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Contrast and stimulus duration dependence of perceptual surround suppression in older adults

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ABSTRACT

Most natural visual tasks involve the extraction of visual features from suprathreshold contrast backgrounds, hence an understanding of how ageing impacts on contrast mechanisms is essential to understand elderly visual function. Previous studies have revealed increased perceptual surround suppression of contrast in older adults. We aimed to determine whether such age-related effects depend on the centre or surround stimulus contrast as the neurophysiological mechanisms underpinning contrast–contrast suppression depend on such contrast relationships. We also measured surround suppression of contrast for longer duration and shorter duration stimuli to explore for effects of surround adaptation Fifteen younger and 15 older adults performed a centre-surround contrast discrimination task for a variety of centre-surround contrast combinations (20%, 40% and 80% contrast). Stimulus duration was 500 ms. The 40% centre, 80% surround condition was also presented for 100 ms duration. Relative to younger adults, perceptual surround suppression was increased for the older group for low, but clearly suprathreshold, central contrasts (20% contrast), whilst both groups performed similarly for stimuli with high centre contrasts. Data was best fit by a model with both increased inhibitory and excitatory weightings in the older group. Reduced stimulus duration increased perceptual surround suppression for both groups consistent with reduced adaptation to the surround, and did not explain the difference in suppression magnitude between groups. Understanding the stimulus parameters that elicit increased surround suppression in older adults is key to directing future work exploring underlying neural substrates, in addition to potentially being useful for predicting performance on more complicated natural visual tasks such as object and scene perception.

1. Introduction

In recent years, there has been considerable study of the age-related effects on centre-surround cortical mechanisms within the human and primate visual system. Much of this research has been motivated by observations from primate research that are consistent with a reduction in inhibitory function within the ageing visual cortex (Leventhal et al., 2003; Schmolesky et al., 2000). The theory of altered inhibition is supported by neurophysiological evidence for altered cellular properties that are known to depend, at least in part, on inhibition. For example, orientation tuning and direction selectivity of neurons are both reduced in the aged non-human primate primary visual cortex. Conversely, spontaneous and visually evoked neural activity is increased (Leventhal et al., 2003; Schmolesky et al., 2000). Leventhal et al. (2003) showed that after GABA administration to individual V1 cells in aged primate, the percentage of orientation biased neurons increased from 39% to 81% of cells tested. A more recent study has shown that the strength of surround suppression is decreased in suppressive V1 neurons of older primates (Fu et al., 2010). Neurons of older animals that were less orientation and direction selective, exhibited significantly reduced surround suppression (76% of neurons tested). The remaining neurons, that did not show reduced orientation selectivity, exhibited similar suppression to those of younger monkeys. The authors suggested that the findings of age related alterations of orientation and direction tuning (Leventhal et al., 2003; Schmolesky et al., 2000), might be linked to the same mechanism underpinning a decrease in neuronal surround suppression (Fu et al., 2010).

Neuronal centre-surround effects result from a complex network of excitatory and inhibitory connections (Angelucci & Bressloff, 2006; Angelucci & Bullier, 2003; Chisum & Fitzpatrick, 2004) hence any process that alters the balance between inhibition

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and excitation may alter the net balance of these connections. In humans, there are several psychophysical tasks that are understood to provide perceptual analogues of neural centre-surround suppression. One such task is the contrast–contrast phenomenon, where the perceived contrast of a given stimulus can vary depending on the context in which it is presented (Cannon & Fullenkamp, 1991; Yu, Klein, & Levi, 2001). An alternate method that has been used to explore perceptual effects of surround suppression is the motion discrimination task originally described by Tadin et al. (2003). Increasing the size of a high contrast drifting stimulus makes it harder to determine the direction of its motion. This is measured as an increase in duration threshold; the amount of time the stimulus is required to be presented in order to correctly identify the direction of the motion. An increase in duration threshold for large, high contrast stimuli, relative to smaller stimuli, has been suggested to represent surround suppression from the centre-surround antagonistic properties of neurons in visual area V5 (Tadin et al., 2011, 2003).

