Aging effects on collinear facilitation

Yu Man Chan Department of Optometry & Vision Sciences, The University of Melbourne, Parkville, 3010, Australia

Josephine Battista Department of Optometry & Vision Sciences, The University of Melbourne, Parkville, 3010, Australia

Allison M. McKendrick Department of Optometry & Vision Sciences, The University of Melbourne, Parkville, 3010, Australia

Normal aging has been shown to alter performance on several suprathreshold spatial tasks such as contour integration and perceptual measures of center-surround interactions. The purpose of this study was to investigate the effects of aging on collinear facilitation. Despite all related lateral interactions that are presumed to involve neural architecture within primary visual cortex, collinear facilitation differs from contour integration and surround suppression tasks in that it is a purely foveal, threshold phenomenon. Collinear facilitation was measured for 20 younger (19–31 years) and 15 older (59–71 years) adults with measures repeated over two identical test sessions. Contrast thresholds were measured for a central Gabor patch in the presence of flankers of varying interelement distances and orientations. A reduced magnitude of facilitation was found for the older observers. Our results demonstrate abnormalities of spatial interactions in older adults.

Keywords: aging, collinear facilitation, form perception

Citation: Chan, Y. M., Battista, J., & McKendrick, A. M. (2012). Aging effects on collinear facilitation. *Journal of Vision, 12*(6):21, 1–10, http://www.journalofvision.org/content/12/6/21, doi:10.1167/12.6.21.

Introduction

Early stages of form perception require the accurate encoding of orientation information, the subsequent grouping of similar orientations into contours, and then the extraction of global features regarding shapes (Loffler, 2008). Collinear facilitation describes the observation that contrast detection thresholds decrease for foveally presented elements when presented with adjacent stimuli of similar orientation and spatial frequency (Keeble & Hess, 1998; Polat & Sagi, 1993). Collinear facilitation is considered to be an important step in the extraction of contours (Loffler, 2008). The purpose of this study was to investigate the effects of normal aging on collinear facilitation.

Previous studies have shown that healthy normal aging alters visual processing for suprathreshold tasks that depend on spatial interactions. Examples include: center-surround contrast discrimination where it has been shown that surround suppression is increased in older observers (Karas & McKendrick, 2009); contour detection in background noise where the elderly require Gabor elements to be more closely positioned in order to detect a closed contour circle within a noisy background (Del Viva & Agostini, 2007); and shape discrimination of closed contours comprised of individual elements where older observers similarly require more closely spaced elements to detect and discriminate shapes (McKendrick, Weymouth, & Battista, 2010; Roudaia, Bennett, & Sekuler, 2008). These outcomes demonstrate that spatial processing is altered by aging; however, given that spatial interactions vary with stimulus contrast (Chen & Tyler, 2002; Gurnsey, 2011; Melmoth, 2000; Woods, Nugent, & Peli, 2002) and position relative to fixation (Gurnsey, 2011; Petrov, 2006), it is not clear how contextual interactions will be altered for the near threshold, foveal task of collinear facilitation.

Our study aimed to explore the effects of aging on early stages of cortical spatial processing by measuring collinear facilitation using a three-vertically-aligned Gabor stimulus, similar to that used by Polat and Sagi (1993). The distance between elements (interelement distance [IED]) was taken as a measure of spatial processing. Polat and Sagi (1993) reported a sharp increase in the contrast detection threshold of the central Gabor at small IEDs (masking). Facilitation was present at IEDs beyond 2λ (where lambda is the reciprocal of the spatial frequency of the Gabor), with peak facilitation occurring at approximately 3λ for their stimulus configuration. Our first hypothesis was that the IED for peak facilitation would change with age. The observation that more closely spaced elements

doi: 10.1167/12.6.21 Received October 11, 2011; published June 15, 2012 ISSN 1534-7362 © 2012 ARVO

were required for the detection of a contour from a noise background (Del Viva & Agostini, 2007) and for discriminating between shapes comprised of elements (McKendrick et al., 2010), suggests that the distance over which spatial interactions occur is shorter in older observers, at least when all the elements are suprathreshold. An alternate possibility is that neural dropout with age and subsequent cortical rewiring in V1 might result in an increased distance of the lateral connections that underpin collinear facilitation (Connor, Diamond, & Johnson, 1980; Peters, Moss, & Sethares, 2001), hence the critical distance for peak facilitation could instead increase in the elderly. Because the lateral extent of receptive field properties of cortical visual neurons alters with the contrast of the stimulus presented to the receptive field center (Kapadia, Westheimer, & Gilbert, 1999; Sceniak, Hawken, & Shapley, 2002; Sceniak, Ringach, Hawken, & Shapley, 1999; Wielaard & Sajda, 2005), the results of previous studies of suprathreshold spatial interactions do not allow for direct interpretation of the likely outcomes for the threshold task of collinear facilitation.

Our second hypothesis was that there would be a smaller magnitude of facilitation in older observers relative to younger adults. The exact mechanisms underpinning collinear facilitation are incompletely understood, however, one suggested model proposes that collinear flankers produce lateral excitation along filters of optimal orientation (Polat, 1999). Long-range horizontal connections are capable of temporal synchronization (Singer & Gray, 1995), and it has been proposed that synchronization is important to facilitation (Yen & Finkel, 1998). Aging increases spontaneous neural activity within the primate visual system (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000), which has the potential to disrupt facilitation, assuming facilitative processes are dependent on synchronization of neural activity, and that similar processes occur in humans.

