DR. BAO N NGUYEN (Orcid ID : 0000-0002-3097-619X)

DR. ALLISON MCKENDRICK (Orcid ID : 0000-0003-1972-1222)

Article type : Feature Issue Manuscript

Title page

Full title: Ageing elevates peripheral spatial suppression of motion regardless of divided attention

Running head: Ageing effects on peripheral motion suppression

Authors' names and institutional affiliation: Soa Park; Bao N Nguyen; Allison M McKendrick

Department of Optometry and Vision Sciences, The University of Melbourne, Parkville, Victoria, Australia

Corresponding author:

Allison M McKendrick

E-mail address: allisonm@unimelb.edu.au

Keywords: ageing, divided attention, centre-surround suppression, motion perception, peripheral vision, spatial suppression

Author contributions: SP & AMM: Involved in all aspects of study conception and design; data acquisition, analysis and interpretation; and drafting and critically revising the manuscript. BN: Involved in data interpretation and drafting and critically revising the manuscript.

Abstract

Purpose: It is more difficult to perceive the direction of motion of larger, high contrast patterns than smaller, low contrast patterns due to spatial suppression. Spatial suppression of motion is considered important to the segmentation of moving objects in the visual environment. Previous studies have shown that such spatial suppression of motion is reduced in older adults in central vision, to the extent that older adults can have better sensitivity than younger adults for foveally presented stimuli. Our study was designed to explore whether spatial suppression of motion is similarly reduced for older adults in parafoveal regions and whether divided attention impacts on suppression strength because attention is known to impact on spatial interactions.

Methods: Twenty younger (19-34 years) and 18 older (61-77 years) adults completed a single task, where observers identified the direction of a drifting Gabor patch of variable size (σ of the Gaussian envelope = 0.5, 1, 2, 3, 4°) presented at 10 degrees of visual angle while observing a central fixation marker, and a dual task, where observers were required to divide their attention across two stimuli, the peripheral drifting Gabor patch and a central rapid serial visual presentation (RSVP) stream.

Results: Older adults showed increased spatial suppression of motion relative to younger adults for both tasks (main effect of group: $p<0.001$). Dividing attention elevated thresholds for both age groups to a similar extent (main effect of attention: $p=0.002$), but did not specifically alter spatial interactions (group x attention interaction: $p=0.13$).

Conclusions: Older adults require significantly longer than younger adults to correctly identify stimulus motion, and demonstrate increased spatial suppression of motion, in peripheral vision. When considered alongside previous evidence for reduced suppression for central fixation, our study provides evidence for substantial differences between foveal and parafoveal mechanisms of spatial suppression.

Introduction

The process of ageing results in wide ranging changes to visual function.[1, 2] One specific aspect of visual function altered by ageing is perceptual spatial suppression, otherwise known as centre-surround suppression.[3-7] For moving stimuli, spatial suppression is considered to assist the visual system to segregate different moving objects from their backgrounds[8] and to provide cues in mid-peripheral vison to subsequently direct saccadic eye movements to objects of interest.[9-11] To investigate perceptual surround suppression of motion, a commonly used task is a motion discrimination procedure which measures the stimulus duration required to accurately determine the direction of motion of Gabor patches of varying sizes and contrasts.[12] Increasing the size of a high-contrast Gabor stimulus makes it more difficult to correctly determine its motion direction, as demonstrated by an increase in duration thresholds.[12] This task is widely considered as a perceptual analogue of neuronal surround suppressive mechanisms in visual cortex (possibly specifically the middle temporal area MT[13,14,15]), where suppression is driven by a combination of local feedforward and areal feedback mechanisms to the neuronal receptive field surround.[16-19]

Several studies report reduced, or a trend for reduced, surround suppression on the motion direction discrimination task in healthy older adults relative to younger adults as demonstrated by shorter duration thresholds for larger, higher contrast stimuli in the older adult group.[3-7] The mechanisms underpinning this effect are somewhat unclear, with initial theories proposing that reduced motion spatial suppression strength may reflect decreased gamma-aminobutyric acid (GABAergic) inhibition in the elderly.[3] More recent reports demonstrate increased GABA concentration in human older adult visual cortex measured with magnetic resonance spectroscopy,[7] increased perceptual suppression in the contrast domain,[5, 6, 20-23] and slowed binocular rivalry switching implying stronger inhibition.[24, 25] Consequently, a simple theory of reduced cortical inhibition in older adults does not provide a clean explanation for these observations. Furthermore, more recent neurophysiological studies in primates,[26] and neuroimaging studies in humans,[27] provide consistent evidence that this type of spatial suppression of motion is not primarily driven by GABAergic inhibition.

Notably, for the perceptual tasks, previous studies of the effects of age on spatial suppression of motion have tested central vision. It is not necessarily the case that similar outcomes will be found when using non-central fixation. Using an centre-surround contrast perception task, Nguyen & McKendrick[22] specifically compared the effects of near and far surrounds on contrast perception at a fixation eccentricity of 6 degrees in order to more directly relate perceptual findings to the eccentricity at which receptive field properties of primate neurons are studied in neurophysiological studies.[11] Intriguingly, the magnitude of surround suppression in older and younger adults differed for both eccentricities but in opposite directions, possibly reflecting different wiring between foveal and parafoveal (6 degrees) surround representations neuronally. Consequently, in this study, we first considered whether surround suppression of motion differs between older and younger adults for non-foveal fixation (specifically at 10° eccentricity from fixation which we refer to hereafter as "peripheral"), and whether the measured difference is phenomenologically similar to that previously reported for central fixation (a weakening of surround inhibition in central vision in older adults).

Additionally, in this study we considered the effect of divided attention on peripheral surround suppression of motion. Previous studies demonstrate that directing attention to peripheral locations can improve performance on a texture segregation task,[28] and can alter neurophysiological spatial integration in awake-behaving primate experiments.[29, 30] Specific to motion perception, one recent study reported that healthy younger adults showed a paradoxical improvement in motion discrimination when dividing their attention across two simultaneous tasks.[31] In the study by Motoyoshi and colleagues, observers were required to identify the coherent global motion of a random-dot kinematogram (RDK), and two digits from a rapid serial visual presentation (RSVP) stream. The tasks were spatially overlapping. Divided attention improved observers' motion sensitivity, which the authors attributed to a decrease in spatial suppression with concomitant expansion of spatial motion integration when attention was directed away from the motion task.[31] In the case of spatial suppression of motion for Gabor stimuli, dividing attention might decrease suppression because it has been shown that attention can increase the effective stimulus contrast.[32]

Dividing attention is important to performance on many daily visual tasks, for example driving, and has been previously shown to be more difficult in the elderly (for example, using the Useful Field of View Test, see reviews by Owsley[1, 33], and as a more general phenomenon see meta-analysis[34]). We therefore investigated how older and younger adults perform when they must divide their attention across two concurrent spatially separated tasks: a motion direction discrimination task (presented peripherally at 10° eccentricity), and identification of numbers from a RSVP stream presented at two different speeds to vary the difficulty of the attentional task.

In summary, our study was designed to answer the following questions:

1) Are the previously observed effects of ageing on centrally fixated spatial suppression of motion also observed for fixation at 10 degrees eccentricity? Alternately, similarly to surround suppression of supra-threshold contrast, is there a distinct phenomenological difference in the impact of age on foveally fixated and non-foveal suppressive phenomena?
2) Does divided attention reduce surround suppression of motion direction discrimination, similarly to the previously reported effects of attention on global motion integration?
3) Is there an interaction between the effects of attention and age, such that older adults show greater impact of dividing attention on spatial suppression of motion due to the need to harness greater attentional resources to maintain task performance?

