

Aging alters intraocular but not interocular foveal center surround contrast suppression

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Numerous previous studies have shown that healthy aging results in increased foveal center surround contrast suppression when the center and surround patterns are presented to both eyes. The mechanistic cause of this observation is not well established. Neurophysiological and psychophysical studies have shown that different mechanisms of parafoveal center surround suppression can be tapped by manipulating viewing conditions to present the center and surround to the same eye (intraocular viewing) or to different eyes (interocular viewing), or by manipulating stimulus parameters such as duration. Here, we tested intraocular and interocular foveal center surround contrast suppression for stimuli of 40 ms and 200 ms duration in 18 younger and 18 older adults. For both groups, foveal intraocular center surround contrast suppression decreased with longer stimulus duration whereas interocular surround suppression did not, confirming contributions from separate mechanisms to these forms of suppression. Intraocular center surround contrast suppression was increased in older adults compared to younger adults; however, interocular suppression was similar in both groups. Our results indicate that aging differentially affects distinct forms of suppression arising at various levels of the visual pathway.

Introduction

Healthy aging alters perceptual surround suppression (Betts, Taylor, Sekuler, & Bennett, 2005; Karas & McKendrick, 2009, 2011, 2012, 2015; Yazdani, Serrano-Pedraza, Whittaker, Trevelyan, & Read, 2015). One type of perceptual surround suppression manifests when the perceived contrast of a suprathreshold

pattern is reduced by a surrounding high-contrast pattern (Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989). This effect is commonly referred to as center surround contrast suppression. Previous studies have investigated the effect of aging on center surround contrast suppression under various conditions in order to improve understanding of the underlying cause for this observed behavioral phenomenon, and demonstrate that the effect is robust for a wide variety of stimulus parameter manipulations. For different stimulus types such as contrast noise textures (Karas & McKendrick, 2009), static gratings (Karas & McKendrick, 2011), and drifting gratings (Karas & McKendrick, 2012), and different stimulus durations such as 100 ms and 500 ms (Karas & McKendrick, 2015), older adults consistently show increased center surround contrast suppression relative to younger adults.

An additional stimulus parameter that has been manipulated previously is the contrast of the center and the surround components of the stimulus (Karas & McKendrick, 2015). For lower contrast center patterns (20%), older adults showed increased suppression relative to younger adults (Karas & McKendrick, 2015). However, the amount of suppression was similar between groups when the center contrast was high (80%; Karas & McKendrick, 2015). These findings would be expected if there are two center surround contrast suppression mechanisms that exist in human foveal vision, one elicited by a low contrast center and the other elicited by a high contrast center, and if aging predominantly affects the suppression mechanism evoked when the center contrast is low. Indeed, low and high contrast stimuli elicit two distinct forms of surround suppression in the receptive fields of primate

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V1 neurons (Webb, Dhruv, Solomon, Tailby, & Lennie, 2005), which are thought to be the neural correlates of perceptual center surround contrast suppression.

Knowledge of how different stimulus properties can alter the strength of surround suppression in visual cortical neurons can be used to inform the design of experiments to disentangle which neuronal mechanisms of surround suppression are affected by the healthy aging process. There are several key results from such neurophysiological experiments that specifically motivated our experiments. First, stimulation of the classical receptive field of V1 neurons with a low contrast target invokes a suppressive surround mechanism with broad spatiotemporal tuning, whereas a high contrast target invokes a suppressive surround mechanism with sharp spatiotemporal tuning (Levitt & Lund, 1997; Webb et al., 2005). The broadly tuned mechanism is predominantly intraocular (within eye) and is not susceptible to contrast adaptation (Webb et al., 2005). This has previously been referred to as the “early” mechanism by Webb et al. (2005), and is thought to originate at the level of the lateral geniculate nucleus (LGN) or at the input layers of V1 (Webb et al., 2005). In comparison, the narrowly tuned mechanism is interocular (between eyes), affected by contrast adaptation and referred to as the “late” mechanism arising beyond the input layers of V1 (Webb et al., 2005). Second, three types of connections that are considered to contribute to surround suppression in primary visual cortex (V1)—feedforward connections from LGN, horizontal connections within V1, and feedback projections from extrastriate cortices to V1—differ in their timing properties (Angelucci & Bressloff, 2006). Intra-V1 horizontal connections carry information at a slower speed (Bringuier, Chavane, Glaeser, & Fregnac, 1999) than extrastriate feedback connections (Girard, Hupe, & Bullier, 2001). These intra-V1 horizontal connections and extrastriate feedback connections are considered to give rise to two distinct components of surround suppression: a stronger, transient suppression and a weaker, sustained suppression respectively (Bair, Cavanaugh, & Movshon, 2003).

