Aging alters surround modulation of perceived contrast

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It is well established that many visual functions deteriorate with age. Perhaps counter-intuitively, a recent study revealed that older people actually require less time to discriminate the direction of motion of large, high contrast stimuli than younger adults (L. R. Betts, C. P. Taylor, A. B. Sekuler, & P. J. Bennett, 2005). L. R. Betts et al. (2005) proposed their finding as evidence for a reduction of cortical inhibitory function within the aging visual system. There is some neurophysiological support for this suggestion, as broadening of visual cortical neural tuning consistent with reduced inhibitory function has been observed in older animals. Here we explore the perceptual consequences of center-surround suppression within the healthy aging human visual system and report data from a center-surround contrast discrimination task (the Chubb contrast illusion). We predicted that older observers would demonstrate less center-surround suppression than younger subjects (consistent with reduced inhibition). Our data does not support this prediction as perceived contrast was altered more by surround modulation in the older than younger group (t(33) = 2.53, p = 0.02). A possible explanation for our findings is a decrease in perceptual brightness induction in the elderly group. Brightness induction relies on neural synchronization which might be disrupted by aging.

Keywords: aging, contrast discrimination, surround modulation, contrast matching


Introduction

Recent neurophysiological studies in primate (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000) and cat (Hua et al., 2006) have demonstrated that the orientation and direction selectivity of neurons in primary visual cortex (area V1) is altered in aging animals. In addition to demonstrating a significant reduction in orientation and direction tuning, these studies also showed that older visual cortex shows increased spontaneous and visually evoked neural activity. The observation of reduced neural response tuning led Schmolesky et al. (2000) to hypothesize that age may negatively affect GABAergic connections in V1, leading to a reduction in inhibitory function in the visual cortex. Inhibition is central to a number of aspects of visual processing, including neural response selectivity for orientation and direction, hence a reduction in inhibition could explain the reduced orientation and direction tuning of aged visual neurons. This was further studied by Leventhal et al. (2003) who hypothesized that the application of GABA and GABA agonists on individual V1 cells would restore orientation and direction tuning. In support of their hypothesis, they found that after GABA administration some of the cells responded strongly to a narrow range of preferred orientations and directions and exhibited nearly no response to non-preferred orientations and directions (Leventhal et al., 2003).

Another example of cortical visual processing that relies on inhibitory function is surround suppression. There are a number of psychophysical visual tasks that enable the demonstration of surround suppression in the human visual system (Chubb, Sperling, & Solomon, 1989; Petrov, Carandini, & McKee, 2005; Polat & Sagi, 1993; Tadin, Lappin, Gilroy, & Blake, 2003). Tadin et al. (2003) demonstrate surround suppression in the visual motion processing pathways by establishing that increasing the size of a high contrast moving pattern counter-intuitively makes it more difficult to perceive its direction of motion. Tadin et al. (2003) proposed surround inhibition as the mechanism for this decrease in motion sensitivity for larger higher contrast stimuli. The unusual perceptual phenomena described by Tadin et al. (2003) motivated an investigation by Betts, Taylor, Sekuler, and Bennett (2005) into center-surround visual motion processing by elderly people. Betts et al. (2005) sought to ascertain whether surround inhibition deteriorated with age. If so, the performance of older people would be expected to be less affected by large high contrast stimulation in the surround of neural receptive fields than younger people. Indeed, their study showed that older people were able to discriminate the direction of motion of large, high contrast stimuli in shorter durations than younger adults (Betts et al., 2005). From this finding, Betts et al. (2005) suggested that it was the reduction in efficacy of inhibitory mechanisms which produce surround suppression in neurons in the visual motion...
processing pathways that was responsible for the age differences in spatial suppression. A reduction in the inhibition of large and potentially uninteresting features of the visual system is unfortunately likely to be a disadvantage for real world visual tasks.

Visual processing occurs via partially anatomically and functionally distinct pathways. Tadin et al. (2003) demonstrated that their paradigm showed features consistent with what is known about response properties and receptive field size of neurons in cortical area MT (a key area for visual motion processing in the extrastriate visual cortex). Given that evidence consistent with changes in inhibitory function in primate is present for V1 neurons, it seems likely that perceptual alterations consistent with reduced center-surround cortical inhibitory function in V1 would also be measurable in elderly humans. In this study we used a center-surround visual task (the Chubb contrast illusion (Chubb et al., 1989)) to explore the perceptual consequences of center-surround suppression in the elderly. The Chubb illusion is illustrated in Figure 1 and involves the presentation of a small low contrast textured patch surrounded by an annulus of same texture but of much higher contrast. The presence of the high contrast surround, results in the central patch appearing to be of lower contrast than it truly is, that is, the contrast perception of the central patch is suppressed by the high contrast surround. The experiments were designed to test the prediction that the high contrast surround would have less effect in older subjects than younger subjects (consistent with reduced inhibition), and hence that the older participants would perceive the central target to be closer to its real contrast than the younger group. Somewhat intriguingly, we found the complete opposite result to that we predicted. Our older group showed a greater alteration in perceived contrast of the target as a consequence of the surround than the younger group.

