Spatial characteristics of center-surround antagonism in younger and older adults

Lisa R. Betts  
Centre for Vision Research, York University, Toronto, ON, Canada

Allison B. Sekuler  
Department of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, ON, Canada

Patrick J. Bennett  
Department of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, ON, Canada

Sensitivity to motion direction is affected by stimulus size, contrast (D. Tadin & J. S. Lappin, 2005; D. Tadin, J. S. Lappin, L. A. Gilroy, & R. Blake, 2003), and observer age (L. R. Betts, C. P. Taylor, A. B. Sekuler, & P. J. Bennett, 2005). Here, we investigated the effect of spatial frequency on motion discrimination and how sensitivity changes in older adulthood. We measured stimulus duration thresholds for younger (18–30 years) and older (60–75 years) observers using drifting Gabor gratings that differed in size, spatial frequency, and contrast. A simple model characterized age differences in the threshold-vs.-size functions. The model parameter fits were consistent with an age-related decrease in the strength of spatial suppression. The model also provided good fits to the thresholds when plotted as a function of the total stimulus contrast energy, which suggests that age-related changes in summation and suppression can be modeled as reduced sensitivity to contrast energy. The summation parameter scaled according to stimulus spatial frequency in younger observers only. Suppression strength decreased as a function of spatial frequency in both age groups. Our findings provide additional evidence for age-related changes in summation and suppression mechanisms and suggest that the total contrast energy in the stimulus plays an important role in determining sensitivity to motion direction in both younger and older adults.

Keywords: motion perception, aging, spatial suppression, spatial summation, spatial frequency, inhibition, contrast energy, classical receptive field, non-classical receptive field


Introduction

Sensitivity to visual motion in a leftward versus rightward discrimination task is constrained by both stimulus size and contrast (Betts, Taylor, Sekuler, & Bennett, 2005; Tadin & Lappin, 2005; Tadin, Lappin, Gilroy, & Blake, 2003). The stimulus duration required to perceive the correct direction of low contrast targets decreases (i.e., performance improves) as stimulus area increases—that is, observers demonstrate spatial summation at low stimulus contrast. The opposite result occurs with high contrast stimuli: Thresholds increase with increasing stimulus size, a phenomenon known as spatial suppression. Similar effects have also been reported for contrast discrimination, orientation discrimination, color matching, and binocular rivalry tasks (Mareschal & Sharpley, 2004; Paffen, Alais, & Verstraten, 2005; Paffen, Tadin, te Pas, Blake, & Verstraten, 2006; Paffen, van der Smagt, te Pas, & Verstraten, 2005; Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004; Petrov, Carandini, & McKee, 2005; Xing & Heeger, 2001; Yu, Klein, & Levi, 2003; Zenger-Landolt & Heeger, 2003). The pervasiveness of contrast-dependent spatial suppression and summation in visual tasks suggests a strong role for these mechanisms in very early stages of visual information processing, perhaps even before the inputs of the two eyes are combined (Paffen, van der Smagt et al., 2005; Paffen et al., 2004). Center-surround antagonism also affects the strength of the motion aftereffect, implicating the involvement of cortical mechanisms (Tadin et al., 2003; Tadin, Paffen, Blake, & Lappin, 2008). Thus far, spatial summation and spatial suppression in motion discrimination tasks in human observers have been measured with only a limited subset of stimulus configurations, namely broadband random dot cinematograms and low spatiotemporal frequency Gabor patterns (Betts et al., 2005; Tadin & Lappin, 2005; Tadin et al., 2003). The present experiments used Gabor patterns that varied in size, contrast, and spatial frequency to gain a better understanding of how spatial suppression and summation mechanisms operate over a range of spatial scales.

The effect of size and contrast manipulations on behavioral motion discrimination thresholds is thought to be associated with the center-surround organization of visual neuron receptive fields, in which the response to the
central classical receptive field (CRF) is modulated by the presence of a stimulus in the surrounding region, known as the non-classical receptive field (nCRF; for recent reviews, see Fitzpatrick, 2000; Lamme, 2004). The balance of excitation and inhibition between the excitatory center and modulatory surround, known as center-surround antagonism, depends on stimulus contrast. For example, neurons in primary visual cortex often show strong excitation to a high contrast stimulus that is well matched to the size of the CRF. Once the stimulus diameter exceeds the CRF, it encroaches on the inhibitory surround, which suppresses the neuron’s response. However, when stimulus contrast is low, the influence of the inhibitory surround typically is lessened and the cell’s response continues to increase with increasing stimulus size. Contrast-dependent changes in center-surround antagonism have been shown throughout the primate visual pathway, including the retina, lateral geniculate nucleus (LGN), V1, V2, middle temporal area (MT), and medial superior temporal area (MST; Cavanaugh, Bair, & Movshon, 2002; Eifuku & Wurtz, 1998; Kapadia, Westheimer, & Gilbert, 1999; Levitt & Lund, 1997; Pack, Hunter, & Born, 2005; Sceniak, Ringach, Hawken, & Shapley, 1999; Solomon, Lee, & Sun, 2006; Solomon, White, & Martin, 2002), all of which contain neurons sensitive to motion direction. Although the mechanisms that produce surround inhibition are not fully understood, the prevalent view is that the inhibitory influence from the nCRF at high stimulus contrast is enforced by GABAergic interneurons (Fitzpatrick, 2000; but see Ozeki et al., 2004).