Distinct perceptual surround suppression mechanisms have likewise been demonstrated in human observers. Perceptually, center and surround patterns are shown to one eye (Cai, Zhou, & Chen, 2008; Schallmo & Murray, 2016) or both eyes (Petrov & McKee, 2009) to study the intraocular suppression mechanism, whereas center and surround patterns are shown to different eyes (Cai et al., 2008; Petrov & McKee, 2009; Schallmo & Murray, 2016) to study the interocular suppression mechanism. We will refer to these forms of suppression as intraocular and interocular center surround contrast suppression

respectively. Under comparable parameter manipulations, performance of human observers is qualitatively similar to those revealed by single-cell neurophysiology. Cai et al. (2008) showed that foveal interocular center surround contrast suppression is tightly orientation tuned and arises at a higher level in the visual pathway than intraocular center surround contrast suppression. Schallmo and Murray (2016) found that parafoveal interocular center surround contrast suppression is tightly orientation tuned and susceptible to surround adaptation, whereas parafoveal intraocular center surround contrast suppression is broadly orientation tuned and less affected by surround adaptation. These findings are consistent with the neurophysiological early and late mechanisms reported by Webb et al. (2005). In addition to manipulating the viewing condition (interocular vs. intraocular), different mechanisms of surround suppression have been revealed by altering the stimulus duration. Petrov and McKee (2009) measured perceptual contrast suppression using a contrast detection task and suggested two distinct time courses of surround suppression in human observers: intraocular suppression dominates at shorter stimulus durations (<100 ms) but becomes weaker at longer stimulus durations (≥ 200 ms) and interocular suppression remains same for stimulus durations between 20 ms to 500 ms.

Given previous reports of increased contrast suppression in older adults for low but not high contrast center patterns (Karas & McKendrick, 2015) and that in primate V1 neurons, a low contrast center elicits predominantly low-level, intraocular mechanisms (Webb et al., 2005), we hypothesized that aging would predominantly affect intraocular surround suppression. In addition, we tested two different stimulus durations (40 ms vs. 200 ms) to investigate the time course of surround suppression for both intraocular and interocular mechanisms. We show that older adults have increased intraocular but not interocular center surround contrast suppression, compared to younger adults. Our results are discussed using a framework of physiological surround suppression mechanisms arising at different levels of the visual pathway.

Methods

Apparatus

Stimuli were generated and displayed on a ViewPixx™ system (VPixx Technologies Inc., Saint-Bruno, QC, Canada). The monitor had a resolution of 1920 × 1080 pixels, refresh rate of 120 Hz and mean luminance of 56 cd/m². Matlab™ version 8 with Psychtoolbox

version 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) was used to produce gamma-corrected stimulus images with 12-bit luminance resolution. Stimuli were viewed through a ScreenScope™ mirror stereoscope (StereoAids, Albany, WA, Australia). The stereoscope had a pair of circular apertures of 2.2 cm diameter; at an effective viewing distance of 57 cm, it allowed 14° of monocular visual field.

Participants

Participants were recruited via written advertisements posted around the University of Melbourne, in online forums associated with the University, and in local community newspapers. All participants underwent an optometric examination including a brief history, visual acuity testing, refraction, and anterior and posterior segment examinations to ensure they had best corrected visual acuity of 6/7.5 or better and refractive error less than ± 5 D sphere or 2 D cylinder in each eye. All participants were refractively corrected for the working distance and had a near visual acuity of N6 or better at 57 cm. Participants taking any medication known to affect contrast sensitivity, or with any ocular pathology, were excluded from the study.

Stable fusion of the two eyes' fields of view was required for the testing, particularly for the interocular conditions. To check this, participants were shown a vertical bar in the right eye and a horizontal bar in the left eye and asked to align the two lines to form a perfect cross by adjusting mirrors in the stereoscope and/or with the aid of prisms up to a maximum of 3 prism diopters. Participants who did not have this level of fusion, or whose stability of fusion deteriorated during the course of testing, were excluded from the study. In addition, participants were asked about any misalignments at the end of each interocular condition, in which case that particular measurement was discarded and repeated after a few minutes break or on a different day. We recruited 19 younger and 23 older adults, out of which one younger and one older participant could not perform the contrast matching task reliably. All the remaining younger participants ($n = 18$) had stable binocular fusion, while four out of the remaining 22 older participants could not maintain stable binocular fusion. Hence, the data presented here are from the remaining 36 participants: 18 younger adults (aged 19 to 32 years, mean = 27 years) and 18 older adults (aged 61 to 78 years, mean = 69 years). All participants provided written informed consent prior to taking part in the study. The study protocol adhered to the tenets of Declarations of Helsinki and the study was

approved by the Human Research Ethics Committee of The University of Melbourne.

Stimuli

The stimuli are illustrated in Figures 1A and 1B. A vertically oriented, circular sinusoid of 0.67° radius was used as the center target. An annular ring of vertically oriented sinusoid (inner radius 0.67° , outer radius 4°) was used as the surround target. The center and surround were separated by one pixel to minimize brightness induction at the border between center and surround (Yu, Klein, & Levi, 2001). Both center and surround targets had a spatial frequency of $4\text{ c}/^\circ$ and the same phase with respect to the center. The phase was randomized between each presentation. The center and surround target contrasts were 20% and 40%, respectively. The stimulus duration was either 40 ms or 200 ms. The viewing was either intraocular or interocular. Two thin identical fixation circles (0.1° wide, 12° radius) constructed of random black and white dots with zero disparity were used to indicate the target locations and to facilitate ocular alignment during interocular viewing.

