Vision Research special issue: Calibrating the visual system

Research Article

Title: Orientation-dependency of perceptual surround suppression and orientation decoding of centre-surround stimuli are preserved with healthy ageing

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Abstract (150-200 words):

A key visual neuronal property that is mirrored in human behaviour is centre-surround contrast suppression, which is orientation-dependent. When a target is embedded in a high-contrast surround, the centre appears reduced in contrast, the magnitude of which depends on the relative orientation between centre and surround. Previous reports demonstrate changes in perceptual surround suppression with ageing; however, whether the orientation-dependency of surround suppression is impacted by ageing has not been explored. Here, we tested 18 younger (aged 19-33) and 18 older (aged 60-77) adults. Perceptual surround suppression was stronger for parallel than orthogonal stimuli; however contrary to previous work, here we found no difference in perceptual suppression strength between age-groups. In the same participants, we measured event-related potentials (ERPs) and conducted multivariate pattern analysis to confirm that parallel and orthogonal centre-surround stimuli elicit distinguishable brain activity, predominantly over occipital areas. Despite a delay in the

first prominent ERP component (P1) in response to each pattern, older adults showed similar decoding of orientation information (i.e. distinguish between parallel and orthogonal centre-surround stimuli from 70 ms post-stimulus onset) as younger adults. This suggests that sufficient information to distinguish orientation in centre-surround stimuli becomes available to the older human brain as early as in younger adults.

Keywords (max 6): Orientation; multivariate decoding; surround suppression; electroencephalography; event-related potentials; ageing

Word count (excluding abstract, tables, captions and references): 5329

1. Introduction

A key neuronal property of visual cortex that is mirrored in human behaviour is centre-surround contrast suppression (or surround suppression), which is orientation-dependent. Typically, when a centre stimulus (e.g., a grating) is embedded in a high-contrast surround, the contrast of the centre appears reduced, more so for when the surround is oriented parallel than orthogonal to the centre (Xing & Heeger, 2000, Xing & Heeger, 2001). Surround suppression is considered a form of contrast gain regulation (Carandini & Heeger, 2011). Older adults show altered perceptual surround suppression (for review, see McKendrick, Chan & Nguyen, 2018), but so far no studies have considered whether ageing impacts on the orientation-dependency of perceptual surround suppression. Here, we exploit the fact that there are well-studied differential effects of centre-surround orientation configurations (namely parallel versus orthogonal centre-surround configurations) on this gain control mechanism to explore for differences in orientation-dependent mechanisms of contrast processing between older and younger adults.

Firstly, the strength of surround suppression (and indeed, whether there is suppression or the opposite effect of facilitation) depends on the ratio of contrast between centre and surround (Cannon & Fullenkamp, 1991, Karas & McKendrick, 2015, Xing & Heeger, 2001, Yu, Klein & Levi, 2002). Presenting a low contrast centre within a higher contrast surround has generally uncovered group differences between older and younger adults in perceptual surround suppression (Karas & McKendrick, 2015, Pitchaimuthu, Nguyen & McKendrick,

2017); thus, we take a similar approach here. Secondly, we consider that the visual system must efficiently process differences in orientation (or decode orientation) in order to show orientation-dependent centre-surround suppression – otherwise, surround suppression would be equivalent across different stimulus orientations. In this study, we presented parallel and orthogonal centre-surround stimuli defined along the cardinal meridians because orientation discrimination is typically more sensitive for the vertical and horizontal meridians compared to oblique orientations (Westheimer & Beard, 1998). In our case, in keeping the centre orientation the same, the key stimulus characteristic that is presumed to drive orientation decoding between parallel and orthogonal centre-surround stimuli is the orientation of the surround, being either vertical or horizontal.

Neurophysiology studies report that aged macaque visual cortex comprises fewer neurons with precise orientation tuning than in younger animals (Fu, Yu, Ma, Wang & Zhou, 2013, Schmolesky, Wang, Pu & Leventhal, 2000, Wang, Yu, Fu, Tzvetanov & Zhou, 2018). While parallel centre-surround stimuli are expected to consistently elicit stronger perceptual surround suppression than orthogonal centre-surround stimuli (Xing & Heeger, 2000, Xing & Heeger, 2001), a simple prediction from neurophysiology is that older adults might show less difference in surround suppression between parallel and orthogonal centre-surround stimuli than younger adults. We test this prediction by comparing the magnitude of perceptual surround suppression for parallel and orthogonal centre-surround stimuli between older and younger adult observers.

However, the situation is further complicated because of other evidence that orientation discrimination is preserved in older humans, particularly once differences in contrast sensitivity are taken into account (Delahunt, Hardy & Werner, 2008, Govenlock, Taylor, Sekuler & Bennett, 2009, Wang et al., 2018). This is likely due to behavioural data representing the summed output of a network of cells, such that across a population of cells, the ability to decode orientation might still be preserved. That is, even though there may be fewer tightly orientation-tuned cells in the ageing visual cortex, which at present can only be inferred from studies in macaque (Fu et al., 2013, Schmolesky et al., 2000, Wang et al., 2018), enough cells remain that are highly selective for orientation to preserve orientation perception. In order to tap into the overall response of a large population of

cells, previous authors (Govenlock et al., 2009) have suggested to measure visually evoked potentials using electrophysiology, which may reveal age-related changes in neuronal processing in the absence of age-related changes in perception. In this study, we have therefore used electroencephalography (EEG) to measure brain activity (event-related potentials, ERPs) in response to parallel and orthogonal centre-surround stimuli in older and younger adults. The aim of our electrophysiological experiment was to determine when information first becomes available to the visual system to differentially decode our parallel and orthogonal centre-surround stimuli. We also aimed to determine whether the timing of that information availability differs between older and younger adults.