Our third hypothesis was that the orientation dependence of collinear facilitation would be similar for older and younger adults. Visual evoked potential recordings have revealed poorer orientation selectivity in V1 of aged primates in comparison to young adult primates (Leventhal et al., 2003). Also, single-cell primate neurophysiology shows a loss of orientation tuning of individual neurons with age (Hua et al., 2006; Schmolesky et al., 2000). The suggested mechanism for this broadening of orientation tuning is a reduction in inhibitory strength as some restoration of orientation tuning was shown by application of GABA-antagonists (Leventhal et al., 2003). In contrast, most human psychophysical experiments do not support a significant decline in orientation processing with age (Delahunt, Hardy, & Werner, 2008; Govenlock, Taylor, Sekuler, & Bennett, 2009; McKendrick et al., 2010), however see Roudaia et al., (2008). The magnitude of collinear facilitation depends on the orientation difference between the flankers and the central target, with maximal facilitation for collinear elements (Chen & Tyler, 2002; Polat & Sagi, 1994). We measured collinear facilitation for a range of flanker orientations with the expectation that the orientation selectivity of collinear facilitation would not vary with age.

Methods

Participants

Twenty younger adults (aged 19 to 31 years old, mean = 24 years, SD = 3 years) and 15 older adults (aged 59 to 71 years old, mean = 67 years, SD = 3 years) participated. This sample size was based on previous studies that have found differences between older and younger groups for spatial vision tasks. Similar human psychophysical aging studies in spatial vision have typically used sample sizes between 10 to 20 in each age group (Del Viva & Agostini [2007]: 11 younger observers [Y], 21 older observers [O]; Roudaia et al. [2008]: 12Y, 12O; McKendrick et al. [2010]: 21Y, 21O). A sample size of 12 provides a power of 0.80 for an alpha level of 0.05 if the size of the pooled group variance is estimated to be approximately the same as the expected mean difference.

Volunteers were recruited both from the University of Melbourne and from advertisements placed in community newspapers. Prior to testing, they provided written informed consent as approved by the Human Research Ethics Committee of the University of Melbourne and in accordance with the tenets of the Declaration of Helsinki. Participants had normal ocular health for their age, which was assessed by a brief optometric examination at the commencement of the project. Inclusion criteria included a normal or corrected to normal visual acuity of 6/7.5 or better in both eyes, refractive errors of no more than ±5D spherical and ±2D cylinder, normal findings on slit lamp examination of the anterior eye and lens, and no abnormalities of the optic nerve head or macula region. Exclusion criteria included the consumption of medications known to affect vision and or cortical function, or having systemic conditions that could affect visual or cortical function.

Equipment

Stimuli were displayed on a LG Flatron (795FT) Plus monitor (Frame rate = 100 Hz, 800 × 600 pixels, maximum luminance = 100 cd/m^2) (Seoul, South

Korea) using the ViSaGe system (Cambridge Research Systems, Cambridge, United Kingdom). The monitor was gamma corrected on a weekly basis with the luminance measured using an OptiCal luminance meter (Cambridge Research Systems). Custom software was written in MatLab R2008a (Mathworks, Natick, MA). A chin rest was positioned to ensure a stabilized head position at a binocular viewing distance of 1 m. Participants were individually refractively corrected for this working distance.

Stimuli

The stimuli used were similar to those used by Polat and Sagi (1993) except that we decreased the stimulus spatial frequency from 13.3 to 3 c/deg and increased the flanker contrast from 40% to 60%. These two parameter changes were employed to ensure that stimulus detection was minimally affected by age-related differences in spatial frequency and contrast sensitivity since there is a known decrease in contrast sensitivity at higher spatial frequencies with age (Derefeldt, Lennerstrand, & Lundh, 1979; Owsley, Sekuler, & Siemsen, 1983).

The luminance distribution of a Gabor ($L[x,y \mid x_0,y_0]$) was determined by the following equation (see Figure 1a).

$$L(x,y|x_0,y_0) = \cos\left(\frac{2\pi}{\lambda}\left((x-x_0)\cos\theta + (y-y_0)\sin\theta\right)\right) \exp\left(-\left(\frac{(x-x_0)^2+(y-y_0)^2}{\sigma^2}\right)\right) \quad (1)$$

The position of the Gabor along the horizontal axis was determined by the x value while y determined the position in the vertical axis, with (x_0, y_0) as the center of the patch. Theta (θ) was the orientation of the Gabor in radians, λ was the wavelength and σ was the standard deviation of the Gaussian envelope (Polat & Sagi, 1993). In parts of this experiment where three Gabors were presented (Figure 1b), they were always vertically aligned along the same vertical axis ($x = 0$) while y was altered to show different IEDs. The summation of the three Gabors was:

$$L(x,y|x_0,y_0) = A_m L(x,y|x_0-\Delta x, y_0-\Delta y) + A_t L(x,y|x_0,y_0) + A_m L(x,y|x_0+\Delta x, y_0+\Delta y) + I \quad (2)$$

where A_m referred to the percentage contrast of the masks or flankers, A_t was the contrast of the central Gabor and I was the average screen luminance (Polat & Sagi, 1993). Two horizontal white fixation guiding lines of 0.86° visual angle were always positioned 2° visual angle away from the midline of the screen. IED is defined as a certain number of wavelengths (λ), where $\lambda = \sigma = 0.33°$ visual angle. Figure 1c shows the Gabors placed at 6λ and the flankers oriented at 100° (10° anticlockwise from the vertical axis).