Psychometric procedure

Foveal center surround contrast suppression was investigated under eight conditions: two viewing conditions (intraocular and interocular), two surround conditions (no surround and surround), and two stimulus durations (40 ms and 200 ms). Measurements were taken during two or three test sessions of approximately 2 hr each, with regular rest breaks as required.

We used a temporal two-interval forced choice procedure with a method of constant stimuli (MOCS) to measure the perceived contrast of the central grating patch. The two intervals were separated by an interstimulus interval of 500 ms. Each interval was accompanied by an auditory tone. The first interval always contained the reference pattern. The second interval contained either the target alone (no surround condition) or the target plus surround pattern (surround condition). An example of a trial sequence is illustrated in Figure 1A and 1B.

Participants indicated the interval that contained the central pattern of higher contrast by pressing a button. The contrast of the reference pattern was varied to construct a psychometric function. The reference pattern had one of seven contrast levels. Stimuli at each contrast level were shown 20 times in two blocks of 10 trials each. The contrast levels were chosen based on an initial MOCS of 10 contrast levels presented four times

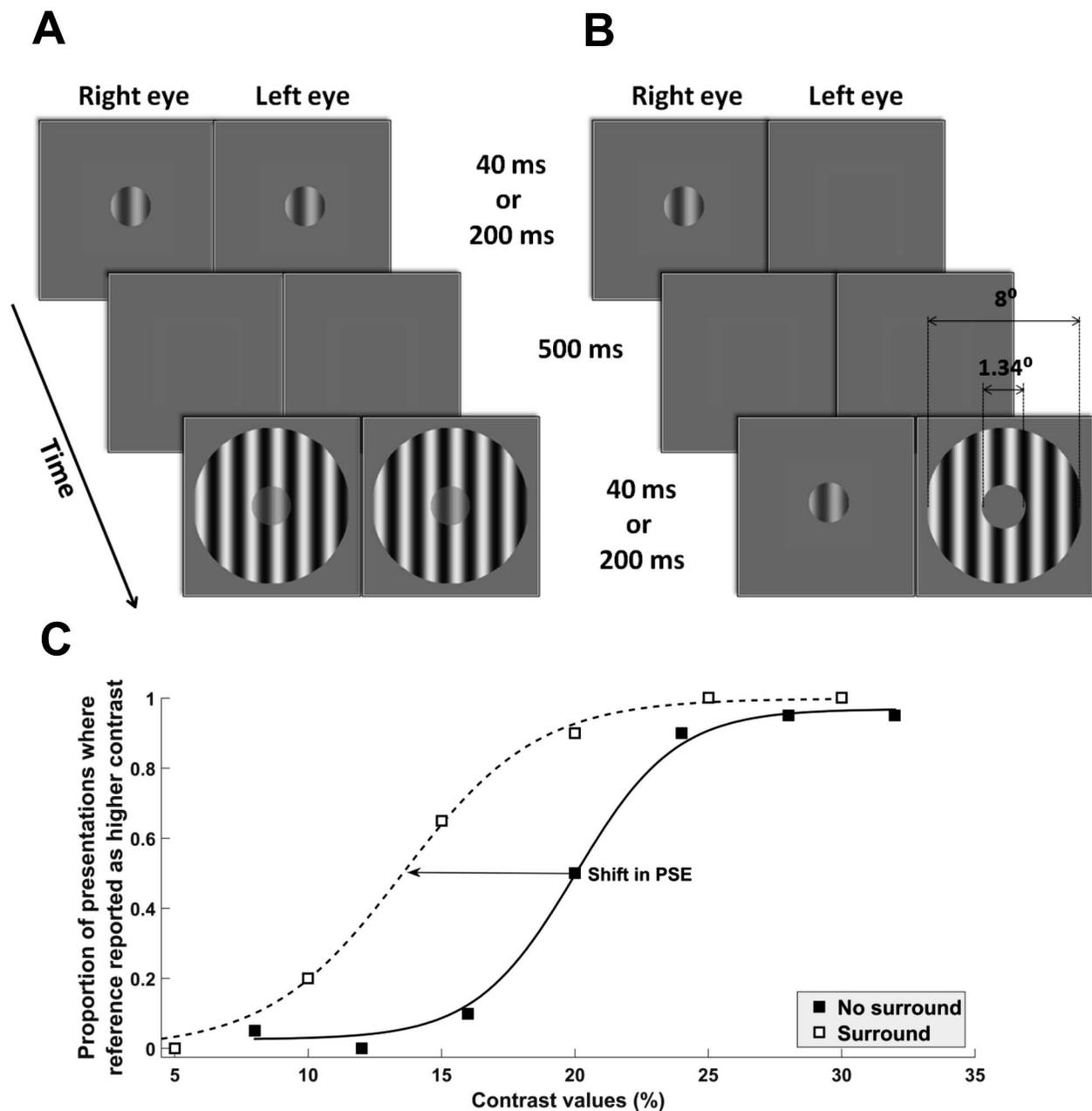


Figure 1. A schematic illustration of stimulus and trial sequence under intraocular (A) and interocular conditions (B), and example psychometric functions from an older participant (C). A leftward shift in the point of subjective equality (PSE) indicates perceptual suppression.

each. This initial MOCS also served as training prior to formal data collection.