A shift in the balance between excitation and inhibition in visual cortex may alter behavioral measures of suppression and summation. Studies of post-mortem human visual cortex suggest that inhibitory synapse composition and neurotransmitter production change across the life span (Boley, Jones, Pinto, & Murphy, 2005; McGeer & McGeer, 1976). Thus, age may have a profound influence on the function of excitatory and inhibitory mechanisms that mediate spatial suppression and summation. Experiments conducted in our laboratory are consistent with the idea that center-surround antagonism in visual motion processing changes with age (Betts et al., 2005): Human observers over 60 years of age with normal vision demonstrated reduced spatial suppression compared to observers in their 20’s. That is, older observers required significantly shorter stimulus durations to judge the direction of motion of large, high-contrast drifting stimuli than younger observers. These results are consistent with the hypothesis that inhibitory mechanisms in visual cortex become less potent with age, thereby reducing the suppressive influence of the non-classical receptive field.

Although the exact details vary across studies, it is generally agreed that age-related reductions in contrast sensitivity become evident beyond 2 c/deg (Arundale, 1978; Bennett, Sekuler, & Ozin, 1999; Burton, Owseley, & Sloane, 1993; Crassini, Brown, & Bowman, 1988; Derefeldt, Lennerstrand, & Lundh, 1979; Elliott, 1987; Owseley, Sekuler, & Siemsen, 1983; Ross, Clarke, & Bron, 1985; Sekuler, Hutman, & Owseley, 1980; Sloane, Owseley, & Alvarez, 1988; Sloane, Owseley, & Jackson, 1988). To determine whether age differences in summation and suppression are linked to stimulus spatial frequency, we tested younger and older observers’ motion direction discrimination over a range of size, contrast, and spatial frequency stimulus configurations.

## Methods

### Participants

We recruited a total of 20 younger observers between the ages of 19 and 30 and 11 older observers between 63 and 75 years of age from the McMaster University student body and the Greater Hamilton Area (Table 1). We specifically attempted to recruit observers to participate in all of the spatial frequency conditions to minimize inter-subject variability, which can be especially prevalent in the older population sample. Because the experiments were conducted over a period of several months there was some attrition, particularly among the younger observers: Two completed all four spatial frequency conditions, three completed 0.5, 2, and 4 c/deg conditions, and two

<table>
<thead>
<tr>
<th>Spatial frequency</th>
<th>Age</th>
<th>N</th>
<th>Near logMAR</th>
<th>Far logMAR</th>
<th>Pelli-Robson</th>
<th>MMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5 c/deg</td>
<td>22.9 (4.5)</td>
<td>8</td>
<td>−0.12 (0.04)</td>
<td>−0.13 (0.05)</td>
<td>1.95 (0)</td>
<td>28.88 (1.55)</td>
</tr>
<tr>
<td></td>
<td>68.0 (4.1)</td>
<td>8</td>
<td>−0.06 (0.10)</td>
<td>−0.05 (0.06)</td>
<td>1.89 (0.08)</td>
<td></td>
</tr>
<tr>
<td>1 c/deg</td>
<td>23.0 (1.4)</td>
<td>8</td>
<td>−0.17 (0.03)</td>
<td>−0.18 (0.03)</td>
<td>1.95 (0)</td>
<td>28.75 (1.49)</td>
</tr>
<tr>
<td></td>
<td>67.9 (1.7)</td>
<td>8</td>
<td>−0.04 (0.03)</td>
<td>0.00 (0.04)</td>
<td>1.91 (0.03)</td>
<td></td>
</tr>
<tr>
<td>2 c/deg</td>
<td>24.0 (5.2)</td>
<td>10</td>
<td>−0.11 (0.09)</td>
<td>−0.10 (0.08)</td>
<td>1.95 (0)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>67.7 (4.0)</td>
<td>9</td>
<td>−0.05 (0.08)</td>
<td>−0.01 (0.07)</td>
<td>1.87 (0.11)</td>
<td>29.22 (1.33)</td>
</tr>
<tr>
<td>4 c/deg</td>
<td>21.6 (3.2)</td>
<td>8</td>
<td>−0.14 (0.06)</td>
<td>−0.13 (0.06)</td>
<td>1.95 (0)</td>
<td>29 (1.55)</td>
</tr>
<tr>
<td></td>
<td>67.5 (4.3)</td>
<td>7</td>
<td>−0.08 (0.09)</td>
<td>−0.01 (0.10)</td>
<td>1.9 (0.08)</td>
<td></td>
</tr>
</tbody>
</table>

Table 1. Participant age, visual acuity measures, and Mini Mental Status Exam scores (older participants only) were collected. Standard deviations are indicated in parentheses.
completed both 0.5 and 4 c/deg conditions. We had greater success in obtaining complete sets of measures from the older observers: Six completed all four spatial frequency conditions, one completed both 1 and 2 c/deg conditions, one completed 0.5 and 2 c/deg conditions, and one completed both 2 and 4 c/deg conditions.

The observers completed a questionnaire to screen for visual abnormalities, such as macular degeneration, cataract, glaucoma, and amblyopia. All observers wore their best optical correction, as required, for the experiment. Near and far logMAR (log of the minimum angle of resolution) acuities were measured using CSV-1000EDRTS eye charts (Precision Vision, LaSalle, Illinois, USA), and Pelli–Robson charts were used to estimate contrast sensitivity (Pelli, Robson, & Wilkins, 1988). Older observers showed a normal age-related decrease in visual acuity compared to younger observers, but the average logMAR acuity in older observers was equal to or less than 0, which is the equivalent of 20/20 Snellen acuity (Table 1). Older observers also completed the Mini Mental Status Examination (MMSE) to screen for any age-related dementia; all participants scored within the normal range for their given age group and level of education (Crum, Anthony, Bassett, & Folstein, 1993; Folstein, Folstein, & McHugh, 1975).