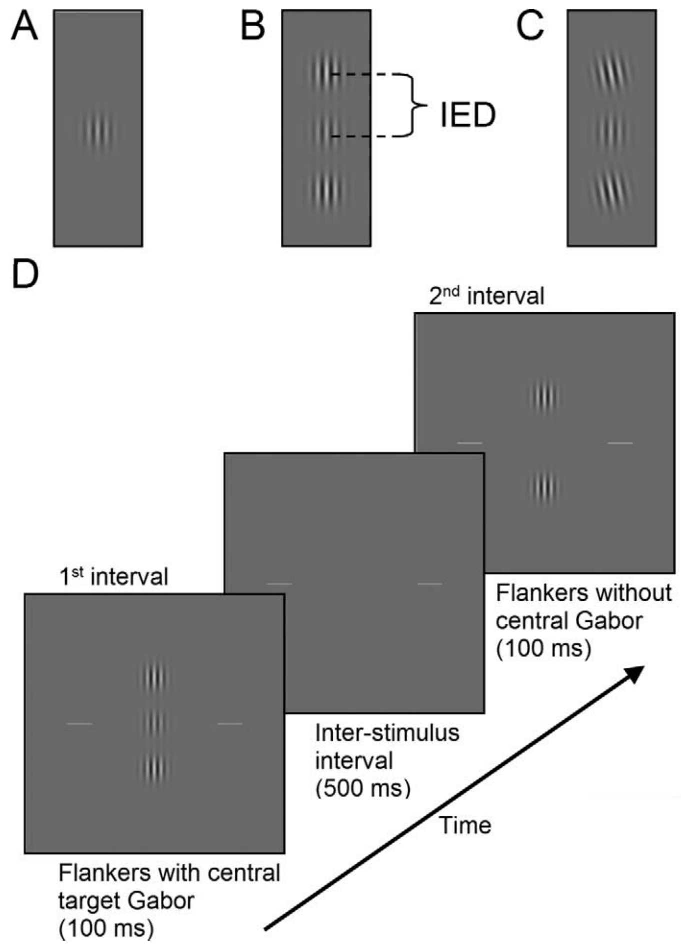

Figure 1. Stimuli and procedure used in this study. Panel a shows an isolated central Gabor patch. Panel b shows the central Gabor in the presence of flankers. Interelement distance (IED) is the separation between the centers of the flankers and the central Gabor. Panel c shows the central Gabor in the presence of flankers with 10° orientation offset, placed at an IED of 6λ. Panel d illustrates the general experimental procedure used in both Experiments 2 and 3. There are two horizontal lines to guide fixation.

Procedure

Contrast detection thresholds for the central Gabor were measured with a 3 down, 1 up staircase in a two-interval-forced-choice (2IFC) design. Contrast was defined as:

$$C = \frac{L_{max} - L_{min}}{L_{max} + L_{min}} \quad (3)$$

where L_{max} is the maximum luminance and L_{min} is the minimum luminance. Staircases terminated after four reversals with the mean of the last two reversals taken as the result of a single staircase. The average of the estimates from the two staircases was taken as the final threshold estimate.

The experiments were conducted in a darkened room. Between stimulus presentations, the screen was a uniform gray at mean luminance (50 cd/m^2) with the fixation guiding lines only. Within the 2IFC design, each stimulus interval was 100 ms with an inter-stimulus interval of 500 ms (Figure 1d). The central Gabor was presented in one of the two stimulus intervals, with the interval chosen at random. Observers indicated which presentation contained the target patch using a button box (Cambridge Research Systems, CB6).

For all participants, practice runs were conducted until they were confident with the task. Data was collected over two sessions of 1–2 hours each, on separate days. Rest breaks were permitted as required. The second session was a repeat of the first session to allow determination of the repeatability of measures.

Three experiments were conducted. Experiment 1 consisted of a simple contrast detection task of a single central Gabor in the absence of flankers. Experiment 2 consisted of nine experimental runs with flankers presented at different IEDs (2.0λ, 2.5λ, 3.0λ, 3.5λ, 4.0λ, 4.5λ, 5.0λ, 5.5λ and 6.0λ) in random order. Experiment 3 consisted of five runs, each at different flanker orientations (95°, 100°, 105°, 110°, and 180°) for an IED of 4λ. Pilot experiments on three experienced observers showed peak facilitation for an IED of 4λ, which is larger than that reported by Polat and Sagi (1993). An increase in peak IED with decreasing spatial frequency is consistent with previous studies (Polat, 2009; Woods et al., 2002).

Analysis

Contrast detection thresholds were analyzed for separate sessions to test for any training effects. Each individual's detection threshold from Experiment 2 was also expressed as log threshold elevation (E), which was defined as, $E = \log(T_f/T_{nf})$. T_f indicates the contrast detection threshold for the flanked condition (Experiment 2) while T_{nf} represents the non-flanked threshold (Experiment 1). Statistical analysis was performed using PASW Statistics version 18.0.2 (IBM, New York) using Repeated Measures Analysis Of Variance (RM-ANOVA). A p-value of less than 0.05 was used to determine statistical significance in the results.

Results

Experiment 1: test-retest of contrast detection of a single Gabor

Figure 2 plots the contrast detection threshold for a single central Gabor for each group (younger: circles; older: triangles) as mean and 95% confidence intervals. A Repeated Measures Mixed Design ANOVA with between-subject factor of group (older versus younger), and within-subjects factor of session, revealed no significant effect of test session (F [1, 33] = 6.70, p = 0.14) but that older observers had a higher mean group threshold than the younger adults (F [1, 33] = 17.98, $p < 0.001$). There was no session by group interaction (F [1, 33] = 1.11, p = 0.30). A general loss in contrast sensitivity with age is consistent with previous reports (Derefeldt et al., 1979; Owsley et al., 1983).

