suppression may be important for object segmentation, yet peripheral surround suppression is understudied. Hence, the first aim of our experiments was to determine whether older adults continue to demonstrate increased surround suppression relative to younger adults for contrast threshold tasks at eccentricities beyond 8°.

Typically, psychophysical studies that have investigated the effects of aging on suppressive effects of contrast sensitivity outside the fovea have only tested the nasal or temporal visual field along the horizontal meridian (8° by Malavita et al., 2017;

Citation: Malavita, M. S., Vidyasagar, T. R., & McKendrick, A. M. (2021). The effect of aging on the eccentricity dependency of orientation anisotropy of perceptual surround suppression. *Journal of Vision*, *21*(1):13, 1–12, https://doi.org/10.1167/jov.21.1.13.

https://doi.org/10.1167/jov.21.1.13 Received June 26, 2020; published January 27, 2021 ISSN 1534-7362

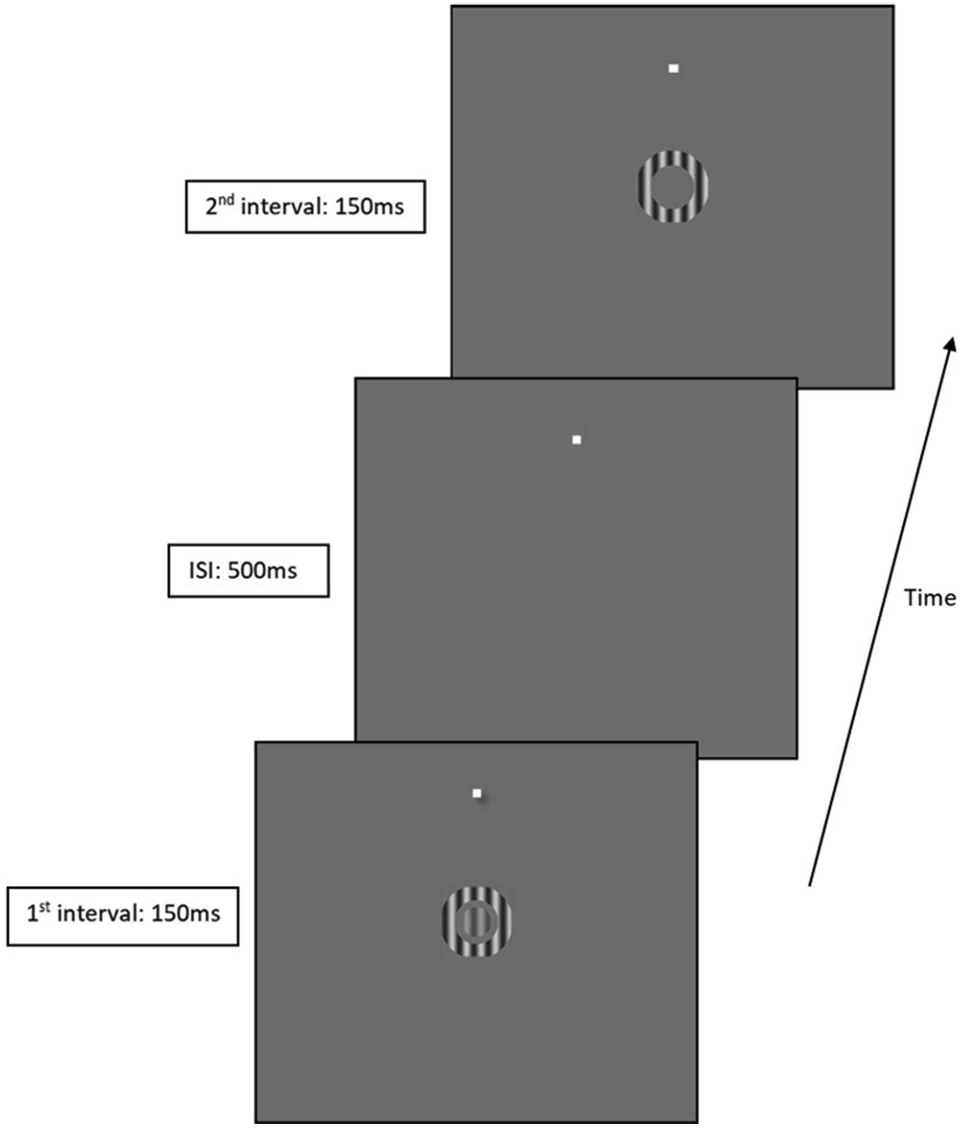

Figure 1. An example stimulus sequence at 270° visual field location. The first or the second interval contained the surround with the target center. Position of the fixation square was changed to test 0° and 315° visual field locations while stimuli were presented on the center of the screen for all conditions. ISI, interstimulus interval.

6° by Nguyen & McKendrick, 2016). However, contrast sensitivity is not homogenous throughout the visual field in either magnitude or orientation biases (Sasaki et al., 2006). Similarly, radial-tangential anisotropies are a pronounced feature of surround suppression (Malavita et al., 2018; Petro & McKee, 2006). We have previously shown that, when there is a surrounding pattern, the orientation biases of the contrast sensitivity depend on both visual field meridian and retinal eccentricity (Malavita et al., 2018). Specifically, we measured the influence of surrounding patterns on contrast detection thresholds for five younger adults in three visual field locations (0°, 225°, and 270°) and at two visual eccentricities (6° and 15°) (Figure 1). Our experiments revealed that surround suppression of contrast detection for parallel centre-surround configurations was increased when the center and surround were oriented horizontally at 6° eccentricity, whereas at 15° eccentricity the same parallel centre-surround configuration (adjusted in size for cortical magnification factor) showed increased suppression when oriented radially to the foveal fixation. Such eccentricity dependency of orientation bias reported in our previous study is qualitatively consistent with studies that have systematically studied contrast detection threshold (Sasaki et al., 2006) and contrast discrimination threshold, but for stimuli without surrounds in human studies (Rovamo, Virsu, Laurinen, & Hyvarinen, 1982; Sasaki et al., 2006), as well as in animal studies (Sasaki et al., 2006).

The second aim of our study was to determine whether the orientation anisotropies of perceptual surround suppression that are evident in younger adults are maintained in older adults. Neurophysiological studies report that the proportion of strongly orientation sensitive neurons in V1 decreases in older rhesus monkeys compared with younger ones (Fu et al., 2010; Leventhal, Wang, Pu, Zhou, & Ma, 2003). If this reported property of primate V1 single neurons is reflected in the older adult human visual system, then orientation preferences in surround suppression may possibly be weakened in older adults.

