SPATIAL SUPPRESSION IN AGING

THE EFFECT OF AGING ON SPATIAL SUPPRESSION

By

LINDSAY E. FARBER, H.B.Sc.

A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Doctor of Philosophy

McMaster University

DOCTOR OF PHILOSOPHY (2015) McMaster University
(Neuroscience Graduate Program) Hamilton, Ontario

TITLE: The effect of aging on spatial suppression
AUTHOR: Lindsay E. Farber, H.B.Sc. (Western University)
SUPERVISORS: Professors Patrick J. Bennett and Allison B. Sekuler
NUMBER OF PAGES: xvii, 130

Abstract

The effect of aging on spatial suppression

Lindsay E. Farber
Doctor of Philosophy
Neuroscience Graduate Program
McMaster University
2015

The research discussed here examines how normal healthy aging affects spatial suppressive mechanisms in a variety of visual tasks using both static and dynamic stimuli. Prior research has suggested that younger adults demonstrate a center-surround antagonistic pattern in which they show spatial summation at low contrast and spatial suppression at high contrast in brief motion direction discrimination tasks. Older adults have been shown to have reduced spatial suppression at high contrast and this is thought to be related to reduced GABAergic inhibition in the visual cortex. The results obtained from this program of research suggest that age-related changes in optical and neural visual mechanisms do not affect spatiotemporal mechanisms for static stimuli when the target is presented with the mask (embedded masking). However, when the mask appears immediately before (forward masking) or after (backward masking) the target, older adults require more contrast to detect the target (Chapter 2). In addition, spatial suppression is not reduced for older adults in a task with moving stimuli presented at long durations, even with increasing speed (Chapter 3). In Chapter 4, we used static stimuli presented at brief durations to induce a sudden motion onset and found that although there was no significant age difference in spatial suppression, there was a trend showing reduced levels of spatial suppression in older adults. These results taken together suggest that inhibitory neural mechanisms in the visual cortex may mediate spatial

suppression for briefly presented stimuli only.

Acknowledgements

I could not have completed my doctoral dissertation without the unwavering support I received from a fantastic team of people. Though I can't acknowledge every individual who provided either professional or personal support during my time as a Ph.D. candidate, I'd like to highlight a few of the most significant contributors to my success in reaching this milestone.

First, I'm so grateful to my graduate supervisors, Dr. Patrick J. Bennett and Dr. Allison B. Sekuler, for their invaluable guidance, scholarly input, and consistent encouragement, which I was so lucky to receive throughout my time spent in their lab. I'd also like to thank my third Ph.D. committee member, Dr. Bruce K. Christensen, the Director of the MiNDS program, Dr. Kathy M. Murphy, and the MiNDS coordinator, Sandra Murphy. Kathy and Sandra, the unique roles that you've played on this journey have meant a great deal to me.

I wouldn't be where I am today—academically or otherwise—without the support of my research lab manager, Donna Waxman, who not only helped me collect important data but also strengthened my stamina with her kind words over the years. My Vision Lab colleagues deserve mention for the warmth they extended to me; I learned a lot from them through our personal and scholarly interactions. I cannot thank our senior participants enough for spending countless hours in our lab, contributing to our research projects.

I'd be remiss if I didn't thank my boss, Dr. Jonathan A. Goler, for his steadfast belief in me, his counsel, and his understanding throughout my time at Moneykey, where I have had the opportunity to work while simultaneously finalizing my thesis.

Finally, I owe so much to my parents, Rachel and Glenn Farber, who cheered me on at every stage of my academic career, longing to see me realize this dream. I also thank my sister, Stacey Farber, for her motivational pep talks and my grandparents, Dr. Robert Farber, Sally Kert, the late Shaynka

Farber, and the late Sheldon Kert for their love. Thank you for encouraging me to work hard and aim higher, and for teaching me to believe that I can accomplish anything I set my mind to.

Contents

List of Figures

List of Tables

List of Abbreviations

2-IFC two-interval forced-choice

ANOVA ANalysis Of VAriance

cd/m^2 Candelas per square meter

CRT cathode-ray tube

CFQ Cognitive Failures Questionnaire

cm centimeters

cpd cycles-per-degree

cps cycles-per-second

deg degrees

dps degrees-per-second

ETDRS Early Treatment Diabetic Retinopathy Study

FARS Fatality Analysis Reporting System

fps frames-per-second

GABA γ-aminobutryic acid

Gabor Windowed sine wave grating

GAD glutamic acid decarboxylase

Hz Hertz

ISI inter-stimulus interval

M Mean

MCI mild cognitive impairment

MDD major depressive disorder

MEGA-PRESS MEscher-GArwood Point REsolved SpectroScopy

MMSE Mini-Mental State Examination

MOA motion onset asynchrony

MoCA Montreal Cognitive Assessment

MREB McMaster Research Ethics Board

MRS magnetic resonance spectroscopy

ms milliseconds

MT middle temporal

MTA motion termination asynchrony

PSE point-of-subjective equality

s seconds

SCZ schizophrenia

SEM Standard Error of the Mean

SOA stimulus onset asynchrony

TMS transcranial magnetic stimulation

TvM threshold-vs.-mask contrast

V1 primary visual cortex/visual area 1

V5 visual area 5

Preface

The main goal of this dissertation is to investigate effects of normal healthy aging on spatial suppression in the visual system. The research presented here is in the form of a sandwich thesis with Chapters 2, 3, and 4 written in journal article format. These chapters are manuscripts that are being prepared for journal submission. Chapter 1 will set the general context for the experiments. Background information specific to each experimental series is provided in the introduction section of its respective chapter. Chapter 5 reviews the findings presented in this dissertation in context with the literature and proposes ideas for future experiments.

After I wrote an initial draft, my dissertation was revised collaboratively with my supervisors Patrick J. Bennett (PJB) and Allison B. Sekuler (ABS). As primary author, I oversaw all aspects of the research presented here. All experimental programming for Chapters 2, 3 and 4 was done by PJB and myself. Donna Waxman, our research manager, collected the data for all experiments. I was responsible for the data analysis in all chapters.

The research here was supported by the Canada Research Chairs program, a grant from the Canadian Institutes of Health Research (CIHR) to PJB and ABS, the CIHR Strategic Training Grant on Communication and Social Interaction in Healthy Aging in Masters Year 1 and PhD Year 1 (PJB and ABS were mentors, and I was a trainee), and an Ontario Graduate Scholarship (OGS), which I was granted in Year 4 of my Ph.D.

Chapter 1

General Introduction

1.1 Why study aging?

Canada's aging population ($\geq$ 65 years of age) has been steadily growing and is projected to increase from 15.3% of the population as of 2013 to approximately 24% by the year 2043 (Statistics Canada, 2014). This demographic trend will have a dramatic effect on every aspect of life in Canada including healthcare, the workforce, transportation and communication. Due to increasing longevity (Statistics Canada, 2012), a large segment of society will have to cope with the sensory, motor, and cognitive deficits that typically accompany normal healthy aging for an increasingly greater portion of their lives. Visual health is critical for seniors to function independently in society, with age-related visual impairments often leading to the need for assisted living, vocational and social services, and disability pensions.