Methods

Participants

Twenty younger adults (19-34 years), and 18 older adults (61-77 years) participated in the study. Ethics approval was granted by the Human Research Ethics Committee of the University of Melbourne and the study protocol adhered to the tenets of the Declaration of Helsinki. Participants provided written consent prior to testing. All participants underwent an ophthalmic examination by a registered optometrist as part of the study including anterior and posterior eye examinations (slit lamp and fundus lens), and assessment of their visual acuity and subjective refraction. Monocular visual acuity was measured at 3m with a logMAR chart and was required to be 0.2 logMAR (Snellen equivalent 6/9.5) or better for inclusion in the study. Experiments were conducted binocularly, and all participants had binocular VA of 6/7.5 or better. Other inclusion criteria were: normal ocular health for age, and refractive error between ±5.00 D spherical, with less than 2 D astigmatism. Any volunteers with systemic conditions or medication usage known to affect visual or cognitive functions were excluded. All participants completed the Mini Mental State Examination (MMSE) and scored 28-30, which is within the normal range.[35]

Apparatus

Experiments were conducted in a darkened room using a Dell Precision T1700 computer (www.dell.com/) with a gamma-corrected Display ++ LCD monitor (screen resolution 1920 x 1080 pixels, frame rate 120 Hz, mean luminance 98 cd/m^2; www.crsltd.com/). Experiments were custom developed in Python using the coder version of PsychoPy V1.85.4 (www.psychopy.org)[36]. A Gazepoint GP3 Eye Tracker and Gazepoint Control x64 v4.1.0 (www.gazept.com) were used for eye tracking to monitor whether participants were maintaining steady central fixation. The binocular viewing distance was 1m from the monitor, maintained using a chin and forehead rest. Participants were refractively corrected for the viewing distance in a trial frame or with own spectacles if appropriate. For most of the older adults, this involved using the subjective refraction results with a +1.00DS for the working distance. Younger adults wore a mixture of trial frames, own spectacles, or no correction depending on their subjective refraction and form of habitual spectacles. No participants wore contact lenses for the experiments.

Visual stimuli

For the motion direction discrimination task, the stimulus was a high contrast (92%) drifting Gabor patch of varying size (σ of the Gaussian envelope = 0.5, 1, 2, 3, 4°) centred at 10° eccentricity to the left of fixation (*Figure 1A*). The spatial frequency of the vertical sine-wave grating was 1 cyc/deg, and the drift rate was 2 deg/sec. The starting phase of the sinewave was varied for each trial. Stimulus duration was varied using two interleaved 3-down 1-up staircases that each converged on the approximate 79% correct response level [37]. Each staircase terminated after six reversals, with the step-size commencing at 8 frames, then being halved at the next two reversals. The threshold estimate of each staircase was taken as the mean of the last four reversals (step-size = 2 frames). The average of the two staircases was taken as the final estimate of the duration threshold for each size tested.

The RSVP stream, a series of four randomised alphabetical letters (chosen from possible letters: A, B, C, D, E, F, G, H, J, K, L, M, N, P, R, T, U, V) and two numerical digits randomly chosen from 1 to 9, was presented centrally (*Figure 1A&B*). At least one letter was always presented between the numbers, and letters were 2 degrees of visual angle in height. The stream was presented at two different speeds (number of frames), 83ms (10 frames/sec) and 117ms (14 frames/sec). Participants were required to identify the numbers interspersed within the stream of letters.

Procedures

Participants completed two task conditions (single-task or dual-task), and two RSVP speed conditions (83ms and 117ms) following sufficient practice runs of each task to ensure comfort with task requirements. The single-task simply required the identification of the direction of drift for the peripheral Gabor (either left or right) while directing their gaze to a central white fixation dot. Auditory feedback was provided for both correct and incorrect responses using auditory tones. For the dual-task condition (conducted at the two RSVP speeds), participants had to divide their attention across two concurrent tasks: the peripheral motion direction discrimination task (which varied stimulus duration using the same interleaved staircase procedure as the single-task) and the central RSVP task. Participants were instructed to identify the two digits (not necessarily in order) from the RSVP stream first, then identify the direction of the Gabor patch. Again, auditory feedback was given. The order of the tasks was randomised with breaks in between. Trials were discarded if the numbers in the RSVP stream were not correctly identified and were repeated (with newly generated RSVP stream).

Data Analysis

Duration thresholds (ms) for each size tested were normalised to the smallest patch size (0.5°) to evaluate the relative change in threshold as a function of size. A suppression index (SI) was calculated as per [3]:

$$Suppression\ Index\ (SI)\ =\ log_{10}\,(threshold\ of\ larger\ size) - log_{10}\,(threshold\ of\ smallest\ size)$$

where the larger sizes were either 1, 2, 3 or 4 degrees, and the smallest size was 0.5 degrees. A positive SI indicates spatial suppression, whereas a negative SI indicates spatial summation. IBM SPSS Statistics V24.0 (https://www.ibm.com/products/spss-statistics) was used for statistical analysis. Mixed analysis of variance (M-ANOVA) were used to compare the means of the younger group to the older group, and to explore interactions between motion stimulus size, RSVP speed, attention, and age group. Effect sizes are reported as partial eta-squared: (η_p^2) for results that reached conventional statistical significance ($p<0.05$).

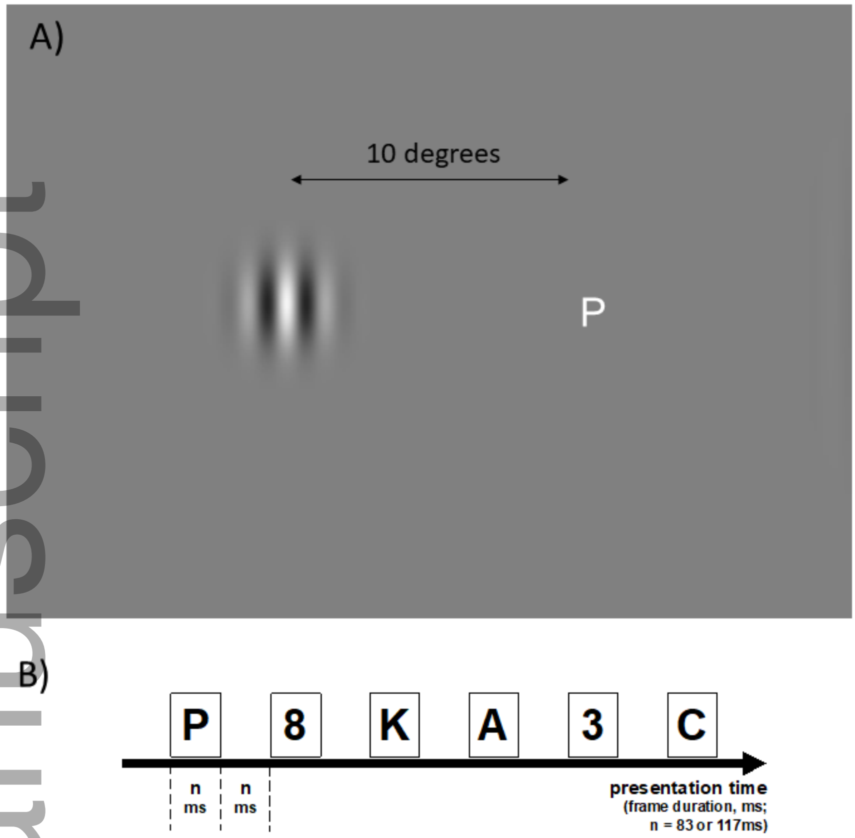


Figure 1. A) Schematic illustration (not to scale) of the positioning of the motion stimulus (Gabor patch) relative to the rapid serial visual presentation (RSVP) stream. B) An example RSVP stream. Four letters and two digits were presented in random order, with the condition that the two digits could not be sequential. The letters and digits were presented at a constant speed of 10 frames/sec (83ms) or 14 frames/sec (117ms) to vary the attentional load in separate runs. The interstimulus duration was equivalent to the letter presentation duration in each run.