Psychometric functions were fitted with the following equation using a maximum likelihood approach:

$$\varphi(c, \mu, \sigma) = FP + (1 - FP - FN)G(c, \mu, \sigma), \quad (1)$$

where φ represents probability of perceiving the stimulus pattern as higher contrast; FP is false positive parameter that represents the lower asymptote of the psychometric function; FN is $1 -$ upper asymptote of the psychometric function; and $G(c, \mu, \sigma)$ is the cumu-

lative Gaussian distribution with mean μ , and standard deviation σ for the stimulus contrast value c ; σ and μ were used as estimates of the spread of the psychometric function (% contrast) and point of subjective equality (% contrast), respectively. Custom written software in R (R Development Core Team, 2014) was used for the curve fitting using the procedures recommended by Wichmann and Hill (2001). The deviance of the fitted model was compared to the deviance distribution derived from Monte Carlo simulations of 10,000 datasets simulated from the fitted

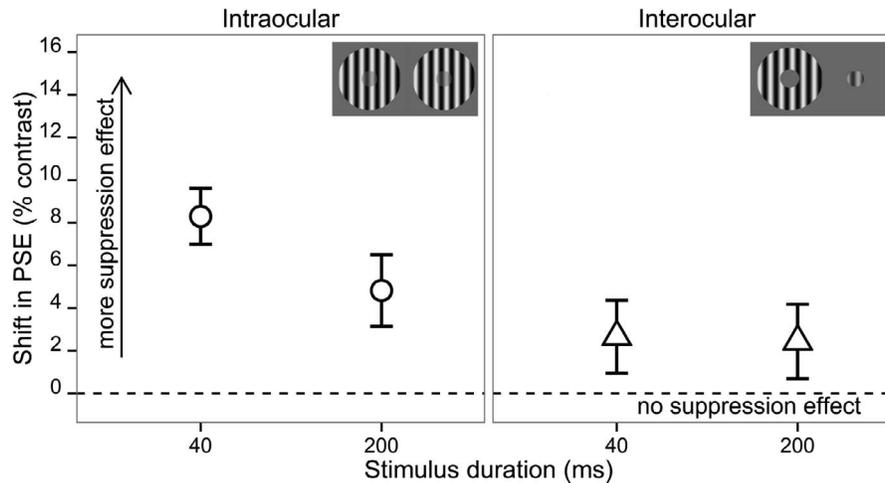


Figure 2. Shift in PSE under intraocular (circles) and interocular (triangles) viewing conditions for younger observers ($n = 18$). Group mean data are presented; error bars represent 95% confidence intervals of the mean. The horizontal dashed line at 0 indicates no suppression; values greater than 0 indicate suppression

model. The probability that a dataset of given size simulated from the fitted model has a deviance as large as or larger than the observed deviance indicates the goodness of fit as a p value. The threshold value was the contrast at which the reference pattern appeared the same contrast as the target (point of subjective equality, or PSE), defined as the 50% point on the fitted function (Figure 1C).

Suppression strength was estimated using the *shift in PSE*, which was calculated as follows:

$$\text{Shift in PSE} = PSE_t - PSE_{t+s}, \quad (2)$$

where PSE_t represents the apparent contrast of the test pattern alone and PSE_{t+s} represents the apparent contrast of the test pattern in the presence of a surround pattern. A shift in PSE of 0 indicates no suppression, a positive value indicates suppression, and a negative value indicates facilitation.

Formal statistics on the data were conducted using IBM SPSS Statistics 20 (SPSS Inc., Chicago, IL). All the data sets were tested for statistical normality (Kolmogorov–Smirnov test) and equal variance (Levene median test). Within-group and between-groups comparisons were tested using repeated measures ANOVA and mixed design ANOVA, respectively.

Results

Intraocular but not interocular suppression decreases with stimulus duration

Figure 2 shows the effect of two stimulus durations on intraocular and interocular surround suppression in

younger adults. Stimulus duration significantly altered the magnitude of intraocular suppression; compared to 40 ms, suppression was reduced almost two-fold for 200 ms. Interocular surround suppression was relatively weaker than intraocular surround suppression and was not influenced by stimulus duration. There was a significant interaction between stimulus duration and viewing condition, RM ANOVA: $F(1, 17) = 19.798, p < 0.001$.