Two of the most common measures of visual function, visual acuity and contrast sensitivity, are known to decline in healthy aging (Sekuler and Sekuler, 2000), and these age-related changes are associated with the general health and quality of life of seniors. Older adults with moderate (20/30) or severely

impaired (20/80) visual acuity in one or both eyes are at a greater risk of sustaining a hip fracture (Felson et al., 1989; Abdelhafiz and Austin, 2003). Visual acuity is also correlated with performance on cognitive assessment tests measuring working memory, associative learning, and concept identification (Gilmore et al., 2006; Salthouse et al., 1996; Lindenberger and Baltes, 1997). Good vision is important for verbal and social communication, especially when one is required to read lips due to age-related hearing loss (Erber, 2002), and without sufficient interpersonal communication, older people can become isolated in society (Berry et al., 2004). These examples demonstrate that when older people lose their vision it affects many aspects of their lives in addition to damaging their emotional well-being. For this reason, it is important to understand how visual loss occurs and discover ways to improve visual function in healthy seniors so that they may maintain a high quality of life. The current dissertation is part of a body of research focusing on gaining a better understanding of the brain's normal aging process with regard to visual functioning.

1.2 Spatial suppression in healthy aging

One important aspect of visual functioning is our ability to detect objects without being distracted by background clutter. This ability is required in everyday situations such as searching for your friend in a crowd and driving through a busy street. Although this ability is critical to navigate complex scenes in the real world, we can study the fundamental principle using relatively simple, psychophysical tasks. Tadin et al. (2003) asked younger adult subjects to indicate the direction of a drifting Gabor (Gaussian-damped sine wave grating) patch that varied in size and contrast. They found an antagonistic effect: when stimulus contrast was low, performance improved as stimulus size increased (spatial summation), but at high contrast performance deteriorated as size increased (spatial suppression). Tadin et al. suggested that center-surround neurons in the middle temporal visual area (MT/V5) are the

physiological basis of spatial suppression (Tadin et al., 2003). Center-surround interactions at the level of MT/V5 have also been proposed as the physiological candidate for spatial suppression in a binocular rivalry experiment using moving stimuli (Paffen et al., 2004). Paffen et al. found that a high-contrast surround grating moving in the same direction as the center stimulus lead to increased dominance of the opposite direction of motion in the center. They suggested that presenting an iso-oriented surround might lower the stimulus strength of the center by inhibiting neuronal responses to the center.

Churan et al. (2008) provided evidence to support the claim that area MT/V5 may be important for spatial suppression. Churan et al. measured neural responses in primate surround-suppressed and non-suppressed MT/V5 neurons to brief motion stimuli at various sizes. They found that surround-suppressed cells were more strongly modulated by motion direction when the stimulus size was small, but that performance deteriorated as size increased. In comparison, non-suppressed cells were not modulated by motion direction at any size. Churan et al. suggested that psychophysical spatial suppression occurs because the output of most MT/V5 neurons provides relatively little information about large, briefly-presented stimuli. Additionally, Tadin et al. (2011) found that spatial suppression disappeared when TMS (transcranial magnetic stimulation) was used to disrupt activity in MT/V5 but not in the primary visual cortex (V1) in younger adults.

Betts et al. (2005) tested both healthy younger and older subjects in a psychophysical direction discrimination task that was similar to an experiment conducted by Tadin et al. (2003). Like Tadin et al., Betts et al. found evidence for spatial suppression in younger subjects: when stimulus contrast was high, increasing stimulus size made direction discrimination more difficult. However, Betts et al. found that spatial suppression was reduced in older adults. Specifically, when contrast was high, the performance of older adults was less affected by changing stimulus size. In fact, performance for older adults was *better* than it was for younger adults in conditions that used large, high-contrast stimuli. Betts et al. suggested that this behavioural find-

ing occurred as a result of the decrease in GABAergic (γ-aminobutryic acid) inhibition in the aging visual system.

1.3 GABA deteriorates in aging

Aging changes the physiological characteristics of visual neurons (Leventhal et al., 2003; Hua et al., 2008; Williams et al., 2010; Pinto et al., 2010). If the responses of such neurons are linked to visual perception, then those physiological changes should produce certain types of changes in visual acuity, contrast sensitivity, and other visual measures. It is important to understand how the visual system changes with age so that we can examine the links between the brain and behaviour.

GABA regulates neural excitation by binding to inhibitory synapses. This regulation is called GABA-mediated inhibition and is thought to play a large role in many visual processes such as orientation tuning (Li et al., 2008), motion direction tuning (Rose and Blakemore, 1974; Sillito, 1979; Tsumoto et al., 1979), and center-surround mechanisms (Schwabe et al., 2006; Angelucci and Bullier, 2003). Currently, there is indirect evidence from animal studies that as the brain ages, GABAergic mechanisms deteriorate. For example, Leventhal et al. (2003) studied orientation tuning in individual V1 neurons in older and younger macaque monkeys. They measured cell responses before and after GABA and muscimol (GABA agonist) were administered electrophoretically in separate experimental sessions. Before drug administration, V1 cells in older animals responded equally well to all orientations and directions. After the agonist was injected, a greater percentage of V1 cells in older animals behaved more like V1 cells in younger animals in that they became more strongly tuned to specific orientations. The researchers concluded that GABA levels deteriorate in V1 and that this deterioration is directly responsible for orientation tuning.

Pinto et al. (2010) later investigated how GABAergic mechanisms in human primary visual cortex change across the lifespan. They quantified the expression of pre and post-synaptic GABAergic markers in post-mortem human V1 and found that levels of GAD65 (glutamic acid decarboxylase—a GABA synthesizing enzyme) and Gephyrin (a GABA receptor anchoring protein) were lower in older than younger adults. They replicated their Gephyrin results in a later experiment (Pinto et al., 2015). Pinto et al. suggested that lower levels of these GABAergic markers may mean that there are lower levels of GABA in the aging visual cortex. However, it is important to note that these GABA markers were not actual direct measures of GABA. Therefore, although this study shows that GABA markers decrease in aging, it does not tell us about actual GABA levels in the aging visual cortex.

Seizure studies also have provided indirect evidence to suggest that GABA levels change in the aging brain. Petroff et al. (1996) found that epileptic seizure patients had significantly lower levels of occipital GABA, measured using MRS (magnetic resonance spectroscopy), than healthy control subjects. Furthermore, the correlations between GABA levels and recent seizures as well as reduced seizure control and lower GABA levels were strong. In a separate epidemiological study, it was found that both the incidence and prevalence of seizures were significantly higher in people over 60 years of age (Tallis et al., 1991). Since seizure levels are related to lower levels of GABA and older adults are more prone to seizures than younger adults, GABA levels may be lower in older adults.