We expected that distinguishable neural responses should be observed in ERPs occipitally as soon as the stimuli are successfully processed. Hence, we focused our analysis on the initial timing of ERPs, specifically at the first prominent deflection observed in the ERP waveforms (the positive P1 component). The P1 is one of the earliest visually-evoked ERP components that reflects when perceptual analysis is being performed, and it is strongly influenced by the physical properties of the stimulus; hence, we consider this component to be significantly influenced by orientation information. In addition to analysing visually evoked ERP waveforms elicited from the occipital region of interest, we exploited the excellent temporal resolution and multivariate nature of EEG signals by applying multivariate pattern analysis techniques (Bode, Sewell, Lilburn, Forte, Smith & Stahl, 2012) to determine when parallel and orthogonal centre-surround stimuli are first differentially represented (or can be decoded) in the brain after the onset of stimulus presentation.

2. Materials and Methods

2.1. Participants

The study was approved by the Human Research Ethics Committee of the University of Melbourne and complied with the Declaration of Helsinki. Eighteen younger adults (13 females, aged 19-33 years) and 18 older adults (13 females, aged 60-77 years) participated after providing written informed consent. All participants met the inclusion criteria of: best corrected monocular visual acuity of 6/7.5 or better, refractive error within ± 5.00 D sphere and -2.00 D cylinder, normal ocular health, no significant lens opacities defined as $\leq$ Grade 1.5 on the Lens Opacities Classification System III scale (Chylack, Wolfe, Singer, Leske,

Bullimore, Bailey, Friend, McCarthy & Wu, 1993), and no systemic conditions (e.g., diabetes, epilepsy) or medications (e.g., antidepressants) that affect visual or cognitive function. All participants were assessed on the Mini Mental State Exam (Folstein, Folstein & McHugh, 1975), achieving normal scores of at least 27 out of a maximum of 30.

2.2. Visual stimuli

The visual stimuli used in this study were the same for both the EEG and behavioral experiments. The centre was always a vertical sinusoidal grating (0.67° radius, 20% contrast, 1 cyc/deg), and the surround was an annulus (4° radius, 40% contrast, 1 cyc/deg, 1 pixel gap separation) with gratings oriented parallel (vertical) or orthogonal (horizontal) to the centre. Figure 1A shows examples of the parallel and orthogonal centre-surround stimuli, and Figure 1B depicts the centre-only (no surround) stimulus. The centre and surround gratings were always in-phase, and phase was randomised for each stimulus presentation.

2.3. Apparatus and general experimental setup

The stimuli were presented on a CRT monitor (Sony Trinitron Multiscan G420, Tokyo, Japan; maximum luminance 105 cd/m^2 , frame rate 75Hz, 1024×768 pixel resolution) via a 32-bit PC (Shuttle, Taiwan) using custom written software Matlab v2015b (The Mathworks, Natick, MA, USA) using Psychtoolbox-3 (Brainard, 1997, Pelli, 1997). Participants were refractively corrected for the working distance (40cm) and viewed the screen binocularly. For both the EEG and behavioural experiments, observers were instructed to fixate at the centre of the screen (i.e. at the centre of the visual stimuli). Fixation was aided during and in between stimulus presentations by four white nonius lines (1° length, see Figure 1).

2.4. EEG experiment

The EEG was continuously recorded at a sampling rate of 512 Hz (DC-coupled with an anti-aliasing filter, -3 dB at 204 Hz) from 64 scalp electrode sites using the international 10-20 montage and BioSemi ActiveTwo system. Additional electrodes at the outer canthus and lower eyelid were used to simultaneously record the electrooculogram for cross-validation of eye blinks. The three visual stimuli (parallel, orthogonal or centre-only) were randomly presented for 150 ms duration and 40 times in one run using a block design (Figure 1B). Overall, each stimulus was presented 240 times over 6 test runs. Up to 20% jitter was added

to vary the timing between presentations (i.e. interstimulus interval ≥ 750 ms), selected at random. In each run, one-third of the stimulus presentations were catch trials where participants were asked to press a button to indicate the detection of a specific pattern (e.g., parallel catch trial) and to not respond to the other patterns. This procedure served to focus attention while not confounding neural responses to the relevant stimuli with motor activity. Only parallel and orthogonal non-button press trials were included in the analysis as we were interested in comparing electrophysiological responses to centre-surround stimuli.

2.5. EEG analysis

EEG data were linearly detrended and re-referenced offline to an average of left and right mastoids. A bandpass filter (0.1-70 Hz) and notch filter (45-55 Hz) were applied sequentially using the “Basic FIR filter (new)” filter in EEGLAB toolbox (Delorme & Makeig, 2004) (zero-phase Hamming windowed sinc finite impulse response filter with default filter order providing a transition bandwidth of 25% of the passband edge; -6dB cutoff frequencies: high pass 0.05 Hz, low pass 70.05 Hz, notch filter 45-54 Hz; transition bandwidths: bandpass 0.1 Hz, notch filter 2 Hz). The low- and high-pass filter cutoffs were chosen *a priori* on the basis of previous EEG filtering recommendations, particularly for preserving the timing of early stimulus-driven components in the ERP waveforms (Widmann, Schroger & Maess, 2015). The continuous EEG recording was time-locked to the onset of the first stimulus presentation using epochs from 200ms pre- to 400ms post-stimulus onset. Epochs with large artefacts (greater than 200 μ V) were manually rejected. An independent component analysis (using EEGLAB) then identified and removed blink artefacts and lateral eye movements. Baseline corrections (200ms pre-stimulus) were applied after each step.