Experiment 2: adding flankers at increasing IEDs

The mean group thresholds are plotted against increasing IEDs for the separate test sessions in Figure 3a. There was no significant difference between sessions (main effect of session: F [1, 33] = 2.25, p = 0.14). As expected from previous literature, threshold differed according to IED (main effect of IED: F [8, 264] = 55.79, $p < 0.001$). There was a significant difference between the age groups (main effect of group: F [1, 33] = 29.32, $p < 0.001$) that did not depend on session (no significant interaction between session and group: F [1, 33] = 0.048, p = 0.83). The main effect of group was dependent on IED (significant interaction between IED

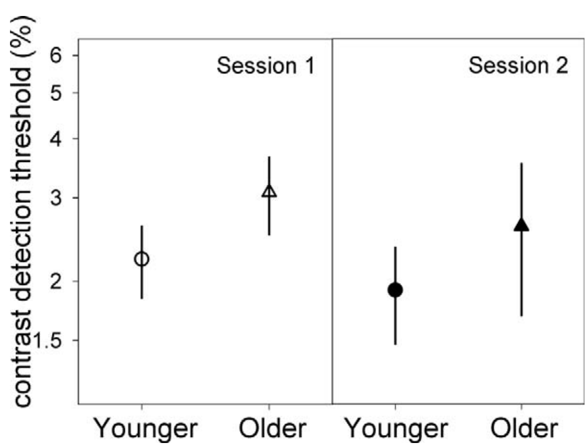

Figure 2. Mean group contrast detection thresholds for the two test sessions for the isolated central Gabor patch (younger adults are denoted by circles, and older adults by triangles). Error bars indicate 95% confidence interval of the mean.

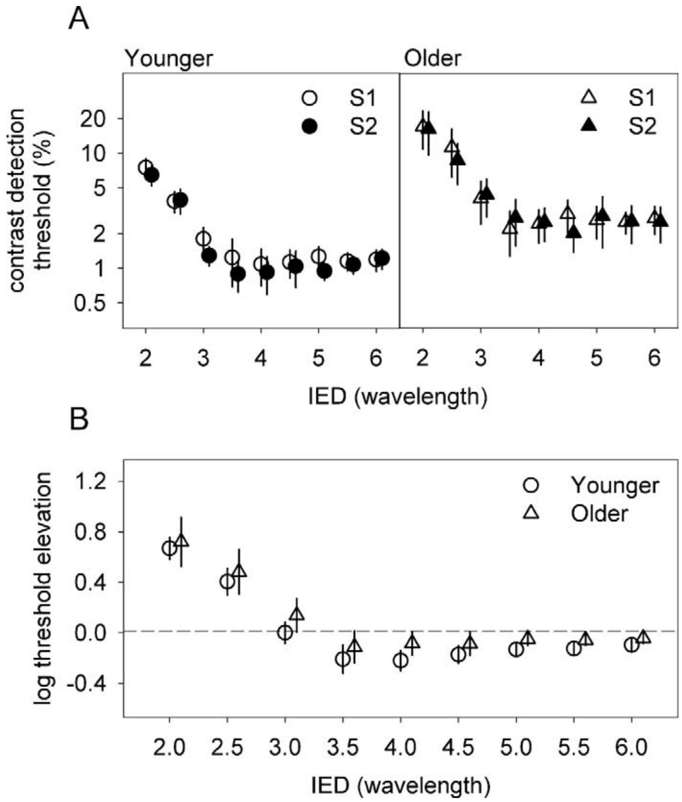

Figure 3. Group mean (±95% CI of the mean) contrast detection thresholds as a function of flanker interelement distance (IED) for younger (circles) and older (triangles) adults. Panel a illustrates the detection thresholds on a percentage log scale as separate sessions (open symbols for session one, filled symbols for session two). Panel b plots the log threshold elevation as a function of IED. The symbols represent group means averaged across both sessions. The data points in Panel b, above the horizontal reference line at zero indicate a masking effect, and below the line signify a facilitation effect. Data points are slightly jittered on the x-axis for clarity.

and group: F [8, 264] = 9.843, $p < 0.001$), as the physical contrast difference between older and younger thresholds was greater for low IED (approximate difference in the mean raw contrast threshold between groups at 2λ of 10% contrast, compared to 1.4% contrast at 6λ).

To allow the inspection of the aging effect on collinear facilitation independent of the difference in contrast sensitivity at baseline, each individual's data was normalized to their own baseline threshold from Experiment 1 to give a log threshold elevation measurement. The normalized thresholds remained significantly different across the IEDs (F [8, 264] = 129.19, $p < 0.001$). There was no significant effect of test session (F [1, 33] = 1.91, $p = 0.18$) and no significant session and group interaction (F [1, 33] = 3.27, p = 0.18), so Figure 3b shows the group means averaged across the two sessions. The log threshold elevation for the older cohort were, on average, higher than those of the younger group (main effect of group: F [1, 33] = 5.16, p = 0.03) across all of the tested IEDs (no significant interaction between IED and group: F [8, 264] = 0.35, $p = 0.95$).