**Equipment**

The experiment was conducted on a Macintosh G4 computer in the Matlab programming environment (v. 5.2), using our own customized software and the Psychophysics and Video Toolboxes (Brainard, 1997; Pelli, 1997). Stimuli were presented on a 20" (51 cm) Sony Trinitron monitor with 1024 × 768 pixel resolution and a 120-Hz refresh rate. Monitor luminance was measured regularly with a PhotoResearch PR650 photometer over the entire period of data collection. The calibration data were regularly with a PhotoResearch PR650 photometer over the entire period of data collection. The calibration data were provided to familiarize the observer to the current block’s 8-bit lookup table and storing them in the display’s 8-bit lookup table. Head position and viewing distance were stabilized with a forehead/chin rest. Responses were collected on a customized button box with an ActiveWire-USB board (ActiveWire, Campbell, CA, USA).

**Stimuli**

The stimuli were vertical sine wave gratings that drifted at a rate of 2 deg/s either to the left or to the right on a uniform gray background (mean luminance = 49.1 cd/m²). Stimulus direction was randomly determined on every trial. The gratings were presented within a radially symmetric, two-dimensional Gaussian envelope. Stimulus size was defined as two standard deviations (2σ) of the Gaussian envelope. At each pixel, luminance contrast, c, was defined as $L_x - L_{ave}$/$L_{ave}$, where $L_x$ represents the contrast of single pixel, and $L_{ave}$ is the average luminance value of the display. Stimulus contrast was defined as the Michelson contrast of the sine wave grating prior to multiplication by the Gaussian envelope and ranged from 2.8% to 92%. Grating spatial frequencies were 0.5, 1, 2, and 4 c/deg, and sizes ranged from 0.175 to 10 degrees of visual angle, depending on the spatial frequency. In a control experiment, the 1 c/deg gratings were also presented at speeds of 2, 4, and 8 deg/s. Stimulus onset and offset were controlled by a square temporal window.

**Procedure**

Stimulus duration was controlled by two independent interleaved staircase procedures. A 2-down, 1-up staircase converged on the stimulus duration needed to produce 71% correct responding, and a 4-down, 1-up staircase converged on the duration needed for 84% correct responding. Both staircases started at 250 ms stimulus duration with initial step sizes of 41.66 ms (5 frames). Step size decreased to 25 ms (3 frames) and 8.3 ms (1 frame) after the third and sixth staircase reversals, respectively.

The observers participated over multiple days of testing for 1–2 hours per day. The observers completed all of the size and contrast conditions for a given spatial frequency condition before continuing on to the next spatial frequency. Stimuli within each spatial frequency condition were blocked according to contrast, size, and speed. Each block contained 150 trials and took approximately 15 minutes to complete. A 2-minute break was provided at the end of each block. Observers completed 3–7 blocks per day.

After getting comfortable in the apparatus, the observer received verbal task instructions from a prepared script. The lights were then turned out so that the monitor was the only light source in the room during testing. The observer adapted to a uniform field of mean luminance for 2 minutes. Ten practice trials with auditory feedback were provided to familiarize the observer to the current block’s spatial frequency, contrast, size, and velocity parameters before the behavioral responses were recorded.

Each trial commenced with a small, high-contrast, black or white fixation point (5 × 5 pixels) in the center of the screen. The fixation point flickered at a rate of 2.5 Hz for 1.6 s and was followed by a blank screen for 0.5 s. The flicker was implemented to reduce adaptation to the square and to attract attention to the center of the screen. The grating was then pulsed onto the screen for the specified stimulus duration after which the screen again turned blank. The screen remained blank until the observer made a response. Auditory feedback was provided on every trial. The fixation point reappeared.
2 s after the response to allow for any motion aftereffect to subside; the subsequent trial began immediately upon the reappearance of the fixation square. Average luminance remained constant throughout each trial.

Analysis

The data from both staircases were combined and a single psychometric function was estimated for each observer by computing the best-fitting (maximum likelihood criterion) Weibull function. Duration threshold was defined as the 77% correct point ($d' = 1.05$) on the psychometric function.

In some cases the data were not well described by the Weibull function and yielded thresholds that were outside of the range of tested stimulus durations. Such thresholds were defined as invalid and were not included in the analyses. Although this occurred rarely (younger, 12/745 acquired thresholds; older, 29/647 acquired thresholds), a few subjects obtained invalid thresholds in more than three conditions and were therefore excluded from further analysis. Exclusions included one younger and two older observers from the 2 c/deg condition, and one younger and two older observers from the 4 c/deg condition. An additional two naive older observers were tested exclusively with the 4 c/deg stimulus but were not included in the final analysis and were not recruited for further experiments because they were unable to perform the task over a broad range of stimulus sizes and contrasts.

The mean duration thresholds for younger and older observers in a portion of this study (1 c/deg stimuli moving at 2 deg/s) were published previously (Betts et al., 2005). Here we report the median values of the same data set along with values for newly obtained data sets to enable an examination of results across a fuller range of stimulus conditions than previously examined.

Model

At each level of contrast, duration thresholds were fit with the equation:

$$f(x) = p_1 x^{k_1} + p_2 x^{k_2}$$  \hspace{1cm} (1)

where $x$ is the stimulus diameter in degrees of visual angle. The parameters $p_1$ and $p_2$ determine the vertical positions of the ascending and descending portions of the curves. The $k_1$ and $k_2$ parameters determine the slopes of the ascending and descending portions of the threshold functions. Bloch’s Law states that contrast sensitivity is proportional to the square root of stimulus duration; summation across time is linear, up until a critical duration (e.g., Barlow, 1958; Legge, 1978; Luntinen, Rovamo, & Näsänen, 1995). In the present experiments we performed the inverse measurement: Stimulus duration was varied while the contrast was held constant. We incorporated linear temporal summation into our model by fixing the spatial summation (i.e., descending) portion of the curve, controlled by the parameter $k_1$, at a value of $-2$. We used the same $k_1$ value in both groups of observers, as aging does not affect the linearity of spatial summation mechanisms (Zele, O’Loughlin, Guymar, & Vingrys, 2006). The remaining parameters ($k_2, p_1$, and $p_2$) were allowed to freely vary between zero and infinity.