Intraocular but not interocular suppression is increased in older adults

Figure 3 compares intraocular and interocular surround suppression for the younger and older adults. Consistent with previous literature, older adults had stronger suppression than younger adults for intraocular viewing (Karas & McKendrick, 2015; Figure 3, left panel). Under interocular viewing, both younger and older adults showed similar strengths of suppression (Figure 3, right panel). Interocular suppression was relatively weaker than intraocular suppression; however, the amount of interocular suppression was significantly different from zero: main effect of surround, $F(1, 34) = 18.951, p < 0.001$ (see Figure S1 in supplementary material). There was a significant interaction between Age \times Viewing Condition, $F(1, 34) = 6.751, p = 0.014$, and between Age \times Stimulus Duration, $F(1, 34) = 5.492, p = 0.025$. In addition, there was a trend toward a significant three-way interaction, Age \times Viewing Condition \times Stimulus Duration, $F(1, 34) = 3.838, p = 0.058$. When separating the viewing conditions, the Age \times Duration Interaction was significant for the intraocular condition, $F(1, 34) = 10.25, P = 0.003$, but not for the interocular condition,

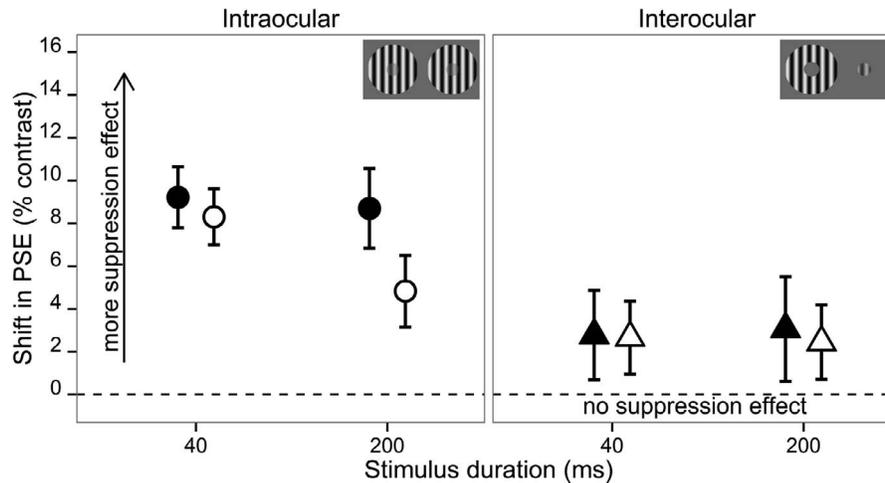


Figure 3. Mean shift in PSE data of younger (open symbols, $n = 18$) and older (closed symbols, $n = 18$) adults under intraocular (circles) and interocular (triangles) viewing conditions. Error bars represent 95% confidence intervals of the mean. The horizontal dashed line at 0 indicates no suppression; values greater than 0 indicate suppression

$F(1, 34) = 0.25$, $p = 0.62$. For full reporting of the ANOVA related to this experiment refer to Tables S1, S2, and S3 in supplementary material.

Intraocular center surround contrast suppression: Binocular viewing is not different from monocular viewing

In the previous experiment, we found that foveal intraocular center surround contrast suppression is increased in older adults, while interocular suppression is unaltered. In our experiments, intraocular suppression was studied under binocular viewing similar to that of Petrov and McKee (2009). In theory, binocular viewing is a combination of monocular and interocular viewing, which makes it difficult to discern the origin of altered surround suppression along the visual pathway in older adults. Therefore, as a control experiment, we compared intraocular center surround contrast suppression under monocular and binocular viewing conditions in a subset of 10 younger adults (aged 21 to 31 years, mean 28 years) and 10 older adults (aged 61 to 74 years, mean 67 years) who had participated in the main study and were able to attend for the additional experiment. Figure 4 shows the strength of monocular and binocular surround suppression in this subset of younger and older adults. In both groups, monocular and binocular suppression strength were similar: main effect of viewing condition, $F(1, 18) = 1.09$, $p = 0.31$. In addition, there was no interaction between viewing condition and age, $F(1, 18) = 1.67$, $p = 0.21$, indicating that aging effects on suppression strength are not dependent on whether the center surround stimulus was presented monocularly or binocularly. The three-way interaction between viewing condition, stimulus dura-

tion, and age was not statistically significant, $F(1, 18) = 0.311$, $p = 0.584$.

In order to determine whether the subset of participants that completed the control experiment were representative of the larger group, we report the interocular suppression data from this subset of participants as collected in the previous experiment (see Figure S2 in the supplementary material). In both groups, interocular suppression was less than binocular and monocular suppression similar to the main experiment: main effect of viewing condition, $F(2, 36) = 45.33$, $p < 0.001$; Viewing Condition \times Stimulus Duration, $F(2, 36) = 7.713$, $p = 0.002$. However, the interaction between viewing condition and age was not significant, $F(2, 36) = 0.95$, $p = 0.395$, nor was the three-way interaction between viewing condition, stimulus duration, and age, $F(2, 36) = 0.216$, $p = 0.806$. Post hoc Bonferroni comparisons indicate that overall monocular and binocular strength were similar ($p = 0.934$), but interocular suppression strength was significantly different from the two other conditions ($p < 0.001$; see Tables S4, S5, and S6 in supplementary material for complete reporting of ANOVA tables related to this experiment). Together with our results from Figure 3, this suggests that whether the surround is present in the same eye as the center target (intraocular) or in a different eye (interocular) is important, rather than whether the whole pattern is viewed by a single eye (monocular) or both eyes (binocular).