Results

Effect of ageing on peripheral surround suppression of motion

Figure 2A plots the performance of older and younger adults on the peripheral motion direction discrimination task for the single task condition. Analysis was performed using a 2x2 mixed ANOVA with the between subject factor of age-group and the within subject factor of size. *Figure 2A* shows that duration thresholds increased with stimulus size for both groups (main effect of size: $F(4, 144) = 21.61$, $p < 0.001$, $\eta_p^2 = 0.37$). The average thresholds of older observers were consistently greater than those of younger observers across all sizes (main effect of group: $F(1,36) = 7.70$, $p = 0.008$, $\eta_p^2 = 0.17$). Differences between groups were the greatest at the two biggest sizes, 12° and 16° (size and group interaction: $F(4,144) = 5.36$, $p < 0.001$, $\eta_p^2 = 0.15$). When converted into suppression indices, both younger and older observers showed increased spatial suppression with increasing stimulus size (*Figure 2B*; 2x2 mixed ANOVA with the between subject factor of age-group and the within subject factor of size: main effect of size: $F(3, 108) = 46.83$, $p < 0.001$, $\eta_p^2 = 0.62$). However, older adults demonstrated consistently more suppression than younger observers (main effect of group: $F(1, 36) = 4.70$, $p = 0.03$, $\eta_p^2 = 0.11$). The difference in suppression between groups was most prominent for the bigger sizes compared to smaller sizes (size and group interaction: $F(3, 108) = 4.27$, $p = 0.01$, $\eta_p^2 = 0.11$).

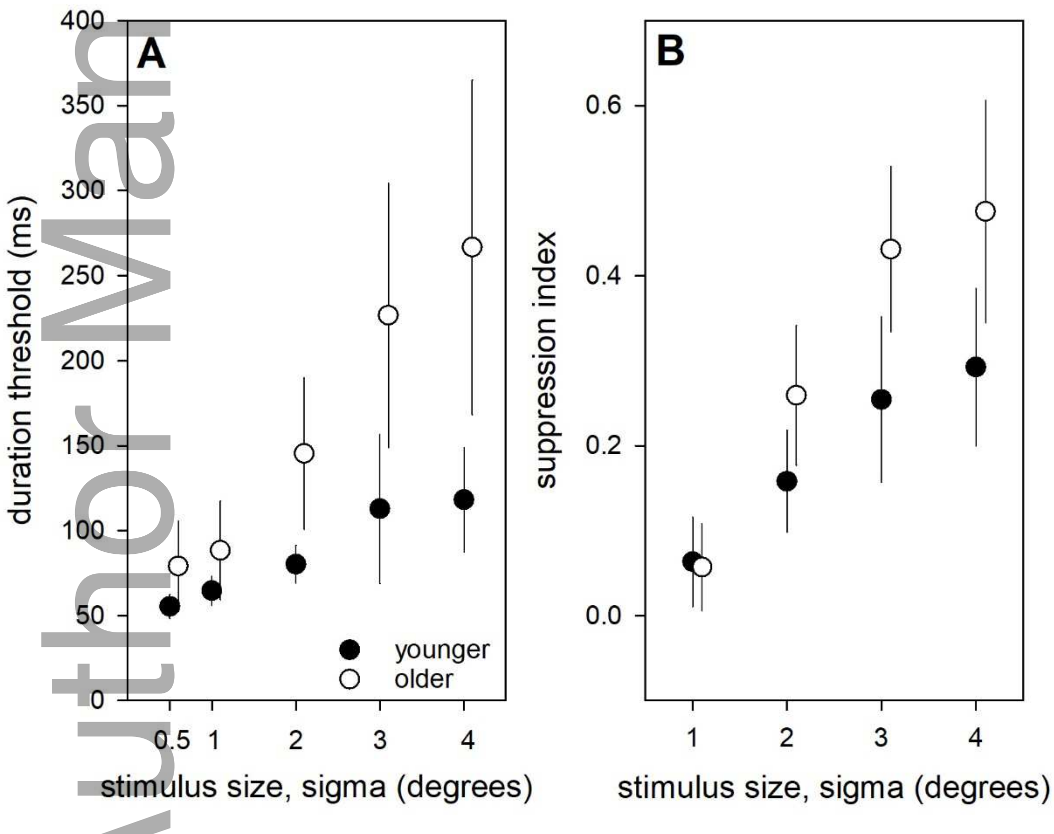


Figure 2. Results for the peripheral motion direction discrimination single task condition. (A) Average duration thresholds (ms) of older adults (open circles, n=18) and younger adults (filled circles, n=20) across increasing stimulus size. (B) Average suppression index (SI) of

older and younger adults across increasing stimulus size. Positive SI values indicate spatial suppression. Error bars are the 95% confidence intervals of the mean. Data have been nudged slightly on x-axis for clarity.

Effect of RSVP stream speed on peripheral surround suppression of motion

Figure 3 shows the effect of RSVP stream speed on peripheral surround suppression. M-ANOVA was performed with the between subject factor of age-group and within subject factors of size and RSVP stream speed. Across both groups, there was no difference in duration threshold (*Figure 3A*, main effect of speed: $F(1, 35) = 0.56$, $p = 0.46$) nor suppression index (*Figure 3B*, main effect of speed: $F(1, 35) = 0.004$, $p = 0.95$) between the two dual task conditions. Consistent with the single task condition (*Figure 2*), older adults showed greater duration thresholds and suppression indices than younger adults (main effect of group; duration threshold: $F(1, 35) = 22.63$, $p < 0.001$, $\eta_p^2 = 0.39$, suppression index: $F(1, 35) = 8.85$, $p = 0.005$, $\eta_p^2=0.20$), particularly with larger sized stimuli (size x group interaction; duration threshold: $F(4, 140) = 10.58$, $p < 0.001$, $\eta_p^2 = 0.33$ suppression index: $F(3, 105) = 4.82$, $p = 0.004$, $\eta_p^2=0.21$). However, the difference between groups was not dependent on the RSVP stream speed (speed x group interaction; duration threshold: $F(1, 35) = 0.74$, $p = 0.40$, suppression index: $F(1, 35) = 0.66$, $p = 0.42$). There were no significant three-way interactions between RSVP stream speed, stimulus size and group.

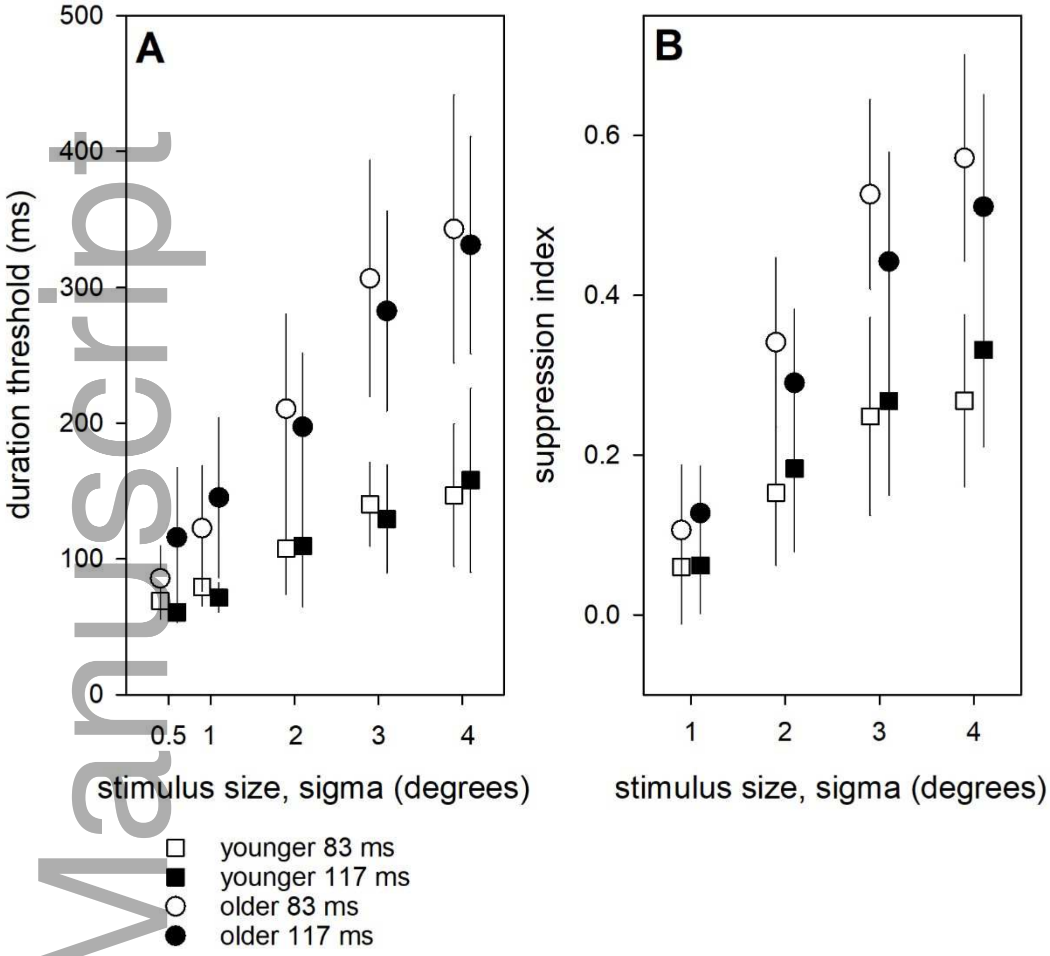


Figure 3. Results for the peripheral motion direction discrimination dual task conditions. (A) Average duration thresholds (ms) of older adults (circles, n=17 and younger adults (squares, n=20) across increasing stimulus size. There were two speeds of the rapid serial visual presentation (RSVP) sequence, 83ms, open symbols and 117ms, filled symbols. (B) Average suppression index (SI) of older and younger adults across increasing stimulus size. Positive SI values indicate spatial suppression. Error bars are the 95% confidence intervals of the mean. Data have been nudged slightly on x-axis for clarity.