Methods

Participants

Eighteen younger adults (aged 18 to 30, mean = 24, stdev = 4.02) and 17 older adults (aged 60 to 72, mean = 66, stdev = 4.47) participated in the study. Participants were recruited by responding to a written advertisement placed in electronic newsletters associated with the University of Melbourne and in community newspapers. The study was approved by the Human Research Ethics Committee of The University of Melbourne and all participants provided written informed consent prior to taking part in the project. All volunteers underwent a full ocular examination (including assessment of anterior and posterior ocular structures, and intraocular pressure).

Figure 1. Stimuli used in the surround contrast discrimination task. Stimuli were presented consecutively to participants who indicated which of the two intervals had the higher contrast. The target stimulus (front panel) was surrounded by an annulus of 95% contrast and had a radius of 4 degrees. The target was presented for 500 ms followed by a 500 ms interstimulus interval before a second stimulus was displayed (back panel). The smaller center stimulus had a radius of 0.67 degrees and seven different contrast levels were randomly presented. All targets were comprised of 4 c/deg bandpass filtered noise.
Inclusion criteria included: normal ocular health for age, visual acuity of 6/7.5 or better, refractive error of no more than ±5.00 diopters spherical and ±2.00D astigmatism. Participants were not allowed to be taking medications known to affect visual function, and were not permitted to have systemic conditions known to affect visual function (for example: diabetes).

**Stimuli and procedures**

The computerized psychophysics experiments were conducted using a personal computer with a gamma-corrected Sony G520 21 inch CRT monitor (frame rate 100 Hz, resolution 1264 × 947 pixels, maximum luminance of 100 cd/m²). Custom software was written in Matlab 7.0 (Mathworks, Natik, MA, USA) and the stimuli were displayed using a VSG 2/5 graphics system (Cambridge Research Systems, Kent, UK). Participants viewed the center of the screen from a distance of 50 cm with their chin and head stabilized using a chin and forehead rest. All measures were conducted within a single test session of approximately 2 hours in duration.

The stimuli used for the experiments are shown in Figure 1. The stimulus parameters were based on those used by Dakin, Carlin, and Hemsley (2005) who used the Chubb illusion (Chubb et al., 1989) to explore for psychophysical correlates of reduced cortical inhibition in people with schizophrenia. Our experimental design was similar to that of Dakin et al. (2005), with the exception that we reduced the spatial frequency of the stimulus from 8 to 4 c/deg. We reduced the spatial frequency to reduce differences in contrast sensitivity between our older and younger groups as contrast sensitivity is increasingly reduced as spatial frequency increases in the elderly (Owsley, Sekuler, & Siemsen, 1983). The central gray textured stimulus had a radius of 0.67 degrees and was comprised of 4 cycle per degree band-pass filtered noise (1 octave bandwidth). In some conditions, the target was embedded in an annulus (4 degrees in radius) of the same textured noise but of 95% contrast (front panel of Figure 1).

**Contrast discrimination**

Participants performed two contrast discrimination tasks: one to determine their ability to discriminate a difference in contrast between two central target patches, the other to determine how their performance changed when the target was presented within a different surrounding visual context (the annulus, the task illustrated in Figure 1). Each task used a two-interval forced choice methodology. For the condition where the target was presented alone, in the first interval the target patch was presented at a fixed contrast of 40% for 500 ms. After an inter-stimulus interval of 500 ms, a second patch of variable contrast was presented, also for 500 ms. Observers were instructed to indicate which of the two intervals they perceived as having the higher contrast. The contrast of the patch presented in the second interval was varied to enable a psychometric function to be obtained using a method of constant stimuli (MOCS). Seven contrast levels were randomly interleaved and were each presented 30 times. Each participant initially performed an abbreviated MOCS (13 levels, presented 4 times each) that was used to select the range of the final 7 contrasts used in more extensive procedure. A similar procedure was used for the second contrast discrimination task: the “surround” condition. In this case, the 40% contrast target patch presented in the first interval was surrounded by a high contrast textured annulus (as illustrated in Figure 1). All other features of the task were identical to the “no surround” condition.