Previous literature has suggested different mechanisms for the facilitation and masking effects (Georgeson, 1987; Mullen, 1994), Facilitation is specific to the spatial and contrast properties of the target stimulus, whereas masking is a more general phenomenon (Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). We analyzed our data in a combined ANOVA; however, the separation of mechanisms could be used to justify separate analysis of the inhibitory and excitatory IEDs. Such additional analysis for our data shows the magnitude of the facilitation effect was significantly smaller in the older group (main effect of group: F [1, 33] = 7.60, $p = 0.01$), but that masking effects between 2.0λ and 3.0λ were not significantly altered with age (main effect of group: F [1, 33] = 1.43, $p = 0.24$). Effect sizes (Cohen's d) were calculated at each IED and averaged across the facilitative range to give an average of 0.42; compared to an averaged effect size of 0.32 for the masking range. It is important to note that the difference in numbers of observations within these analyses (3 IEDs for masking; 5 for facilitation) means that the power to detect a difference for the masking situation will be less than that for facilitation. Overall, a conservative conclusion is that the data does not support that masking and facilitation are altered to different extents by aging. However, this similarity in magnitude of effect does not necessarily imply similar causality.

To determine whether the IED for peak facilitation alters with age, the IED at which the lowest contrast detection threshold occurred, was extracted from each participant's data, and the distributions were compared using a Kolmogorov-Smirnov test. The majority of the older observers had peak facilitation at 3.5λ while most of the younger observers peaked at 4.0λ. Overall, however, the distributions did not differ significantly (K-S, D = 0.233, $p = 0.68$).

We also fit each participant's data with a Difference of Gaussian (DoG) model, using maximum likelihood estimation as an alternate approach to obtaining the IED of peak facilitation. A narrower Gaussian fitted the masking region while a broader Gaussian fitted the flatter facilitatory region. The subtraction of the broader Gaussian from narrower one resulted in a DoG model. Figure 4 depicts examples of the DoG model fit to a younger (left panel) and an older (right panel) participant's data. The IED at which peak facilitation was demonstrated for each individual was extracted. The older observers peaked at an average IED of 4.52 (SD = 0.94) and the average was 4.29 (SD = 0.62) for the younger group. Overall, the distributions

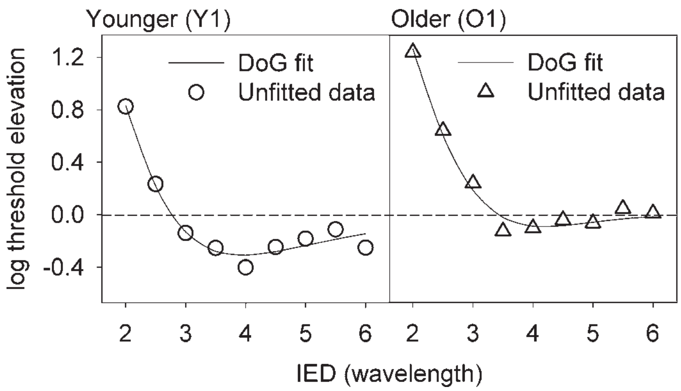

Figure 4. Log threshold elevation plotted as a function of flanker interelement distance (IED) for a single younger, Y1 (circles), and an older, O1 (triangles) adult. The lines represent the Difference of Gaussian (DoG) model fit for the individual's data.

did not differ significantly (unpaired t-test: t[33] = 0.88, $p = 0.39$).

Experiment 3: orientation tuning of collinear facilitation

Figure 5a plots the group mean thresholds as a function of flanker orientation for the separate test sessions. Contrast detection thresholds were significantly higher in the older group (F [1, 33] = 31.32, $p <$ 0.001). There was also a significant session effect (F [1, 33] = 4.79, $p = 0.04$) but the session-group interaction was not significant (F [1, 33] = 2.03, $p = 0.16$).

To explore the changes in orientation selectivity relative to the baseline no-flanker condition, individual data were normalized similarly as in Experiment 2 to obtain log threshold elevation measures. There was no significant session effect in this normalized data (F [1, 33] = 2.04, $p = 0.16$), nor a significant session by group interaction (F [1, 33] = 0.579, $p = 0.452$). Therefore the individual data were averaged across both sessions and the group means are plotted against flanker orientation in Figure 5b. The horizontal asymptote indicates the mean group detection threshold with no flankers. The older group performed significantly different from the younger cohort (main effect of group: F [1, 33] = 6.03, p = 0.02), showing on average elevated thresholds even after normalization. This main effect of group depended on orientation (significant interaction between orientation and group: F [1, 165] = 3.97, $p = 0.002$). A paired t-test was performed at each flanker orientation and corrected for multiple comparisons using Holm-Bonferroni method (Holm, 1979). The paired group means were significantly different at flanker orientations of 105° (t[14] = –0.447, $p = 0.006$) and 180° (t[14] = 3.453, $p = 0.004$). The results of the paired t-test at 90° was t(14) = 2.819, $p = 0.014$, which does not quite meet the required Holm-Bonferroni corrected p-value of 0.0125.