Another observation from our previous study of peripheral spatial suppression of contrast (Malavita et al., 2018) was a relative increase in suppression strength for orthogonal surround stimuli with increasing eccentricity. Specifically, at 6° eccentricity, if the surround orientation was orthogonal to the center grating, there was hardly any suppression relative to the parallel surround condition. In comparison, at 15° eccentricity, suppression was maintained even for orthogonal surrounds (Malavita et al., 2018). This observation extended previous studies that have shown weak or nonexistent suppression for orthogonal surrounds in parafoveal vision using psychophysics (Petrov & McKee, 2009) and using functional magnetic resonance imaging (Silver, Shenhav, & D'Esposito, 2008) through the demonstration of reduced orientation tuning of surround suppression for more eccentric viewing. Most studies that have studied changes to perceptual centre-surround suppression in older adults have not considered orthogonal centre-surround stimuli (Betts, Sekuler, & Bennett, 2009; Betts, Taylor, Sekuler, & Bennett, 2005; Karas & McKendrick, 2009, 2011, 2012, 2015), but have instead concentrated on parallel configurations because such stimulus arrangements show the maximum suppressive effects for a given spatial frequency and surround contrast (Cannon & Fullenkamp, 1991; Xing & Heeger, 2000). A notable exception is the study by Yazdani et al. (2015), who reported that both parallel and orthogonal surround suppression of contrast detection thresholds were increased in older adults at 4.2° eccentricity with the effect only reaching conventional statistical significance for the orthogonal condition. The authors argued that the statistical results may have arisen owing to an increased variability in their parallel surround data. It is worth noting that although Yazdani et al. (2015) tested subjects between 19.4 and 69.1 years of age, the mean age was 42.3 years with only six participants above the age of 60 years. Aside from the study of Yazdani et al. (2015), the orientation dependency of surround suppression of contrast threshold tasks outside the fovea has not been explored in older adults, nor have the retinotopic biases. Hence, the third aim of our experiments was to measure the strength of surround suppression of contrast detection for both parallel and orthogonal surround orientations at 6° and 15° eccentricities.

Thus, our experiments were designed to determine whether older adults show more suppression than younger adults at both 6° and 15°, to explore whether the eccentricity dependency of orientation anisotropy differs between age groups, and to determine whether there are any age-related differences in the complex patterns of suppression strength that depend on the relationships between the center-surround configurations and retinotopic location.

Methods

Participants

Nineteen younger (age, 18–32 years; mean age, 24 years) and 20 older adults (age, 60–77 years; mean age, 67 years) were recruited via university staff newsletters and local newspaper advertisements. Participants signed a written informed consent form and the study was approved by the University of Melbourne Human Research Ethics Committee (HREC # 144157.2) according to a protocol consistent with the Declaration of Helsinki. Subjects with distance best corrected visual acuity in the left eye equal or better than 6.0/7.5 with corrective spectacle power of less than ±5 diopters sphere and less than 2 diopters astigmatism were included. Slit lamp biomicroscopy and ophthalmoscopy were conducted to ensure the absence of ocular pathology and those with cataract grading above 1 in The Lens Opacities Classification System III were not included in the study (Chylack et al., 1993). A supra-threshold glaucoma screening test (white-on-white Goldmann Size III targets) was performed using the Octopus 600 perimeter (Haag-Streit AG, Köniz, Switzerland) (Takahashi et al., 2017; Turpin, Myers, & McKendrick, 2016) and only those participants with no visual field defects were included.

Stimuli and procedures

Stimuli were written in Matlab v7.6 (Mathworks, Natick, MA) and displayed on a gamma-corrected monitor (G520 Trinitron; Sony, Tokyo, Japan; framerate, 100 Hz; resolution, 1024 × 768 pixels, maximum luminance = 100 cd/m^2) interfaced with a ViSaGe graphics system (Cambridge Research Systems, Ltd., Kent, UK). Viewing distance was 573 mm for stimuli presented at 6° and 400 mm for 15° eccentricity. This change in viewing distance enabled us to achieve the relevant stimulus size and spatial frequency (described in detail elsewhere in this article), while keeping the fixation marker on the monitor. Refractive error was corrected for working distance with a trial frame where required. The specific presbyopic correction for each viewing distance was applied. The room was dimly lit under monocular viewing conditions (left eye). The participant's chin and forehead were rested against a stand to secure steady positioning throughout the experiment. The examiner monitored the gaze position of the participant via a compact mirror placed at the monitor to ensure a constant gaze was held throughout the testing period. Participants were given regular breaks to avoid fatigue and testing was completed in two sessions each of approximately 2 hours in duration.

The stimulus configurations and the sequence of presentations are illustrated in Figure 2. The target stimulus was a circular sinusoidal grating presented at 6° or 15° eccentricity. Parameters at 6° were as follows: center radius 1°, inner surround radius 1.5°, outer surround radius 2.5°, and spatial frequency 1 c/°. The test stimuli were always presented at the center of the screen to ensure that the luminance variations across the screen did not interfere with contrast sensitivity measurements. Participants were asked to fixate on a fixation spot (0.1° radius, white) that was presented at the corresponding visual field distance from the center of the monitor. Data were collected with center alone (horizontal, vertical, radial, and tangential orientations) and center surrounded by a 40% contrast, parallel or orthogonal, annular grating of the same phase (randomly altered from trial to trial) and spatial frequency in separate blocks. Three testing locations were used: horizontal nasal (0°), oblique inferior (315°), and inferior (270°) from foveal fixation (see Figures 2 and 3). In each test location, the detection threshold was estimated for the horizontal, vertical, radial, and tangential center orientations with and without the surround annulus. The stimulus presentations of eccentricity (6° or 15°), surround condition (with or without), stimulus location (0°, 315°, or 270°), center orientation (horizontal, vertical, radial, or tangential), and surround orientation (parallel or orthogonal) were precomputed to be balanced between subjects.

A two-interval forced choice psychophysical method was used to determine the contrast detection threshold. The stimulus duration was 150 ms throughout the experiment and there was an interstimulus interval of 500 ms. The observer's task was to press a button (CB6, Cambridge Research Systems) to denote the interval that contained the target. The target contrast was varied using a three-down, one-up staircase with a step size of 20% of the previous contrast level (Wetherill & Levitt, 1965). The staircase was terminated after four reversals and the last two reversals were averaged. Each threshold estimate was repeated twice and the average of the two was taken for analysis. A ratio of the contrast detection threshold with and without the surround was taken as the suppression ratio. A ratio of 1 denotes no suppression.

