Mismatched summation mechanisms in older adults for the perception of small moving stimuli.

Thomas J. McDougall[1], Bao N. Nguyen[2], Allison M. McKendrick[2] and David R. Badcock[1]

1. School of Psychological Science, The University of Western Australia,
2. Department of Optometry and Vision Sciences, The University of Melbourne, Australia

Abstract

Previous studies have found evidence for reduced cortical inhibition in ageing visual cortex. Reduced inhibition could plausibly increase the spatial area of excitation in receptive fields of older observers, as weaker inhibitory processes would allow the excitatory receptive field to dominate and be psychophysically measureable over larger areas. Here, we investigated ageing effects on spatial summation of motion direction using the Battenberg summation method, which aims to control the influence of locally generated internal noise changes by holding overall display size constant. This method produces more accurate estimates of summation area than conventional methods that simply increase overall stimulus dimensions. Battenberg stimuli have a checkerboard arrangement, where check size (luminance-modulated drifting gratings alternating with mean luminance areas), but not display size, is varied and compared with performance for a full field stimulus to provide a measure of summation. Motion direction discrimination thresholds, where contrast was the dependent variable, were measured in 14 younger (24-34 years) and 14 older (62-76 years) adults. Older observers were less sensitive for all check sizes, but the relative sensitivity across sizes, also differed between groups. In the older adults, the full field stimulus offered smaller performance improvements compared to that for younger adults, specifically for the small checked Battenberg stimuli. This suggests ageing impacts on short-range summation mechanisms, potentially underpinned by larger summation areas for the perception of small moving stimuli.

Introduction

Age-related declines in human visual motion processing cannot be entirely due to increased intraocular light scatter or increased optical aberrations that accompany ageing, as degrading visual acuity in younger observers does not impair direction discrimination (Ball & Sekuler, 1986; Owsley, 2011). Rather, motion processing deficits may be the consequence of dysfunctional inhibitory mechanisms in the ageing brain (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000). Liang et al. (2010), using single cell recording techniques, found reduced direction selectivity, increased spontaneous activity and decreased signal-to-noise in visual cortical areas MT and V1 of older macaques, which were suggested to arise, at least in part, from reduced age-related efficacy of inhibition.

One potential effect of reduced inhibition with ageing is disrupted balance of the excitatory-inhibitory receptive field properties of centre-surround visual cortical neurons. These neurons increase their response, due to summation of neural responses, as increasingly larger stimuli moving in the cell's preferred direction are presented inside the classical receptive field (CRF, Allman, Miezin, & McGuinness, 1985). Once the spatial extent of the stimulus spreads beyond the CRF boundary, concurrently stimulating the extra-classical surround region, the neuron's response is suppressed. The suppressive strength of the inhibitory receptive field of V1 cells has been reported to be reduced in older primates (Fu et al., 2010), a finding often attributed to a global decrease in GABA-mediated inhibition in the ageing brain (Hua, Kao, Sun, Li, & Zhou, 2008; Hua et al., 2006; Leventhal et al., 2003). In humans, post-mortem V1 samples from older adults (2 samples over 55 years old) contained reduced amounts of pre- and post-synaptic GABAergic markers compared to younger adults (2 samples between 18 and 45 years old). Conversely, there is also emerging evidence for increased GABA levels in visual cortex of aged

macaques (Liao, Han, Ma, & Su, 2016) and a recent study of human subjects found that pharmacologically increasing GABA-mediated neural inhibition lead to weaker spatial suppression and increased summation (Schallmo et al., 2017). Therefore, despite neurophysiological evidence for changes in GABA circuitry with ageing, these changes are complex and only partially understood, and whether these changes are related to increases/decreases in suppression/summation remains speculative at present.

A visual perceptual task used to examine visual cortical centre-surround summation and suppression of motion in humans was introduced by Tadin, Lappin, Gilroy, and Blake (2003). For low contrast drifting stimuli (Gabor patches) of increasing size, observers need shorter presentation times to correctly discriminate motion direction, due to spatial summation (Anderson & Burr, 1987, 1991). However, for high contrast stimuli of increasing size, longer presentation times are required for correct motion direction discrimination, an outcome that is considered to be a perceptual consequence of surround inhibition of motion-selective neurons in visual cortical areas MT/V5 (Tadin et al., 2003). To investigate the excitatory-inhibitory balance in visual cortex with age, Betts, Taylor, Sekuler, and Bennett (2005) measured performance on the motion direction discrimination task of Tadin et al. (2003) in older and younger observers. Older observers had shorter duration thresholds than younger observers for large, high contrast drifting Gabor stimuli. Later, Betts, Sekuler, and Bennett (2012) were able to best account for the effects of ageing by increases in the model parameter that governed the size of the excitatory receptive field (the gain model), rather than changes in suppression strength, and speculated that changes in GABAergic functioning could allow for the excitatory receptive field to expand. Following this notion that age may be associated with a general increase in excitatory receptive field size, which may produce an expansion of the area over which excitation can be measured,