Results

Duration thresholds versus stimulus size

Figure 1 shows the duration thresholds for younger and older observers over a range of contrasts as a function of stimulus size in all spatial frequencies. Both younger and older observers’ duration thresholds showed a strong interaction between stimulus size and contrast. At lower contrasts, the curves predominantly decreased with increased stimulus size, consistent with spatial summation. However, even at 2.8% contrast, many of the curves also contained an ascending segment, indicating a switch from summation to spatial suppression for sufficiently large stimuli. As contrast increased, summation changed to suppression at progressively smaller stimulus sizes so that at the highest contrasts, only spatial suppression was evident. Thus, for the four spatial frequencies tested here, spatial summation occurred at low contrast and gradually switched to spatial suppression as stimulus contrast increased. These results are consistent with previous reports that measured stimulus duration thresholds for low spatial frequency and random dot stimuli (Tadin & Lappin, 2005; Tadin et al., 2003).

The ascending portions of the curves rose at a reduced rate in older observers. Consequently, older observers’ thresholds were actually briefer than younger observers’ thresholds for larger, higher contrast stimuli at all spatial frequencies tested. These findings indicate that the age-related reduction in spatial suppression for 1 c/deg drifting Gabors reported previously (Betts et al., 2005) generalizes over the range of spatial frequencies tested here.

The solid lines through the data points in Figure 1 correspond to the fits from Equation 1. The model fits accounted for approximately 86% of the total variance in younger observers (mean Pearson $R^2 = 0.856, \sigma = 0.194$) and 90% of the total variance in older observers (mean Pearson $R^2 = 0.904, \sigma = 0.204$). The values of the best-fitting parameters are shown in Figure 2. Also shown are the 95% confidence intervals for each parameter, which were estimated using a non-parametric bootstrap (BCa-type interval, 999 repetitions; Efron & Tibshirani, 1993).
In both age groups, the value of $p_1$, which governs the vertical position of the descending portion of Equation 1, declined with increasing contrast at each spatial frequency: For contrasts greater than 10%, $p_1$ was essentially zero. These results are consistent with the claim that spatial summation was significantly diminished at moderate and high contrasts in both groups of observers. The value of $p_1$ generally was higher in older observers when stimulus contrast was 2.8%, although the age difference was statistically significant only in conditions that used a 1 and 4 c/deg pattern. Could age-related differences in contrast sensitivity explain this result? If so, older observers should have higher duration thresholds at low contrasts, regardless of stimulus size. We conducted independent comparisons of the mean thresholds at 2.8% contrast from younger and older observers for the smallest and largest stimuli in each spatial frequency condition. To control for the inflation of Type I error due to multiple comparisons (8 in total), we evaluated significance at $p < 0.01$. At the smallest stimulus sizes, older observers’ thresholds were significantly higher at 1 and 2 c/deg (1 c/deg: $t_{(13)} = 3.214, p < 0.01$; 2 c/deg: $t_{(14)} = 3.560, p < 0.01$), consistent with an age-related reduction in contrast sensitivity. For the largest stimuli, however, there were no significant differences between age groups at any of the spatial frequencies tested. These results suggest that age-related changes in spatial summation may be due to a shift in sensitivity to stimulus size, rather than contrast, whereby older observers require larger stimuli to produce the same motion discrimination thresholds as younger observers.

In younger observers, the parameter controlling the vertical position of the ascending segment of the curve, $p_2$, increased slightly at high contrasts and did not vary significantly across spatial frequency. The parameter controlling the slope, $k_2$, on the other hand, was not systematically related to stimulus contrast but declined from 0.4–0.5 when the spatial frequency was 0.5 c/deg, to approximately 0.2 when the spatial frequency was 4 c/deg. Taken together, these results suggest that spatial frequency was fixed, raising stimulus contrast increased spatial suppression in younger observers by increasing the height of the ascending part of Equation 1 rather than altering its slope. When contrast was fixed, however, increasing spatial frequency reduced spatial suppression in young observers primarily by reducing the slope of the ascending part of the threshold-vs.-size function.

In older observers, $p_2$ increased with contrast with the 1 c/deg stimulus but varied as a quadratic function of contrast in the other frequency conditions. This quadratic trend meant that $p_2$ was smallest at intermediate contrasts and greatest at low and high stimulus contrasts. The ascending slopes exhibited the opposite trend: $k_2$ reached its highest value at intermediate contrasts and was reduced at low and high contrasts. The exception occurred at 0.5 c/deg, where $k_2$ did not vary over contrasts ranging from 0.042 to 0.46. No systematic relationship was observed between stimulus spatial frequency and either the $k_2$ or $p_2$ parameters. These trends in $p_2$ and $k_2$ indicate that the strength of spatial suppression in older observers peaked at intermediate stimulus contrast levels and fell off as contrast exceeded 10%.

Figure 1. Median duration thresholds (seconds) in all spatial frequency conditions are plotted as a function of the stimulus size ($2\sigma$ of the Gaussian envelope) for younger (left column, open symbols) and older (right column, solid symbols) observers. The smooth lines through the data are the fitted curves from Equation 1. The slope of the descending portion of Equation 1 ($k_1$) was held constant at −2.

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Of the two parameters used to fit the suppressive portions of the threshold-versus-size curves, age differences in $k_2$ were most evident. Examination of Figure 2 shows that $k_2$ was significantly lower in older observers in the majority (i.e., 12 out of 18) of stimulus conditions, whereas age differences in $p_2$ were much more variable. Hence, age-related changes in spatial suppression were consistently related to decreases in the slopes, rather than the vertical positions, of the ascending portions of the threshold curves.