Occipital GABA levels have also been shown to decrease with the increase of cognitive failures experienced in daily life (as measured by the CFQ (Cognitive Failures Questionnaire) (Broadbent et al., 1982)), indicating that there is a correlation between low GABA levels and the incidence of cognitive failures (Sandberg et al., 2014). In addition, the prevalence of cognitive impairment has been linked to increased age (Graham et al., 1997). Since lower GABA levels are associated with the incidence of cognitive failures, and the prevalence of cognitive failures increases with age, there might be lower GABA levels in

older adults.

1.4 GABA and spatial suppression

Although GABA levels have not been correlated with spatial suppression in the aging population, this link has been observed in studies involving other special populations. For example, (Golomb et al., 2009) tested MDD (major depressive disorder) patients and controls in Tadin et al. (2003)'s direction discrimination task and found that the patients exhibited decreased spatial suppression. Prior to that, Sanacora et al. (1999, 2004) measured occipital GABA levels in MDD patients and controls using MRS. They found that MDD patients had significantly lower occipital GABA concentrations than healthy control subjects. Similarly, Tadin et al. (2006a) discovered that patients with SCZ (schizophrenia) had weakened center-surround interactions. They assessed SCZ patients and controls (a different set of controls than in the Tadin et al. (2003) study) in the direction discrimination task, and found that the patients showed less spatial suppression. Later, Yoon et al. (2010) measured GABA concentration in the visual cortex using MRS and found that it was significantly reduced in SCZ patients as compared to healthy controls. In these studies, there were correlations between GABA levels and spatial suppression at the level of the group rather than the individual. Based on these findings, it appears that visual cortical GABA levels are linked to spatial suppression.

In addition, there is neurophysiological evidence to support the link between GABA and surround suppression. Following Leventhal et al. (2003)'s finding that V1 cells in older monkeys are more broadly tuned to direction and orientation than V1 cells in younger monkeys, Fu et al. (2010) measured the response of V1 neurons in younger and older monkeys to central stimuli as well as central-plus-surround stimuli at various orientations. Fu et al. found that V1 cells in older monkeys showed reduced suppression indices compared with the V1 cells in younger monkeys. Therefore, there is a correlation between

the degradation of selectivity in V1 cells, reduced GABA levels, and reduced surround suppression in the aging brain.

1.5 Static versus dynamic stimuli

One caveat to the link established between psychophysically derived estimates of suppression and GABA is that only a single task has been used to measure spatial suppression in elderly adults: the direction discrimination task originally used by Tadin et al. (2003). Many other psychophysical tasks have been used to investigate spatial suppression, and although some have produced results that align with Tadin's classic summation and suppression patterns at low and high contrast (Gorea, 1985; Tadin et al., 2003, 2006b, 2008; Churan et al., 2009; van der Smagt et al., 2010), others have not (Karas and McKendrick, 2009, 2011, 2012, 2015).

Differences in the results reported in these studies addressing spatial suppression could be due to the way in which stimuli were presented. It has been shown that in studies addressing spatial suppressive mechanisms, younger adults consistently show greater spatial suppression as contrast increases no matter if the stimuli are static (Karas and McKendrick, 2009, 2011, 2015) or dynamic (Gorea, 1985; Tadin et al., 2003, 2006b, 2008; Churan et al., 2009; van der Smagt et al., 2010; Karas and McKendrick, 2012). However, it is important to note that evidence for an *age-related* decline in spatial suppression has not been found in all of these static or dynamic psychophysical tasks.

Karas and McKendrick published four papers investigating spatial suppression effects in aging (Karas and McKendrick, 2009, 2011, 2012, 2015). They found that in their tasks measuring perceived contrast, older adults showed greater spatial suppression than younger adults no matter if the stimuli were static and presented for 500 ms (Karas and McKendrick, 2009, 2011, 2015) or 100 ms Karas and McKendrick (2015) or dynamic and presented for 500 ms

(Karas and McKendrick, 2012). However, when they conducted a direction discrimination task using dynamic stimuli, replicating Tadin et al. (2003) and Betts et al. (2005)'s high contrast condition, they did not find evidence for an age difference in suppression Karas and McKendrick (2012). Their raw duration threshold results, however, revealed that older observers showed greater suppression at the small size and less suppression at the large size than younger observers, which was similar to what Betts et al. showed. Therefore, there seems to be a trend that spatial suppression decreases slightly in aging in dynamic direction discrimination tasks (Betts et al., 2005; Karas and McKendrick, 2012).

Using the same dynamic direction discrimination task originally reported in Tadin et al. (2003), Tadin et al. (2011) found that applying TMS on area MT/V5 in younger adults impaired spatial suppression. They showed that disrupting area MT/V5 improved performance for the younger adults in the large, high-contrast condition resembling the behavioural results for older adults in Betts et al.'s 2005 study. In contrast, they found that when V1 was disrupted using TMS, performance did not change. Tadin et al.'s 2011 experiment shows that there is a direct relationship between area MT/V5 and spatial suppression using dynamic gratings. Since GABA levels were not directly measured in this experiment, conclusions cannot be made regarding GABA levels with and without TMS to area MT/V5 or V1. Taken together, these observations imply that age-related neural changes may be taking place in area MT/V5.

Evidence from our lab (the Vision and Cognitive Neuroscience Lab at McMaster University) supports the hypothesis that stimulus type affects age-related changes in surround suppression. For example, Govenlock (2010) conducted an orientation tuning experiment with static stimuli. Orientation tuning has been shown to be linked directly to GABA levels (Sato et al., 1996). Younger and older subjects were instructed to detect a horizontal signal that was masked by variably-oriented patterns. They anticipated that a mask with the same orientation as the target would necessitate a stronger signal in younger adults. Given that animal neurophysiology research has found

significant detuning of senescent orientation-selective V1 (Schmolesky et al., 2000) and V2 (Yu et al., 2006) neurons, they hypothesized that older adults would show broader psychophysical orientation tuning. Surprisingly, they did not find an age effect on psychophysical orientation tuning with static stimuli. However, Tsotsos (2012) employed a masking paradigm using moving stimuli to investigate directionally-selective mechanisms in the aging brain. Subjects were asked to discriminate the direction of moving signal dots embedded in noise dots. Unlike Govenlock, Tsotsos found that older adults were less sensitive to motion direction and demonstrated broader tuning. These studies support the claim that the coding of moving and static stimuli are differentially affected by aging in humans.

1.6 Thesis overview

The evidence reviewed in this chapter indicating that GABA levels deteriorate in aging, and that there is an association between low visual cortical GABA concentration and reduced spatial suppression, raises the possibility that spatial suppressive mechanisms may diminish in the healthy aging brain. Studies on spatial suppression in older adults have employed different methodologies and have found opposing results. To better characterize spatial suppressive mechanisms in senescence, I conducted a series of visual psychophysical tasks in healthy younger (age range: 17-30 years) and older (age range: 60-90 years) adult humans.