we aimed to directly investigate summation, as distinct from surround suppression (by using low contrast stimuli), to better characterise the motion summation mechanisms in older human observers.

Given previous reports of increased spontaneous activity in motion sensitive neurones of older macaques (Liang et al., 2010), it is important to control for internal noise differences with ageing when measuring summation. Thus, in this study, we employed the Battenberg summation method, originally introduced by Meese (2010) as a way of dissociating changes in signal area from changes in internal noise, by keeping overall display size constant. Battenberg stimuli have a checkerboard arrangement covering a fixed retinal area, where check size is manipulated to measure improvement in contrast detection threshold as the check size increases (spatial summation). For gratings that vary in diameter, the number of stimulated detectors is thought to increase as the overall retinal size of a stimulus increases, with each detector contributing its own intrinsic amount of internal noise. Importantly, internal noise levels remain constant using the Battenberg stimulus – i.e. if the number of monitored detectors depends primarily on the overall stimulus size, then threshold changes only reflect signal summation properties, providing a cleaner measure of signal summation behaviour. It is especially useful to control for overall stimulus size in light of recent work by Liu, Haefner, and Pack (2016) in alert behaving primates, which found that neuronal noise correlations were most closely aligned with signal correlations for responses to larger moving stimuli, thus limiting performance benefits with increasing size (spatial summation). A further advantage of the Battenberg paradigm is that it provides insight into the different stages of summation. That is, smaller sized checks are thought to tap short-range mechanisms, whereas larger check sizes measure of the potency of long-range summation mechanisms (McDougall, Dickinson, & Badcock, 2016; Meese, 2010).

We hypothesised that if older adults have a more expansive excitatory receptive field, then spatial summation will be measurable over a larger area. Moreover, the Battenberg method allowed us to look at the functioning of short-range and long-range summation mechanisms, separably, to determine whether ageing affects the summation properties of one or both of these mechanisms.

Method

Apparatus

Stimuli were generated using MATLAB 7.6.0 (Mathworks, Natick, Ma, USA) and presented on a Sony Trinitron Multiscan G520 Monitor (screen resolution: 1024 × 768, refresh rate: 100Hz; Tokyo, Japan) from the frame store (256MB) of a Cambridge Research Systems ViSaGe graphics system. Observers viewed the monitor binocularly from a distance of 65.5cm, which was maintained using a chin-rest. Participants were optimally refracted for this viewing distance. Testing took place in a darkened room (ambient luminance < 1cd/m^2). The background screen luminance was set at 50cd/m^2. In this study, contrast is defined as Michelson contrast in percent;

$$C_{M\%} = \left(\frac{L_{max} - L_{min}}{L_{max} + L_{min}}\right) \times 100 \qquad (1)$$

where L is luminance. This will also be expressed in dB units (Baker & Meese, 2011; Meese,

$$C_{dB} = 20\log_{10}(C_{M\%}) \qquad (2)$$

2010) where;

Participants

Participants were recruited from the University of Melbourne community and from a database of previous research participants. The study was approved by the University of Melbourne Human Research Ethics committee. Participants provided written informed consent before participating, and the study protocol was compliant with the tenets of the Declaration of Helsinki. Two groups participated: 14 younger adults aged 24 to 34 years (mean age: 27 years, standard deviation = 3 years, 7 males) and 14 older adults aged 62 to 76 years (mean age: 69 years, standard deviation = 5 years, 6 males). Best corrected visual acuity was required to be 6/7.5 or better with a refractive error between ±5.00D spherical and ±2D cylinder astigmatism. Slit lamp and ophthalmoscopy examinations were conducted to ensure normal posterior and anterior ocular health. All participants had clear ocular media, defined as Grade 1.5 or less on the Lens Capacities Classification System III scale (Chylack et al., 1993). Participants were excluded for systemic conditions (e.g., migraine, epilepsy and diabetes), or medications (e.g., anti-depressant medications), known to affect visual performance or cortical function.