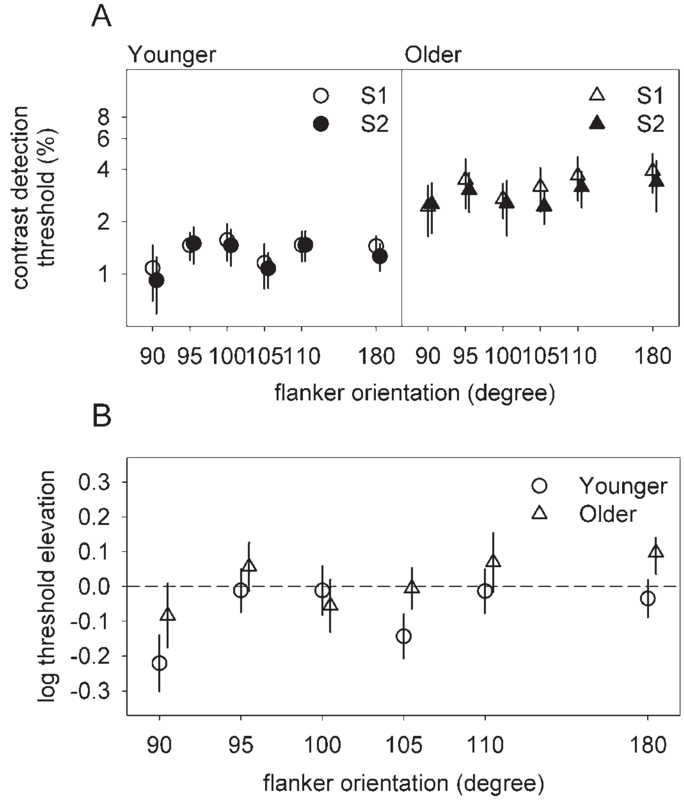

Figure 5. Group mean (±95% CI of the mean) contrast detection thresholds as a function of flanker orientation for younger (circles) and older (triangles) adults. Panel a illustrates the detection thresholds on a percentage log scale as separate sessions (open symbols for session one, filled symbols for session two). Panel b plots the log threshold elevation as a function of flanker orientation. The symbols represent group means averaged across both sessions. The data points, in Panel b, above the horizontal reference line at zero, indicate a masking effect, and below the line signify a facilitation effect. Data points are slightly jittered on the x-axis for clarity.

Discussion

This study investigated whether aging alters collinear facilitation. The data demonstrates a smaller magnitude of facilitation for older participants in comparison to younger adults, in the presence of increased masking. The IED for peak facilitation did not differ between the age groups and the orientation selectivity did not differ in a systematic fashion.

Consistent with previous studies, this study showed a general decrease in contrast sensitivity with normal aging (Derefeldt et al., 1979; Owsley et al., 1983). Both Owsley et al. (1983) and Derefeldt et al. (1979) showed the presence of an age related decrease in contrast sensitivity, especially with high spatial frequency stimuli (Derefeldt et al., 1979; Owsley et al., 1983). However, the percentage difference between the groups in our project (14.21%) was larger than that in the study by Derefeldt et al. (1979, 4.82%). This discrepancy might be due to the narrower bands of the age groups in our experiment. The difference in age between groups in our study was approximately 40 years; however, there was only 30 years difference between groups in the study of Derefeldt et al. (1979). The larger the age gap, the greater the magnitude of difference between their group contrast thresholds (Owsley et al., 1983).

Older adults showed a shift in the strength of collinear effects: an increase in masking and a decrease in facilitation. Before discussing more complex neural mechanisms of spatial vision, it is important to consider whether these results are likely explicable by the reduced contrast sensitivity and presumed increased optical scatter in the older group. Previous study shows that facilitation strength does not alter significantly over a wide range of flanker contrasts (10%–75% contrast in Polat. 1999; and 20%–80% in pilot data collected on our stimuli, data not shown); however, masking strength reduces markedly with decreasing flanker contrast (Polat, 1999). Given that our data shows a decrease in facilitation in the presence of an increase in masking strength, the findings are not consistent with previous reports of the effects of reduced flanker contrast. Optical scatter will blur the stimuli across a slightly larger retinal area, hence stimuli will have effectively shorter IEDs: that is the data shown in Figure 3 would represent a horizontal shift in the data between groups. In this situation, the expected trend is for older adults to have a slightly larger IED for optimal facilitation in addition to apparently more facilitation at slightly wider separation distances. Our data is not supportive of this situation.

Experiment 2 does not support our hypothesis of a shift in the IED for peak facilitation in the older group. This finding is inconsistent with behavioral results from Del Viva and Agostini (2007) and McKendrick et al. (2010) that showed that the elderly required elements to be more closely positioned in order to be integrated into contours. The difference in spatial processing between our study and Del Viva & Agostini (2007) and McKendrick et al. (2010) could be due to the different nature of the experiments. The contour detection and discrimination tasks in their studies involved both foveal and peripheral vision. There is evidence for differences in foveal and peripheral processing of collinear stimuli (Tailby, Cubells, & Metha, 2001), with significantly decreased facilitation at 1° to 2° eccentricity (Shani & Sagi, 2005). In addition, the closed contour stimuli used in their studies were always suprathreshold whereas collinear facilitation is a contrast detection threshold task. Collinear facilitation and contour integration are intermediate processes that feed into form perception but seemingly recruit different underlying neural circuits.

Experiment 3 showed that collinear facilitation effects for both the younger and older observers were tightly tuned to orientation. Both age groups exhibited facilitation with collinear flankers and no/minimal facilitation for other orientations. Our facilitatory effects were very tightly orientation tuned; however, comparison with previous studies is difficult as larger orientation step sizes have been used in previous work (for example 15° step sizes in Polat & Sagi [1993] and 45° in Polat et al. [1994]) There was no systematic difference in performance between groups that would indicate a difference in the orientation tuning of collinear facilitation. However, the groups did perform differently when the flankers were orthogonal to the central target (the 180° condition in Figure 5) where the older adults showed some suppression of the ability to detect the central target. There is evidence for differences in mechanisms involved in center-surround processing for orthogonal versus collinear gratings (Petrov, Carandini, & Suzanne, 2005). Further work is required to determine whether specific alterations to these processes are informative regarding the selectivity, or otherwise, of age-related changes to the mechanisms of long-range spatial interactions.