Effect of divided attention on peripheral surround suppression of motion

Given performance for both groups was similar for the two RSVP stream speeds tested, we compared single versus dual task performance for the 117ms condition using a M-ANOVA with within-subjects factors of size and task (single or dual), and between subjects factor of group. Overall, duration thresholds for the dual-task condition were higher than for the single-task condition (*Figure 4A*, main effect of attention: $F(1, 36) = 11.46$, $p = 0.002$, $\eta_p^2=0.24$), indicating that divided attention increased the duration thresholds required to correctly identify the direction of stimulus motion. Older adults also measured higher thresholds across all tasks relative to younger adults (main effect of group: $F(1, 36) = 11.10$, $p = 0.002$, $\eta_p^2=0.23$). However, the impact of dividing attention on duration threshold did not differ between the groups (non-significant group x attention interaction: $F(1, 36) = 2.43$, $p = 0.13$).

When data was converted into suppression indices, there was no difference in suppression strength between the single-task and the dual-task for both age groups (*Figure 4B*, main effect of attention: $F(1, 36) = 0.69$, $p = 0.41$; attention x group interaction: $F(1, 36) = 0.08$, $p= 0.79$). Hence, the effect of dividing attention was to elevate the thresholds but not in a size dependent fashion (no interaction between attention and size ($F(3, 108) = 0.18$, $p=0.91$). There were no significant three-way interactions between task, stimulus size and group.

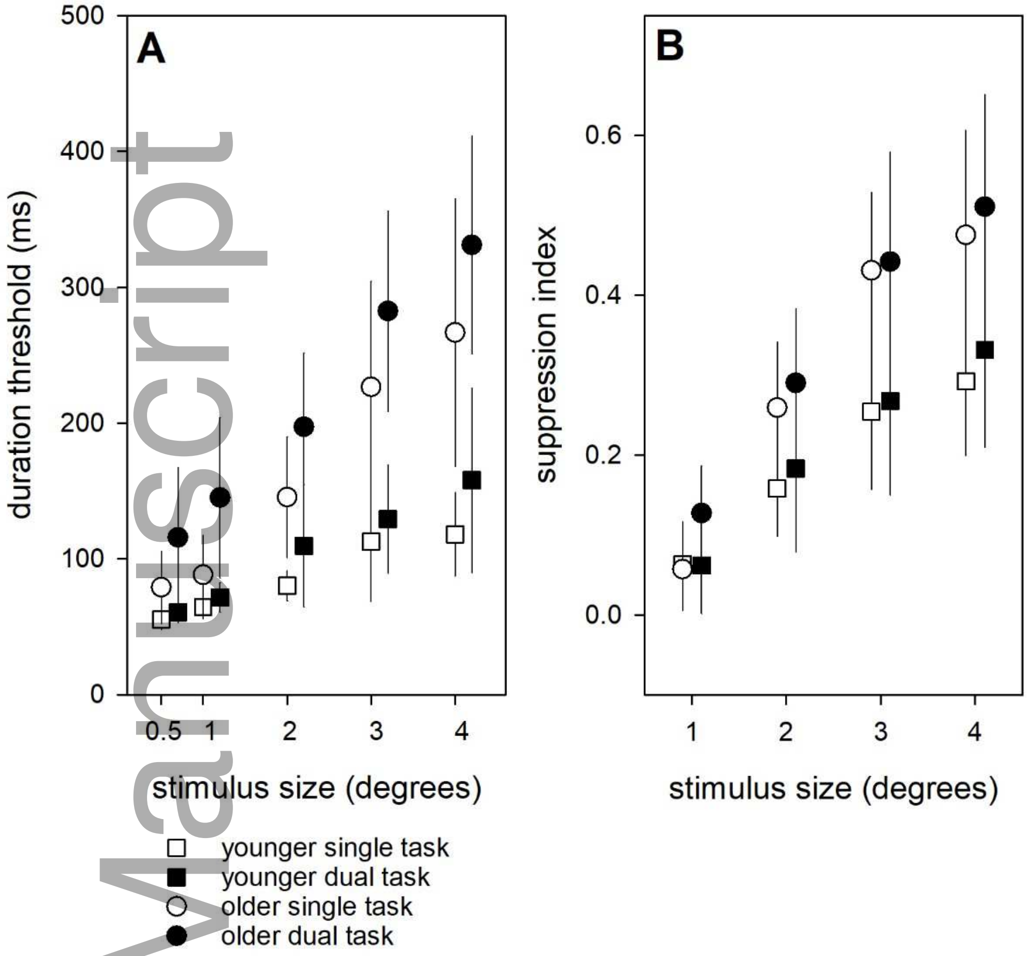


Figure 4. Results for the peripheral motion direction discrimination single versus dual task conditions. (A) Average duration thresholds (ms) of older adults (circles, n=18) and younger adults (squares, n=20) across increasing stimulus size in the single task (open symbols) and dual task (filled symbols) conditions. (B) Average suppression index (SI) of older and younger adults across increasing stimulus size. Positive SI values indicate spatial suppression. Error bars are the 95% confidence intervals of the mean. Data have been nudged slightly on x-axis for clarity.

Discussion

This study explored how older adults' ability to determine the direction of motion of a briefly presented object differed to younger adults, and whether performance was affected when attention was directed to a central task. The specific task of interest was a spatial motion direction discrimination task, which is considered a perceptual analogue of neuronal centre-surround interactions. Both older and younger groups exhibited increased duration thresholds and suppression strengths with increasing stimulus size, demonstrating spatial suppression with increasing stimulus size. Older adults required longer stimulus durations to correctly identify the direction of motion of the target than younger adults, particularly for the larger stimuli. This size dependent elevation of threshold indicates greater surround suppression in the older group in peripheral vision. Dividing attention increased thresholds for both groups to a similar extent.

Perceptual surround suppression of motion has received considerable attention in the literature because of relatively close links between the stimulus features that alter human perception and primate neurophysiology.[11] In the context of healthy ageing, only foveal vision has previously been tested, with studies showing that surround suppression of motion is reduced in the elderly in the fovea.[3, 7, 38] Indeed, one study found that suppression was reduced to the extent that older adults actually had lower thresholds for the detection of motion of large high contrast gratings than younger adults.[3] We do not replicate that effect when testing outside the fovea. Instead, our data collected at 10 degrees of visual angle indicates stronger surround suppression of motion in older adults.

Although we did not measure foveal surround suppression in this study, we deliberately used the same variable size motion discrimination task and stimulus as previous reports in central vision.[3, 7, 12, 39] It is also notable that the effect of elevated suppression in our older adult group was found across three separate experimental conditions (undivided attention and two divided attention conditions) demonstrating repeatability of the result.. The data for these experimental conditions was collected in separate blocks, with the block order randomised between participants and groups to avoid systematic learning or fatigue effects.