For threshold estimation at 15°, the fixation point was presented at 15° and the rest of the procedure was similar to that at 6°. Stimulus size and spatial frequency were scaled for cortical magnification factor using the function described by

$$M = (1 + aE + bE^3)^{-1} M_0,$$

where for the nasal horizontal meridian a = 0.33 and b = 0.00007; for the temporal horizontal meridian a = 0.29 and b = 0.000012; for the superior vertical meridian a = 0.42 and b = 0.000012; for the inferior vertical meridian a = 0.42 and b = 0.000055; M_0 is the value for magnification (7.99 mm/°) for the most central fovea; and E is the eccentricity in degrees (Rovamo & Virsu, 1979). The average magnification factors of nasal horizontal (0°) and inferior vertical meridians (270°) were used to calculate the stimulus size and its spatial frequency. Parameters at 15° were as follows: center radius 2.05°, inner surround radius 3.08°, outer surround radius 5.13°, and spatial frequency 0.48 c/°. The surround contrast remained at 40% for all conditions.

Data analysis

Data were analyzed using SPSS (Version 20.0.; IBM Corp, Armonk, NY). The normality and sphericity of the data were tested using the Kolmogorov–Smirnov normality test and Mauchly's sphericity test. A mixed analysis of variance (ANOVA) was conducted to compare the suppression ratios between age groups and various within-subject factors, as detailed in the Results section. A p value of less than 0.05 was considered as the criterion for statistical significance. Effect sizes are reported as partial eta-squared: (η_p^2) for results that reached conventional statistical significance, $p < 0.05$. Two subjects (one younger and one older) were excluded from the study owing to incorrect task performance (repeated loss of fixation) and the data were analyzed for 18 younger and 19 older adults. Raw data is provided in Supplementary Material A (for eccentricity of 6 degrees) and Supplementary Material B (for eccentricity of 15 degrees).

Results

Older adults have increased surround suppression of contrast at 6° and 15°

Figures 2 and 3 show the individual and mean suppression ratios for the horizontal and vertical orientations (Figure 2) and the radial and tangential orientations (Figure 3) at 6° and 15° eccentricities

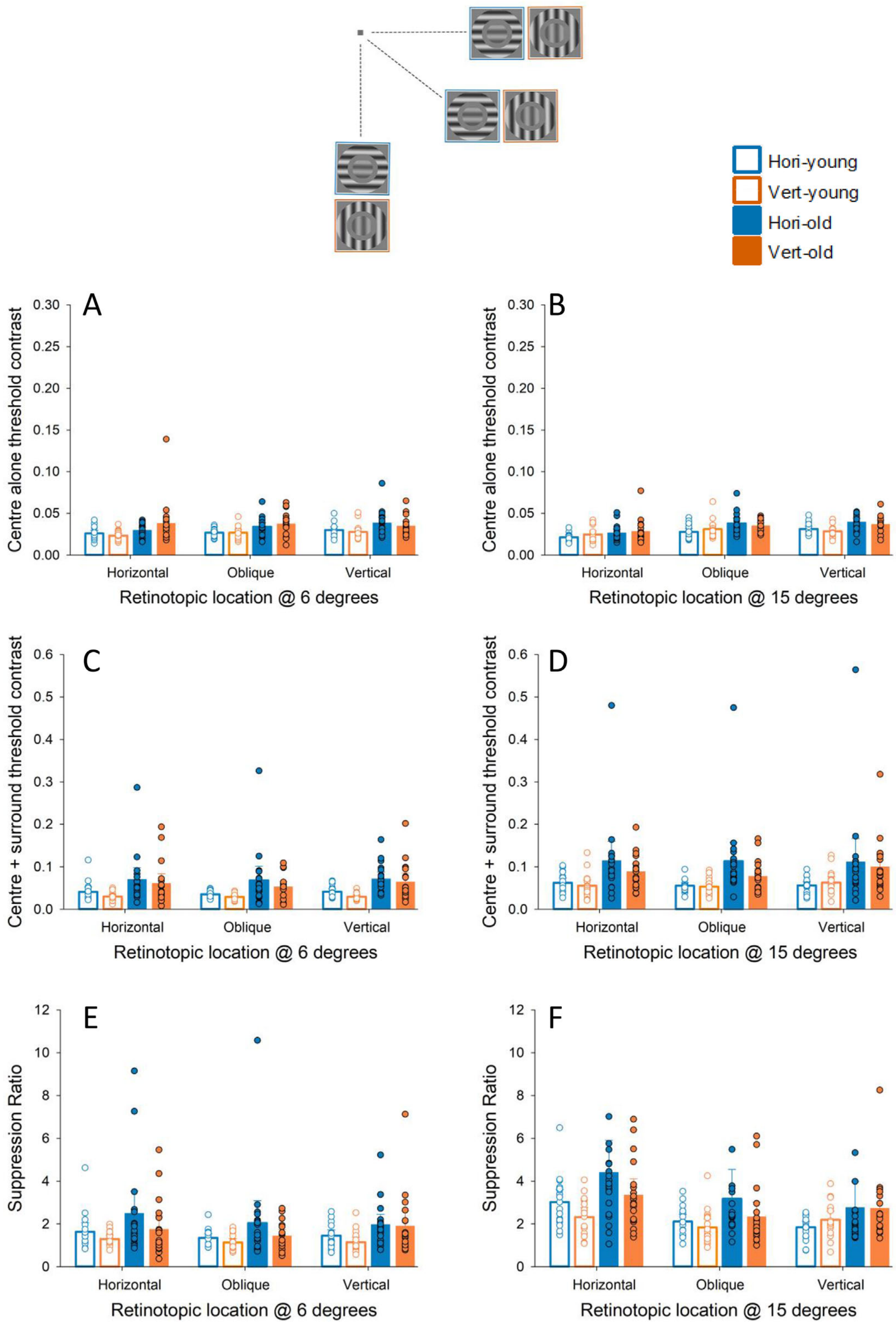

Figure 2. An illustration of parallel center-surround stimuli with horizontal and vertical orientations, center alone contrast threshold, center + surround contrast threshold, and suppression ratio for younger (open circles and bars) and older (filled circles and bars) adults at horizontal, oblique and vertical visual field locations at 6° (left panels) and 15° (right panels) eccentricities. Error bars correspond to 95% confidence interval of the mean.