Duration threshold versus stimulus contrast energy

Numerous studies of spatial summation have found that contrast thresholds are inversely proportional to the size of the stimulus in both static (Banks, Sekuler, & Anderson, 1991; Barlow, 1958; Davila & Geisler, 1991; Hoekstra, van der Goot, van den Brink, & Bilsen, 1974; Howell & Hess, 1978; Inui, Mimura, & Kani, 1981; Rovamo, Luntinen, & Näsänen, 1993; Savoy & McCann, 1975; Wilson, 1970) and moving (Anderson & Burr, 1987, 1991) gratings, up to a critical area. Over this linear summation range, first described by Piper (1903), the total contrast energy in the stimulus is constant. Similarly, physiological studies of spatial summation in V1 and MT receptive fields showed that neurons linearly sum responses to pairs of low contrast stimuli presented within the CRF, indicating that the neurons are driven by the overall stimulus energy presented within the excitatory receptive field (DeAngelis, Ohzawa, & Freeman, 1993; Heuer & Britten, 2002).

In the present experiment, we manipulated stimulus size and contrast, both of which contribute to the total amount of energy in the stimulus. Consequently, a large, low-contrast stimulus may contain an equal amount of energy as a smaller high-contrast stimulus. We wondered whether our results of size- and contrast-dependent spatial suppression and summation would be better described as a function of stimulus energy, $\Sigma c^2$, the sum of the stimulus squared contrast. If so, stimuli of different sizes and contrasts, but equal contrast energy, should produce equivalent duration thresholds.

To evaluate the effect of stimulus contrast energy on motion discrimination duration thresholds, we used Equation 1 to fit the log-transformed, median duration threshold data as a function of stimulus energy, $\Sigma c^2$, rather than as a function of stimulus size (smooth lines, Figure 3). As before, we fixed the slope of the descending portion of the curve to follow linear summation. In this case, however, duration thresholds were measured as a function of squared contrast, and so $k_1$ was held constant at $-1$. The $k_2$, $p_1$, and $p_2$ parameters varied freely. As before,
bootstrapped 95% confidence intervals were estimated for each parameter. The model fit the data moderately well, with average $R^2$ values of 0.725 ($\sigma = 0.180$) and 0.800 ($\sigma = 0.184$) for younger and older observers. The best-fitting parameters from the curve fits are shown in Figure 4. Significant age differences were apparent in parameter $p_1$ at 0.5, 2, and 4 c/deg, indicating an age-related decrease in sensitivity to low energy stimuli. The $p_2$ estimates did not vary significantly with age, but $k_2$ was reduced in the older group at 0.5, 1, and 4 c/deg, in keeping with an age-related reduction in spatial suppression at higher contrast energies. To summarize, when duration thresholds are shown as a function of stimulus contrast energy, it can be seen that i) older observers were generally less sensitive than younger observers to stimuli with low contrast energy, and ii) age differences in spatial suppression were characterized by changes in the slope, rather than the vertical position of the threshold-versus-energy functions.

By collapsing contrast and size into a single measure of stimulus contrast energy, the influence of spatial frequency became more readily apparent. In younger observers $p_1$ decreased monotonically as a function of spatial frequency, indicating that less stimulus contrast energy was required to discriminate the motion direction as spatial frequency increased. In older observers thresholds decreased only between 0.5 and 1 c/deg; beyond 1 c/deg, a constant amount of stimulus energy was required to perform the motion discrimination task. Therefore, age differences in motion direction discrimination interact with stimulus spatial frequency over the range of stimulus energy associated with spatial summation.

The $k_2$ parameter also varied with spatial frequency for both groups of observers; younger $k_2$ values flattened out beyond 1 c/deg, while older $k_2$ values decreased monotonically with increasing spatial frequency. In comparison, the $p_2$ functions were flat across spatial frequency conditions in both age groups. These results indicate that in both age groups, the strength of suppression is strongest at low spatial frequencies, and that the strength of suppression is related to the slope, rather than the vertical position, of the threshold-versus-energy functions, regardless of the observer’s age.

Inspection of the model residuals revealed that the fits were not uniform over the entire range of contrast energy. We examined whether the deviations from the best-fitting curves in Figure 3 were related systematically to the stimulus. If the deviations were random, then they should be related to neither stimulus size nor contrast. To test this idea, linear models were constructed that related each set of log-transformed deviations to stimulus size and contrast. Because there were eight models (two age groups in four conditions), and there were two parameters (i.e., size and contrast) in each model, we used a criterion of $p < 0.01$ to determine statistical significance. Only one effect was significant: the deviations from thresholds

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Figure 3. Stimulus duration thresholds for younger (open symbols) and older (closed symbols) observers are plotted as a function of stimulus energy, the sum of the squared contrast at each pixel in the display. The smooth lines through the equation show the best-fitting curves for Equation 1 as a function of stimulus energy with $k_1$ fixed at $-1$. The different sizes are represented by the same symbols as in Figure 1.

Figure 4. Fitted parameters for the threshold-versus-energy functions are shown as a function of spatial frequency for younger and older observers. Error bars indicate the bootstrapped 95% confidence intervals.
measured in younger subjects in the 1 c/deg condition were significantly associated with stimulus size \( F_{(3,18)} = 7.57, p < 0.01 \). This effect can be seen in Figure 3; as the size of the 1 c/deg stimulus increased, so did the deviation of the thresholds from the fitted model. In all other cases the deviations from the best-fitting energy model were not linearly associated with stimulus contrast or size. Overall, then, stimulus contrast energy is a good predictor of the summation and suppression effects seen in younger and older observers.