The neuronal circuitry that underpins neuronal surround suppression involves a complex network of feedforward, lateral and feedback circuits.[16-19] While most psychophysical studies are conducted using central fixation, neurophysiological experiments typically avoid the immediate foveal representation due to the complexity of very dense and small receptive fields. Consequently, comparisons between neurophysiology and parafoveal vision are likely to yield closer linkages than foveal testing.[11] Indeed, differences in foveal and parafoveal vision can provide interesting insights into the neurophysiology of human vision.[22] The current study, in combination with previous work, demonstrates that the healthy ageing process results in opposite phenomenological effects on surround suppression of motion between the fovea and the parafovea: namely a reduction in suppression foveally, but a strengthening of suppression at 10 degrees. Contrasting effects of ageing across the visual field on surround suppression of perceived contrast have previously been reported.[22] Surround suppression of perceived contrast is stronger in older adults than younger adults in the fovea, but weaker than younger adults at 6 degrees.[22] Motion suppression and contrast suppression do not assess the same mechanisms,[38] however, the study of adults of varying age reveals evidence of eccentricity dependent circuitry that is differentially affected by the ageing process for both perceptual phenomena.

In the original study reporting reduced surround suppression of motion in older adults,[3] the authors suggested that their foveally measured perceptual findings may be related to reduced inhibitory GABAergic mechanisms in the senescent brain. Previous primate studies have shown that senescent visual cortical neurones are less selective for orientation than younger animals,[40-42] and that some of the tuning can be restored by the application of GABA agonists.[43] This finding has been widely interpreted as possible evidence for reduced GABAergic inhibition in the visual brain as a consequence of ageing. However, more recent human brain imaging using magnetic resonance spectroscopy demonstrates increased GABA levels in human primary visual cortex (V1) in older people [7]. Elevated GABA was regionally specific to V1 and inversely correlated with perceptual surround suppression of motion measured foveally.[7] Peripheral motion suppression was not measured in that study, however, our current finding of increased perceptual surround suppression of motion outside of the fovea is more aligned with increased rather than decreased availability of GABA, if indeed GABA estimates are of relevance to spatial suppression of motion. Firstly, GABA estimates from magnetic resonance spectroscopy do not provide evidence for bioavailability, but more importantly, recent evidence demonstrates that manipulation of

$GABA_A$ receptors has little influence on surround suppression of motion measured either neurophysiologically in primate [26], or psychophysically in humans[27]. Clearly, a simple model of reduced inhibitory neurotransmitter availability in older adult visual cortex does not align with recent neuroimaging or perceptual evidence[7]. Future experiments linking GABA estimates to perceptual surround suppression across the visual field, and across the lifespan, may provide useful additional information to help further our understanding of the linkage, in any, between these factors.

In our experiments, the orientation of the Gabor patch was vertical, hence the motion direction was horizontal. As the patch was displaced horizontally from fixation, the motion was therefore centrifugal. It has previously been reported that there are strong centrifugal biases in motion perception for short duration stimuli presented at 40 degrees eccentricity resulting in the velocity of the stimulus appearing faster than veridical.[44] It is not clear whether this effect is present at eccentricities significantly closer to fixation such as used herein (10 degrees). If present, there is the possibility that perception of our shorter duration stimuli (smaller sizes) might be influenced by this bias, and potentially more so for the younger adults because their thresholds were lower. Future experiments may like to consider varying the orientation of the Gabor to test this possibility directly. It is worth noting that centrifugal biases exist in the strength of surround suppression of contrast depending on the direction from fixation and eccentricity in the visual field.[45] We have recently explored perceptual centre-surround contrast suppression in older and younger adults to explore for differences in orientation anisotropies at 6 degrees and 15 degrees eccentricity.[46] Both groups showed stronger suppression for stimuli that were oriented cardinally at 6 degrees, and radially at 15 degrees, relative to other orientation pairings. Similar to our current experiment, older adults showed stronger suppressive effects that younger adults at these non-foveal eccentricities, however no differences in orientation biases were found between groups.[46]

Dividing attention resulted in elevated duration thresholds overall but did not change motion suppression indices. Our study was partially motivated by a previous observation that dividing attention paradoxically resulted in an improvement in sensitivity to motion cues encoded in random dot kinematograms.[31] Motoyoshi and colleagues proposed that dividing attention across two concurrent tasks would broaden the spatial region over which motion is integrated, by weighting network responses to summation of information rather than suppression. [31] There are notable differences in the experimental methods used, perhaps most significantly the spatial separation that we imposed between the location of attention (foveally fixated RSVP stream) and the motion stimulus (peripherally displaced). This displacement likely means that any localised variation in the area of summation/suppression around the attended location might not extend to the receptive fields relevant to our target Gabor. In contrast, Motoyoshi *et al*[31] embedded the RSVP stream in the centre of the RDK stimulus. We decided on spatial separation to prevent obscuration of our small Gabor targets by the RSVP stream, and to avoid alternate motion cues arising from stimulus overlap. Our study design is more similar to the Useful Field of View test, in which a central target is attended while a judgement is required regarding a peripheral stimulus that decreases in stimulus duration.[47] Previous studies demonstrate poorer performance of older adults on the Useful Field of Vision Test than younger adults (see reviews by Owsley[1, 33]). Here we show that duration thresholds are elevated in both groups, rather than a specific decline in the performance for the older adults. Our older adults were healthy, high functioning volunteers, interested in engaging in research studies, with minimal medication usage.

We used two RSVP stream speeds in an attempt to explore the effect of attentional load, and specifically to see whether a larger difference in performance between the older and younger adults might manifest when the task was more difficult (faster RSVP stream). Previous work demonstrated an interaction between RSVP stream speed and improved motion sensitivity under dual-task conditions.[31] We did not find a statistically significant effect of RSVP speed on motion direction discrimination performance, nor an interaction between speed and group. It is possible that the difference between 83 ms and 117 ms was not enough to elicit a measurable difference in performance. The choice of RSVP streams speed was based on the availability of integer numbers of frames and the logistical requirement that both older and younger observers could still reliably perform the task (i.e. not too fast that it was impossible). One older adult could not perform the RSVP task accurately at the faster speed (83ms) and pilot testing in younger adults for shorter durations was considerably more difficult (data not shown) hence not used for the main experiments.

In summary, we find that the strength of surround suppression of motion is increased in older adults in peripheral vision, which predicts that older adults will have more difficulty in segregating moving objects from their backgrounds in natural visual environments. Under divided attention, both younger and older groups required a longer stimulus duration to correctly determine the direction of motion of a drifting stimulus, however the relative magnitude of surround suppression did not alter with divided attention. Indeed, older adults had elevated surround suppression under all conditions tested. In terms of raw thresholds, for the largest high contrast stimuli under divided attention, the older adults required a stimulus duration that was more than twice that of the younger adults (approximately 342ms relative to 146ms). This observed effect is opposite to previous reports of performance using the same task tested foveally, where older adults have shorter thresholds than younger: a finding attributed previously to reduced spatial suppression. Our study highlights the importance of studying perceptual performance at different eccentricities, in order to both understand how older adults experience natural visual environments and to reveal important properties of the human visual system.

Disclosure

The authors report no conflicts of interest and have no proprietary interest in any of the materials mentioned in this article.

Acknowledgements

This work was supported by Australian Research Council Discovery Projects DP140100157 and DP180102596 to author AMM.

References

1. Owsley C. Aging and vision. *Vision Res* 2011;51:1610-1622.
2. McKendrick AM, Chan YM & Nguyen BN. Spatial vision in older adults: perceptual changes and neural bases. *Ophthalmic Physiol Opt* 2018;38:363-375.