To investigate decoding of orientation information between parallel and orthogonal centre-surround stimuli, we undertook a spatial multivariate pattern classification analysis using epoched data from all recording channels and timepoints by applying support vector machine classification as implemented in the Decision Decoding ToolBOX (DDTBOX) Matlab package (Bode, Feuerriegel, Bennett & Alday, 2019). For each participant we used small moving analysis time-windows of non-overlapping steps of 10ms, covering the first 200ms of the trial, to investigate whether the distributed spatial patterns in the EEG could predict the processing of parallel and orthogonal stimuli. Each analysis step (for each participant)

was based on ten iterations of a ten-fold cross-validation procedure (by independently dividing the data in 10 sets, training on all-but-one sets and testing on the left-out set). This resulted in 100 independent analyses, and these results were then averaged for each analysis time window to derive a conservative estimate of the classification accuracy for each time window for each participant. Each step's results were then individually statistically tested across participants against an empirical chance distribution of results obtained by performing a shuffled-labels classification analysis. This shuffled-labels analysis was identical to the real classification analysis and used the same 10 iterations of all 10 cross-validation steps with exactly the same data and the same labels, but a random allocation of labels to data (Bode et al., 2019, Chan, Pianta, Bode & McKendrick, 2017). The advantage of this procedure is that the real classification results could be compared to an empirical chance distribution based on the same data, generated independently for each time window, rather than against a theoretical chance level. In a second group level analysis, the real results from each age group were then statistically tested against each other (rather than against chance) for each analysis step to test the main hypothesis that there were differences in the temporal availability of information. Corrections for multiple comparisons were performed using cluster-based permutation tests based on the cluster mass statistic (cluster inclusion alpha = 0.05, permutation samples = 5000).

Although the advantage of EEG over other measures of neural activity (e.g., functional magnetic resonance imaging) lies in its superior temporal resolution, we additionally made use of the available spatial information in a feature weights analysis to indicate the likely spatial origins of the signals that most strongly contributed to successful classification. For this, standardised absolute feature weights were extracted for each successful (above chance) multivariate pattern analysis and averaged across the data points contained in each analysis time window. Averaging across data points within analysis time windows resulted in one average feature weight per channel, allowed for estimating the relative importance of different channels to this particular classification process. We applied the correction algorithm that is implemented in DDTBOX to make the feature weights interpretable (Haufe, Meinecke, Gorgen, Dahne, Haynes, Blankertz & Biessmann, 2014). Given that the stimuli were visual in nature, we expected large feature weights for electrodes over visual (occipital) areas for significant classification time windows.

We also investigated the electrophysiological responses to the whole centre-surround stimulus by characterising the timing and amplitude of the first component of the ERP waveforms elicited from the midline occipital electrode, Oz, where visually evoked activity is expected to predominate. The most straightforward way to characterise timing of a waveform deflection is to measure the peak latency (i.e. the timepoint at which the deflection reaches its local maximum or minimum), which is the approach taken by the International Society for the Clinical Electrophysiology of Vision for measuring the timing of clinical visual evoked potentials (Odom, Bach, Brigell, Holder, McCulloch, Mizota, Tormene & International Society for Clinical Electrophysiology of Vision, 2016). Clinical visual evoked potentials, however, are elicited using stimuli chosen for their ability to evoke maximal visual responses (e.g., high Michelson contrast $\geq 80\%$, pattern-reversal, checkerboard stimuli covering at least 15° of visual field). In our case, we expected that our centre-surround stimuli (low Michelson contrast between 20-40%, pattern-onset grating stimuli covering maximum 8° of visual field) would not elicit the same high amplitude deflections as seen using clinical protocols. Moreover, the peak of a component occurs well after its onset, and given that the motivation for our study was to explore timing differences in the *onset* of neural processing between older and younger observers, we have therefore focused on the very first sign of stimulus-driven brain activity (the P1 component). Our ERP outcome measure was the P1 50% fractional area latency metric (the timepoint at which 50% of the total positive area for the P1 deflection was observed), an approach recommended by previous authors (Kiesel, Miller, Jolicoeur & Brisson, 2008, Woodman, 2010) where EEG signals may have low signal-to-noise or when the waveform does not conform to the canonical shape, which is especially the case when analysing individual waveforms. The P1 amplitude was taken as the instantaneous amplitude corresponding to the 50% fractional area latency, using the ERP measurement tool in ERPLAB (Lopez-Calderon & Luck, 2014).

2.6. *Perceptual experiment and analysis*

A schematic representation of the perceptual experiment is shown in Figure 1C. Participants were presented with visual stimuli in two intervals, separated by 500ms. The first interval always contained the centre-only stimulus (variable contrast), and the second interval

contained the reference centre-surround stimulus of fixed contrast (20% contrast centre, 40% contrast surround). Participants chose the interval where the centre was highest in contrast (two interval forced choice procedure). Where the two intervals appeared equal in contrast, participants were instructed to balance their choices of the first or second interval to minimise response bias towards one button. Three conditions were tested in separate runs: centre-only (i.e. no surround in the second interval), parallel and orthogonal.

The outcome measure of interest was the perceived contrast of the centre. Seven different contrast levels of the first interval stimulus were randomly presented 20 times using a Method of Constant Stimuli (MOCS) to enable a psychometric function to be estimated. Each participant initially performed an abbreviated MOCS (13 levels, presented 4 times each) as a practice run, which was also used to select the range of contrast levels to be tested in the main experiment. Individual data were fitted with a modified cumulative Gaussian (Wichmann & Hill, 2001) (Equation 1) using a maximum-likelihood fitting procedure in Microsoft Excel (Microsoft, Redmond, WA, USA).

$$\psi(t) = FP + (1 - FP - FN) \times G(t, \mu, \sigma) \quad (\text{Equation 1})$$

where $G(t, \mu, \sigma)$ is the cumulative Gaussian distribution with mean μ and standard deviation σ for value t . FP and FN represent the false positive and false negative error rates, respectively, assuming that false responses are made independently of the underlying Gaussian distribution of responses. The mean of the fitted psychometric function (μ), or the 'point of subjective equality' (PSE), when both the reference and target stimulus appeared subjectively the same, was analysed.