Contrast matching of isolated patterns is similar between younger and older adults

Interpretation of our findings assumes that all participants were reliable observers and able to perform

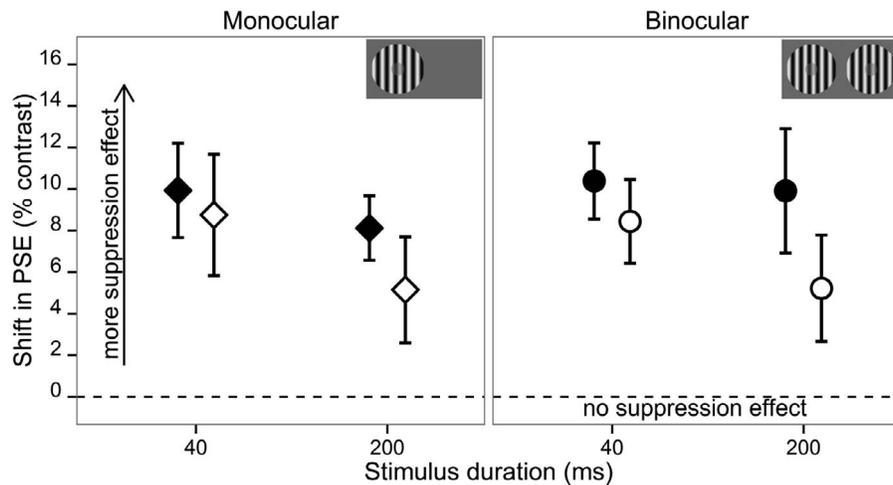


Figure 4. Mean shift in PSE data of younger (open symbols, $n = 10$) and older (closed symbols, $n = 10$) adults under monocular (diamonds) and binocular (circles) viewing conditions. Error bars represent 95% confidence interval of the mean. The horizontal dashed line at 0 indicates no suppression; values greater than 0 indicate suppression.

the contrast matching judgments with sufficient precision. To check the ability of our participants to perform the matching task, we also inspected the PSEs (Figure 5A) and spreads of the psychometric functions obtained for the isolated grating patch (Figure 5B). For psychometric function spreads in the presence of surrounds see Figure S3 in supplementary material. Both older and younger adults reliably matched the reference grating to the test grating's physical contrast (20%; horizontal dashed lines in Figure 5A). The PSE and the spread of the contrast matching functions were not different between younger and older adults, or between different viewing conditions in the absence of surround: PSE, Viewing Condition \times Stimulus Duration, $F(1, 34) = 0.151$, $p = 0.700$; main effect of age, $F(1, 34) = 3.620$, $p = 0.066$; spread, Viewing Condition \times

Stimulus Duration, $F(1, 34) = 1.034$, $p = 0.316$; main effect of age, $F(1, 34) = 0.844$, $P = 0.365$.

Discussion

Increased contrast suppression in older adults for low but not high contrast central stimulation (Karas & McKendrick, 2015) has been previously reported. In primate V1 neurons, a low-contrast central stimulus elicits predominantly intraocular mechanisms, whereas a high-contrast center invokes interocular mechanisms (Webb et al., 2005). Based on these two findings, we hypothesized that aging might affect low-level intraocular surround suppression mechanisms to a larger extent than interocular mechanisms. Consistent with

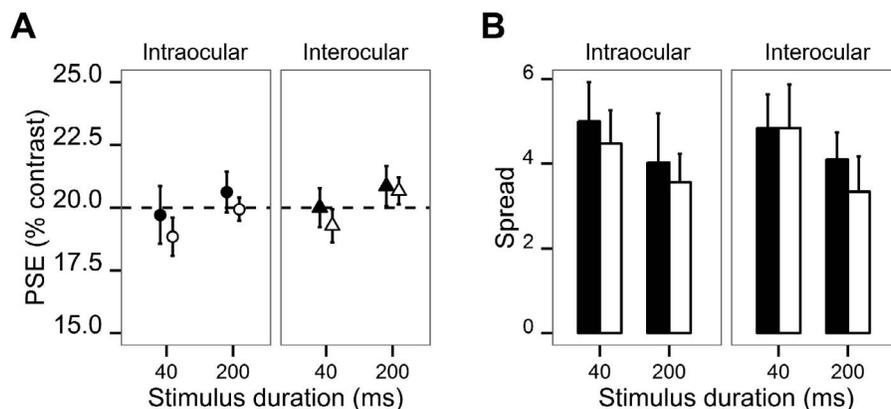


Figure 5. Contrast matching data of the isolated grating (veridical contrast = 20%). Point of subjective equality (PSE; A) and spread of the psychometric functions (B) of younger (open symbols) and older (closed symbols) adults under intraocular and interocular viewing conditions. Error bars represent 95% confidence interval of the mean. Horizontal dashed line in the left panel indicates veridical perception.

this hypothesis, we found that older adults have similar foveal interocular center surround contrast suppression strength as younger adults (Figure 3, right panel). However, older adults have increased foveal intraocular center surround contrast suppression (Figure 3, left panel). This latter finding is consistent with previous studies (Karas & McKendrick, 2009, 2011, 2012, 2015); however, interocular experiments in older adults have not been previously reported.