Effects of stimulus speed

In all of the stimulus conditions tested thus far, the speed of motion was held constant at 2 deg/s. However, stimulus speed may be an important variable to consider when studying age differences in motion perception. Older observers typically require greater stimulus speeds to detect motion, discriminate motion direction, and to estimate the speed of moving objects (Atchley & Andersen, 1998; Raghuram, Lakshminarayanan, & Khanna, 2005; Snowden & Kavanagh, 2006). In one particularly pertinent example, it was shown that relative to younger observers, older adults tended to overestimate the velocity of slow-moving vehicles and underestimate the velocity of fast-moving vehicles (Scialfa, Guzy, Leibowitz, Garvey, & Tyrrell, 1991).

To determine whether age-related changes in perceived stimulus speed contribute to age-related changes in summation and suppression, we obtained duration thresholds for 1 c/deg stimuli moving at 2, 4, and 8 deg/s from an additional three younger and three older observers. Once again, we fit Equation 1 to duration thresholds as a function of stimulus contrast energy, keeping the \( k_1 \) slope parameter fixed at \(-1\). Increasing the stimulus speed improved duration thresholds in both groups of observers, as indicated by the downward shift in all of the fitted curves (Figure 5A). The vertical position of the descending portions of the threshold-versus-contrast energy curves, \( p_1 \), did not vary with stimulus speed in younger observers. An effect of age was seen at 2 deg/s, however, with greater \( p_1 \) values in the older observers. Thus at low contrast energy and low stimulus speed older observers required a faster motion signal to discrimination motion direction, which could be related to age differences in perceived stimulus speed.

Age differences were particularly evident over the ascending portions of the threshold-vs.-energy curves, i.e., during suppression. Younger observers’ thresholds were greater than older observers’ thresholds at the largest contrast energy. This trend was reflected in the parameters controlling the height and slope of the ascending portions of the curves (Figure 5B), in which older observers obtained consistently greater \( p_2 \) and shallower \( k_2 \) values than younger observers. Older observers’ \( k_2 \) values

Figure 5. (A) Duration thresholds and (B) fitted parameters (Equation 1) for motion direction discrimination of 1 c/deg Gabor s are plotted as a function of stimulus contrast energy for three different speeds.
decreased with increasing speed, indicating reduced suppression at higher speed, whereas younger observers’ \( k_2 \) values showed the opposite trend, indicating a slight increase in suppression at higher speed. It was not possible to derive valid bootstrapped confidence intervals for the fitted parameters with our small sample size. Nevertheless, the interaction between speed and age on suppression suggests that a simple age-related difference in perceived speed cannot account for the observed pattern of results.

By measuring duration thresholds over a range of stimulus speeds it was also possible to determine whether observers discriminated stimuli on the basis of motion or on spatial displacements (i.e., spatial phase; Boulton, 1987; Nakayama & Tyler, 1981; Scobey & Johnson, 1981; Seiffert & Cavanagh, 1999; Snowden, 1992; Snowden & Braddick, 1990). If observers used a change in position as a cue, then the magnitude of the phase shift required for correct discrimination of motion direction should remain constant across a range of stimulus speeds. When duration thresholds were converted to changes in phase, we found that the magnitude of the phase shift required to discriminate the stimulus direction increased significantly with increasing stimulus speed in both younger and older observers in almost all conditions. This result is inconsistent with the constant-displacement hypothesis and suggests instead that both younger and older observers used motion to discriminate stimulus direction.

**Discussion**

Recent work from our laboratory showed that the typical pattern of spatial summation and suppression in motion discrimination tasks changes across the life span (Betts et al., 2005). Surprisingly, direction discrimination duration thresholds were lower (i.e., briefer) in older observers for large, high contrast stimuli, consistent with an age-related decline in spatial suppression. In our previous work, we used 1 c/deg stimuli to minimize age-related differences in contrast sensitivity. The current study extends these findings to show that older observers obtained lower duration thresholds than younger observers for large, high contrast Gabors ranging in spatial frequency from 0.5 to 4 c/deg (Figure 1) and ranging in speed from 2 to 8 deg/s (Figure 5).

**Model results**

We implemented a simple model (Equation 1) to better characterize the effect of stimulus size on duration thresholds at different levels of contrast (Figure 2). In both groups of observers, the parameter associated with spatial summation \( p_1 \) decreased as a function of stimulus contrast, indicating a shift away from summation at higher contrast values. The main effects of age were evident in the slopes \( (k_2) \), rather than the vertical positions \( (p_2) \), of the ascending (i.e., suppressive) portions of the threshold-versus-size curves. In the majority of contrast and spatial frequency conditions (12/18 threshold measures; non-overlapping error bars in Figure 2), shallower slope estimates were obtained from older observers, a finding that is consistent with an age-related decline in suppression strength from the non-classical receptive field of direction-sensitive mechanisms. Additionally, the pattern of results for the older observers’ \( k_2 \) estimates suggest that suppression was actually greater for intermediate levels of contrast. This pattern of results points to the possibility that aging may cause the gain mechanism controlling the suppressive components of motion-detection units to saturate at relatively low levels of contrast. Subsequent increases in contrast have few, or even reversed, effects on spatial suppression.

A more general overview of the age differences in summation and suppression was revealed when the duration thresholds were plotted as a function of the stimulus contrast energy, which effectively collapsed the data across size and contrast (Figure 3). The model provided reasonable fits to these threshold-versus-energy functions, suggesting that stimulus energy is an important factor to consider in the investigation of center-surround antagonism.