Parallel centre-surround stimuli elicit surround suppression (where the perceived contrast of the centre is reduced in the presence of the surround), which is stronger than for orthogonal centre-surround stimuli (Xing & Heeger, 2000, Xing & Heeger, 2001). To compare visual perception between parallel and orthogonal centre-surround stimuli, a suppression index was calculated ($1 - \text{PSE 'surround'}/\text{PSE 'no surround'}$). A positive suppression index indicates

suppression (maximum suppression = 1), a negative index indicates facilitation, and an index of 0 indicates no effect of the surround.

Figure 1. Schematic of the test stimuli and procedures. (A) Parallel and orthogonal centre-surround stimuli examples. (B) Schematic of the EEG test procedure. Three stimuli (centre-only, parallel and orthogonal centre-surround stimuli) were randomly presented in a blocked design while the EEG was continuously recorded, with at least 750 ms between stimulus presentations (interstimulus interval = ISI). Each run included 40 presentations of each stimulus. For each run, a different ‘target’ (one of the three stimuli) was chosen. Participants pressed a button when they saw the designated target appear. (C) Schematic of the visual perception test procedure. The first interval always contained the centre-only stimulus, followed by 500 ms ISI. The second interval contained the comparison stimulus. Here, only the parallel centre-surround stimulus is shown as the comparison stimulus, but the actual runs consisted of a centre-only condition (as baseline comparison), a parallel centre-surround stimulus condition and an orthogonal centre-surround stimulus condition. Participants pressed a button to indicate which interval contained the centre that appeared higher in contrast. For both the EEG and behavioural experiments, fixation was aided by four white nonius lines that stayed on during the entire run.

2.7. Statistical analysis

Statistical analysis was conducted using SPSS version 25.0 (IBM Corp, Armonk, NY, USA). Data were confirmed to be normally distributed using a Kolmogorov-Smirnov test.

Comparisons between younger and older groups were performed using a repeated-measures analysis of variance (RM-ANOVA) for analysis of the occipital ERP P1 50% fractional area latency, instantaneous P1 amplitude at the 50% fractional area latency and perceptual suppression index data (within factor: surround orientation). Statistical analyses for the multivariate analysis of the EEG data were conducted as described above using DDTBOX group-level statistics functions (Bode et al., 2019). This enabled us to determine when decoding between parallel and orthogonal centre-surround stimuli occurred for the younger and older groups separately, taking into account multiple statistical comparisons across the range of time windows.

3. Results

3.1. EEG results: multivariate pattern analysis

Overall, the percentage of discarded EEG trials (due to manual rejection of large artefact and incorrect button presses) was not different between age groups (median [IQR]; younger: 2.19% [2.40%], older: 2.29% [3.02%]; Mann-Whitney rank sum test: $U=143.5$, $p=0.57$). The number of analysed EEG trials was also similar between older and younger participants for both the parallel centre-surround stimulus (median [IQR]; younger: 157 [4], older: 158 [8], Mann-Whitney rank sum test: $U=154$, $p=0.81$) and orthogonal centre-surround stimulus (median [IQR]; younger: 157 [2], older: 156 [6], Mann-Whitney rank sum test: $U=136.5$, $p=0.42$).

Taking into account neural activation patterns across the entire brain, rather than at a specific region of interest, the multivariate pattern analyses demonstrated that both older and younger adults showed successful decoding between parallel and orthogonal centre-surround stimuli within the first 200 ms post-stimulus onset (Figure 2; above-chance classification accuracy). After correcting for the multiple time window comparisons for the entire -200 pre-stimulus to 200 post-stimulus period, we found that successful decoding first occurred at the same time window (70-80 ms) in both older and younger groups (purple shaded area), indicating that the differential representation of parallel and orthogonal centre-surround stimuli was not delayed with healthy ageing. When the two groups were compared across multiple time windows, there was no difference in decoding (with multiple comparisons taken into consideration). Feature weights analysis at the first three time

(70-80 ms, 80-90 ms, 90-100 ms) are predominantly localised to the occipital areas (red on heat maps) for both (A) younger and (B) older observers.

3.2. EEG results: visual evoked ERPs at the midline occipital electrode

We then focused on a specific region of interest (the occipital pole) to characterise the visual evoked potentials in response to parallel and orthogonal centre-surround stimuli. The first prominent ERP component that was observed at the midline occipital (Oz) electrode in response to the parallel and orthogonal centre-surround stimuli was a positive deflection at approximately 80-90 ms (Figure 3). For the P1 50% fractional area latency metric, there was no single time window width appropriate to bracket the entire P1 component of interest for both older and younger average group waveforms (Figure 3) and also for all of the individual waveforms. We therefore chose a time window width of 50-130 ms for the older group and 50-100 ms for the younger group (because in some younger participants, the onset of the next positive component occurred within the 100-150 ms window). Data were excluded from this sub-analysis if the waveform at the midline occipital electrode (Oz) was not positive during the defined time window. Thus, in Table 1, individual amplitude and latency data are available for 14 younger and 17 older participants. Note that data from the four younger participants and one older participant who were excluded from the amplitude and latency sub-analysis are included in the group ERP waveforms (Figure 3), and included in the primary multivariate decoding analysis given overall signal quality across channels was acceptable.