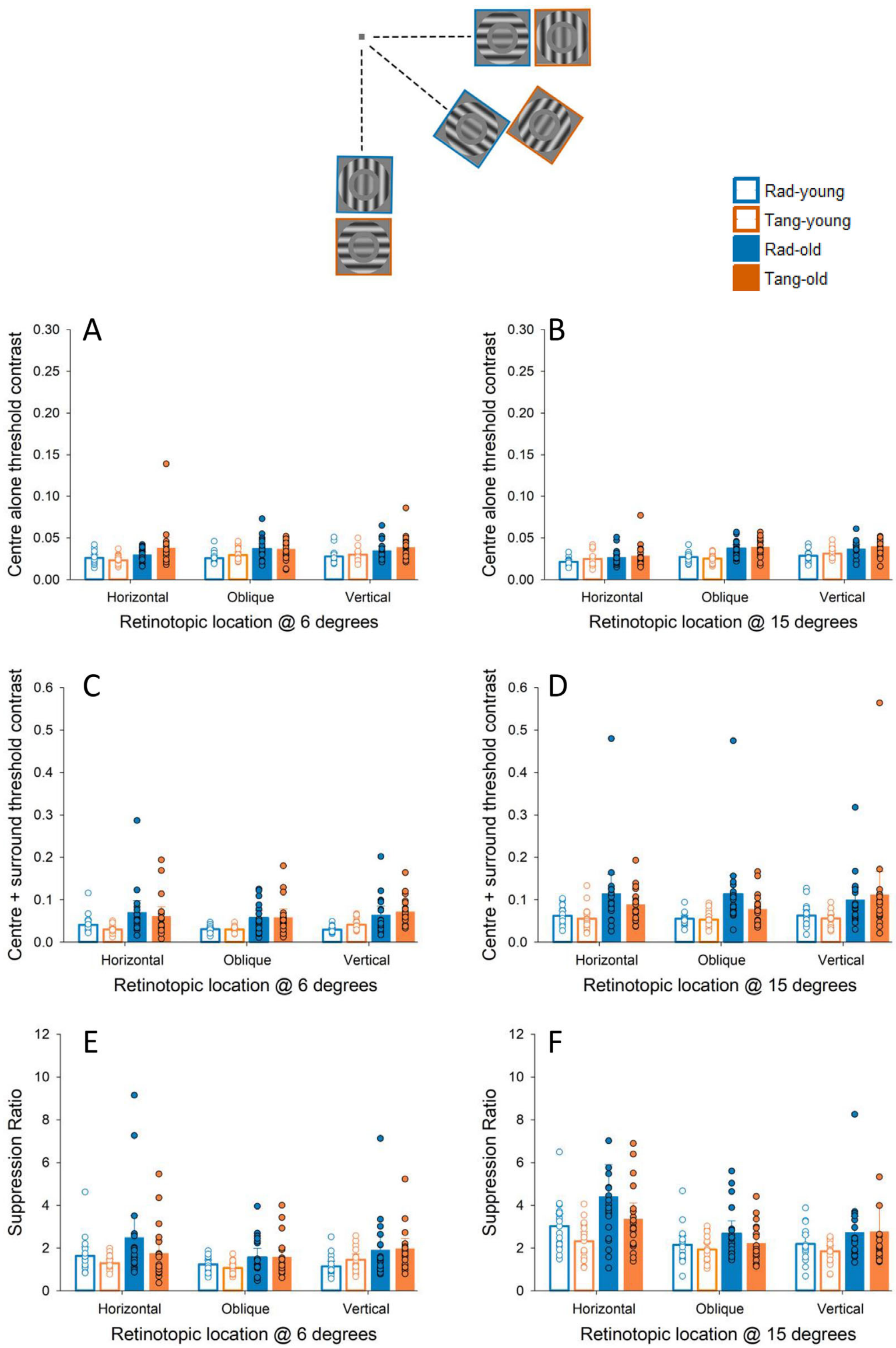

Figure 3. An illustration of parallel center-surround stimuli with radial and tangential orientations, center alone contrast threshold, center + surround contrast threshold, and suppression ratio for younger (open circles and bars) and older (filled circles and bars) adults at horizontal, oblique and vertical visual field locations at 6° (left panels) and 15° (right panels) eccentricities. Error bars correspond to 95% confidence interval of the mean.

for younger (open circles and bars) and older adults (filled circles and bars). Our first aim was to determine whether there is a significant effect of physiological aging on surround suppression of contrast detection at 15° eccentricity. Mixed ANOVA tests were conducted to compare the suppression strengths of age groups at 6° and 15° eccentricities separately for parallel center-surround stimuli. Visual field location (horizontal, oblique, and vertical) and orientation (horizontal and vertical) were within-subject factors and age group was the between-subjects factor. There was a main effect of age at 6° (Figure 2E), F (1, 35) = 5.03, $p < 0.05$, $\eta_p^2 = 0.08$, and at 15° (Figure 2E), F (1, 35) = 4.6, $p < 0.05$, $\eta_p^2 = 0.06$ (as visualized by the filled bars showing larger suppression ratios than the open bars). The group mean suppression ratios were 1.3 and 1.9 for young and older adults, respectively, at 6° eccentricity and they were 2.2 and 3.0 at 15° eccentricity.

Eccentricity dependency of orientation asymmetry of surround suppression of contrast detection is similar for younger and older adults

We then compared the eccentricity dependency of the orientation asymmetry observed in each group, for conditions where the center and surround of the stimulus were matched in orientation. We chose parallel center-surround orientation (maximum suppression) to determine if there is a horizontal–vertical orientation bias at 6° or 15° eccentricity separately. We considered the two eccentricities separately for analysis based on a priori expectations from our prior study (Malavita et al., 2018) that demonstrated notably different orientation effects between these two eccentricities (specifically a cardinal orientation bias at 6° and a radial orientation bias at 15°). Visual field location (horizontal, oblique, and vertical) and orientation (horizontal and vertical) were within-subject factors and age group was the between-subjects factor. There was a main effect of orientation at 6° (Figure 2E), F (1, 35) = 5.5, $p < 0.05$, $\eta_p^2 = 0.14$, but no such effect at 15° (Figure 2F), F (1, 35) = 2.2, $p = 0.15$. There was no interaction between the within-subject factors (orientation and visual field location) and age, indicating that increased suppression for horizontal stimuli at 6° is a feature in both age groups.