In Chapter 2, I employed spatiotemporal masking techniques to assess psychophysical suppressive mechanisms in normal aging. Subjects were instructed to detect a horizontally-oriented Gabor stimulus that was masked with either a small central overlay, a surround annulus, or a combination of the central and surround masks in a 2-IFC (two-interval forced-choice) task. The target was presented either immediately before (backward masking), during (embedded masking), or immediately after (forward masking) mask presentation. This

methodology was previously used in younger observers by Saarela and Herzog (2008), who found that masking was strongest for the central and combination masks at the backward and forward masking time points. However, there was less masking for the combination mask. They reasoned that although the surround mask on its own had a very small effect, the surround portion of the combination mask reduced the strength of the central mask area. Assuming that older observers have less visual cortical GABA and that this is related to reduced spatial suppression, then the surround portion of the combination mask should *not* reduce the strength of the central area of the mask. Therefore, we would expect the central and combination masking thresholds to be similar across the temporal conditions. Contrary to that prediction, however, we found that older adults showed the same spatiotemporal masking patterns as their younger counterparts, but with slightly higher contrast thresholds overall.

One possible explanation for the discrepancy between reports of reduced visual cortical GABA and diminished psychophysical spatial suppression in aging, and no effect of age in our spatiotemporal masking study when the target was presented during mask presentation, is that the reduced spatial suppression effect observed in older adults is found in studies using dynamic as opposed to static stimuli. Moving stimuli are known to be processed in area MT/V5 (Churan et al., 2008; Tadin et al., 2011). In our spatiotemporal task, the stimuli were static. Therefore, if the age difference for simultaneously presented target and mask stimuli occurs when the stimuli are dynamic, then perhaps the age-related neural change is located in area MT/V5.

I examined this idea in the experiments presented in Chapter 3, in which I presented drifting stimuli to observers and varied the size and contrast. Instead of measuring duration thresholds like Betts et al. (2005), I measured perceived speed in a task similar to the one used by van der Smagt et al. (2010). In this 2-IFC task, observers were asked to indicate the stimulus interval containing the grating drifting at a faster speed. Consistent with the results reported by van der Smagt et al., we found that younger observers showed spatial

suppression at high contrast. However, we did not find spatial summation at low contrast in our younger observers. If aging diminishes the effects of spatial suppression on motion tasks, then we would expect older adults to show reduced spatial suppression in this perceived speed task. The results presented in Chapter 3 provided no evidence that spatial suppression is reduced in aging in this motion task. Younger and older subjects showed similar patterns in their results.

It is important to note that in our Chapter 3 experiments, the drifting stimuli were presented to subjects for a relatively long time (500 ms), whereas duration thresholds measured in Tadin et al. (2003) and Betts et al. (2005)'s studies were much more brief (40-100 ms). Since surround suppressed cells in MT/V5 show stronger tuning to motion direction with briefly presented stimuli ($\sim$ 40 ms) than non-suppressed cells (Churan et al., 2008), perhaps we needed to use a briefer stimulus to find an age difference in psychophysical spatial suppression.

The experiments discussed in Chapter 4 addressed this issue. I employed Churan et al. (2009)'s methodology in which a static vertically-oriented Gabor stimulus was presented for a brief duration and underwent a phase-shift in the middle of the stimulus presentation. Observers were asked to indicate the direction of the movement (i.e., left or right), with stimulus size and contrast varied across conditions. Churan et al. (2009) had found the classic pattern of spatial summation at low contrast and spatial suppression at high contrast in their younger observers. We hypothesized that if older adults have weaker surround suppression mechanisms then they would show reduced spatial suppression at high contrast in this brief motion task. We found that the strength of spatial suppression for older adults at high contrast was still strong in this experiment. Although we did not find a statistical age difference in the magnitude of spatial suppression at high contrast, there was a trend showing less spatial suppression in older than younger adults.

Altogether, the results from this dissertation suggest that the previously

held belief that spatial suppression generally declines in healthy older humans is not accurate and a more nuanced understanding of surround suppression is required. Chapters 2, 3, and 4 contain a more detailed description of each experimental series. The General Discussion of this dissertation, Chapter 5, contains a discussion of how the results reported here can be reconciled with other related literature as well as ideas for future research directions.

References

Abdelhafiz, A. H., Austin, C. A., Jan 2003. Visual factors should be assessed in older people presenting with falls or hip fracture. Age Ageing 32 (1), 26–30.

Angelucci, A., Bullier, J., 2003. Reaching beyond the classical receptive field of v1 neurons: horizontal or feedback axons? J Physiol Paris 97 (2-3), 141–54.

Berry, P., Mascia, J., Steinman, B. A., 2004. Vision and hearing loss in older adults: Double trouble. Care Manag J 5 (1), 35–40.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., Feb 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–6.

Broadbent, D. E., Cooper, P. F., FitzGerald, P., Parkes, K. R., Feb 1982. The Cognitive Failures Questionnaire (CFQ) and its correlates. Br J Clin Psychol 21 (Pt 1), 1–16.

Churan, J., Khawaja, F. A., Tsui, J. M. G., Pack, C. C., Nov 2008. Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT. Curr Biol 18 (22), R1051–2.

Churan, J., Richard, A. G., Pack, C. C., 2009. Interaction of spatial and temporal factors in psychophysical estimates of surround suppression. J Vis 9 (4), 15.1–15.

Erber, N. P., 2002. Hearing vision communication and older people. Clavis Publishing, Melbourne.

Felson, D. T., Anderson, J. J., Hannan, M. T., Milton, R. C., Wilson, P. W., Kiel, D. P., Jun 1989. Impaired vision and hip fracture: The Framingham Study. J Am Geriatr Soc 37 (6), 495–500.

Fu, Y., Wang, X. S., Wang, Y. C., Zhang, J., Liang, Z., Zhou, Y. F., Ma, Y. Y., Aug 2010. The effects of aging on the strength of surround suppression of receptive field of v1 cells in monkeys. Neuroscience 169 (2), 874–81.

Gilmore, G. C., Spinks, R. A., Thomas, C. W., Mar 2006. Age effects in coding tasks: componential analysis and test of the sensory deficit hypothesis. Psychol Aging 21 (1), 7–18.

Golomb, J. D., McDavitt, J. R. B., Ruf, B. M., Chen, J. I., Saricicek, A., Maloney, K. H., Hu, J., Chun, M. M., Bhagwagar, Z., Jul 2009. Enhanced visual motion perception in major depressive disorder. J Neurosci 29 (28), 9072–7.

Gorea, A., 1985. Spatial integration characteristics in motion detection and direction identification. Spat Vis 1 (2), 85–102.

Govenlock, S. W., 2010. Visual channels in aging. Ph.D. thesis, McMaster University.

Graham, J. E., Rockwood, K., Beattie, B. L., Eastwood, R., Gauthier, S., Tuokko, H., McDowell, I., Jun 1997. Prevalence and severity of cognitive impairment with and without dementia in an elderly population. Lancet 349 (9068), 1793–6.