Stimuli

Battenberg stimuli have a checkerboard arrangement, consisting of signal checks alternating with uniform luminance checks. In this study, the signal checks contained luminance-modulated, drifting sine wave gratings with a spatial frequency of 3c/°. Uniform checks were 0% contrast and had the same mean luminance as the display background. The size of the check regions within the Battenberg stimulus containing signal could be varied to measure dependence on local signal area without adjusting the overall stimulus size; 10° across all conditions. Four different check sizes were used (Figures 5.1A-D): 0.71°, 1.43°, 2.0°, 3.33° to test performance

for the Battenberg stimuli, as well as the 'full' stimulus (square of 10° side length) with no blank regions (Figure 5.1E).

The luminance variation across space and time ($L[x, t]$) of a drifting sine wave grating is:

$$L[x, t] = L_m[1 + c \cdot \cos(2\pi f_s \cdot x + 2\pi f_t \cdot t + \phi)] \tag{3}$$

where L_m is the mean luminance of the display, c is amplitude, f_s is the spatial frequency, f_t is the temporal frequency and ϕ adjusts the phase of the grating. The checks were smoothed at the edge using a raised sine envelope that occupied a uniform width strip equal to 10% of the distance from the centre to the nearest edge of the square check. The blurring in the corners was therefore √2 wider.
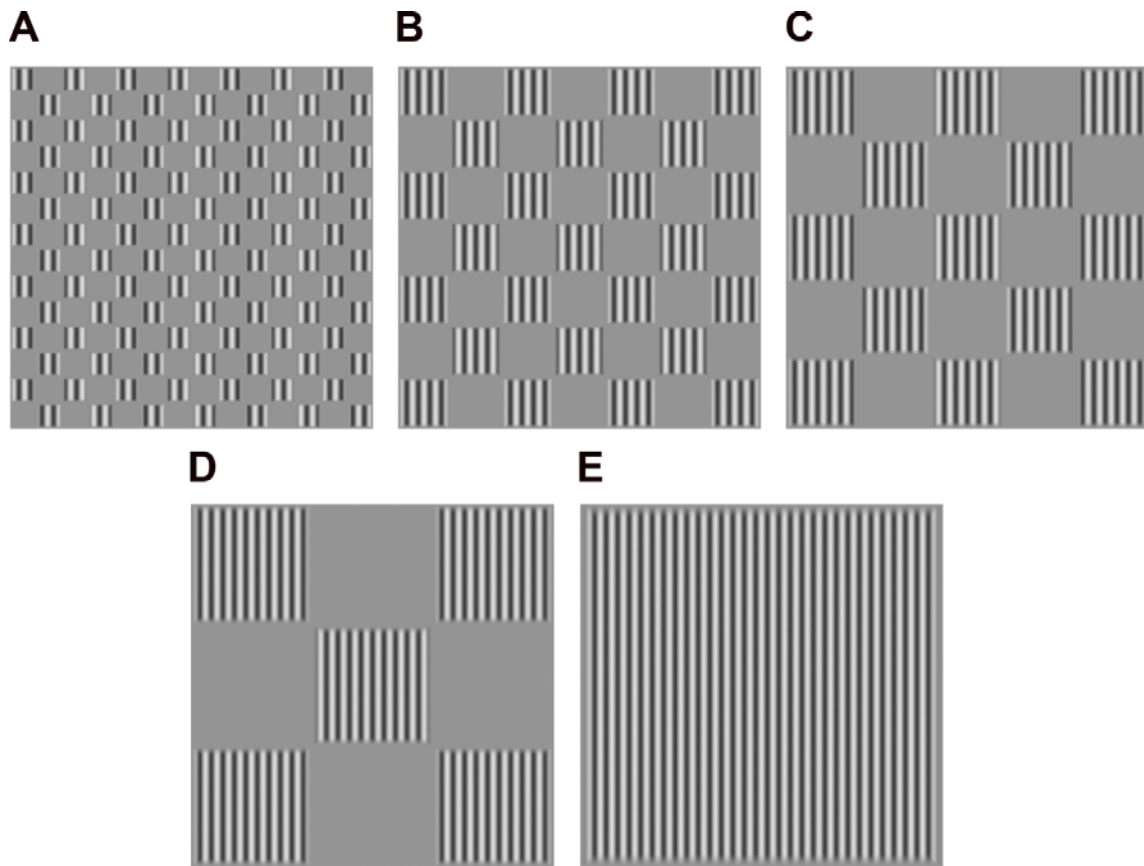
Figure 5.1. Examples of the stimuli used. The four Battenberg patterns had check edge sizes of

0.71°, 1.43°, 2.0° and 3.33°, (A-D respectively). The full stimulus (E) had a side length of 10°.