We first checked if ERP waveforms elicited from the midline occipital (Oz) electrode were different in response to parallel versus orthogonal centre-surround stimuli. While the P1 50% fractional area latency was not different between parallel and orthogonal centre-surround stimuli (main effect of surround orientation: $F(1,29)=2.59$, $p=0.12$), P1 amplitudes were larger for parallel compared to orthogonal centre-surround stimuli for all participants (main effect of surround orientation: $F(1,29)=14.47$, $p=0.001$). These findings are consistent with our pattern classification analysis results that occipital responses to parallel and orthogonal centre-surround stimuli were different and measurable in ERPs. We then considered the effect of ageing. Older adults showed delayed P1 50% fractional area latencies relative to the younger group (Table 1; RM-ANOVA main effect of group:

F(1,29)=14.25, $p=0.001$), but the delay did not depend on orientation (group x surround orientation interaction: F(1,29)=0.23, $p=0.63$). P1 amplitudes were also larger in the older group compared to the younger participants (Table 1; main effect of group: F(1,29)=4.28, $p=0.048$). However, there was no orientation-dependent difference between groups in P1 amplitude (group x surround orientation interaction: F(1,29)=1.67, $p=0.21$).

Table 1. Summary of amplitude and latency parameters determined for each individual participant (group mean $\pm$ standard deviation) from the ERP waveforms recorded from the midline occipital electrode, Oz.

Stimulus	Outcome measure	Younger (n=14)	Older (n=17)
Parallel centre-surround stimulus	P1 50% fractional area latency	77 ± 6 ms	88 ± 9 ms
	P1 amplitude	3.37 ± 2.03 μ V	5.57 ± 3.64 μ V
Orthogonal centre-surround stimulus	P1 50% fractional area latency	77 ± 6 ms	87 ± 10 ms
	P1 amplitude	2.68 ± 1.63 μ V	4.17 ± 2.31 μ V

Figure 3. Group averaged ERP waveforms. ERPs recorded from the midline occipital electrode, Oz, in response to parallel (black) and orthogonal (red) centre-surround stimuli for (A) younger ($n=18$) and (B) older participants ($n=18$). The defined time window for P1 fractional peak latency measurement (grey shaded area) was 50-100 ms for the younger group and 50-130 ms for the older group. P1 amplitude was measured as the instantaneous positive amplitude at the 50% fractional peak latency timepoint.

3.3. Perceptual results: orientation-dependent centre-surround contrast suppression

We confirmed previous findings that parallel centre-surround stimuli elicited stronger suppression than orthogonal centre-surround stimuli (main effect of surround orientation: $F(1,34)=152.5$, $p<0.0001$). In Figure 4, the suppression indices for both older and younger groups were higher for parallel compared to orthogonal stimuli, indicating stronger suppression for parallel centre-surround stimuli. However, there was no differences between groups in suppression strength (main effect of group: $F(1,34)=0.12$, $p=0.74$) and no

orientation-dependent difference between the groups (group x surround orientation interaction: $F(1,34)=0.37$, $p=0.55$).

Figure 4. Perceptual suppression indices in response to parallel and orthogonal centre-surround stimuli. Younger individual data are shown as filled symbols ($n=18$) and the older individual data are shown as unfilled symbols ($n=18$). The higher the suppression index, the lower the perceived contrast of the centre pattern in the presence of a surround. Group mean data $\pm$ 95% confidence intervals of the mean are shown.

4. Discussion

To address our main aim of determining when parallel and orthogonal centre-surround stimuli are differentially represented in the brain response, we used multivariate pattern analysis of ERPs to confirm that the stimuli show distinguishable neural responses predominantly at an occipital location. The major advantage of EEG is the ability to track fast brain processes in time. We could therefore determine, at a resolution of tens of milliseconds, that differences in orientation between parallel and orthogonal centre-surround stimuli were reflected occipitally at 70-80 ms post-stimulus onset. This timing was observed in both older and younger observers, which argues against a disadvantage of ageing. Rather, our finding implies that the accumulation of sensory evidence to

differentiate between our specific parallel and orthogonal centre-surround configurations (here, decode between vertical and horizontal information in the surround given that the centre orientation remained constant) was not impaired in older adults.

Our experimental paradigm involved both behavioural and EEG testing; however, these were not conducted simultaneously. We deliberately kept the tests separate and created a 'passive' EEG test paradigm in order to investigate decoding of orientation information directly from brain activity, rather than inferring from behavioural data (Casco, Barollo, Contemori & Battaglini, 2017) that inherently involves an additional confound of motor responses, and possibly different attentional allocation. In our perceptual task, we did not measure the speed with which observers could respond to the parallel and orthogonal centre-surround stimuli, nor an explicit orientation judgement per se. Rather, we measured the well-studied effect of surround orientation on the perceived contrast of a central target (perceptual surround suppression), for which decoding of orientation information (here, the difference between vertical and horizontal information in the surround) is critical. Centre-surround contrast suppression did not differ between older and younger groups for the specific stimulus configurations used herein, which appears consistent with our main electrophysiological finding that efficient orientation decoding was preserved in the older adult brain.

While our multivariate analysis of the EEG compared when the pattern of responses to the parallel centre-surround stimulus was different to the pattern of responses to the orthogonal centre-surround stimulus, we also characterised the timing and amplitude of the ERP waveforms elicited in response to the whole centre-surround stimulus configuration. Since ageing is associated with reduced contrast sensitivity (Owsley, 2011), and reduced contrast sensitivity is associated with increased latency of visual evoked potentials (Brusa, Jones, Kapoor, Miller & Plant, 1999), it was not surprising that we replicated typical findings of delayed ERP waveforms in our older adults (Dustman, Shearer & Emmerson, 1993, Tobimatsu, 1995) at the midline occipital electrode, Oz (which can be assumed to mostly originate from early visual cortices). A delay in electrophysiology is typically construed to be disadvantageous. Age-related latency changes are assumed to reflect a delay in signal conduction, possibly due to changes in neurotransmitter function, increased synaptic delay,