Hua, T., Kao, C., Sun, Q., Li, X., Zhou, Y., Jan 2008. Decreased proportion of GABA neurons accompanies age-related degradation of neuronal function in cat striate cortex. Brain Res Bull 75 (1), 119–25.

Karas, R., McKendrick, A. M., 2009. Aging alters surround modulation of perceived contrast. J Vis 9 (5), 11.1–9.

Karas, R., McKendrick, A. M., Nov 2011. Increased surround modulation of perceived contrast in the elderly. Optom Vis Sci 88 (11), 1298–308.

Karas, R., McKendrick, A. M., 2012. Age related changes to perceptual surround suppression of moving stimuli. Seeing Perceiving 25 (5), 409–24.

Karas, R., McKendrick, A. M., Mar 2015. Contrast and stimulus duration dependence of perceptual surround suppression in older adults. Vision Res.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., Ma, Y., May 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–5.

Li, G., Yang, Y., Liang, Z., Xia, J., Yang, Y., Zhou, Y., Aug 2008. GABA-mediated inhibition correlates with orientation selectivity in primary visual cortex of cat. Neuroscience 155 (3), 914–22.

Lindenberger, U., Baltes, P. B., Sep 1997. Intellectual functioning in old and very old age: cross-sectional results from the Berlin Aging Study. Psychol Aging 12 (3), 410–32.

Paffen, C. L. E., te Pas, S. F., Kanai, R., van der Smagt, M. J., Verstraten, F. A. J., 2004. Center-surround interactions in visual motion processing during binocular rivalry. Vision Res 44 (14), 1635–9.

Petroff, O. A., Rothman, D. L., Behar, K. L., Mattson, R. H., Dec 1996. Low brain GABA level is associated with poor seizure control. Ann Neurol 40 (6), 908–11.

Pinto, J. G. A., Hornby, K. R., Jones, D. G., Murphy, K. M., 2010. Developmental changes in GABAergic mechanisms in human visual cortex across the lifespan. Front Cell Neurosci 4, 16.

Pinto, J. G. A., Jones, D. G., Williams, C. K., Murphy, K. M., 2015. Characterizing synaptic protein development in human visual cortex enables alignment of synaptic age with rat visual cortex. Front Neural Circuits 9, 3.

Rose, D., Blakemore, C., May 1974. Effects of bicuculline on functions of inhibition in visual cortex. Nature 249 (455), 375–7.

Saarela, T. P., Herzog, M. H., 2008. Time-course and surround modulation of contrast masking in human vision. J Vis 8 (3), 23.1–10.

Salthouse, T. A., Hancock, H. E., Meinz, E. J., Hambrick, D. Z., Nov 1996. Interrelations of age, visual acuity, and cognitive functioning. J Gerontol B Psychol Sci Soc Sci 51 (6), P317–30.

Sanacora, G., Gueorguieva, R., Epperson, C. N., Wu, Y.-T., Appel, M., Rothman, D. L., Krystal, J. H., Mason, G. F., Jul 2004. Subtype-specific alterations of gamma-aminobutyric acid and glutamate in patients with major depression. Arch Gen Psychiatry 61 (7), 705–13.

Sanacora, G., Mason, G. F., Rothman, D. L., Behar, K. L., Hyder, F., Petroff, O. A., Berman, R. M., Charney, D. S., Krystal, J. H., Nov 1999. Reduced cortical gamma-aminobutyric acid levels in depressed patients determined by proton magnetic resonance spectroscopy. Arch Gen Psychiatry 56 (11), 1043–7.

Sandberg, K., Blicher, J. U., Dong, M. Y., Rees, G., Near, J., Kanai, R., Feb 2014. Occipital GABA correlates with cognitive failures in daily life. Neuroimage 87, 55–60.

Sato, H., Katsuyama, N., Tamura, H., Hata, Y., Tsumoto, T., Aug 1996. Mechanisms underlying orientation selectivity of neurons in the primary visual cortex of the macaque. J Physiol 494 (Pt 3), 757–71.

Schmolesky, M. T., Wang, Y., Pu, M., Leventhal, A. G., Apr 2000. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. Nat Neurosci 3 (4), 384–90.

Schwabe, L., Obermayer, K., Angelucci, A., Bressloff, P. C., Sep 2006. The role of feedback in shaping the extra-classical receptive field of cortical neurons: a recurrent network model. J Neurosci 26 (36), 9117–29.

Sekuler, R., Sekuler, A. B., 2000. Oxford Textbook of Geriatric Medicine, 2nd Edition. No. pp. 874-880. Oxford University Press, New York.

Sillito, A. M., Apr 1979. Inhibitory mechanisms influencing complex cell orientation selectivity and their modification at high resting discharge levels. J Physiol 289, 33–53.

Statistics Canada, May 2012. Life expectancy at birth, by sex, by province. URL http://www.statcan.gc.ca/tables-tableaux/sum-som/l01/cst01/health26-eng.htm

Statistics Canada, Sept 2014. Population projections for Canada, Provinces and Territories, 2013 to 2063. URL http://www.statcan.gc.ca/pub/91-520-x/2014001/tbl/tbl2.4-eng.htm

Tadin, D., Kim, J., Doop, M. L., Gibson, C., Lappin, J. S., Blake, R., Park, S., Nov 2006a. Weakened center-surround interactions in visual motion processing in schizophrenia. J Neurosci 26 (44), 11403–12.

Tadin, D., Lappin, J. S., Blake, R., Mar 2006b. Fine temporal properties of center-surround interactions in motion revealed by reverse correlation. J Neurosci 26 (10), 2614–22.

Tadin, D., Lappin, J. S., Gilroy, L. A., Blake, R., Jul 2003. Perceptual consequences of centre-surround antagonism in visual motion processing. Nature 424 (6946), 312–5.

Tadin, D., Paffen, C. L. E., Blake, R., Lappin, J. S., 2008. Contextual modulations of center-surround interactions in motion revealed with the motion aftereffect. J Vis 8 (7), 9.1–11.

Tadin, D., Silvanto, J., Pascual-Leone, A., Battelli, L., Jan 2011. Improved motion perception and impaired spatial suppression following disruption of cortical area MT/V5. J Neurosci 31 (4), 1279–1283.

Tallis, R., Hall, G., Craig, I., Dean, A., Nov 1991. How common are epileptic seizures in old age? Age Ageing 20 (6), 442–8.

Tsotsos, L. E., 2012. The effects of aging on motion perception in healthy older adults. Ph.D. thesis, McMaster University.

Tsumoto, T., Eckart, W., Creutzfeldt, O. D., Jan 1979. Modification of orientation sensitivity of cat visual cortex neurons by removal of GABA-mediated inhibition. Exp Brain Res 34 (2), 351–63.

van der Smagt, M. J., Verstraten, F. A. J., Paffen, C. L. E., Aug 2010. Center-surround effects on perceived speed. Vision Res 50 (18), 1900–4.