3. Betts LR, Taylor CP, Sekuler AB & Bennett PJ. Aging reduces center-surround antagonism in visual motion processing. *Neuron* 2005;45:361-366.
4. Deng H, Chen W, Kuang S & Zhang T. Distinct aging effects on motion repulsion and surround suppression in humans. *Front Aging Neurosci* 2017;9:363.
5. Karas R & McKendrick AM. Increased surround modulation of perceived contrast in the elderly. *Optom Vis Sci* 2011;88:1298-1308.
6. Karas R & McKendrick AM. Contrast and stimulus duration dependence of perceptual surround suppression in older adults. *Vision Res* 2015;110:7-14.
7. Pitchaimuthu K, Wu QZ & Carter O, *et al*. Occipital GABA levels in older adults and their relationship to visual perceptual suppression. *Sci Rep* 2017;7:14231.
8. Tadin D, Park WJ, Dieter KC, Melnick MD, Lappin JS & Blake R. Spatial suppression promotes rapid figure-ground segmentation of moving objects. *Nat Commun* 2019;10:2732.
9. Petrov Y, Carandini M & McKee S. Two distinct mechanisms of suppression in human vision. *J Neurosci* 2005;25:8704-8707.
10. Petrov Y & McKee SP. The effect of spatial configuration on surround suppression of contrast sensitivity. *J Vision* 2006;6:224-238.
11. Shushruth S, Nurminen L, Bijanzadeh M, Ichida JM, Vanni S& Angelucci A. Different orientation tuning of near- and far-surround suppression in macaque primary visual cortex mirrors their tuning in human perception. *J Neurosci* 2013;33:106-119.
12. Tadin D, Lappin JS, Gilroy LA & Blake R. Perceptual consequences of centre-surround antagonism in visual motion processing. *Nature* 2003;424:312-315.
13. Pack CC, Hunter JN & Born RT. Contrast dependence of suppressive influences in cortical area MT of alert macaque. *J Neurophysiol* 2005;93:1809-1815.
14. Liu LD, Haefner RM & Pack CC. A neural basis for the spatial suppresion of visual motion perception. *eLife* 2016;5:e16167.
15. Tadin D, Silvanto J, Pascual-Leone A & Battelli L. Improved motion perception and impaired spatial suppression following disruption of cortical area MT/V5. *J Neurosci* 2011;31:1279-1283.
16. Angelucci A & Bullier J. Reaching beyond the classical receptive field of V1 neurons: horizontal or feedback axons? *J Physiol Paris* 2003;97:141-154.

17. Nurminen L & Angelucci A. Multiple components of surround modulation in primary visual cortex: multiple neural circuits with multiple functions? *Vision Res* 2014;104:47-56.

18. Schwabe L, Obermayer K, Angelucci A & Bressloff PC. The role of feedback in shaping the extra-classical receptive field of cortical neurons: a recurrent network model. *J Neurosci* 2006;26:9117-9129.

19. Angelucci A, Bijanzadeh M, Nurminen L, Federer F, Merlin S & Bressloff PC. Circuits and mechanisms for surround modulation in visual cortex. *Annu Rev Neurosci* 2017;40:425-451.

20. Karas R & McKendrick AM. Aging alters surround modulation of perceived contrast. *J Vis* 2009;9:11 11-19.

21. Pitchaimuthu K, Nguyen BN & McKendrick AM. Aging alters intraocular but not interocular foveal center surround contrast suppression. *J Vis* 2017;17:16.

22. Nguyen BN & McKendrick AM. Foveal and parafoveal contrast suppression are different: Mechanisms revealed by the study of healthy aging. *J Vis* 2016;16:10.

23. Nguyen BN & McKendrick AM. Visual contextual effects of orientation, contrast, flicker, and luminance: All are affected by normal aging. *Front Aging Neurosci* 2016;8:79.

24. Ukai K, Ando H & Kuze J. Binocular rivalry alternation rate declines with age. *Percept Mot Skills* 2003;97:393-397.

25. Jalavisto E. The phenomenon of retinal rivalry in the aged. *Gerontologia* 1964;49:1-8.

26. Liu LD, Miller KD & Pack CC. A unifying motif for spatial and directional surround suppression. *J Neurosci* 2018;38:989-999.

27. Schallmo MP, Kale AM & Millin R, *et al*. Suppression and facilitation of human neural responses. *eLife* 2018;7:e30334.

28. Yeshurun Y & Carrasco M. Attention improves or impairs visual performance by enhancing spatial resolution. *Nature* 1998;396:72-75.

29. Roberts M, Delicato LS, Herrero J, Gieselmann MA & Thiele A. Attention alters spatial integration in macaque V1 in an eccentricity-dependent manner. *Nature Neurosci* 2007;10:1483-1491.

30. Ito M & Gilbert CD. Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron* 1999;22:593-604.

31. Motoyoshi I, Ishii T & Kamachi MG. Limited attention facilitates coherent motion processing. *J Vis* 2015;15:1.
32. Carrasco M, Ling S & Read S. Attention alters appearance. *Nature Neurosci* 2004;7:308-313.
33. Owsley C. Visual processing speed. *Vision Res* 2013;90:52-56.
34. Verhaeghen P, Steitz DW, Sliwiniski MJ & Cerella J. Aging and dual-task performance: A meta-analysis. *Psychol Aging* 2003;18:443-460.
35. Folstein MF, Folstein SE & McHugh PR. "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *J Psychiatr Res* 1975;12:189-198.
36. Peirce JW. PsychoPy--Psychophysics software in Python. *J Neurosci Meth* 2007;162:8-13.
37. Wetherill GB & Levitt H. Sequential estimation of points on a psychometric function. *Br J Math Stat Psychol* 1965;18:1-10.
38. Yazdani P, Serrano-Pedraza I, Whittaker RG, Trevelyan A & Read JC. Two common psychophysical measures of surround suppression reflect independent neuronal mechanisms. *J Vis* 2015;15:21.
39. Karas R & McKendrick AM. Age related changes to perceptual surround suppression of moving stimuli. *Seeing Perceiving* 2012;25:409-424.
40. Fu Y, Yu S, Ma Y, Wang Y & Zhou Y. Functional degradation of the primary visual cortex during early senescence in rhesus monkeys. *Cereb Cortex* 2013;23:2923-2931.
41. Schmolesky MT, Wang Y, Pu M & Leventhal AG. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neurosci* 2000;3:384-390.
42. Wang Z, Yu S, Fu Y, Tzvetanov T & Zhou Y. Aging potentiates lateral but not local inhibition of orientation processing in primary visual cortex. *Front Aging Neurosci* 2018;10:14.
43. Leventhal AG, Wang Y, Pu M, Zhou Y & Ma Y. GABA and its agonists improved visual cortical function in senescent monkeys. *Science* 2003;300:812-815.
44. Zhang R, Kwon OS & Tadin D. Illusory movement of stationary stimuli in the visual periphery: evidence for strong centrifugal prior in motion processing. *J Neurosci* 2013;33:4415-4423.

45. Malavita MS, Vidyasagar TR & McKendrick AM. Eccentricity dependence of orientation anisotropy of surround suppression of contrast-detection threshold. *J Vis* 2018;18.

46. Malavita MS, Vidyasagar TR & McKendrick AM. The effect of aging on the eccentricitiy dependency of orientation anisotropy of perceptual surround suppression of contrast detection. *42nd European Conference on Visual Perception.* Leuven; *Perception*, 2019; 48: 1–236.

47. Ball K & Owsley C. The useful field of view test: a new technique for evaluating age-related declines in visual function. *J Am Optom Assoc* 1993;64:71-79.

FIGURE CAPTIONS

Figure 3. A) Schematic illustration (not to scale) of the positioning of the motion stimulus (Gabor patch) relative to the rapid serial visual presentation (RSVP) stream. B) An example RSVP stream. Four letters and two digits were presented in random order, with the condition that the two digits could not be sequential. The letters and digits were presented at a constant speed of 10 frames/sec (83ms) or 14 frames/sec (117ms) to vary the attentional load in separate runs. The interstimulus duration was equivalent to the letter presentation duration in each run.

Figure 4. Results for the peripheral motion direction discrimination single task condition. (A) Average duration thresholds (ms) of older adults (open circles, n=18) and younger adults (filled circles, n=20) across increasing stimulus size. (B) Average suppression index (SI) of older and younger adults across increasing stimulus size. Positive SI values indicate spatial suppression. Error bars are the 95% confidence intervals of the mean. Data have been nudged slightly on x-axis for clarity.