The exact physiological mechanisms underpinning the age-related alteration of intraocular surround suppression are still unclear. Visual signals from the two eyes first converge at the layers beyond the input layers of V1 (Hubel & Wiesel, 1968). While it is impossible to pinpoint specific neural location using psychophysical measures, our data indirectly suggests that the predominant age-related alterations in surround suppression of contrast occurs at a processing stage before binocular combination of visual signals; that is, prior to or at the level of the input layers of V1.

Aging and suprathreshold contrast perception

Since our study suggests that aging alters intraocular (low-level) but not interocular surround suppression mechanisms, we first consider the possible confound of precortical threshold contrast sensitivity deficits and optical factors such as reduced retinal illumination in older adults. Although aging results in reduced threshold contrast sensitivity (Owsley, Sekuler, & Siemsen, 1983), it has no effect (Tulunay-Keesey, Ver Hoeve, & Terkla-McGrane, 1988) or marginal effect on suprathreshold contrast matching (Mei, Leat, & Hovis, 2007), which is the task we employed here. In addition, aging results in reduced retinal illuminance due to senile miosis (Winn, Whitaker, Elliott, & Phillips, 1994). However, its influence on suprathreshold contrast perception phenomena is negligible (Betts, Sekuler, & Bennett, 2007; Betts et al., 2005; Elliott, Whitaker, & MacVeigh, 1990). The spread of the psychometric function, which can be considered as a measure of contrast discriminability, was not different between younger and older adults (Figure 5B). Hence, the observed perceptual differences between younger and older adults in the presence of surround seems unlikely to be driven by age-related retinal illuminance differences or threshold contrast sensitivity differences.

Mechanisms of surround suppression

Intraocular and interocular surround suppression have previously been studied in observers with normal vision (Cai et al., 2008; Chubb et al., 1989; Meese & Hess, 2004; Petrov & McKee, 2009; Schallmo &

Murray, 2016). With the exception of Chubb et al. (1989), all studies have reported significant interocular suppression, including ours. Alternate frameworks have been suggested as a basis of interpreting interocular suppression data such as the mathematical model proposed by Meese and Hess (2004). This model, referred to as the late binocular summation model, was able to describe suppression data in their two experimental observers. Such a framework might provide some future utility in interpreting changes to surround suppression in the elderly; however, this would require a different experimental design and approach than that used herein.

There are several other studies that have reported distinct intraocular and interocular components of perceptual surround suppression in human vision (Cai et al., 2008; Petrov & McKee, 2009; Schallmo & Murray, 2016). In particular, our study was motivated by Petrov and McKee's (2009) work that showed distinct surround suppression mechanisms of contrast detection in human parafovea could be elicited by manipulating stimulus duration and viewing eye. Here, it is important to note that surround suppression of contrast detection is quite different from that of contrast matching. Suppression of contrast matching manifests under foveal and parafoveal vision whereas suppression of contrast detection manifest only in parafoveal vision (Petrov, Carandini, & McKee, 2005). Petrov and McKee (2009) showed that interocular parafoveal center surround contrast suppression was weaker than intraocular suppression for a range of stimulus durations (20 ms to 500 ms). In contrast, the strength of intraocular parafoveal contrast suppression peaked at approximately 40 ms, but then gradually reduced and reached the level of interocular suppression around 200 ms. This prompted us to use stimulus durations of 40 ms and 200 ms as we required some constraints on numbers of durations included in order to maintain a test session length suitable for older adults.

A possible interpretation of Petrov and McKee's (2009) data is that when interocular mechanisms are isolated using a dichoptic viewing setup, neural responses for different stimulus durations are generated from within the same neural population. Consequently, similar amounts of suppression are derived for the two stimulus durations. On the other hand, under intraocular viewing conditions, perceptual surround suppression for shorter stimulus durations are generated by strong, transient neural mechanisms, whereas responses for longer stimulus durations are generated by weak, sustained neural mechanisms (Petrov & McKee, 2009). This transient and sustained mechanism interpretation is consistent with physiological mechanisms reported in primate V1 receptive fields (Bair et al., 2003). In line with the neural schema of transient and sustained

mechanisms of surround suppression, for younger adults we show that foveal intraocular suppression has different stimulus duration dependency than interocular surround suppression similar to parafoveal surround suppression mechanisms of contrast detection.

Conclusion

Our study demonstrates that aging predominantly alters foveal intraocular center surround contrast suppression but not interocular suppression. In addition, our study provides evidence suggesting existence of distinct forms of intraocular and interocular surround suppression that can be tapped by manipulating stimulus duration similar to that of parafoveal mechanisms (Petrov & McKee, 2009). The exact mechanisms behind altered intraocular surround suppression in healthy aging remain unclear. To further our understanding of the normal aging process, future physiological studies investigating intraocular and interocular surround suppression mechanisms in senescent V1 receptive fields are warranted.