A similar analysis was performed to determine if there is a radial orientation bias at 15°. Visual field position (horizontal, oblique, and vertical) and orientation (radial and tangential) were within-subject factors and age group was the between-subjects factor. There was a main effect of orientation (Figure 3F), F (1, 35) = 15, $p < 0.001$, $\eta_p^2 = 0.3$, at 15° but no such effect at 6° (Figure 3E), F (1, 35) = 1.3, $p = 0.26$. In summary, there was a radial orientation bias at 15°, which was consistent across both age groups, [F (1, 35) = 0.08, $p = 0.78$, as visualized by the greater suppression ratios for blue bars relative to orange bars in Figure 3F. Note that the blue bars at the horizontal location also denote the horizontal orientation, but the overall radial effect is significant only at 15° eccentricity.

Comparing parallel with orthogonal center-surround configurations

We aimed to determine whether there is a significant effect of age on the relative change in suppression strength between parallel and orthogonal center-surround combinations. Figure 4 shows individual and group mean values for parallel (blue) and orthogonal (orange) suppression ratios for horizontal (Figure. 4A) and vertical (Figure 4B) center orientations at 6° (as horizontal orientation bias was evident at 6°) and for radial (Figure 4C) and tangential (Figure 4D) center orientations at 15° eccentricities (as radial orientation bias was evident at 15°). A three-way ANOVA at 6° (3 retinotopic locations × 2 center orientations × 2 surround orientations) showed a main effect of the center, F (1, 35) = 4.8, $p = 0.036$, $\eta_p^2 = 0.12$, and surround, F (1, 35) = 45, $p < 0.001$, $\eta_p^2 = 0.56$, orientations. Further, there were interactions between center orientation × surround orientation, F (1, 35) = 5.5, $p = 0.025$, $\eta_p^2 = 0.14$, surround orientation × age group, F (1, 35) = 4.5, $p = 0.041$, $\eta_p^2 = 0.11$, and a significant main effect of age, F (1, 35) = 4.9, $p = 0.032$, $\eta_p^2 = 0.13$. There was no significant interaction between center orientation × age group, F (1, 35) = 0.48, $p = 0.49$. As expected from the literature, parallel surrounds generated greater perceptual suppression than orthogonal. As observed in Malavita et al. (2018), the horizontal center configuration was more susceptible to suppression than the vertical case. As indicated by the significant interaction between the surround orientation and age, the older age group showed a relatively greater elevation of suppression for parallel (open vs. filled blue bars in Figures 4A and B) than orthogonal conditions (open vs. filled orange bars in Figures 4A and B) when compared with the younger age group.

The data for 15° is shown in Figures 4C and D, displayed as radial and tangential retinotopic configurations. A three-way ANOVA (3 retinotopic locations × 2 center orientations × 2 surround orientations) showed a main effect of location, F (2, 70) = 15, $p < 0.001$, $\eta_p^2 = 0.3$; center orientation, F (1, 35) = 16.5, $p < 0.001$, $\eta_p^2 = 0.32$; surround orientation, F (1, 35) = 83, $p < 0.001$, $\eta_p^2 = 0.7$; and a main effect of age group, F (1, 35) = 4.8, $p = 0.035$, $\eta_p^2 = 0.12$. There were also interactions between location × surround orientation, F (2, 70) = 12.4, $p < 0.001$, $\eta_p^2 = 0.26$, and center orientation × surround orientation, F (1, 35) = 8.5, $p = 0.006$, $\eta_p^2 = 0.2$. There were no significant