A simple theory of reduced inhibitory function in ageing, leads to predictions of reduced perceptual surround suppression in older adults. There is support for this in the literature. Betts et al. (2005) found by using the motion discrimination task (Tadin et al., 2003), that older adults produced shorter duration thresholds for large, high contrast stimuli, indicating that they were better able to discriminate the direction of motion of a large, high contrast stimulus than younger adults. The improvement in performance with age was suggested to be due to a decrease in surround suppression. However, contrast–contrast tasks lead to the opposite result. Using the contrast–contrast discrimination task, we have previously shown that perceptual surround suppression is increased in older adults leading to greater contrast suppression. An increase in contrast suppression in older groups is replicable, and has been observed for high contrast textured stimuli (Karas & McKendrick, 2009), grating stimuli, both in-phase and out-of phase between centre and surround (Karas & McKendrick, 2011) and for drifting stimuli (Karas & McKendrick, 2012). The seemingly conflicting findings for the motion duration task and the centre-surround contrast task are potentially informative regarding the mechanisms underpinning these perceptual phenomena and the intersection of these with the ageing process. A disconnect between the outcomes of these measures is not the case for other conditions where centre-surround tasks have been used as perceptual analogues of cortical inhibition such as migraine and schizophrenia (Battista, Badcock, & McKendrick, 2010, 2011; Dakin, Carlin, & Hemsley, 2005; Tadin et al., 2006). While there are a number of differences between the motion duration task and the perceived contrast task, key differences are the uniformity of contrast across the stimulus for the motion task (relative to the different centre-surround contrasts in the perceived contrast task); and considerable differences in stimulus duration (thresholds of approximately 100 ms for the motion task, and typical stimulus displays of 500 ms for the contrast task). The purpose of our current experiments was to determine whether either the centre-surround contrast configuration or stimulus duration, can shed light on why older adults show increased rather than the predicted decrease of suppression with the contrast–contrast task.

Both neurophysiological (Cavanaugh, Bair, & Movshon, 2002b; Levitt & Lund, 1997; Schwabe et al., 2010) and psychophysical (Cannon & Fullenkamp, 1991; Xing & Heeger, 2001; Yu, Klein, & Levi, 2001) experiments demonstrate that the balance between suppression and excitation depends on the ratio of contrast between centre and surround. Behaviourally, the amount of surround suppression versus enhancement is typically dependent on the contrast ratios between centre and surround, with surround suppression when the surround contrast is higher than the centre and surround enhancement when the surround contrast is lower than the centre contrast (Ejima & Takahashi, 1985; Xing & Heeger, 2001). Centre-surround interactions at a cellular level in V1 also depend on centre and surround contrast (Levitt & Lund, 1997; Webb et al., 2005), with response properties suggesting different input mechanisms depending on contrast. When stimuli are high contrast, surround suppression is strongly orientation tuned, with suppressive effects present when the orientation of the centre and surround are matching (Levitt & Lund, 1997). At low contrast, suppressive effects do not display this orientation tuning (Levitt & Lund, 1997). Webb et al. (2005) varied the contrast between the centre and surround, and showed that when the centre contrast was low, V1 suppressive tuning was broadband and monocularly driven and when the centre contrast was high, spatiotemporal tuning was sharp and binocularly driven. The authors suggest that the origins of the different contrast dependent surround suppression responses include early in the visual pathway (possible the LGN or input layers of V1) and then later, within V1 and/or feedback from extrastriate areas (Webb et al., 2005). This evidence for the mechanisms of contrast suppression being dependent on contrast relationships between the centre and surround areas forms motivation for our first experiment in this study.

We also investigated the effect of reducing stimulus duration for the perceived contrast task. When a stimulus is high contrast, surround adaptation results in the surround being less effective at suppressing the centre with increasing stimulus duration (Cavanaugh, Bair, & Movshon, 2002a; Patterson, Wissig, & Kohn, 2013; Wissig & Kohn, 2012). It is plausible that the increase in surround suppression demonstrated by older adults for centre-surround contrast stimuli, is not due to an increased suppressive effect per se, but due to a reduction in adaptation. In this case, older and younger adults should perform similarly for shorter presentation durations (where surround adaptation has not yet been activated) but perform differently at longer presentation durations after surround adaptation is present. Our second experiment tests this hypothesis.

2. Materials and methods

The current study included two groups: 15 young adults (20–30 years) and 15 older adults (65–79 years). Ethics approval was granted by the Human Research Ethics Committee of The University of Melbourne and all participants provided written consent prior commencing the research according to a protocol consistent with the Declaration of Helsinki. Participants attended for two sessions of up to 2 h in duration. The first visit included a general eye examination (refraction, ophthalmoscopy, slit lamp and tonometry) to ensure study eligibility. Participants' best corrected visual acuity was required to be 6/7.5 or better with a refractive error limit of ±5D spherical with 2D of astigmatism. Normal findings of ocular health assessment for age including anterior eye and optic nerve assessment were required. Participants also provided information about their general health, to exclude people with systemic conditions known to affect visual function (for example, diabetes, migraine, schizophrenia, and epilepsy) or who were taking medications known to affect visual function (e.g., anti-anxiety or anti-depressant medications).

Experiments were conducted using a personal computer with a gamma-corrected Sony G520 21-inch CRT monitor (frame rate 120 Hz, resolution 800×600 pixels, and maximum luminance 100 cd/m^2). Custom software was written in Matlab 7.0 (Mathworks, Natick, MA, USA) and stimuli were displayed using