Example psychometric functions from a single younger observer are shown in Figure 2. From the psychometric functions we obtained measures of the spread of the function (an estimate of the precision of the observer in making a contrast discrimination judgment) and threshold (enabling the calculation of bias from the reference contrast). Estimates of spread and threshold were obtained by fitting the data with a modified Cumulative Gaussian (Wichmann & Hill, 2001):

\[
\Psi(t) = 1 - \left( FP + (1 - FP - FN) \times G(t, \mu, \sigma) \right),
\]

where \(G(t, \mu, \sigma)\) is the Cumulative Gaussian distribution with mean \(\mu\) and standard deviation \(\sigma\) for value \(t\). FP and FN represent the false positive and negative rates respectively. This equation gives a psychometric function that accounts for false responses by assuming that a false response is made independently of the underlying Gaussian distribution of responses. Curves were fit using a bootstrap procedure (1000 repetitions) enabling 95% confidence limits to be estimated for the threshold (\(\mu\)) and spread (\(\sigma\)) parameters. For this experiment, the threshold (\(\mu\)) represents the contrast level for which the reference subjectively appeared the same as the target patch (the point-of-subjective equality (PSE)).

All participants received substantive training prior to the collection of formal data. Participants were randomized to perform either the “surround” or “no surround” condition first and this was counterbalanced between older and younger groups to avoid order dependent effects of learning or fatigue between groups.

**Contrast detection**

As it is well known that normal aging reduces contrast sensitivity (Elliott, 1987; Morrison & McGrath, 1985; Owsley et al., 1983; Sekuler & Hutman, 1980; Wright &
Drasdo, 1985) contrast detection thresholds were also measured for the central target stimulus to establish the magnitude of this effect for our stimulus. A yes-no procedure was used where observers had to nominate if they saw the target stimulus appear by pressing a button. The stimulus was displayed for 500 ms and observers had 1.5 sec to respond. Contrast thresholds were measured using two interleaved staircases (3 down, 1 up) each of 6 reversals. The mean of the last four reversals was calculated as the result of a single staircase. This procedure was performed twice and the mean of the results of all staircases was returned as the final threshold estimate.

Statistics

Statistical analysis was performed using SigmaStat 3.0 (SPSS, Chicago, IL, USA). All data sets were tested for conformation to statistical normality (Kolmogorov-Smirnov test) and equal variance (Levene Median test). To compare performance between elderly and younger groups, parametric tests (t-tests or ANOVA where appropriate) were used for data distributions that did not depart from statistical normality. The non-parametric Mann-Whitney Rank Sum Test was used for distributions where data departed from a normal distribution.

Results

Contrast discrimination thresholds

Figure 3 shows group mean performance (±95% confidence limits for the mean) for the contrast discrimination tasks. Panel 3a shows the best estimates of the point-of-subjective equality (PSE) returned from the curve fitting. When the target was not surrounded by the annulus, the groups performed similarly with both younger and older groups matching the 40% contrast target patch with a patch that was close to 40% contrast (no significant difference between groups, t(33) = 0.127, p = 0.90). When the surround was present (right hand side of panel 3a), both groups showed a bias in their perception of the target’s contrast, with the patch appearing to be significantly less than 40% contrast. The mean PSE for the

Figure 2. Example psychometric function for one younger observer. Panel (a) shows the raw data for the no surround (filled symbols) and surround (unfilled symbols) conditions. Fitted curves are the mean cumulative Gaussian returned by the bootstrapping procedure. The curves have similar slopes but different points-of-subjective equality, with the surround causing the target patch to appear to be of lower contrast than the veridical contrast of 40% (dotted vertical line). Panels (b) and (c) show the fitted curves for the no-surround and surround separately with the shaded area illustrating the 95% confidence limits of the curve fits.
older group was significantly less than that for the younger group ($t(33) = 2.53, p = 0.02$), indicating that contrast perception was more biased by the presence of the annulus for the older than the younger group. This finding was opposite to our hypothesis. Panel 3c shows the distribution of the width of the 95% confidence limit of the PSE as determined from the bootstrapping procedure (see Figure 2). Data is shown as the median and 95th percentile. There was no difference between groups for this measure for either the no surround (Mann-Whitney Rank Sum Test, $p = 0.30$) or surround condition (Mann-Whitney Rank Sum Test, $p = 0.88$), indicating that the confidence in the estimates returned from the psychometric functions was the same in the two groups.