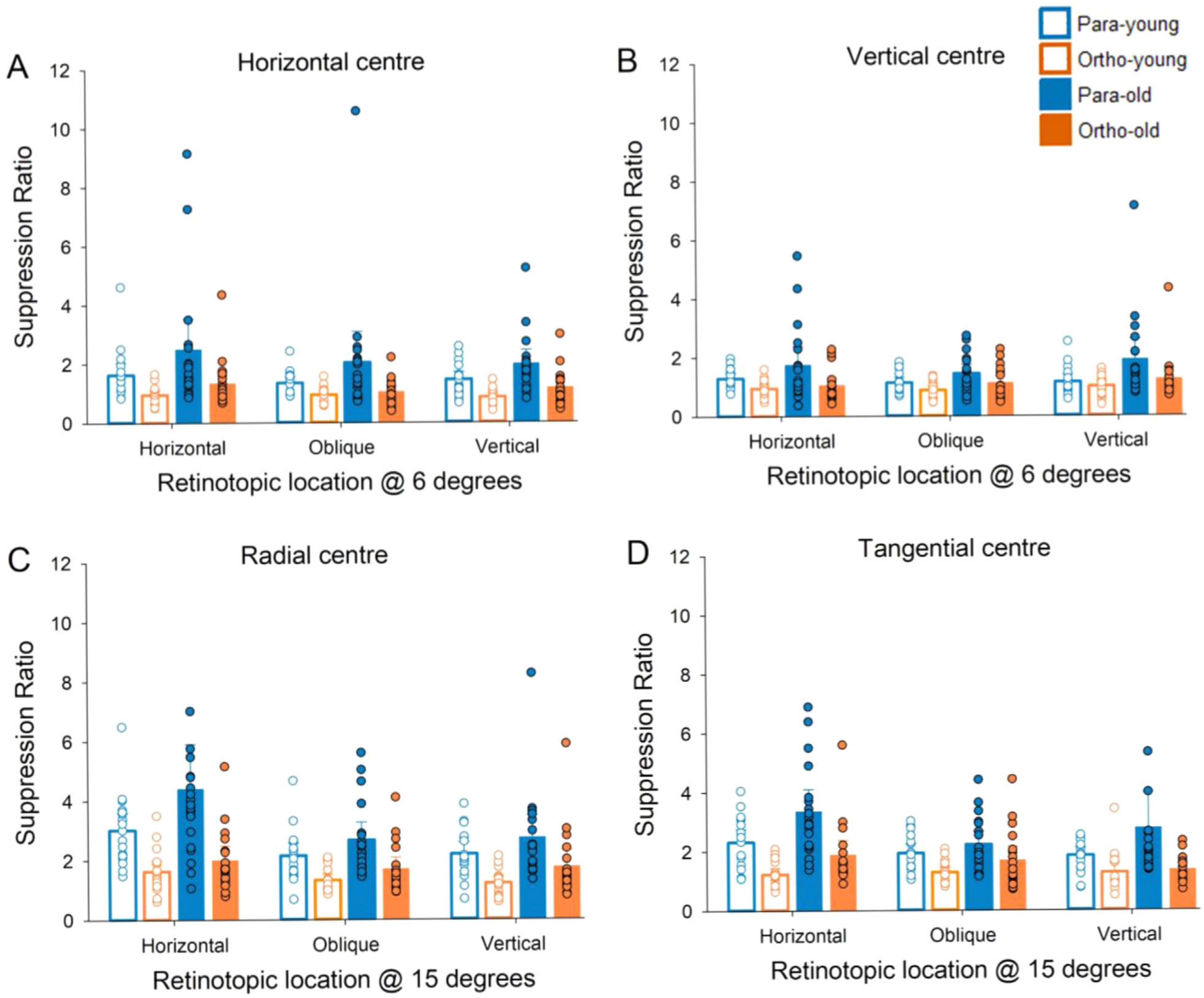

Figure 4. Parallel (blue) and orthogonal (orange) surround suppression ratios for horizontal (**A**) and vertical (**B**) center orientations at horizontal, oblique and vertical visual field locations at 6° and radial (**C**) and tangential (**D**) center orientations at horizontal, oblique and vertical visual field locations at 15° eccentricities. Open circles and bars denote data of young adults and filled circles and bars denote data of older adults. Error bars correspond to 95% confidence interval of the mean.

interactions between surround orientation × age group, $F(1, 35) = 2.4$, $p = 0.13$ or center orientation × age group, $F(1, 35) = 0.1$, $p = 0.73$. Suppression strength was greatest at the horizontal visual field location and further increased for parallel over orthogonal surround orientation. Suppression strength was greater in older adults in general regardless of the surround orientation or center orientation (open vs. filled bars in Figures 4C and D).

Discussion

Malavita et al. (2017) reported that older adults have an increased surround suppression of contrast detection at 8° visual eccentricity for parallel, vertical center-surround orientations on the horizontal visual axis (i.e., a tangential orientation at 0° visual field meridian) (Malavita et al., 2017). The first objective of the current study was to evaluate whether surround suppression of contrast detection is also stronger in older adults for eccentricities beyond 8°. Despite the stimulus conditions being somewhat different between the current experiment and that described in Malavita et al. (2017) (i.e., full vs. half surround annuli), the current experiment found that older adults have increased surround suppression relative to younger adults at both 6° and 15° eccentricities. Consequently, these data and those reported in Malavita et al. (2017) suggest that an increase of perceptual surround suppression of contrast detection outside the fovea in the elderly is a robust and replicable finding.

Although the current experiment replicated the finding of the Malavita et al. (2017), according to Nguyen and McKendrick (2016), older adults have decreased surround suppression compared with that in foveal vision when tested using supra-threshold stimuli (contrast matching task) at 6° parafoveal vision. It should be noted that both the task and stimuli were very different between the study of Nguyen and McKendrick (2016) and the present study. In particular, our current experiment describes contrast detection threshold tasks, whereas Nguyen and McKendrick (2016) used supra-threshold contrast matching tasks (20% and 40% contrasts for center and surround, respectively). Perceived contrast is thought to depend on the mean level of responses, whereas detection thresholds depend on the signal-to-noise ratio of neural responses. Indeed, detection thresholds under conditions of surround suppression are likely indicative of the responses of the least suppressed detectors (Petrov & McKee, 2006). Previous modelling of contrast response functions for center-surround measures of perceived contrast have suggested that increased weighting of both inhibitory and excitatory parameters is required to fit foveal older adult contrast response functions relative to those of younger adults (Karas & McKendrick, 2015). Future work might consider a detailed study of both the threshold and suprathreshold conditions in the same individuals at different retinal eccentricities to more fully understand the effects of aging on surround suppression of contrast. Table 1 further summarizes previous research on the effect of aging on surround suppression.

The second question of this study was to find out if the eccentricity dependency of center-surround interactions on surround suppression of contrast detection are altered in older adults. There was no evidence that orientation anisotropies are different between age groups either at 6° or 15° eccentricity. Specifically, there was a horizontal orientation bias at 6° and a radial orientation bias at 15° for parallel center-surround stimuli in both age groups. The finding of similar orientation anisotropies in young and older adults is consistent with previous psychophysical studies that reported unaltered orientation selectivity (Govenlock, Taylor, Sekuler, & Bennett, 2009; Karas & McKendrick, 2012) and tuning properties (Delahunt, Hardy, & Werner, 2008) in older human adults. Single-cell neurophysiological studies previously raised the possibility of reduced orientation sensitivity as a consequence of aging (Leventhal et al., 2003; Schmolesky, Wang, Pu, & Leventhal, 2000). The discrepancy between the psychophysical and physiological studies may simply mean that the reported observation in single-cell neurophysiology is not carried through overall visual perception or that this particular single cell study on anaesthetized animals is not comparable to psychophysical studies on humans. However, it should be noted that we did not investigate orientation tuning bandwidth here, since we examined suppressive effects only for parallel and orthogonal center-surround orientations (i.e. 0° and 90° apart center-surround orientations).

The third aim of the current experiment was to determine whether older adults have increased surround suppression for both parallel and orthogonal surround configurations and to explore the effect of center and surround orientation on suppression strength as a function of retinotopic location. The results indicated that in both age groups, parallel and orthogonal surround suppression ratio of contrast detection was significantly increased for a horizontal center at 6°, relative to the vertical condition (Figure 4A vs. Figure 4B) and it was more significant for a parallel surround than an orthogonal surround (blue bars against orange bars in Figure 4A). At 15° eccentricity, where surround suppression is typically stronger for radial configurations, suppression was significantly increased for radial than tangential center orientation in both age groups (Figure 4C vs. Figure 4D). Although the current experiment reports the maximum suppression strength for parallel center-surround orientations consistent with previous literature (Xing & Heeger, 2000), we suggest that studies that investigate orientation tuning bandwidths should consider the relative center-surround orientation of the stimulus with reference to retinotopic visual field location in addition to eccentricity to obtain maximum sensitivity of orientation differences. Finally, as can be seen in the Figure 4, surround suppression for the orthogonal condition (orange bars) at 6° eccentricity (Figures 4A and B) is almost completely released (suppression ratio close to 1 as indicated by dashed lines) whereas at 15° eccentricity (Figures 4C and D) suppression can be still seen for orthogonal surrounds. This result is consistent with previous evidence of surround suppression showing less dependency on the difference in orientation between the center and surround with more eccentric viewing (Malavita et al., 2018; Petrov & McKee, 2009; Silver et al., 2008).