and/or axonal or myelin loss resulting in decreased conduction velocity (see review by (Tobimatsu, 1995). However, our results suggest that a delay in signal processing through the visual pathway is not necessarily associated with a delay in the onset of sensory information becoming available for successful decoding of orientation information. Rather, we find that the ageing visual system may be capable of compensating for a delay in visual processing of the whole centre-surround stimulus at an occipital location (perhaps due to reduced contrast sensitivity) by having the same timecourse of initial orientation decoding between parallel and orthogonal centre-surround stimuli as younger adults, which was detectable with our multivariate analysis when considering activity patterns across the entire brain. The larger response amplitudes at relevant regions of interest (i.e. increased amplitude of visually evoked response at the midline occipital electrode, as found here) could further reflect compensatory mechanisms (for example, we have recently demonstrated increased steady-state visual evoked potential amplitude in healthy older adults that possibly compensates for the simultaneous reduction in retinal evoked responses, relative to younger adults, see Lek, Nguyen, McKendrick & Vingrys, 2019), but this remains speculative at this stage. Taken together with our behavioural data, the surround stimulus appears to be just as effective at eliciting perceptual suppression in older adults relative to their younger counterparts (possibly a result of gain control to compensate for the delay in signal passing through the visual system).

Interestingly, for both older and younger participants, the P1 amplitude of the ERP waveforms elicited at the midline occipital (Oz) electrode was higher for parallel centre-surround stimuli relative to orthogonal centre-surround stimuli. This result may at first seem surprising given that parallel centre-surround stimuli produce greater surround suppression of perceived contrast. Human functional magnetic resonance imaging has shown reduced magnitude of the haemodynamic blood oxygen-level dependent response from visual cortex in response to parallel compared to orthogonal centre-surround stimuli (McDonald, Mannion, Goddard & Clifford, 2010, Schallmo, Grant, Burton & Olman, 2016, Williams, Singh & Smith, 2003, Zenger-Landolt & Heeger, 2003). Similarly, in ERP studies, response amplitudes are reduced more so when central target stimuli are surrounded by parallel than orthogonal flanking stimuli (Joo, Boynton & Murray, 2012, Khoe, Freeman, Woldorff & Mangun, 2004). Unlike previous ERP studies (Joo et al., 2012, Khoe et al., 2004), however,

we did not collect data for the surround annulus alone, as we were focused on keeping the visual stimuli identical for the perceptual and EEG experiments. Moreover, the onset of the centre and surround stimuli was synchronous in this study, whereas previous studies of contextual effects have presented the surround or flanking stimuli before and after the appearance of the centre target (Haynes, Roth, Stadler & Heinze, 2003, Joo et al., 2012, Joo & Murray, 2014, Ohtani, Okamura, Yoshida, Toyama & Ejima, 2002, Schallmo, Kale & Murray, 2019), in order to isolate the responses to the target and surround/flankers in time. Hence, we could not isolate the effect of the surround on the response from the centre only. Future work could consider analysing the difference signal between the centre-surround stimulus and a surround only condition (see for example the logic presented by Khoe et al., 2004) to properly investigate the contextual effect on the centre, which would presumably mirror the strength of perceptual suppression (not the intent of our present study). In the absence of measuring EEG responses to the surround annulus alone, we are also unable to comment on whether the electrophysiological responses were dominated exclusively by the surround (given that the surround was almost six times the spatial extent of the centre) and can only interpret that our occipital ERP waveforms reflect the response to the whole centre-surround configuration.

The main focus of our behavioural experiment was to investigate the possibility of between-group differences in the orientation dependency of centre-surround contrast suppression. In recent years, numerous studies have exclusively explored *parallel* centre-surround contrast suppression in younger and older adults (reviewed in McKendrick et al., 2018), with the most common finding being an increase in suppression strength in older adults for foveally presented targets (Karas & McKendrick, 2009, Karas & McKendrick, 2011, Karas & McKendrick, 2012, Karas & McKendrick, 2015, McKendrick, Weymouth & Battista, 2013, Nguyen & McKendrick, 2016a, Nguyen & McKendrick, 2016b, Pitchaimuthu et al., 2017). We did not replicate that well-established effect here. While we had similar inclusion and exclusion criteria and task requirements as previous work, we did however use centre-surround stimuli of different contrast and lower spatial frequency than in some previous studies. Our stimulus choice here clearly elicits the general phenomenon of orientation-dependent centre-surround contrast suppression (see Figure 4), but did not reveal group differences in suppression strength. While not key to our current exploration of orientation

effects, this observation suggests possible spatial and contrast dependencies that may be important for future work aiming to understand ageing effects on centre-surround contrast suppression (e.g. see also Karas & McKendrick, 2015).

Perceptual centre-surround effects have been characterised in the literature using a range of methodologies; decisions around our particular experimental paradigm were made based on prior experience and practical reasons. The motivation for using a fixed order of presentation for the behavioural experiment (see Figure 1C, centre-alone presented first, centre-surround stimulus presented second) was to maintain consistency and familiarity with the two-interval forced choice task. It is our experience working with largely untrained observers that the task is less confusing if the order is fixed and expected. Furthermore, the large, higher contrast surround results in some local adaptation, and presenting the surround in the second interval prevents temporal masking/adaptation effects from the surround influencing the perception of the centre-alone stimulus. We also included the no surround PSE in the denominator of the suppression index (rather than examining the surround PSE alone), as the suppression index provides an individualised metric that takes into account any imprecision in perceived contrast (possibly due to a response bias in the button pressing for a two-interval forced choice task – for example, a tendency to press the dominant hand button more often if uncertain). Furthermore, calculation of a ratio enables comparison of suppression strength across different studies, where stimulus parameters may differ and therefore impact on the absolute magnitude of the shift in PSE observed.