As with the previous analysis that used size as the independent variable, the analyses based on contrast energy found age differences in the slope of the summation/ascending curve (i.e., parameter \( k_2 \)) consistent with reduced suppression in older observers. However, age differences in the summation/descending curves also became evident: At 0.5, 2, and 4 c/deg, \( p_1 \) was greater in older observers than younger observers, which suggests that aging reduces sensitivity at the low end of the range of contrast energies tested here. This result supports the hypothesis that older observers require greater stimulus energy to reach the optimal level of performance in the motion discrimination task than younger observers. The required increase in stimulus energy could be obtained either by raising the contrast or enlarging the stimulus area, a finding that is consistent with previous work suggesting that the area of complete summation is larger in older observers (Hiller & Kline, 2001; Owlsley & Sekuler, 1982; but see Brown, Peterken, Bowman, & Crassini, 1989; Dannheim & Drance, 1971; Latham, Whitaker, & Wild, 1994; Zele et al., 2006). Our results also support the hypothesis that the linearity of spatial summation is preserved with age (Zele et al., 2006).

Interestingly, age differences in summation may be related to stimulus speed. Older observers obtained greater \( p_1 \) values than their younger counterparts for 1 c/deg stimuli moving at 2 deg/s, but the age differences vanished at 4 and 8 deg/s (Figure 5). Previous studies have also
documented age-related reductions in motion detection, discrimination, and speed estimation at slower speeds (Atchley & Andersen, 1998; Raghuram et al., 2005; Snowden & Kavanagh, 2006). Our findings imply that increased stimulus speed, rather than temporal frequency, provides the main benefit to the older observers at low contrast, as age differences were evident for 2 and 4 c/deg stimuli moving at 2 deg/s, but not for the 1 c/deg stimuli moving at 4 and 8 deg/s. Future studies with greater sample sizes are required to fully understand the relationship between speed and temporal frequency on spatial summation mechanisms, and how these mechanisms are affected in normal healthy aging.

Spatial frequency scaling

The effect of spatial frequency on summation and suppression became more apparent when thresholds were modeled as a function of contrast energy (rather than stimulus size and contrast). In younger observers, the value of the fitted parameter $p_1$ (Figure 4) decreased monotonically with increasing spatial frequency. When thresholds are plotted on log–log axes, reducing $p_1$ shifts the threshold curve leftward along the abscissa. Therefore, the reduction in $p_1$ can be interpreted as indicating that the transition from summation to suppression occurred at lower contrast energy as spatial frequency increased. This result is consistent with previous psychophysical studies that showed spatial-frequency-dependent scaling of the complete area of spatial summation (Anderson & Burr, 1987; Banks et al., 1991; Howell & Hess, 1978; Legge, 1978; Luntinen et al., 1995; Näsänen, Kukkonen, & Rovamo, 1993; Rovamo et al., 1993; Virsu & Rovamo, 1979). Similarly, physiological estimates of V1 neuron grating summation fields, a measure that is often taken as the spatial extent of the classical receptive field, also scales according to spatial frequency selectivity (Cavanaugh et al., 2002; De Valois, Albrecht, & Thorell, 1982). In general, the critical area that marks the maximum spatial summation is inversely proportional to spatial frequency squared, i.e., the critical area decreases as a function of spatial frequency with a slope of $-2$ (Howell & Hess, 1978; Luntinen et al., 1995; Virsu & Rovamo, 1979). Although we did not specifically measure the critical area of summation, it is worth noting that the slope of the $p_1$ parameter, shown in Figure 4 as a function of spatial frequency, was $-1.57$, suggesting that our model can provide at least a rough estimate of spatial frequency scaling.

The relationship between motion discrimination sensitivity and spatial frequency in older observers was less clear: $p_1$ values reached a plateau after 1 c/deg, suggesting a breakdown in spatial frequency scaling. Although this result could be attributed to age-related changes in the contrast sensitivity function, performance may improve given a sufficient increase in stimulus contrast energy by either enlarging the target or increasing contrast. Importantly, such an increase in stimulus energy might then engage the suppressive mechanisms in younger observers, thereby impairing their performance.

As previously noted, the slopes of the suppression/ascending portions of the threshold curves varied as a function of spatial frequency in both younger and older observers. This effect is most clearly seen in the older observers in Figure 4; by 4 c/deg, the $k_2$ value was effectively zero, suggesting that suppression is virtually non-existent in older observers for high spatial frequencies. In younger observers the curve flattened out after 1 c/deg, consistent with a lower, non-zero, limit to the strength of spatial suppression. As such, spatial suppression may be a phenomenon that is mediated primarily by low spatial frequency channels. Consistent with previous findings, we also found that suppression may increase slightly as a function of speed in younger observers (Figure 5B; Lappin, Nyquist, & Tadin, 2006), suggesting that suppression mechanisms are likely to display tuning in both spatial and temporal domains, which in turn may be differentially affected by the normal aging process.

Energy summation and suppression?

Popular physiological models of surround suppression (e.g., Cavanaugh et al., 2002; Sceniak et al., 1999) emphasize the effect of stimulus size or contrast, rather than the total amount of stimulus energy, on neuronal responses. The incorporation of physiologically based parameters into size and contrast-dependent models of motion perception may help elucidate the mechanisms underlying age-related changes in summation and suppression in visual motion processing. Two models proposed by Tadin and Lappin (2005) that incorporated contrast and size-dependent changes in receptive field structure, in line with the physiological literature, provided good fits to psychophysical duration thresholds. An additional model, which yoked the strength of the inhibitory surround to the activation of the excitatory center, is more consistent with a mechanism that depends on stimulus contrast energy. Our data suggest that models of motion processing based on stimulus contrast energy may further enhance our understanding of age effects on both summation and suppression mechanisms in visual motion processing.