Keywords: aging, surround suppression, intraocular, interocular, contextual interaction, dichoptic

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References

- Angelucci, A., & Bressloff, P. C. (2006). Contribution of feedforward, lateral and feedback connections to the classical receptive field center and extra-classical receptive field surround of primate V1 neurons. In S. Martinez-Conde, S. L. Macknik, L. M. Martinez, J. M. Alonso, & P. U. Tse (Eds.), *Progress in Brain Research* (Vol. 154, pp. 93–120). Amsterdam, The Netherlands: Elsevier.
- Bair, W., Cavanaugh, J. R., & Movshon, J. A. (2003). Time course and time-distance relationships for surround suppression in macaque V1 neurons. *Journal of Neuroscience*, *23*(20), 7690–7701.
- Betts, L. R., Sekuler, A. B., & Bennett, P. J. (2007). The effects of aging on orientation discrimination. *Vision Research*, *47*(13), 1769–1780.
- 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.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Bringuier, V., Chavane, F., Glaeser, L., & Fregnac, Y. (1999). Horizontal propagation of visual activity in the synaptic integration field of area 17 neurons. *Science*, *283*(5402), 695–699.
- Cai, Y., Zhou, T., & Chen, L. (2008). Effects of binocular suppression on surround suppression. *Journal of Vision*, *8*(9):9, 1–10, doi:10.1167/8.9.9. [PubMed] [Article]
- 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.
- Chubb, C., Sperling, G., & Solomon, J. A. (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Sciences, USA*, *86*(23), 9631–9635.
- Elliott, D., Whitaker, D., & MacVeigh, D. (1990). Neural contribution to spatiotemporal contrast sensitivity decline in healthy ageing eyes. *Vision Research*, *30*(4), 541–547.
- Girard, P., Hupe, J. M., & Bullier, J. (2001). Feedforward and feedback connections between areas V1 and V2 of the monkey have similar rapid conduction velocities. *Journal of Neurophysiology*, *85*(3), 1328–1331.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, *195*(1), 215–243.
- Karas, R., & McKendrick, A. M. (2009). Aging alters surround modulation of perceived contrast. *Journal of Vision*, *9*(5):11, 1–9, doi:10.1167/9.5.11. [PubMed] [Article]
- Karas, R., & McKendrick, A. M. (2011). Increased surround modulation of perceived contrast in the elderly. *Optometry and Vision Science*, *88*(11), 1298–1308.
- Karas, R., & McKendrick, A. M. (2012). Age related changes to perceptual surround suppression of

- moving stimuli. *Seeing and Perceiving*, 25(5), 409–424.
- Karas, R., & McKendrick, A. M. (2015). Contrast and stimulus duration dependence of perceptual surround suppression in older adults. *Vision Research*, 110, 7–14.
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception*, 36(14), 1–16.
- Levitt, J. B., & Lund, J. S. (1997). Contrast dependence of contextual effects in primate visual cortex. *Nature*, 387(6628), 73–76.
- Meese, T. S., & Hess, R. F. (2004). Low spatial frequencies are suppressively masked across spatial scale, orientation, field position, and eye of origin. *Journal of Vision*, 4(10):2, 843–859, doi:10.1167/4.10.2. [PubMed] [Article]
- Mei, M., Leat, S. J., & Hovis, J. (2007). Supra-threshold contrast matching and the effects of contrast threshold and age. *Clinical and Experimental Optometry*, 90(4), 272–281.
- Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research*, 23(7), 689–699.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Petrov, Y., Carandini, M., & McKee, S. (2005). Two distinct mechanisms of suppression in human vision. *Journal of Neuroscience*, 25(38), 8704–8707.
- Petrov, Y., & McKee, S. (2009). The time course of contrast masking reveals two distinct mechanisms of human surround suppression. *Journal of Vision*, 9(1):21, 1–11, doi:10.1167/9.1.21. [PubMed] [Article]
- R Development Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Schallmo, M. P., & Murray, S. O. (2016). Identifying separate components of surround suppression. *Journal of Vision*, 16(1):2, 1–12, doi:10.1167/16.1.2. [PubMed] [Article]
- Tulunay-Keesey, U., Ver Hoeve, J. N., & Terkla-McGrane, C. (1988). Threshold and suprathreshold spatiotemporal response throughout adulthood. *Journal of the Optical Society of America A: Optics and Image Science*, 5(12), 2191–2200.
- Webb, B. S., Dhruv, N. T., Solomon, S. G., Tailby, C., & Lennie, P. (2005). Early and late mechanisms of surround suppression in striate cortex of macaque. *Journal of Neuroscience*, 25(50), 11666–11675.
- Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63, 1293–1313.
- Winn, B., Whitaker, D., Elliott, D. B., & Phillips, N. J. (1994). Factors affecting light-adapted pupil size in normal human subjects. *Investigative Ophthalmology and Visual Science*, 35(3), 1132–1137. [PubMed] [Article]
- 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, 1–14, doi:10.1167/15.13.21. [PubMed] [Article]
- Yu, C., Klein, S. A., & Levi, D. M. (2001). Surround modulation of perceived contrast and the role of brightness induction. *Journal of Vision*, 1(1):3, 18–31, doi:10.1167/1.1.3. [PubMed] [Article]