5. Conclusions

Our study takes advantage of the excellent temporal resolution of EEG, combined with multivariate pattern classification analyses, to determine whether parallel and orthogonal centre-surround stimuli are differentially processed by the ageing human brain. We also tested whether ageing affects the orientation-dependency of perceptual centre-surround contrast suppression. Ageing did not detrimentally affect the temporal neural processing of the specific parallel and orthogonal centre-surround stimuli used herein, nor did it impact on the perception of those same stimuli. The findings suggest that older people have preserved decoding of parallel and orthogonal centre-surround stimuli at a neural network

level, by accumulating sensory information at the same time as younger adults, which appears to preserve their visual performance on a task that depends on orientation.

Acknowledgements

This work was supported by an Australian Research Council Discovery Project Grant (DP140100157) to AMM. The authors wish to thank Dr Daniel Feuerriegel for technical support with the Decision Decoding ToolBOX (DDTBOX) Matlab package.

References

- Bode, S., Feuerriegel, D., Bennett, D., & Alday, P.M. (2019). The Decision Decoding ToolBOX (DDTBOX) - A Multivariate Pattern Analysis Toolbox for Event-Related Potentials. *Neuroinformatics*, 17 (1), 27-42.
- Bode, S., Sewell, D.K., Lilburn, S., Forte, J.D., Smith, P.L., & Stahl, J. (2012). Predicting perceptual decision biases from early brain activity. *Journal of Neuroscience*, 32 (36), 12488-12498.
- Brainard, D.H. (1997). The Psychophysics Toolbox. *Spat Vis*, 10 (4), 433-436.
- Brusa, A., Jones, S.J., Kapoor, R., Miller, D.H., & Plant, G.T. (1999). Long-term recovery and fellow eye deterioration after optic neuritis, determined by serial visual evoked potentials. *J Neurol*, 246 (9), 776-782.
- Cannon, M.W., & Fullenkamp, S.C. (1991). Spatial interactions in apparent contrast: inhibitory effects among grating patterns of different spatial frequencies, spatial positions and orientations. *Vision Res*, 31 (11), 1985-1998.
- Carandini, M., & Heeger, D.J. (2011). Normalization as a canonical neural computation. *Nat Rev Neurosci*, 13 (1), 51-62.
- Casco, C., Barollo, M., Contemori, G., & Battaglini, L. (2017). The Effects of Aging on Orientation Discrimination. *Front Aging Neurosci*, 9, 45.
- Chan, Y.M., Pianta, M.J., Bode, S., & McKendrick, A.M. (2017). Spatio-temporal patterns of event-related potentials related to audiovisual synchrony judgments in older adults. *Neurobiol Aging*, 55, 38-48.
- Chylack, L.T., Jr., Wolfe, J.K., Singer, D.M., Leske, M.C., Bullimore, M.A., Bailey, I.L., Friend, J., McCarthy, D., & Wu, S.Y. (1993). The Lens Opacities Classification System III. The Longitudinal Study of Cataract Study Group. *Arch Ophthalmol*, 111 (6), 831-836.
- Delahunt, P.B., Hardy, J.L., & Werner, J.S. (2008). The effect of senescence on orientation discrimination and mechanism tuning. *J Vis*, 8 (3), 5 1-9.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods*, 134 (1), 9-21.
- Dustman, R.E., Shearer, D.E., & Emmerson, R.Y. (1993). EEG and event-related potentials in normal aging. *Prog Neurobiol*, 41 (3), 369-401.
- Folstein, M.F., Folstein, S.E., & McHugh, P.R. (1975). "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *J Psychiatr Res*, 12 (3), 189-198.

Fu, Y., Yu, S., Ma, Y.Y., Wang, Y.C., & Zhou, Y.F. (2013). Functional Degradation of the Primary Visual Cortex During Early Senescence in Rhesus Monkeys. *Cerebral Cortex*, 23 (12), 2923-2931.

Govenlock, S.W., Taylor, C.P., Sekuler, A.B., & Bennett, P.J. (2009). The effect of aging on the orientational selectivity of the human visual system. *Vision Res*, 49 (1), 164-172.

Haufe, S., Meinecke, F., Gorgen, K., Dahne, S., Haynes, J.D., Blankertz, B., & Biessmann, F. (2014). On the interpretation of weight vectors of linear models in multivariate neuroimaging. *Neuroimage*, 87, 96-110.

Haynes, J.D., Roth, G., Stadler, M., & Heinze, H.J. (2003). Neuromagnetic correlates of perceived contrast in primary visual cortex. *J Neurophysiol*, 89 (5), 2655-2666.

Joo, S.J., Boynton, G.M., & Murray, S.O. (2012). Long-range, pattern-dependent contextual effects in early human visual cortex. *Curr Biol*, 22 (9), 781-786.

Joo, S.J., & Murray, S.O. (2014). Contextual effects in human visual cortex depend on surface structure. *J Neurophysiol*, 111 (9), 1783-1791.

Karas, R., & McKendrick, A.M. (2009). Aging alters surround modulation of perceived contrast. *J Vis*, 9 (5), 11 11-19.

Karas, R., & McKendrick, A.M. (2011). Increased surround modulation of perceived contrast in the elderly. *Optom Vis Sci*, 88 (11), 1298-1308.

Karas, R., & McKendrick, A.M. (2012). Age related changes to perceptual surround suppression of moving stimuli. *Seeing Perceiving*, 25 (5), 409-424.

Karas, R., & McKendrick, A.M. (2015). Contrast and stimulus duration dependence of perceptual surround suppression in older adults. *Vision Res*, 110 (Pt A), 7-14.