It is important to realize that we constrained our model to reflect physiological and psychophysical evidence that stimulus energy is summed linearly across the receptive field, up until a maximum value. As such, the descending slope value ($k_1$) was fixed at $-2$ (Figure 1) or $-1$ (Figure 3) for duration thresholds plotted as a function of stimulus size and contrast energy, respectively. The goodness of the model fits, as well as visual inspection of the descending region of the curves, confirm that this constraint on the model was reasonable in both groups.
of observers for the range of spatial frequencies and speeds tested. For larger/higher energy stimuli, the model fits indicate that the strength of spatial suppression is certainly not proportional to stimulus energy in either group, with log-log slopes ($k_2$) consistently less than 1 in all spatial frequencies (Figures 2 and 4). Taken together, our model results confirm the current opinion that spatial summation and suppression are mediated by different neural mechanisms and suggest that the mechanisms underlying spatial suppression are more vulnerable to aging than those that mediate spatial summation.

Aging and receptive field structure

Potential physiological explanations for the age-related increase in summation area include a loss of retinal ganglion cells, which may lead to topographic reorganization and enlarged receptive field sizes for senescent cortical neurons (Gilbert & Wiesel, 1992; Schefrin, Bieber, McLean, & Werner, 1998). Surprisingly, age-related anatomical changes in the primate retinogeniculostriate pathway are quite subtle (Spear, 1993). Photoreceptor loss in the retina is primarily restricted to rods (Curcio, 2001), and while ganglion cell density of the whole retina decreases significantly with age, the macular region is well preserved (Harman, Abrahams, Moore, & Hoskins, 2000). A less complicated explanation is that reduced retinal illuminance in older observers due to optical factors such as decreased pupil size and increased lens opacity (Weale, 1992) is sufficient to enlarge summation fields. Indeed, when the age-related decrease in retinal illuminance is controlled by lowering the display luminance in younger observers the spatial extent of summation is equated between the two age groups (Betts et al., 2005). In comparison, reduced illuminance does not account for reduced spatial suppression in older observers. In previous work, we found that reducing retinal illuminance of younger observers by one log unit did not affect estimates of spatial suppression (Betts et al., 2005). The differential effect of retinal illuminance on summation and suppression suggest that these two processes rely upon different neural mechanisms.

Can reduced effective contrast explain the age differences in suppression? If inhibitory mechanisms simply required greater stimulus contrast to induce suppression, older observers’ thresholds should start to increase at a rate similar to younger observers at higher stimulus contrast energies, resulting in a rightward shift along the x-axis in Figure 3. In this scenario, the ascending slope values, estimated by the fitted $k_2$ parameter, would be equivalent in both age groups. However, the slope values were consistently lower in older observers, an effect that did not interact with stimulus spatial frequency (Figure 4). As such, it is unlikely that reduced suppression in older observers is due to age-related changes in effective stimulus contrast.

For similar reasons, it is also unlikely that that we observed less suppression in older observers because we did not test with sufficiently large stimuli. If the effect of age simply increased the spatial extent of the nCRF, we would not expect differences in the $k_2$ slope parameters. Instead, we found shallower slopes in older observers, consistent with a reduction in the strength, rather than an increase in size, of suppression from the nCRF.

A more intriguing explanation for lessened suppression in older observers is a decline in the efficacy of inhibitory mechanisms, particularly the neurotransmitter GABA, in the visual cortex. Importantly, the relationship between GABA levels in the human occipital lobe and behavior in our motion discrimination task has recently been examined. Using MRI spectroscopy, Golomb and colleagues reported reduced quantities of occipital cortex GABA in recovered depressed patients. Interestingly, a separate group of recovered depressed patients showed significantly reduced spatial suppression in the motion discrimination task (Golomb et al., 2008). Furthermore, reduced suppression in motion direction discrimination has also been found in schizophrenic patients with severe negative symptoms, a population with known disruptions in visual motion processing (Tadin et al., 2006) that is also thought to have reduced efficacy of the GABAergic system (e.g., Lewis, Hashimoto, & Volk, 2005). The ways in which inhibition could be reduced in healthy older observers are myriad, but two likely sources are discussed here.

First, it has been shown that GABAergic mechanisms that mediate orientation and motion direction tuning in monkey V1 are compromised in older monkeys (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000). Further evidence for reduced GABAergic functioning in older visual cortex comes from post-mortem brain tissue samples from human donors. Boley et al. (2005) recently reported an age-related reduction in GAD 67, a GABA synthesizing enzyme, in brain tissue samples over 50 years of age. Additionally, the composition of the GABA$_A$ receptor subtype changed with age, and in fact appeared to regress toward a more immature form of receptor protein configurations. These studies provide converging evidence that both the production of GABA and its effect at the post-synaptic receptor change with age. Such changes in neurotransmitter function may be an underlying factor in the behavioral age differences observed here.

A second potential site of age-related changes in cortical function comes from the physiological finding that the timing of feedback mechanisms in senescent visual cortex is disrupted (Wang, Zhou, Ma, & Leventhal, 2005). Myelination irregularities have also been reported in older primate visual cortex (Peters, Moss, & Sethares, 2000). Several studies suggest that feedback mechanisms from higher visual areas, such as the motion sensitive middle temporal cortex, are likely involved in spatial suppression (Bair, Cavanaugh, & Movshon, 2003; Cavanaugh et al., 2002; Hupé et al., 1998; Levitt & Lund, 1992).
even slight delays or advances in the feedback signal could significantly interfere with the timing of the circuit. It is our hope that future research will clarify how the temporal properties of the visual signal change with age at the neuronal level.

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Corresponding author: Lisa R. Betts.
Email: lbetts@yorku.ca.
Address: Centre for Vision Research, Room 0009 CSEB, York University, 4700 Keele Street, Toronto, Ontario M3J 1P3, Canada.

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