Although single cell electrophysiologic recordings demonstrate a decreased number and specificity of orientation selective cells in V1 in aged primates (Schmolesky et al., 2000), our project and several other psychophysical experiments show preserved behavioral orientation selectivity (Govenlock et al., 2009; McKendrick et al., 2010) and tuning with age in humans (Delahunt et al., 2008). While our study cannot explain the discrepancy between single-cell primate data and human behavioral results, possible explanations include: the presence of cortical rewiring or plasticity in the aging human brain as a compensatory mechanism (Connor et al., 1980; Delahunt et al., 2008; Peters et al., 2001); the pooling of orientation information across a population of neurons being sufficient to encode orientation adequately even if single neurons show some reduction in orientation selectivity; or that some observations from the primate are not carried through to the human system.

It has been suggested that collinear facilitation may arise due to the flankers resulting in reduced uncertainty about the position of the central patch (Petrov, Verghese, & McKee, 2006). Our study does not provide direct support nor disagree with the uncertainty model of Petrov et al. (2006). Older observers could receive less facilitatory benefit if they have more noise in their ability to encode position, however changes to position coding are quite minimal with age (Moore, Richards, & Hood, 1984; Whitaker, Elliott, & MacVeigh, 1992). Additional experiments would be required to determine this, for example by applying positional jitter of the elements horizontally in a collinear facilitation task. Despite the fact that others have shown that more than uncertainty reduction is required to explain facilitation (Williams & Hess, 1998; Wu & Chen, 2010), it does not rule out uncertainty reduction as playing a role in our data completely.

It has been proposed that aging results in a reduction of inhibition within the visual system (Dustman, Emmerson, & Shearer, 1996; Leventhal et al., 2003; Schmolesky et al., 2000). A reduction of inhibition predicts lesser suppressive effects, and increased facilitation: the opposite of the findings herein. Instead, our data is consistent with recent reports of increased perceptual surround suppression for suprathreshold center-surround stimuli (Karas & McKendrick, 2011a, 2011b; Karas & McKendrick, 2009). Increased suppressive effects might also, at least partially, underpin deficits in contour integration (Del Viva & Agostini, 2007; Roudaia et al., 2008) as facilitatory benefits associated with optimally aligned contours would be reduced. The mechanisms underlying these effects, and the relationship between the threshold and suprathreshold tasks, require further study; however, it is clear that spatial vision processes requiring long-range interactions are altered with advancing age.

Conclusion

This study demonstrates that normal aging alters lateral interactions between closely placed elements and adds to a growing body of work that suggests that a major effect of aging on the visual system is to alter the balance between suppressive and facilitatory interactions.

Acknowledgments

The authors would like to thank Dr Anne Weymouth for assisting in the optometric assessment of the participants. This research was supported by the Australian Research Council Discovery Project 0877923 (AMM); AMM is supported by Australian Research Council FT0990930.

Commercial relationships: none.
Corresponding author: Allison M. McKendrick.
Email: allisonm@unimelb.edu.au.
Address: Department of Optometry & Vision Sciences, The University of Melbourne, Parkville, 3010, Australia.

References

Chen, C. C., & Tyler, C. W. (2002). Lateral modulation of contrast discrimination: Flanker orientation effects. *Journal of Vision, 2*(6):(8) 520–530, http://www.journalofvision.org/content/2/6/8, doi:10.1167/2.6.8. [PubMed] [Article].

Connor, J. R., Jr., Diamond, M. C., & Johnson, R. E. (1980). Aging and environmental influences on two types of dendritic spines in the rat occipital cortex. *Experimental Neurology, 70*(2), 371–379.

Del Viva, M. M., & Agostini, R. (2007). Visual spatial integration in the elderly. *Investigative Ophthalmology & Visual Science, 48*(6): 2940–2946, http://www.iovs.org/content/48/6/2940. [PubMed] [Article].

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): 51–9, http://www.journalofvision.org/content/8/3/5, doi:10.1167/8.3.5. [PubMed] [Article].

Derefeldt, G., Lennerstrand, G., & Lundh, B. (1979). Age variations in normal human contrast sensitivity. *Acta Opthalmologica (Copenhagen), 57*(4), 679–690.

Dustman, R. E., Emmerson, R. Y., & Shearer, D. E. (1996). Life span changes in electrophysiological measures of inhibition. *Brain and Cognition, 30*(1), 109–126.

Georgeson, M. A. (1987). Facilitation and masking of briefly presented gratings: Time-course and contrast dependence. *Vision Research, 27*(3), 369–379.

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.

Gurnsey, R., Roddy, G., & Chanab, W. (2011). Crowding is size and eccentricity dependent. *Journal of Vision, 11*(7):15, 1–17, http://www.journalofvision.org/content/11/7/15, doi:10.1167/11.7.15. [PubMed] [Article].

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6*, 65–70.

Hua, T., Li, X., He, L., Zhou, Y., Wang, Y., & Leventhal, A. G. (2006). Functional degradation of visual cortical cells in old cats. *Neurobiology of Aging, 27*(1), 155–162.

Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1999). Dynamics of spatial summation in primary visual cortex of alert monkeys. *Proceedings of the National Academy of Sciences of the United States of America, 96*(21), 12073–12078.

Karas, R., & McKendrick, A. (2011a). Age related changes to perceptual surround suppression of moving stimuli. *Seeing and Perceiving*, E-pub ahead of print September 29, 2011.