All checks drifted in the same direction, randomly selected as left or right at the start of each

trial.

Procedure

To ensure direction selective processing, the minimum contrast required to discriminate

motion direction (left or right) was measured. Stimuli were presented for 300ms in a single

temporal interval marked by an auditory beep, followed by a 1s pause before the next

presentation. Motion direction (left or right) was selected randomly at the start of each trial with

equal probability. Observers were required to indicate by pressing a button box which direction

they believed the pattern to be moving. Auditory feedback was provided. Observers fixated on a cross at the centre of the screen which was present before each trial. On each run, a three-down, one-up staircase procedure was used to converge upon the 79.4% correct performance level (Wetherill, 1963; Wetherill & Levitt, 1965). The procedure terminated after six reversals and threshold was calculated as the mean of the contrast levels for the last two reversals. Each condition (four Battenberg conditions and one full condition) was repeated five times and these were averaged to give a single threshold (the minimum contrast required to discriminate motion direction) per condition.

Results

Figure 5.2 shows raw motion direction discrimination thresholds for the stimuli shown in Figure 5.1. The top panel shows individual results and the bottom panel shows the averaged group data. In Figure 5.3, thresholds have been transformed to indicate summation ratios (contrast threshold for Battenberg/contrast threshold for full stimulus) in dB units, following previous work (Baldwin, Husk, Meese, & Hess, 2014; McDougall et al., 2016; Meese, 2010) This transformation indicates the reduction in the level of summation for each of the Battenberg stimuli, relative to the full stimulus and also adjusts for the overall differences in individual sensitivity to the 'full' stimulus.
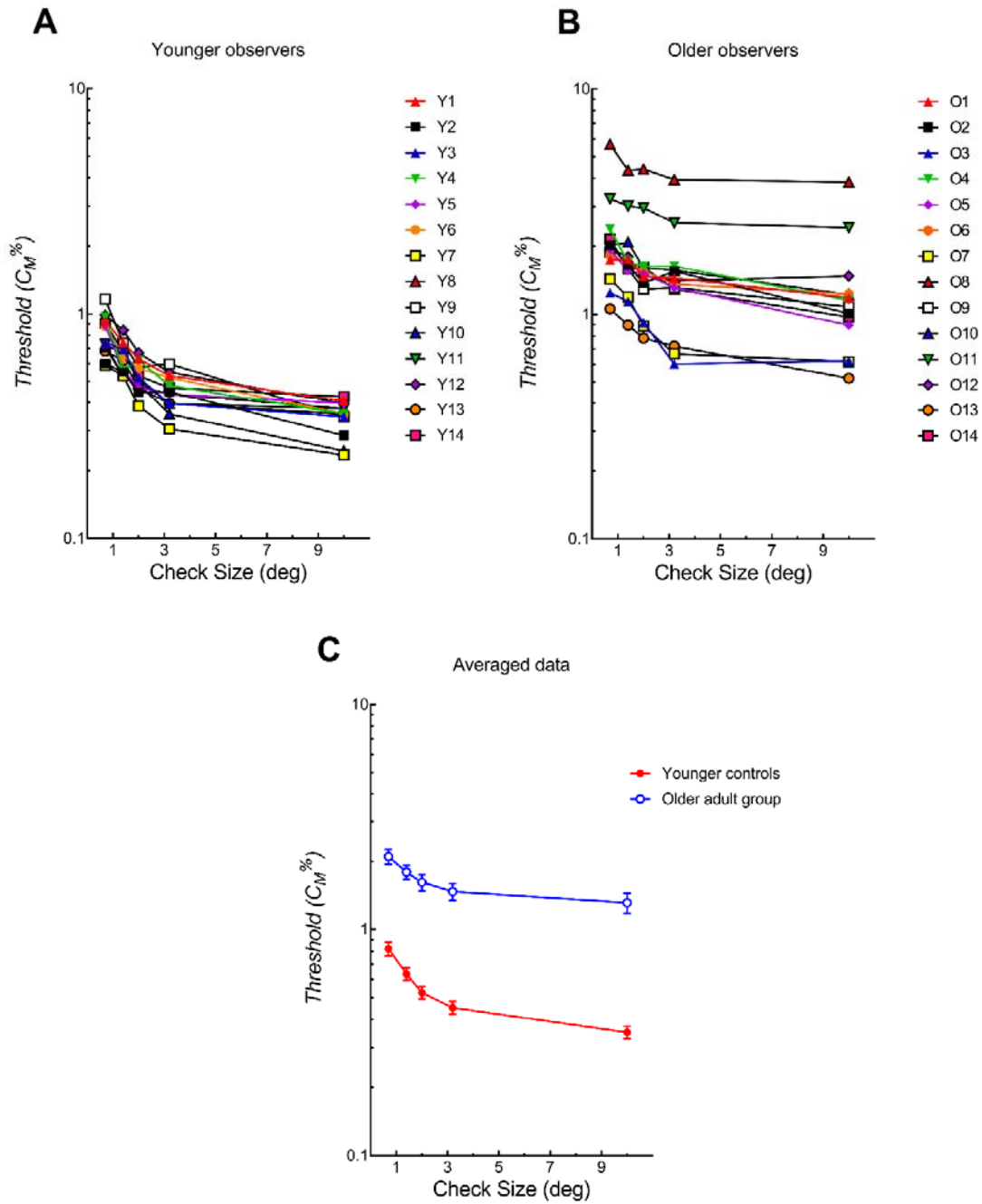
Figure 5.2. Contrast thresholds for the 'full' stimulus and each of the checked Battenberg stimuli for younger (A) and older observers (B) individually. The averaged data for the older and younger groups are plotted in panel C. Error bars represent 95% confidence intervals of the mean.