Group mean data for the spread of the psychometric function (a measure of the ability to discriminate between different contrast targets) is shown in Figure 3b, with the distribution of the 95% confidence limits of the spread estimates from the individual curve fits being shown in Figure 3d as medians and 95th percentiles. The mean spread of the psychometric function did not significantly differ between groups (no surround: $t(33) = 0.906, p = 0.37$; surround: $t(33) = -0.70, p = 0.49$) nor the median 95% confidence limit of the spread estimates (Mann-Whitney Rank Sum Test; no surround: $p = 0.31$, surround: $p = 0.58$). Hence the data shown in Figures 3b and 3d demonstrates that the older and younger groups were equally able to discriminate between stimuli of different contrasts. Several previous studies have shown equivalent contrast discrimination in older and younger groups (Beard, Yager, & Neufeld, 1994; Mei, Leat, & Hovis, 2007).

**Contrast detection thresholds**

It is well established that contrast sensitivity declines with aging (Elliott, 1987; Morrison & McGrath, 1985; Owsley, Gardner, Sekuler, & Lieberman, 1985; Owsley
et al., 1983; Sekuler & Hutman, 1980). Consequently, while Figure 3 shows that the ability to discriminate between different contrasts was equivalent between groups, it should be expected that our older participants would, on average, have poorer contrast sensitivity (elevated contrast detection thresholds). As shown in Figure 4, group mean threshold was elevated for the older participants relative to the younger group (t-test on the log contrast threshold data: \( t(33) = -6.31, p < 0.001 \)).

### Reduced effective contrast stimuli in younger observers

Due to the elevated contrast thresholds of the older group (as shown in Figure 4) the stimuli used for the contrast discrimination task would have been closer to contrast threshold for the older group than the younger group. However, for all participants, the 40% target stimulus was substantially suprathreshold (the most elevated contrast threshold in the older group was 11.8%). To explore whether the difference in contrast sensitivity was likely to explain the enhanced shift of the PSE experienced by the older group, we repeated the contrast discrimination task on a subset of three younger observers for target stimuli of 30% and 20% contrast. The surround conditions for these targets were 71.25% and 47.5% contrast respectively to keep the ratio of center to surround contrast consistent across all conditions. The purpose of this additional experiment was to determine whether manipulating the target and surround stimuli to be closer to the observer’s contrast threshold changed the magnitude of the perceived bias. In order to explain the older observers’ performance, an elevation in bias would need to be observed as the contrast of the stimuli was reduced. Figure 5 shows the performance of the three younger observers for the contrast discrimination task for reduced contrast targets. For each contrast condition and each observer, the magnitude of the perception bias was determined (the difference between the surround and no surround conditions). As the contrast of the target was reduced, so too was the magnitude of the bias. A repeated measured ANOVA revealed this effect to be statistically significant \( (p = 0.02) \), with post-hoc testing (Holm-Sidak method) showing that the bias at 20% contrast was less than that at either 30 or 40% contrast. Figure 5b shows the bias plotted as a ratio of target contrast, and in this case, there is no significant difference between contrast levels (RM-ANOVA, \( p = 0.32 \)) as consistent with Weber like behavior. We recognize that this does not truly simulate the effect of reduced contrast sensitivity in older people. Nevertheless, making the target and surround closer to the subject’s contrast threshold shifted performance in the opposite direction to that necessary to explain the difference between older and younger subjects for the 40% contrast condition (Figure 3). Our older observers would need better contrast sensitivity than the younger cohort for an on-average larger bias to be found in the older group.

### Discussion

Our experiment produced results contrary to those we predicted. We hypothesized that the presence of the
high contrast surround would have less effect on the perceived contrast of the central target for the older adults, consistent with a reduction in inhibitory function within the visual cortex. This expectation was derived from the results of Betts et al. (2005) who found that older people were better able to perceive large, high contrast moving stimuli than were younger people, consistent with a reduction in inhibitory surround strength (Betts et al., 2005). Intriguingly, our results were in the opposite direction to our initial prediction. While this study was primarily interested in changes in visual performance in the elderly that are presumed to arise from cortical mechanisms, the well-known deterioration of optical quality with age also needs consideration. One important factor is decreased retinal illuminance, primarily due to senile miosis (age-related decrease in pupil size) (Winn, Whitaker, Elliott, & Phillips, 1994).