Williams, K., Irwin, D. A., Jones, D. G., Murphy, K. M., 2010. Dramatic loss of ube3a expression during aging of the mammalian cortex. Front Aging Neurosci 2, 18.

Yoon, J. H., Maddock, R. J., Rokem, A., Silver, M. A., Minzenberg, M. J., Ragland, J. D., Carter, C. S., Mar 2010. GABA concentration is reduced in visual cortex in schizophrenia and correlates with orientation-specific surround suppression. J Neurosci 30 (10), 3777–81.

Yu, S., Wang, Y., Li, X., Zhou, Y., Leventhal, A. G., July 2006. Functional degradation of extrastriate visual cortex in senescent rhesus monkeys. Neuroscience 140 (3), 1023–9.

Chapter 2

Spatiotemporal masking effects in the aging visual system

2.1 Abstract

Three experiments were conducted to assess the effects of aging on spatial and temporal visual masking. In Experiment 1, younger (aged $\sim$ 22 years) and older (aged $\sim$ 70 years) observers detected a 4 cpd horizontally-oriented grating that was masked by a small central pattern that overlapped the target, a surround annulus, or a combination of the central and surround masks. Mask contrast was kept constant at 40%, and the target was presented at three different onset times in relation to the mask. Consistent with previous findings with younger observers (Saarela and Herzog, 2008), masking strength was highest for the central and combination masks when target offset coincided with mask onset (backward masking) and when target onset coincided with mask offset (forward masking). Minimal masking was observed with the sur-

round annulus. Similar results were obtained with older observers, although older adults required a higher contrast level to detect the target in all conditions. Since our first experiment did not take into account age differences in sensitivity to the mask, we measured detection thresholds for each of the three mask types and the target (Experiment 2). We found that although older adults were less sensitive to the target and masks overall, thresholds for both age groups were highest for the target, followed by the central mask, and then the surround and combination masks. In Experiment 3, we tested subjects in the same task used in Experiment 1 but added a wider range of mask contrast levels to control for age differences in contrast sensitivity. After normalizing the threshold levels (masking threshold/no-mask threshold) and the contrast levels (mask contrast/mask detection threshold), we found that thresholds for older subjects were higher than younger subjects at the backward and forward masking time points, but not at the embedded masking time point. These results suggest that transient masking affects younger and older subjects differently and that age differences in contrast sensitivity do not explain this finding.

2.2 General Introduction

It is well established that aging affects several aspects of visual perception, including contrast sensitivity, visual acuity, and motion detection (Andersen and Ni, 2008; Billino et al., 2008; Glass, 2007; Sekuler and Sekuler, 2000; Owsley et al., 1983). However, the specific effects of spatial and temporal masking in aging are not understood. We know that different types of spatial masks affect behavioural responses. For example, a surround grating can decrease perceived contrast of (Cannon and Fullenkamp, 1991; Olzak and Laurinen, 1999; Snowden and Hammett, 1998; Xing and Heeger, 2000; Yu et al., 2001) as well as reduce neural responses to (Blakemore and Tobin, 1972; Cavanaugh et al., 2002; Fries et al., 1977; Jones et al., 2001; Maffei and Fiorentini, 1976; Nelson and Frost, 1978; Sengpiel et al., 1997; Webb et al.,

2005) a central target. In addition, superimposed overlay gratings (i.e., masks that spatially overlap with the target) can increase or decrease central target detection thresholds (Derrington and Henning, 1989; Foley, 1994; Legge and Foley, 1980; Petrov et al., 2005; Ross and Speed, 1991; Saarela and Herzog, 2008, 2009). In terms of spatial effects of masking in aging very little is known, but Chan et al. (2012) showed that iso-oriented flankers produce less facilitation in older than younger adults indicating that older adults may have abnormalities in spatial interactions.

In addition to spatial effects, the degree of masking depends on stimulus onset timing and presentation order. Saarela and Herzog (2008) manipulated both spatial and temporal masking in a study with younger adults. Results for one observer are shown in Figure 2.1. Subjects were instructed to detect a central target stimulus (40 ms in duration) in a 2-IFC task. They measured target contrast detection thresholds. A mask stimulus (100 ms duration) was also presented at each stimulus interval. There were three spatial mask conditions: a central mask, a surround mask, and a combination mask. Mask-target SOA (stimulus onset asynchrony) also varied across conditions: Negative SOAs indicate that the target appeared before the mask, positive SOAs indicate that the target appeared after the mask, and zero SOA indicates that the target and mask appeared on the screen at the same time. Saarela and Herzog found that a central mask produced strong masking when the mask was presented before (i.e., forward masking) or after (i.e., backward masking) the target stimulus, and relatively weak masking when the mask and target patterns overlapped in time. For example, in Figure 2.1 masking peaked in conditions when the mask-target SOA was -40 ms and 100 ms. Churan et al. (2009) also showed that suppression is strongest in younger adults when an iso-oriented central mask stimulus is presented briefly and immediately before a target (forward masking), after a target (backward masking) or at both time points. Interestingly, Saarela and Herzog (2008) found that a central-plus-surround (combination) mask produced significantly less backward masking then a central mask, but that the two patterns produced equivalent masking at other

SOAs. One interpretation of this result is that, in the backward masking condition, the addition of the surround considerably reduced the strength of (i.e., suppressed) the central mask.

Several studies have demonstrated age differences in backward masking. For example, Kline and Szafran (1975) conducted a backward masking study in younger and older adults, presenting target and mask stimuli monoptically to the right eye. The mask (a random visual noise array consisting of line segments) always appeared after the target (2-digit numbers). Kline and Szafran measured the shortest SOA between the target and mask required for an observer to correctly identify two or more of the four 2-digit numbers. They found that older adults required longer SOAs to escape the backward masking effects, concluding that it takes longer for the older visual cortex to clear a sensory message evoked by a visual stimulus. In a follow-up study, Kline and Birren (1975) further examined backward masking effects in aging, but presented the target to the right eye and the mask to the left eye and found similar results, suggesting that this behavioural age effect originates in the brain beyond the optic chiasm and not in the eye. Walsh (1976) also conducted a backward masking study and presented the target (one symmetrical letter with straight lines) to the right eye and the mask (randomly placed straight lines) to the left eye. Like Kline and Szafran and Kline and Birren, Walsh found that older adults required longer SOAs to escape masking. Till and Franklin (1981) also conducted a backward masking study with older adults and presented the target (two-letter combinations) and two types of masks (random visual noise or a pattern mask) to the same eye. Till and Franklin measured the minimum SOA required to correctly identify four consecutive targets, and found that older adults required longer SOAs than younger adults. In all of these studies, spatiotemporal masking effects at different SOAs and with different mask types in aging were not explored since the contrast and size of the mask were not manipulated and the mask always appeared after the target.