Figure 3. Results for the peripheral motion direction discrimination dual task conditions. (A) Average duration thresholds (ms) of older adults (circles, n=17 and younger adults (squares, n=20) across increasing stimulus size. There were two speeds of the rapid serial visual

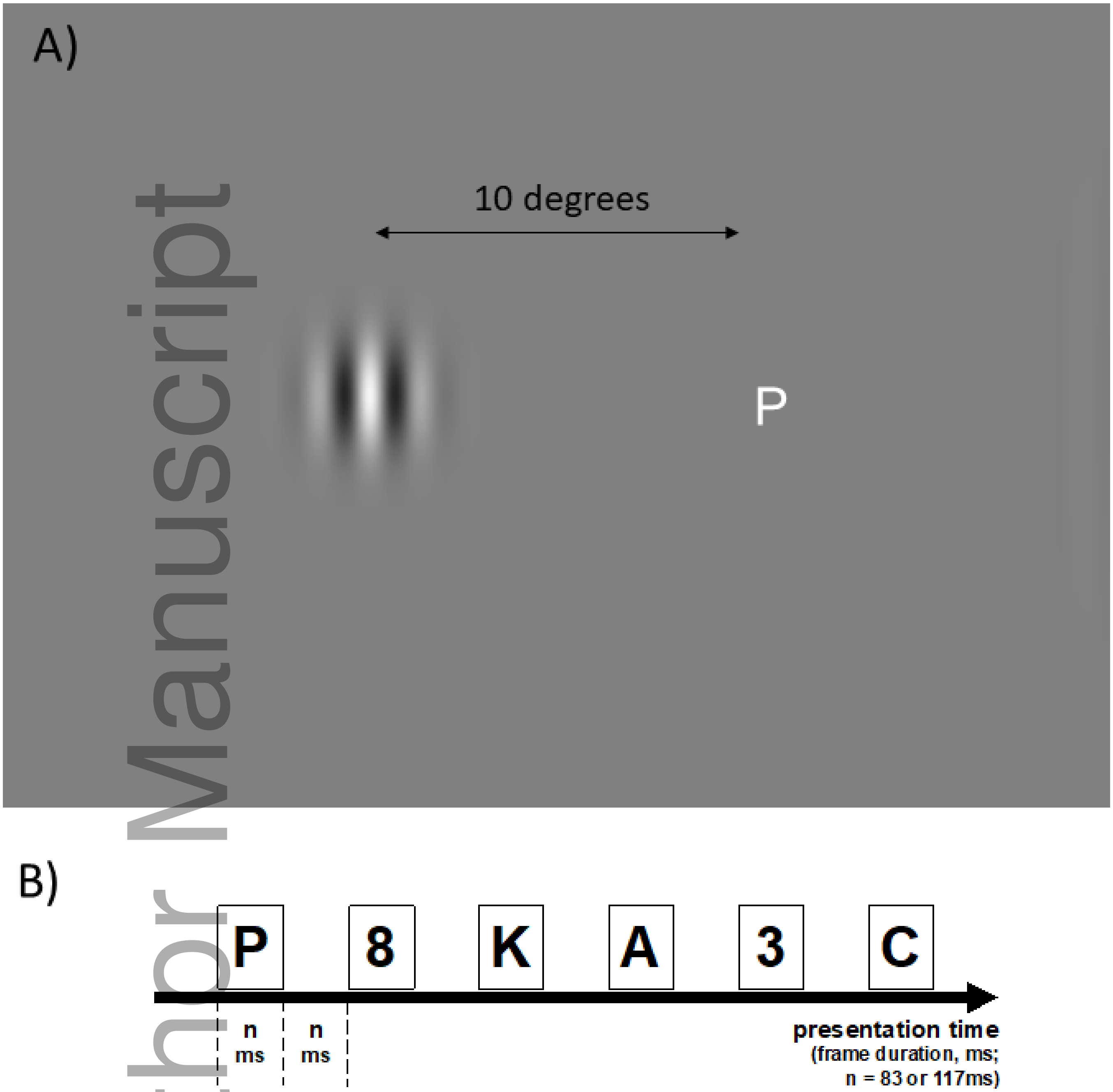
presentation (RSVP) sequence, 83ms, open symbols and 117ms, filled symbols. (B) Average suppression index (SI) of older and younger adults across increasing stimulus size. Positive SI values indicate spatial suppression. Error bars are the 95% confidence intervals of the mean. Data have been nudged slightly on x-axis for clarity.

Figure 4. Results for the peripheral motion direction discrimination single versus dual task conditions. (A) Average duration thresholds (ms) of older adults (circles, n=18) and younger adults (squares, n=20) across increasing stimulus size in the single task (open symbols) and dual task (filled symbols) conditions. (B) Average suppression index (SI) of older and younger adults across increasing stimulus size. Positive SI values indicate spatial suppression. Error bars are the 95% confidence intervals of the mean. Data have been nudged slightly on x-axis for clarity.

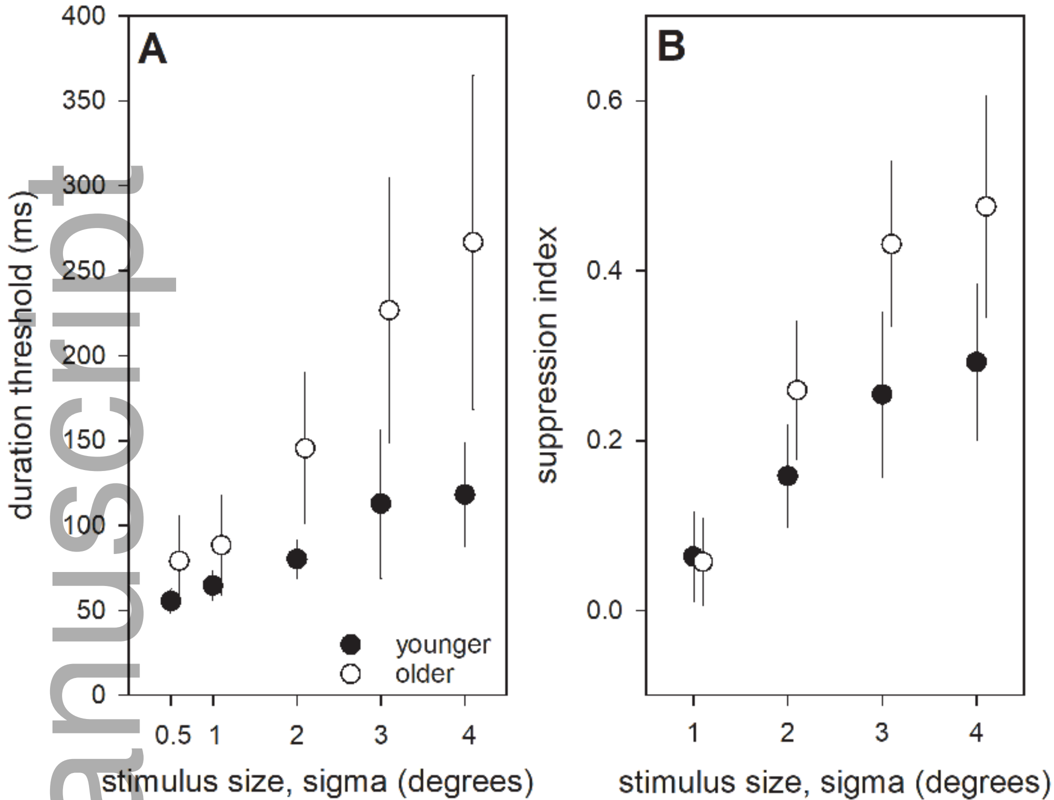
Soa Park graduated with a Bachelor of Science degree with Honours at The University of Melbourne in 2018. After studying Visual Neuroscience during her undergraduate degree, she became interested in vision research and decided to pursue an Honours degree project where she became involved in researching motion perception and ageing with Professor Allison McKendrick. She is now studying medicine at the University of Queensland and hopes to pursue a future career combining both clinical and research interests.

Bao N Nguyen is a lecturer and human visual neuroscientist at the Department of Optometry and Vision Sciences, The University of Melbourne. After graduating with Deans Honours from a Bachelor of Optometry in 2008, she completed a PhD investigating vision anomalies in people with migraine in 2014, both at The University of Melbourne. She has an active research interest in healthy ageing and childhood development of vision, eye diseases such as glaucoma, and systemic conditions such as migraine and human immunodeficiency virus infection. Her contribution to her profession as a clinician-scientist and capacity as an early career researcher have been recognised with a BioMedVic Early Career Clinician Researcher Award, Melbourne Neuroscience Institute Fellowship, Australian College of Optometry Fellowship, and she was most recently inducted in 2020 into the Mentone Girls Grammar School Remarkable Women Hall of Fame as an inspiration for the next generation of girls and young women. Given the generous mentorship and guidance she has received early in her career from senior scientists, she is passionate about mentoring younger peers to pursue careers in STEMM (science, technology, engineering, mathematics, medicine) because she believes a good mentor is key for driving success and empowerment.