It is worth noting that there are many ways to calculate suppression metrics (Mannion, Donkin, & Whitford, 2017). To enable a direct, quantitative comparison with our previous publication (Malavita et al., 2018), we have calculated the suppression ratio using a divisive method in this experiment. However, we also repeated the main analyses using a subtractive method and the key findings were unchanged (data not shown).

Although reported as a different phenomenon, a brief remark on visual crowding and its orientation effects are noteworthy. Similar to perceptual surround suppression, visual crowding becomes stronger in parafoveal vision and shows orientation anisotropy (Toet & Levi, 1992). Toet and Levi (1992) reported that spatial interactions are increased about two to

Study	Task/testing parameter	Centre: surround contrast (%)	Retinal eccentricity (°)	Stimulus orientation	Age groups	Results
Karas & McKendrick, 2009	Contrast matching (perceived contrast)	40:95 (matching reference = variable)	0	Textured noise stimuli	18–30 years (mean age, 24 years); 60–72 years (mean age, 66 years)	Increased surround suppression of perceived contrast in older group
Karas & McKendrick, 2012	Centre-surround contrast perception	40:95 (matching reference = variable Sine wave gratings of 92%	0	Vertical	20–34 years (mean age, 24.7 years); 61–75 years (mean age, 69.1 years)	Increased perceptual surround suppression for drifting, high contrast stimuli in older group Similar surround suppression in both age groups for largest stimulus
	Motion direction discrimina-tion					
McKendrick et al., 2013	Perceived contrast threshold	Variable:matching reference = 40:95	0	Vertical	20–82 years	Increased surround suppression with increasing age
Malavita et al., 2017	Contrast detection threshold	Variable: 95	8	Vertical center and surround orientation presented on horizontal meridian	18–32 years (mean age, 26.1 years); 60–74 years (mean age, 70.3 years)	Increased surround suppression in older group
Nguyen and McKendrick (2016)	Suprathreshold contrast matching	Variable: 40 (matching reference = 20:40)	6	Horizontal center orientation presented on horizontal meridian	24–35 years (mean age, 28 years); 62–78 years (mean age, 69 years)	Reduced near surround suppression in older group with similar far surround suppression in both groups Increased near surround suppression in older group
Yazdani et al. (2015)	Contrast detection threshold	Variable: 25	0 4.2	±45° to the vertical on four cardinal directions	19.4–69.1 years (mean age, 42.3 years)	Increased surround suppression in older adults for orthogonal surround
Current study	Contrast detection threshold	Variable center: 40	6	Horizontal, vertical, radial, and tangential orientations presented at horizontal nasal (0°), oblique inferior (315°) and inferior (270°) meridians	18–32 years (mean age, 24 years); 60–77 years (mean age, 67 years)	Increased surround suppression in older adults with horizontal orientation bias in both age groups
			15			Increased surround suppression in older adults with radial orientation bias in both age groups

Table 1. Summary of studies of perceptual surround suppression in adults of differing ages.

three times (increased crowding) for the orientation discrimination of a central 'T' letter between flanking 'T's along radial axis compared with that along a tangential axis up to 10° parafoveal vision in subjects aged 24 to 34 years. However, to the best of our knowledge, there is no evidence in the literature for a change in orientation anisotropy of crowding in healthy older adults. Among a handful of studies that addressed visual crowding in healthy aging, Astle, Blighe, Webb, and McGraw (2014) and Malavita et al. (2017) reported no effect of aging on visual crowding for letter acuity and orientation discrimination of Gabor tasks respectively. Malavita et al. (2017) tested nasal and temporal visual field locations at 8° eccentricity (similar to Petrov, Popple, & McKee, 2007), whereas Astle et al. (2014) tested only at 10° in the upper visual field. In contrast, a more recent study reported that older adults have increased crowding for a letter acuity task (a similar task to Astle et al., 2014) when tested at 2°, 4°, and 8° eccentricities at 12 visual field locations, suggesting that the crowding may be altered in older adults at specific eccentricities and/or visual field locations (Liu, Patel, & Kwon, 2017). This finding indicates the need for future research to explore the aging effect of visual crowding as a function of eccentricity and visual field location, possibly similar to the conditions used in the current experiment.

In conclusion, perceptual surround suppression of contrast detection is stronger for older adults compared with younger adults at 6° and 15° eccentricities. Retinotopic orientation anisotropies that are present at 6° and 15° are maintained with age (at least for the age range tested in this work). The study of differences between foveal and parafoveal visual perception across the lifespan can contribute to the understanding of neural mechanisms in human vision. The functional impact of strengthened surround suppression in older adults is not yet understood, but likely contributes to age-related differences in object segmentation and the identification of salient features to direct saccadic eye movements.

Keywords: aging vision, surround suppression, contrast detection, peripheral vision, orientation anisotropy

Acknowledgments

Commercial relationships: none.
Corresponding author: Allison M. McKendrick.
Email: allisonm@unimelb.edu.au.
Address: Department of Optometry & Vision Sciences, The University of Melbourne, 200, Berkley Street, VIC 3053, Australia.

References

Astle, A. T., Blighe, A. J., Webb, B. S., & McGraw, P. V. (2014). The effect of aging on crowded letter recognition in the peripheral visual field. *Investigative Ophthalmology and Visual Science, 55*(8), 5039–5045, doi:10.1167/iovs.14-14181.

Betts, L. R., Sekuler, A. B., & Bennett, P. J. (2009). Spatial characteristics of center-surround antagonism in younger and older adults. *Journal of Vision, 9*(1),25, 21–15, doi:10.1167/9.1.25.

Betts, L. R., Taylor, C. P., Sekuler, A. B., & Bennett, P. J. (2005). Aging reduces center-surround antagonism in visual motion processing. *Neuron, 45*(3), 361–366, doi:10.1016/j.neuron.2004.12.041.

Cannon, M. W., & Fullenkamp, S. C. (1991). Spatial interactions in apparent contrast: Inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. *Vision Research, 31*(11), 1985–1998.

Chylack, L. T., Jr., Wolfe, J. K., Friend, J., Khu, P. M., Singer, D. M., McCarthy, D., . . . Rosner, B. (1993). Quantitating cataract and nuclear brunescence, the Harvard and LOCS systems. *Optometry and Vision Science, 70*(11), 886–895.