Karas, R., & McKendrick, A. (2011b). Increased surround modulation of perceived contrast in the elderly. *Optometry & Vision Science, 88*(11), 1298–1308.

Karas, R., & McKendrick, A. M. (2009). Aging alters surround modulation of perceived contrast. *Journal of Vision, 9*(5):11, 1–9, http://www.journalofvision.org/content/9/5/11, doi:10.1167/9.5.11. [PubMed] [Article].

Keeble, D. R., & Hess, R. F. (1998). Orientation masks 3-Gabor alignment performance. *Vision Research, 38*(6), 827–840.

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.

Loffler, G. (2008). Perception of contours and shapes: Low and intermediate stage mechanisms. *Vision Research, 48*(20), 2106–2127.

McKendrick, A. M., Weymouth, A. E., & Battista, J. (2010). The effect of normal aging on closed contour shape discrimination. *Journal of Vision, 10*(2):1, 1–9, http://www.journalofvision.org/content/10/2/1, doi:10.1167/10.2.1. [PubMed] [Article].

Melmoth, D. R., Kukkonen, H., Mäkelä, P. K., & Rovamo, J. M. (2000). The effect of contrast and size scaling on face perception in foveal and extrafoveal vision. *Investigative Ophthalmology & Visual Science, 41*(9): 2811, http://www.iovs.org/content/41/9/2811. [PubMed] [Article].

Moore, T. E., Richards, B., & Hood, J. (1984). Aging and the coding of spatial information. *Journal of Gerontology, 39*(2), 210–212.

Mullen, K. T. (1994). Evidence for separate pathways for color and luminance detection mechanisms. *Journal of the Optical Society of America B: Optical Physics, 11*(12), 3136–3151.

Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research, 23*(7), 689–699.

Peters, A., Moss, M. B., & Sethares, C. (2001). The effects of aging on layer 1 of primary visual cortex in the rhesus monkey. *Cerebral Cortex, 11*(2), 93–103.

Petrov, Y., & McKee, P. (2006). The effect of spatial configuration on surround suppression of contrast sensitivity. *Journal of Vision, 6*(3):4, 224–238, http://www.journalofvision.org/content/6/3/4, doi:10.1167/6.3.4. [PubMed] [Article].

Petrov, Y., Carandini, M., & Suzanne, M. (2005). Two distinct mechanisms of suppression in human vision. *The Journal of Neuroscience, 25*(38), 8704.

Petrov, Y., Verghese, P., & McKee, S. P. (2006). Collinear facilitation is largely uncertainty reduction. *Journal of Vision, 6*(2):8, 170–178, http://www.journalofvision.org/content/6/2/8, doi:10.1167/6.2.8. [PubMed] [Article].

Polat, U. (1999). Functional architecture of long-range perceptual interactions. *Spatial Vision, 12*(2), 143–162.

Polat, U. (2009). Effect of spatial frequency on collinear facilitation. *Spatial Vision, 22*(2), 179–193.

Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., & Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature, 391*(6667), 580–584.

Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research, 33*(7), 993–999.

Polat, U., & Sagi, D. (1994). The architecture of perceptual spatial interactions. *Vision Research, 34*(1):73–78.

Roudaia, E., Bennett, P. J., & Sekuler, A. B. (2008). The effect of aging on contour integration. *Vision Research, 48*(28), 2767–2774.

Sceniak, M. P., Hawken, M. J., & Shapley, R. (2002). Contrast-dependent changes in spatial frequency tuning of macaque V1 neurons: Effects of a changing receptive field size. *Journal of Neurophysiology, 88*(3), 1363–1373.

Sceniak, M. P., Ringach, D. L., Hawken, M. J., & Shapley, R. (1999). Contrast's effect on spatial summation by macaque V1 neurons. *Nature Neuroscience, 2*(8), 733–739.

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.

Shani, R., & Sagi, D. (2005). Eccentricity effects on lateral interactions. *Vision Research, 45*(15), 2009–2024.

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience, 18*, 555–586.

Tailby, C., Cubells, O., & Metha, A. (2001). Enhanced sensitivity for peripherally-presented collinearly-aligned stimulus elements: Contour detection or spatial summation? *Clinical and Experimental Optometry, 84*(6), 354.

Whitaker, D., Elliott, D. B., & MacVeigh, D. (1992). Variations in hyperacuity performance with age. *Ophthalmic and Physiological Optics, 12*(1), 29.

Wielaard, J., & Sajda, P. (2005). Neural mechanisms of contrast dependent receptive field size in V1. In Y. Weiss, B. Scholkopf, & J. Platt (Eds.), *Advances in Neural Information Processing Systems 18*. Cambridge, MA: MIT Press, (pp. 1505–1512).

Williams, C. B., & Hess, R. F. (1998). Relationship between facilitation at threshold and suprathreshold contour integration. *Journal of the Optical Society of America, Optics and Image Science, 15*(8), 2046–2051.

Woods, R. L., Nugent, A. K., & Peli, E. (2002). Lateral interactions: Size does matter. *Vision Research, 42*(6), 733–745.

Wu, C. C., & Chen, C. C. (2010). Distinguishing lateral interaction from uncertainty reduction in collinear flanker effect on contrast discrimination. *Journal of Vision, 10*(3):8, 1–14, http://www.journalofvision.org/content/10/3/8, doi:10.1167/10.3.8. [PubMed] [Article].

Yen, S. C., & Finkel, L. H. (1998). Extraction of perceptually salient contours by striate cortical networks. *Vision Research, 38*(5), 719–741.