We did not experimentally investigate the effect of retinal illuminance on our methodology because of the pre-existence of substantial evidence that retinal illuminance does not explain the deterioration of contrast processing in older adults. Indeed, many studies which have looked at contrast sensitivity and contrast related tasks have eliminated retinal illuminance as the major cause of changes seen in older observers (Betts, Sekuler, & Bennett, 2007; Betts et al., 2005; Elliott, Whitaker, & MacVeigh, 1990; Sloane, Owsley, & Alvarez, 1988). Similar to Betts et al. (2005), we could have run an additional control experiment involving neutral density filters on our younger participants in order to emulate the retinal illuminance reduction of the older participants. Alternately, we could have dilated the pupils of the older participants so that they would appear more like those of the younger participants. However, with the above-mentioned literature eliminating retinal illuminance as a cause of difference on other contrast processing measures, we consider it unlikely that retinal illuminance is the major cause of the differences seen in this present study.

Due to their reduced contrast sensitivity the experimental stimuli were a reduced effective contrast for the older group. Spatial summation area varies with stimulus contrast: for example; the preferred stimulus size of a V1 neuron increases with decreases in stimulus contrast (Tailby, Solomon, Peirce, & Metha, 2007). Consequently, a reduced effective contrast for the older participants would predict integration over a larger spatial area. Betts, Sekuler, and Bennett (2009) have recently explored spatial summation in older and younger participants for center-surround motion stimuli and conclude that alterations in spatial summation predicted by reduced effective contrast sensitivity in older observers are insufficient to explain their results. In our study, given that the experimental target was of fixed size, an increase in central spatial summation area would presumably result in a reduced area of surround, hence potentially less inhibitory strength. Such a situation would predict the older group to demonstrate reduced surround suppression when compared to younger adults. This predicted finding would be consistent with our original hypothesis, however is opposite to that supported by the data.

With that in mind, these findings are likely to reflect differences in neural function, but what might these differences be? As demonstrated in this experiment and in many previous studies, a stimulus’ perceived contrast is influenced by surrounding stimuli. It is well known that grating-type stimuli with surrounds of the same orientation (referred to as iso-oriented) are suppressed due to lateral inhibition (Cannon & Fullenkamp, 1991, 1996). However, when stimuli are surrounded with either a cross-oriented surround or a surround out of phase with the center stimulus (Cannon & Fullenkamp, 1991; Yu, Klein, & Levi, 2001) the opposite result is obtained, that is, there is little suppression, and sometimes stimulus contrast enhancement. One mechanism used to explain such enhancement in perceived contrast is referred to as brightness induction which results from local luminance contrast at the edge of the central target (Biedlerlack et al., 2006; Yu et al., 2001). Our random texture stimulus was not continuous between the center and the surround of the stimulus, hence may have resulted in some degree of brightness induction similar to a phase-shifted grating. We chose a non-continuous border in order to minimize the effect of contextual modulation believed to result from feedback from higher centers (Lotto & Purves, 2001). If present, brightness induction due to phase differences at the border of the center and surround of the stimulus would act to partially negate the impact of the inhibitory surround (that is: brightness induction would make the central target appear higher contrast, whereas the presence of the high contrast annulus would result in surround suppression reducing the perceived contrast of the central stimulus).

While somewhat speculative, it is interesting to consider whether our results could be explained by a reduction in the magnitude of brightness enhancement in our elderly group. A recent physiological study has found that brightness induction is related to neuronal synchronization (Biedlerlack et al., 2006). Their study found that when brightness enhancement is induced by phase offset of gratings between center and surround, the synchronization increases between neurons responding to the center grating, while rates of firing remain unaffected. As previously mentioned, there is considerable evidence for an increase in spontaneous and visually evoked neuronal firing in older animals (Hua et al., 2006; Leventhal et al., 2003; Schnolesky et al., 2000). Furthermore, physiological studies have found some evidence consistent with an increase in intrinsic neural noise in older humans (Betts et al., 2007). If there is, in fact, an increase in spontaneous neuronal firing in older people, then that could decrease synchronization of neuronal firing and, therefore, subsequently decrease the ability to produce brightness enhancement.
Conclusions

This study clearly demonstrates differences in center-surround visual processing as a consequence of normal aging. While psychophysics does not directly assess neural function, our results indicate that complex visual perceptual changes arise as a consequence of normal aging that are consistent with aberrant cortical visual neural function. Further study is required to help identify which specific neural functional alterations are responsible for the differences observed.

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