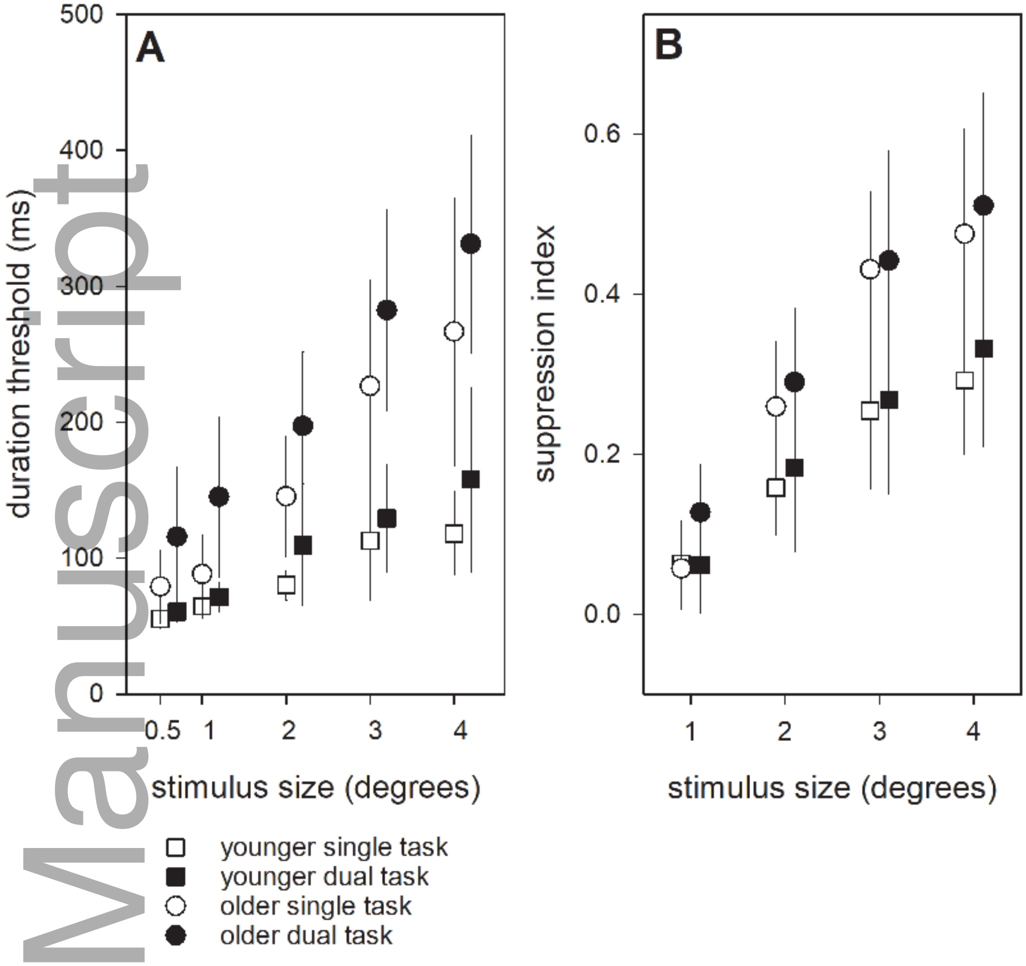
Allison M McKendrick is Professor and Head of Department of Optometry & Vision Sciences at the University of Melbourne. She is the first female to be appointed to the academic level of Professor in the department. She completed her PhD in Optometry & Vision Science at the University of Melbourne. She then spent two years as a postdoctoral researcher at the Devers Eye Institute, Oregon, USA, prior to returning to Australia to take up a prestigious NHMRC Australian Clinical Research Fellowship at the School of Psychology, The University of Western Australia. Her research interests span a breadth of human clinical visual neuroscience. Her laboratory has specific interests in the study of the impacts of healthy aging on the eye and brain, glaucoma, and neurological disorder (in particular migraine). In addition to enhancing understanding of the underlying neural status in these conditions, her research has applied aims including the development of improved clinical tests for the assessment of vision (in particular perimetry and ocular imaging), in addition to improving knowledge of the consequences of vision loss on performance in natural visual environments and day-to-day tasks. Her early career was predominantly surrounded by male colleagues and mentors, who were typically highly supportive but sometimes bemused by the level of juggling of family and work. In particular, she is grateful to her postdoctoral mentor for being prepared to offer her a job despite attending the interview at an international conference jet-lagged with a toddler and a highly visible pregnancy. She endeavours to provide similar support and encouragement to colleagues to take risks and jump at opportunities.



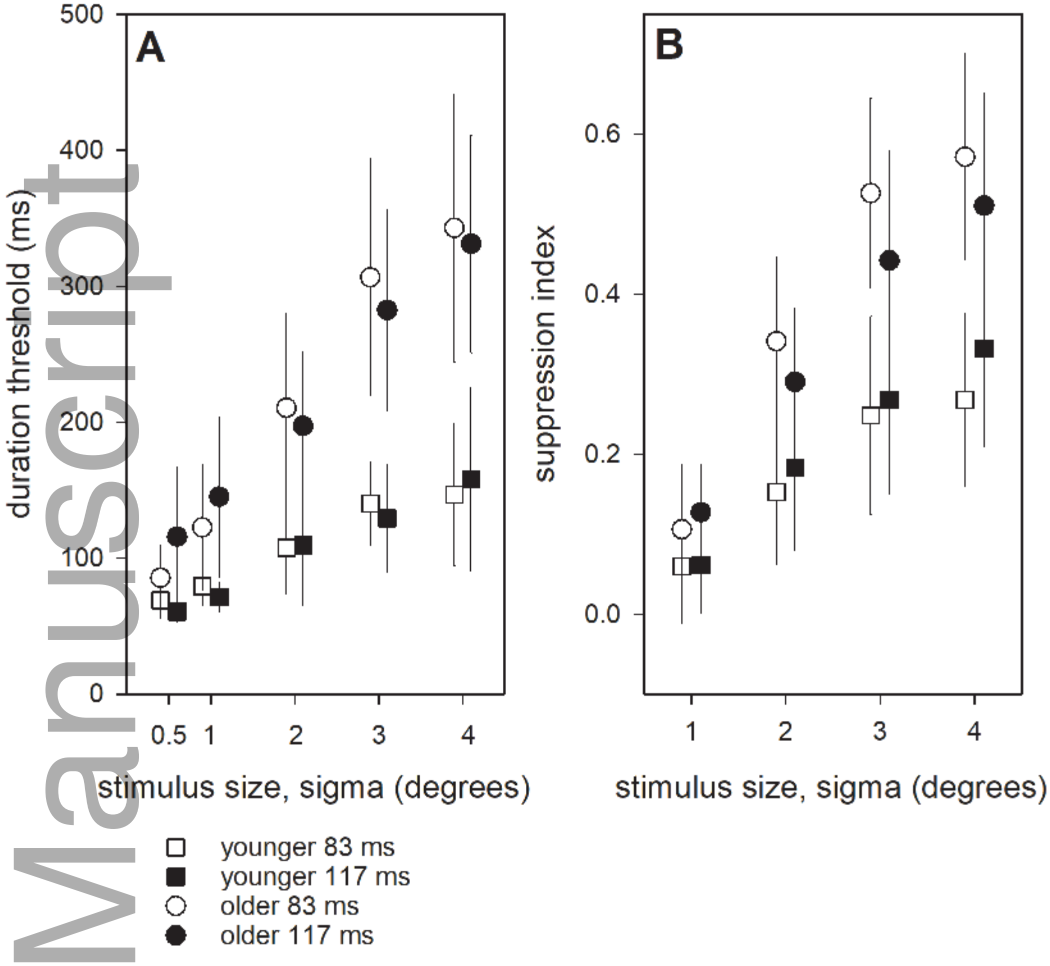
opo_12674_f1.tif



opo_12674_f2.tif



opo_12674_f3.tif



opo_12674_f4.tif