We hypothesized that the spatiotemporal effects on masking observed by Saarela and Herzog (2008) depend on mechanisms that produce spatial sup-

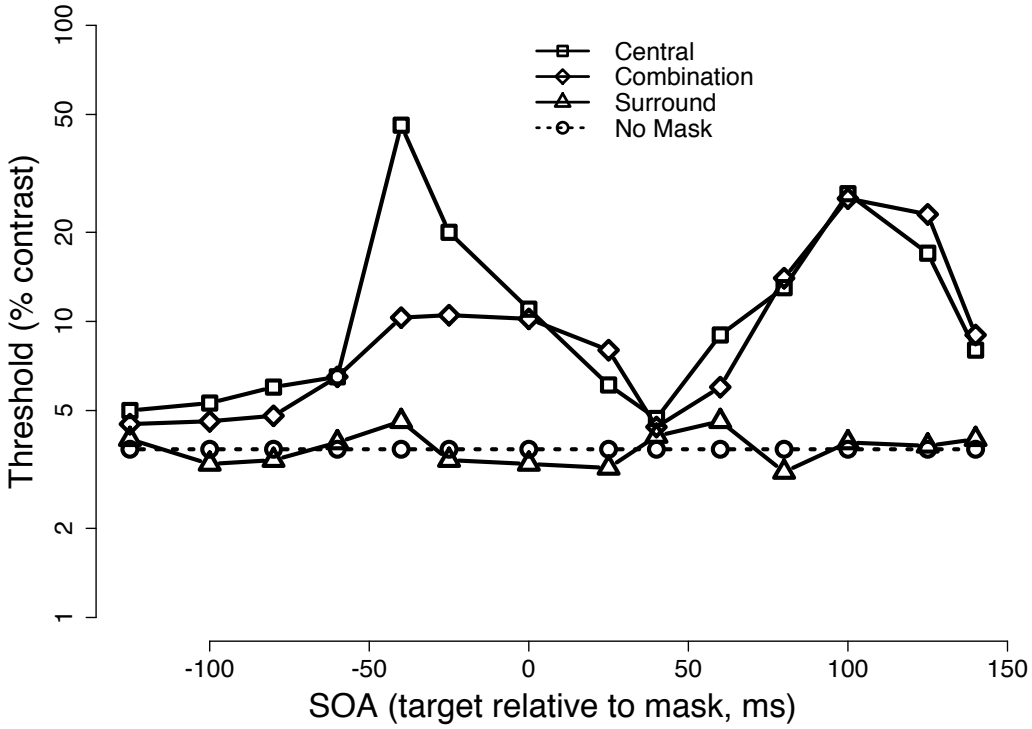


Figure 2.1: Detection thresholds replotted from Figure 3 in Saarela and Herzog (2008). Time course of iso-orientation contrast masking for subject TS. Negative SOAs indicate that the target onset preceded the mask onset. The dashed horizontal lines show the control detection thresholds, measured with the target (no-mask).

pression. Spatial suppression is the phenomenon that, in some conditions, performance worsens as stimulus size increases for high-contrast stimuli. For example, (Tadin et al., 2003) measured the stimulus duration that young observers required to discriminate leftward and rightward drifting sine wave gratings and found that longer durations were required to discriminate large high-contrast gratings than small high-contrast gratings. Tadin et al. hypothesized that spatial suppression was produced by the surround suppression that is found in many visual neurons. Neurophysiological (Leventhal et al., 2003) and anatomical (Pinto et al., 2010; McGeer and McGeer, 1976) studies suggest that aging may selectively impair cortical inhibitory mechanisms, which could result in reduced surround suppression in visual cortical neurons and, consequently, reduced spatial suppression. The hypothesis that spatial suppression is reduced in older adults has received support in some (Betts et al., 2005, 2009), but not all (Karas and McKendrick, 2009, 2011, 2012, 2015), psychophysical studies. In the current study, we examined the effects of aging on center-surround interactions in Saarela and Herzog's masking paradigm.

If the age-related changes in spatial suppression hold in the case of spatial masking, then we should expect to see different effects of the various mask types at different times for older versus younger adults. If spatial suppression is reduced with age, then the surround portion of the combination mask should have less of an effect on the central portion of the mask for older observers. In the absence of an effect of the surround, the combination mask should produce the same threshold patterns as the central mask.

2.3 Experiment 1

2.3.1 Methods

Participants

Twenty-two younger (M = 22.4 years; range: 18 - 30, 10 female) and 22 older (M = 69.5 years; range: 61 - 78, 11 female) observers participated in this experiment. All participants were naïve with respect to the purpose of the experiment and completed a written informed consent form prior to being tested. Near and far visual acuities were measured in all subjects using the SLOAN Two Sided ETDRS (Early Treatment Diabetic Retinopathy Study) Near Point Test and the 4 Meter 2000 Series Revised ETDRS charts (Precision Vision, LaSalle, Illinois, USA). All subjects had normal or corrected-to-normal near and far Snellen visual acuity. Contrast sensitivity was estimated using the Pelli-Robson Contrast Sensitivity Test (Pelli et al., 1988). Older subjects completed the MMSE (Mini-Mental State Examination) (Folstein et al., 1975) and the MoCA (Montreal Cognitive Assessment) (Nasreddine et al., 2005) before psychophysical testing began. All MMSE and MoCA scores were within the normal ranges according to age and education levels. All procedures were approved by the MREB (McMaster Research Ethics Board). Subjects were compensated for their time at a rate of $10/hour. Table 2.1 contains the demographic information for each age group.

Apparatus

The experiment, programmed in MATLAB (version 7.9) with software from the Psychophysics and Video Toolboxes (version 3.0.8) (Brainard, 1997; Pelli, 1997), was conducted on a Macintosh G5 computer. Stimuli were displayed on a 21-inch Sony Trinitron CRT monitor (GDM-F520) with a spatial resolution of 1280 × 1024 pixels (pixel size = 0.014 deg) and a refresh rate of

Table 2.1: Experiment, number of subjects, age, decimal near acuity, decimal far acuity, MMSE and MoCA scores for older subjects. Values in parentheses are standard deviations.