Raw Threshold Analysis

Motion direction discrimination thresholds for both younger and older observers were highest for the Battenberg stimulus with the smallest sized check (0.71°) and decreased as check size increased, indicating that spatial summation occurred to produce improvements in threshold in both groups. A mixed design, two-way, repeated-measures analysis of variance (ANOVA) was conducted with contrast threshold as the dependent variable, and check size (0.71°, 1.43°, 2.0°, 3.33°, and 'full') and group (younger vs older) as independent variables. The analysis revealed a significant main effect of group, $F(1,26) = 21.683$, $p < .001$, partial $\eta^2 = .455$, indicating that older observers had higher contrast thresholds for discrimination of motion direction (Figure 5.2C). Post-hoc tests, with Sidak corrections to control for familywise error rate, confirmed that the threshold increase in older observers was consistent across all stimulus configurations (all p's $< .0014$). The analysis also revealed a significant effect of check size, $F(4, 104) = 107.913$, $p < .001$, partial $\eta^2 = .806$, as expected from spatial summation, in both groups. In addition, there was a significant interaction between age and check size ($F(4, 104) = 9.747$, $p < .001$, partial $\eta^2 = .267$), indicating that check size had different effects in the two age groups. Separate analyses of the older and younger group data revealed that performance was different between all check sizes for the younger group (main effect of group: $F(4,52) = 107.510$, $p < .001$, post-hoc tests with Sidak corrections: all p's $< .01$). There was a similar overall effect of check size for the older group ($F(4,52) = 51.740$, $p < .001$), however, post-hoc tests with Sidak corrections showed no difference in thresholds for the 2.0° vs 3.33° Battenberg stimuli ($p = .078$), whereas all other comparisons were statistically significant (all p's $< .05$).
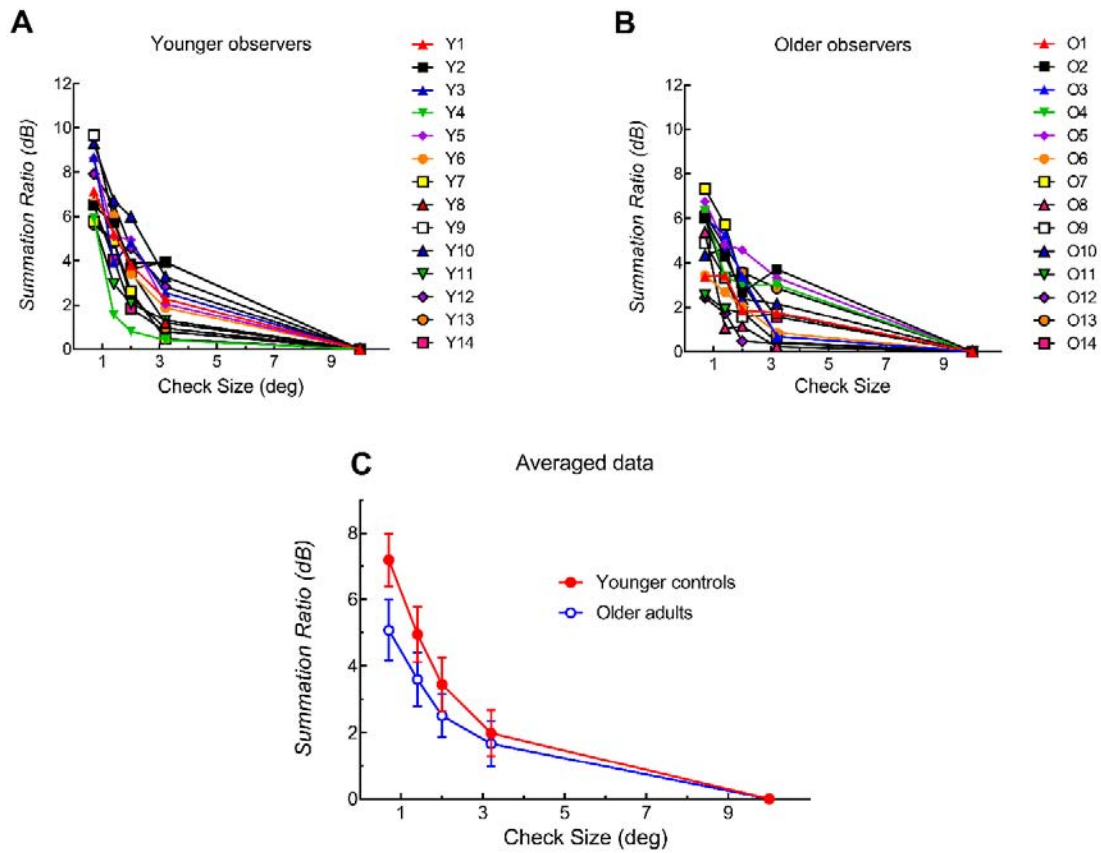
Figure 5.3. Individual summation ratios (Battenberg/Full) for younger (A) and older observers (B). The averaged summation ratio data for the younger and older groups are plotted in Panel C. Error bars represent the 95% confidence intervals around the mean.