Delahunt, P. B., Hardy, J. L., & Werner, J. S. (2008). The effect of senescence on orientation discrimination and mechanism tuning. *Journal of Vision, 8*(3), 5 1–9, doi:10.1167/8.3.5.

Fu, Y., Wang, X. S., Wang, Y. C., Zhang, J., Liang, Z., Zhou, Y. F., . . . Ma, Y. Y. (2010). The effects of aging on the strength of surround suppression of receptive field of V1 cells in monkeys. *Neuroscience, 169*(2), 874–881, doi:10.1016/j.neuroscience.2010.05.015.

Govenlock, S. W., Taylor, C. P., Sekuler, A. B., & Bennett, P. J. (2009). The effect of aging on the orientational selectivity of the human visual system. *Vision Research, 49*(1), 164–172, doi:10.1016/j.visres.2008.10.004.

Karas, R., & McKendrick, A. M. (2009). Aging alters surround modulation of perceived contrast. *Journal of Vision, 9*(5):11, 11–19, doi:10.1167/9.5.11.

Karas, R., & McKendrick, A. M. (2011). Increased surround modulation of perceived contrast in the elderly. *Optometry and Vision Science, 88*(11), 1298–1308, doi:10.1097/OPX.0b013e31822f4d51.

Karas, R., & McKendrick, A. M. (2012). Age related changes to perceptual surround suppression of moving stimuli. *Seeing and Perceiving, 25*(5), 409–424, doi:10.1163/187847611X595873.

Karas, R., & McKendrick, A. M. (2015). Contrast and stimulus duration dependence of perceptual surround suppression in older adults. *Vision*

Research, 110(Pt A), 7–14, doi:10.1016/j.visres.2015.02.016.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science, 300*(5620), 812–815, doi:10.1126/science.1082874.

Liu, R., Patel, B. N., & Kwon, M. (2017). Age-related changes in crowding and reading speed. *Scientific Reports, 7*(1), 8271, doi:10.1038/s41598-017-08652-0.

Malavita, M. S., Vidyasagar, T. R., & McKendrick, A. M. (2017). The effect of aging and attention on visual crowding and surround suppression of perceived contrast threshold. *Investigative Ophthalmology and Visual Science, 58*(2), 860–867, doi:10.1167/iovs.16-20632.

Malavita, M. S., Vidyasagar, T. R., & McKendrick, A. M. (2018). Eccentricity dependence of orientation anisotropy of surround suppression of contrast-detection threshold. *Journal of Vision, 18*(7), 5, doi:10.1167/18.7.5.

Mannion, D. J., Donkin, C., & Whitford, T. J. (2017). No apparent influence of psychometrically-defined schizotypy on orientation-dependent contextual modulation of visual contrast detection. *PeerJ, 5*, e2921

McKendrick, A. M., Weymouth, A. E., & Battista, J. (2013). Visual form percxeption from age 20 through 80 years. *Investigative Ophthalmology and Visual Science, 54*(3), 1730–1739, doi:10.1167/iovs.12-10974.

Nguyen, B. N., & McKendrick, A. M. (2016). Foveal and parafoveal contrast suppression are different: Mechanisms revealed by the study of healthy aging. *Journal of Vision, 16*(3), 10, doi:10.1167/16.3.10.

Petrov, Y., Carandini, M., & McKee, S. (2005). Two distinct mechanisms of suppression in human vision. *Journal of Neuroscience, 25*(38), 8704–8707, doi:10.1523/JNEUROSCI.2871-05.2005.

Petrov, Y., & McKee, S. P. (2006). The effect of spatial configuration on surround suppression of contrast sensitivity. *Journal of Vision, 6*(3), 4, doi:10.1167/6.3.4.

Petrov, Y., & McKee, S. P. (2009). The time course of contrast masking reveals two distinct mechanisms of human surround suppression. *Journal of Vision, 9*(1):21, 21–11, doi:10.1167/9.1.21.

Petrov, Y., Popple, A. V., & McKee, S. P. (2007). Crowding and surround suppression: Not to be confused. *Journal of Vision, 7*(2):12, 11–19, doi:10.1167/7.2.12.

Rovamo, J., & Virsu, V. (1979). An estimation and application of the human cortical magnification factor. *Experimental Brain Research, 37*(3), 495–510.

Rovamo, J., Virsu, V., Laurinen, P., & Hyvarinen, L. (1982). Resolution of gratings oriented along and across meridians in peripheral vision. *Investigative Ophthalmology and Visual Science, 23*(5), 666–670.

Sasaki, Y., Rajimehr, R., Kim, B. W., Ekstrom, L. B., Vanduffel, W., & Tootell, R. B. (2006). The radial bias: A different slant on visual orientation sensitivity in human and nonhuman primates. *Neuron, 51*(5), 661–670, doi:10.1016/j.neuron.2006.07.021.

Schmolesky, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience, 3*(4), 384–390, doi:10.1038/73957.

Silver, M. A., Shenhav, A., & D'Esposito, M. (2008). Cholinergic enhancement reduces spatial spread of visual responses in human early visual cortex. *Neuron, 60*(5), 904–914, doi:10.1016/j.neuron.2008.09.038.

Snowden, R. J., & Hammett, S. T. (1998). The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. *Vision Research, 38*(13), 1935–1945.

Takahashi, N., Hirasawa, K., Hoshina, M., Kasahara, M., Matsumura, K., & Shoji, N. (2017). Diagnostic ability and repeatability of a new supra-threshold glaucoma screening program in standard automated perimetry. *Translational Vision Science & Technology, 6*(3), 7, doi:https://doi.org/10.1167/tvst.6.3.7.

Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research, 32*(7), 1349–1357.

Turpin, A., Myers, J. S., & McKendrick, A. M. (2016). Development of visual field screening procedures: A case study of the octopus perimeter. *Translational Vision Science & Technology, 5*(3), 3, doi:10.1167/tvst.5.3.3.

Wetherill, G. B., & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology, 18*, 1–10.

Xing, J., & Heeger, D. J. (2000). Center-surround interactions in foveal and peripheral vision. *Vision Research, 40*(22), 3065–3072.

Yazdani, P., Serrano-Pedraza, I., Whittaker, R. G., Trevelyan, A., & Read, J. C. (2015). Two common psychophysical measures of surround suppression reflect independent neuronal mechanisms. *Journal of Vision, 15*(13), 21, doi:10.1167/15.13.21.