



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



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ABSTRACT

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

1. Introduction

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

One potential effect of reduced inhibition with aging is disrupted balance of the excitatory-inhibitory receptive field properties of center-surround visual cortical neurons. These neurons increase their response, due to summation of neural responses, as increasingly larger stimuli moving in the cell's preferred direction are presented inside the

classical receptive field (CRF, Allman, Miezin, & McGuinness, 1985). Once the spatial extent of the stimulus spreads beyond the CRF boundary, concurrently stimulating the extra-classical surround region, the neuron's response is suppressed. The suppressive strength of the inhibitory receptive field of V1 cells has been reported to be reduced in older primates (Fu et al., 2010), a finding often attributed to a global decrease in GABA-mediated inhibition in the aging brain (Hua, Kao, Sun, Li, & Zhou, 2008; Hua et al., 2006; Leventhal et al., 2003). In humans, post-mortem V1 samples from older adults (2 samples over 55 years old) contained reduced amounts of pre- and post-synaptic GABAergic markers compared to younger adults (2 samples between 18 and 45 years old). Conversely, there is also emerging evidence for increased GABA levels in visual cortex of aged macaques (Liao, Han, Ma, & Su, 2016) and a recent study of human subjects found that pharmacologically increasing GABA-mediated neural inhibition lead to weaker spatial suppression and increased summation (Schallmo et al., 2017). Therefore, despite neurophysiological evidence for changes in GABA circuitry with aging, these changes are complex and only partially understood, and whether these changes are related to increases/decreases

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in suppression/summation remains speculative at present.

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

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

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

2. Method

2.1. Apparatus

Stimuli were generated using MATLAB 7.6.0 (Mathworks, Natick, Ma, USA) and presented on a Sony Trinitron Multiscan G520 Monitor (screen resolution: 1024 × 768, refresh rate: 100 Hz; Tokyo, Japan) from the frame store (256 MB) of a Cambridge Research Systems ViSaGe graphics system. Observers viewed the monitor binocularly from a distance of 65.5 cm, which was maintained using a chin-rest. Participants were optimally refracted for this viewing distance. Testing took place in a darkened room (ambient luminance < 1 cd/m²). The background screen luminance was set at 50 cd/m². In this study, contrast is defined as Michelson contrast in percent;

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

where L is luminance. This will also be expressed in dB units (Baker & Meese, 2011; Meese, 2010) where;

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

2.2. Participants

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

2.3. Stimuli

Battenberg stimuli have a checkerboard arrangement, consisting of signal checks alternating with uniform luminance checks. In this study, the signal checks contained luminance-modulated, drifting sine wave gratings with a spatial frequency of 3c/°. Uniform checks were 0% contrast and had the same mean luminance as the display background. The size of the check regions within the Battenberg stimulus containing signal could be varied to measure dependence on local signal area without adjusting the overall stimulus size; 10° across all conditions. Four different check sizes were used (Fig. 1A–D): 0.71°, 1.43°, 2.0°, 3.33° to test performance for the Battenberg stimuli, as well as the full stimulus (square of 10° side length) with no blank regions (Fig. 1E).

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

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

where L_m is the mean luminance of the display, c is amplitude, f_s is the spatial frequency, f_t is the temporal frequency and ϕ adjusts the phase of the grating. The checks were smoothed at the edge using a raised sine envelope that occupied a uniform width strip equal to 10% of the distance from the center to the nearest edge of the square check. The

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