Summation Ratio Analysis

The magnitude of summation across check sizes can be examined by calculating summation ratios (Battenberg/Full-sized stimulus), consistent with previous work (McDougall et al., 2016; Meese, 2010). This also normalises the data for the overall differences in thresholds between the two groups (higher thresholds in older observers). A two-way, repeated measures ANOVA conducted on the summation ratio data (Figure 5.3) indicated a main effect of check

size, $F(4, 104) = 200.700$, $p < .001$, partial $\eta^2 = .885$, a main effect of group, $F(1, 26) = 7.418$, $p = .011$, partial $\eta^2 = .199$, and a significant interaction $F(4,104) = 6.460$, $p = .011$, partial $\eta^2 = .186$ (Figure 5.3C). Post-hoc t-tests, with Sidak corrections, were conducted on the main effect of group to further explore this interaction. A significant difference in summation ratio between the older and younger observers was found for the 0.71° condition ($p < .0001$, Cohens $d = .246$) and 1.43° condition ($p = 0.032$, Cohens $d = .745$), but the groups did not differ for the larger check sizes (2.0° and 3.33°, $p = 0.216$ and $p = 0.922$, respectively).

Discussion

This study used the Battenberg paradigm to examine the effects of ageing on contrast summation for motion direction discrimination. Older adults had higher motion direction discrimination thresholds overall, consistent with previous research (Owsley, 2011). Both groups showed the same trend of lower thresholds as stimulus size increased. To assess summation we calculated a summation ratio, which conveniently normalises for differences in overall contrast threshold for the largest stimulus. For the younger observers the results follow the typical summation behaviour seen in previous Battenberg stimulus studies (McDougall et al., 2016; Meese, 2010) and the closely related Swiss Cheese stimulus study (Baker & Meese, 2011). Using Meese's (2010) interpretation, the initial peak in summation for the smallest check size is consistent with short-range summation within linear filters (stage one). The summation ratios drop as check size increases but a relatively high summation ratio of 2dB was maintained for the largest check size in both groups (Figure 5.3C) and did not drop to low levels typically associated with probability summation; i.e. when 1.5dB is used as the fiducial value equivalent to a fourth-root summation rule (McDougall et al., 2016; Meese, 2010). Therefore, summation is unlikely to be compatible with a process of probabilistic summation of responses across multiple,

independent, detectors and is more likely to be subserved by a stage of long-range signal summation (stage two) within receptive fields that, in this case, extends over an area at least as large as 3.33°. Given that this was evident for both groups, it suggests that normal long-range summation mechanisms are in place for these sizes, irrespective of age.