Khoe, W., Freeman, E., Woldorff, M.G., & Mangun, G.R. (2004). Electrophysiological correlates of lateral interactions in human visual cortex. *Vision Res*, 44 (14), 1659-1673.

Kiesel, A., Miller, J., Jolicoeur, P., & Brisson, B. (2008). Measurement of ERP latency differences: a comparison of single-participant and jackknife-based scoring methods. *Psychophysiology*, 45 (2), 250-274.

Lek, J.J., Nguyen, B.N., McKendrick, A.M., & Vingrys, A.J. (2019). An Electrophysiological Comparison of Contrast Response Functions in Younger and Older Adults, and Those With Glaucoma. *Invest Ophthalmol Vis Sci*, 60 (1), 442-450.

Lopez-Calderon, J., & Luck, S.J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Front Hum Neurosci*, 8, 213.

McDonald, J.S., Mannion, D.J., Goddard, E., & Clifford, C.W. (2010). Orientation-selective chromatic mechanisms in human visual cortex. *J Vis*, 10 (12), 34.

McKendrick, A.M., Chan, Y.M., & Nguyen, B.N. (2018). Spatial vision in older adults: perceptual changes and neural bases. *Ophthalmic Physiol Opt*, 38 (4), 363-375.

McKendrick, A.M., Weymouth, A.E., & Battista, J. (2013). Visual form perception from age 20 through 80 years. *Invest Ophthalmol Vis Sci*, 54 (3), 1730-1739.

Nguyen, B.N., & McKendrick, A.M. (2016a). Foveal and parafoveal contrast suppression are different: Mechanisms revealed by the study of healthy aging. *J Vis*, 16 (3), 10.

Nguyen, B.N., & McKendrick, A.M. (2016b). Visual Contextual Effects of Orientation, Contrast, Flicker, and Luminance: All Are Affected by Normal Aging. *Front Aging Neurosci*, 8, 79.

Odom, J.V., Bach, M., Brigell, M., Holder, G.E., McCulloch, D.L., Mizota, A., Tormene, A.P., & International Society for Clinical Electrophysiology of Vision. (2016). ISCEV standard for clinical visual evoked potentials: (2016 update). *Doc Ophthalmol*, 133 (1), 1-9.

Ohtani, Y., Okamura, S., Yoshida, Y., Toyama, K., & Ejima, Y. (2002). Surround suppression in the human visual cortex: an analysis using magnetoencephalography. *Vision Res*, 42 (15), 1825-1835.

Owsley, C. (2011). Aging and vision. *Vision Res*, 51 (13), 1610-1622.

Pelli, D.G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis*, 10 (4), 437-442.

Pitchaimuthu, K., Nguyen, B.N., & McKendrick, A.M. (2017). Aging alters intraocular but not interocular foveal center surround contrast suppression. *J Vis*, 17 (1), 16.

Schallmo, M.P., Grant, A.N., Burton, P.C., & Olman, C.A. (2016). The effects of orientation and attention during surround suppression of small image features: A 7 Tesla fMRI study. *J Vis*, 16 (10), 19.

Schallmo, M.P., Kale, A.M., & Murray, S.O. (2019). The time course of different surround suppression mechanisms. *J Vis*, 19 (4), 12.

Schmolesky, M.T., Wang, Y., Pu, M., & Leventhal, A.G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nat Neurosci*, 3 (4), 384-390.

Tobimatsu, S. (1995). Aging and pattern visual evoked potentials. *Optom Vis Sci*, 72 (3), 192-197.

Wang, Z., Yu, S., Fu, Y., Tzvetanov, T., & Zhou, Y. (2018). Aging Potentiates Lateral but Not Local Inhibition of Orientation Processing in Primary Visual Cortex. *Front Aging Neurosci*, 10, 14.

Westheimer, G., & Beard, B.L. (1998). Orientation dependency for foveal line stimuli: detection and intensity discrimination, resolution, orientation discrimination and vernier acuity. *Vision Res*, 38 (8), 1097-1103.

Wichmann, F.A., & Hill, N.J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Percept Psychophys*, 63 (8), 1293-1313.

Widmann, A., Schroger, E., & Maess, B. (2015). Digital filter design for electrophysiological data--a practical approach. *J Neurosci Methods*, 250, 34-46.

Williams, A.L., Singh, K.D., & Smith, A.T. (2003). Surround modulation measured with functional MRI in the human visual cortex. *J Neurophysiol*, 89 (1), 525-533.

Woodman, G.F. (2010). A brief introduction to the use of event-related potentials in studies of perception and attention. *Atten Percept Psychophys*, 72 (8), 2031-2046.

Xing, J., & Heeger, D.J. (2000). Center-surround interactions in foveal and peripheral vision. *Vision research*, 40 (22), 3065-3072.

Xing, J., & Heeger, D.J. (2001). Measurement and modeling of center-surround suppression and enhancement. *Vision research*, 41 (5), 571-583.

Yu, C., Klein, S.A., & Levi, D.M. (2002). Facilitation of contrast detection by cross-oriented surround stimuli and its psychophysical mechanisms. *J Vis*, 2 (3), 243-255.

Zenger-Landolt, B., & Heeger, D.J. (2003). Response suppression in v1 agrees with psychophysics of surround masking. *Journal of Neuroscience*, 23 (17), 6884-6893.

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Title:

Orientation-dependency of perceptual surround suppression and orientation decoding of centre-surround stimuli are preserved with healthy ageing

Date:

2020-11

Citation:

Nguyen, B. N., Chan, Y. M., Bode, S. & McKendrick, A. M. (2020). Orientation-dependency of perceptual surround suppression and orientation decoding of centre-surround stimuli are preserved with healthy ageing. *Vision Research*, 176, pp.72-79. <https://doi.org/10.1016/j.visres.2020.07.015>.

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