Inspecting the manner in which the magnitude of summation changes as check size reduces allows us to examine short-range summation mechanisms. The average summation ratio for the younger observers for the smallest check size suggests that the full stimulus (which contains twice the amount of contrast signal) offered more than a doubling in threshold improvement, whereas for the older observers the full stimulus offers slightly less than a doubling in threshold improvement. It is important to point out that the average summation ratio for the younger observers for the smaller check sizes was 7.1dB which is 1dB more than the expected linear summation (6dB) within filter mechanisms, based on previous Battenberg summation studies. However, the majority of observers cluster around 6dB to 6.5dB (see Figure 5.3A), which would suggest normal linear within-receptive field summation (a halving in threshold with a doubling in total signal) in most of our young observers. The more systematic change is the reduction in summation ratio for smaller checks in the older adults. This suggests abnormal spatial summation properties of short-range mechanisms with ageing. This may be due to increased summation area of these short-range mechanisms that are responsible for processing the smaller check sizes, and as such there is less of a benefit when extra signal is added (the 'full' stimulus), producing a reduction in relative sensitivity between the small check stimuli and the larger full field stimulus.

Given that previous studies show minimal contribution of motion surround suppression at low contrast (Hunter & Born, 2011; Pack, Hunter, & Born, 2005; Tadin, 2015; Tadin et al.,

2003), the results here are more likely to be a consequence of a dissociative change in summation mechanisms in older observers. This would be consistent with the gain model proposed by Betts et al. (2012) which predicts an increase in the size of the excitatory CRF's responsive to motion. This model is less likely to be explained by changes in GABA mediated inhibition in the ageing brain, however it is possible that changes in GABA can potentially allow for expansion of the excitatory receptive field, and therefore this link cannot be ruled out entirely (Betts et al., 2012). This has some support from a recent study by Schallmo et al. (2017) which examined human MT complex (hMT+) using magnetic resonance spectroscopy and found that GABA concentration was correlated with better motion perception in general, but was not correlated with the strength of spatial suppression specifically.

Differences in motion summation and suppression have been reported in other clinical populations. For example Foss-Feig, Tadin, Schauder, and Cascio (2013) found increased spatial summation for low contrast motion stimuli in a group of individuals diagnosed with autism spectrum disorder (ASD). A recent a psychophysical study found that the differences in spatial summation for motion direction discrimination in ASD were specific to small stimuli (Schauder, Park, Tadin, & Bennetto, 2017), similar to what is seen here in this study for older adult observers. Schauder et al. (2017) used computational modelling to reveal larger excitatory receptive field sizes in ASD as the mechanism responsible for summation differences for perception of smaller stimuli. Our data, for older observers, also implicates larger receptive field sizes for the perception of small moving stimuli. Both ageing and autism have been proposed to have imbalances in excitation and inhibition (Leventhal et al., 2003; Rubenstein & Merzenich, 2003) and in both groups this may manifest as larger measurable excitatory receptive fields.

Conclusions

We have used Battenberg stimuli to reveal that ageing is associated with an increase in psychophysical summation area for the perception of small moving stimuli at threshold for direction discrimination. This summation enhancement may result in erroneously pooling together signals from distinct, small moving objects, which may lead to spurious percepts for older adults and thus contribute additional motion noise. In the younger visual system, smaller summation areas may be beneficial to increase spatial resolution and better detect local motion differences to facilitate effective motion segmentation in situations where segmentation is more useful (Braddick, 1993; Tadin, 2015) . The control over the influence of noise offered by the Battenberg method changes summation estimates and suggests the procedure should be considered whenever studying groups that are suspected to have imbalanced cortical inhibition and excitation so that resultant differences in summation behaviour can be more clearly ascertained.

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Author/s:
McDougall, TJ; Nguyen, BN; McKendrick, AM; Badcock, DR

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