Experiment	Subjects (N)	Age (μ,σ)	Near Acuity (μ,σ)	Far Acuity (μ,σ)	MMSE (μ,σ)	MoCA (μ,σ)
1	22 younger	22.4 (3.4)	1.44 (0.23)	1.34 (0.31)		
	22 older	69.5 (4.7)	1.05 (0.24)	1.12 (0.24)	29.32 (1.04)	26.33 (3.40)
2	9 younger	18.9 (1.5)	1.45 (0.18)	1.30 (0.19)		
	9 older	69.6 (7.6)	0.97 (0.24)	1.07 (0.31)	29.11 (0.93)	24.88 (3.54)
3a	8 younger	24.0 (4.0)	1.46 (0.24)	1.34 (0.23)		
	8 older	72.8 (6.5)	0.87 (0.23)	0.83 (0.19)	28.38 (1.60)	24.25 (4.77)
3b	11 younger	23.8 (3.5)	1.54 (0.17)	1.47 (0.22)		
	10 older	68.7 (3.5)	1.02 (0.23)	1.23 (0.19)	29.00 (1.25)	27.44 (2.74)
3c	11 younger	24.1 (4.8)	1.53 (0.22)	1.35 (0.25)		
	12 older	69.9 (4.9)	0.94 (0.21)	1.11 (0.26)	28.92 (1.08)	26.64 (2.69)
3d	12 younger	24.2 (4.8)	1.55 (0.26)	1.35 (0.29)		
	9 older	67.8 (3.6)	1.00 (0.20)	1.19 (0.26)	29.00(1.27)	27.00 (2.62)

100 Hz. Average luminance was 65 cd/m^2, and was constant throughout the experiment. The monitor was the only source of light during the testing period. At the viewing distance of 57 cm, the display subtended visual angles of 36.19 deg horizontally and 28.99 deg vertically. Observers' head position and binocular viewing distance were stabilized using a chin/forehead rest. A standard QWERTY Macintosh keyboard was used to record each observer's behavioural responses. This apparatus was used for each experiment described in this chapter.

Stimuli

The target stimulus was a 4 cpd horizontal sine wave Gabor viewed through a Gaussian envelope with a standard deviation of 0.25 deg. The spatial phase of the target was 0 deg relative to the center of the Gaussian envelope (Figure 2.2a). The target always appeared on the screen for 40 ms.

Three types of masks were used in this experiment: a central mask that covered the visible spatial extent of the target (Figure 2.2b), a surround mask that covered a large spatial extent of the screen, but did not cover the target (Figure 2.2c), and a combination mask that was formed by adding the central and surround masks (Figure 2.2d). All of the masks were constructed from a horizontal, 4 cpd sine wave grating that had a Michelson contrast of 40%. The outer diameters of the central, surround and combination masks were 1 deg, 8.42 deg, and 8.42 deg, respectively. The inner diameter of the surround mask was 1 deg. All masks had the same spatial phase as the Gabor target, and the duration of each mask was 100 ms.

Procedure

A 2-IFC procedure measured target contrast detection thresholds with each of the three masks and a baseline condition that did not use a mask. A trial

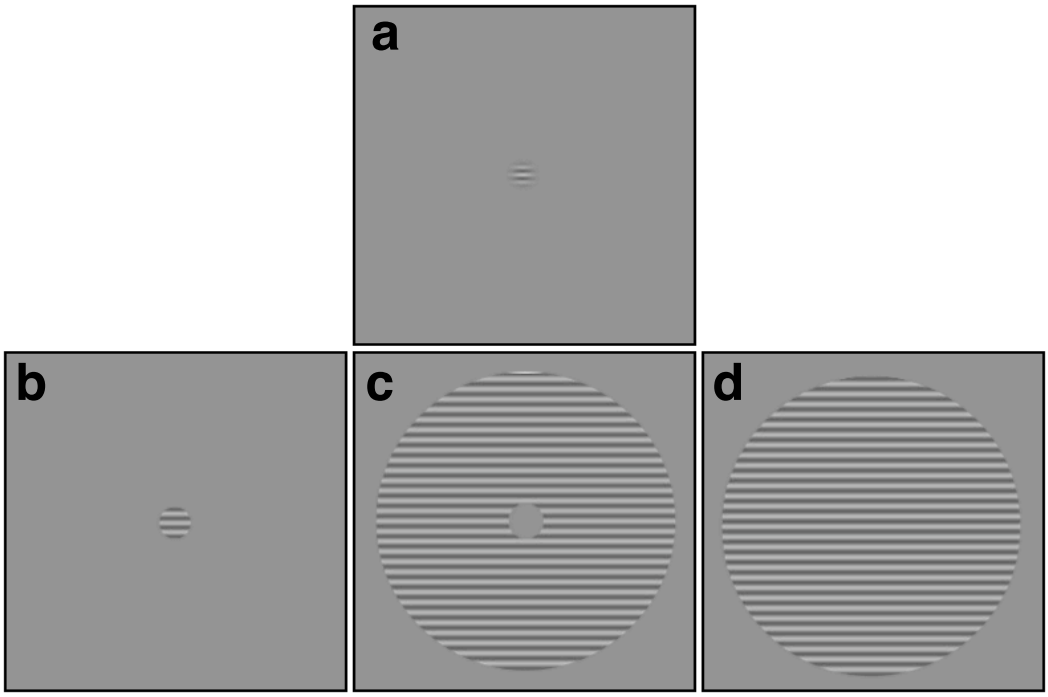


Figure 2.2: (a) The horizontally-oriented target and mask stimuli. The central target Gabor's Gaussian envelope had a standard deviation of 0.25 deg. Three different mask types were used in the experiment: (b) a central mask (outer diameter = 1 deg), (c) a surround mask (inner diameter = 1 deg; outer diameter = 8.42 deg) and (d) a combination of both masks (outer diameter = 8.42 deg).

began when a small (diameter = 4 pixels) high-contrast central fixation point flickered at a rate of 6 Hz for 500 ms to direct the participant's attention to the center of the screen. The fixation point was followed by a delay of 500 ms. Then the two stimulus intervals were presented, separated by an ISI (inter-stimulus interval) of 500 ms. A static fixation point appeared again during the ISI to ensure that subjects were fixating at the center of the screen. Each stimulus interval had a duration of 1.04 s, and the target Gabor was presented in either the first or second stimulus interval. The target was always presented at the mid-point of the temporal interval, and mask onset time varied depending upon the masking condition. In the no-target stimulus interval, the mask appeared at the same time within the interval as the mask in the corresponding target interval. Subjects were told that the target appeared in each interval with equal probability (and their task was to select the interval that contained the target). Auditory feedback, in the form of a 600 Hz tone, was given after incorrect responses. The next trial, beginning with the presentation of the flickering fixation point, started 1.5 s after the subject's response (Figure 2.3).

Target contrast varied across trials using a two-down, one-up staircase procedure that converged on the contrast required to produce 71% correct responding. The initial staircase step size of 0.25 log units was reduced to 0.125, 0.05, and 0.025 log units after the second, fourth, and sixth staircase reversals, respectively. A staircase ended after 50 trials, and threshold was defined as the average stimulus contrast at the last four reversals.

In conditions that used a mask, the mask was presented for 100 ms in the middle of both stimulus intervals (i.e., mask onset occurred 450 ms after the start of each stimulus interval). Target duration was always 40 ms, and target onset time varied across conditions to produce three SOAs. The three SOAs were -40 ms (i.e., onset of target occurred 40 ms before onset of mask), 40 ms (i.e., target onset occurred 40 ms after mask onset), and 100 ms (i.e., target onset occurred 100 ms after mask onset). In the -40 ms SOA condition, the mask appeared just after the offset of the target, and therefore we refer to this SOA as the *backward masking* condition. In the 40 ms SOA condition,

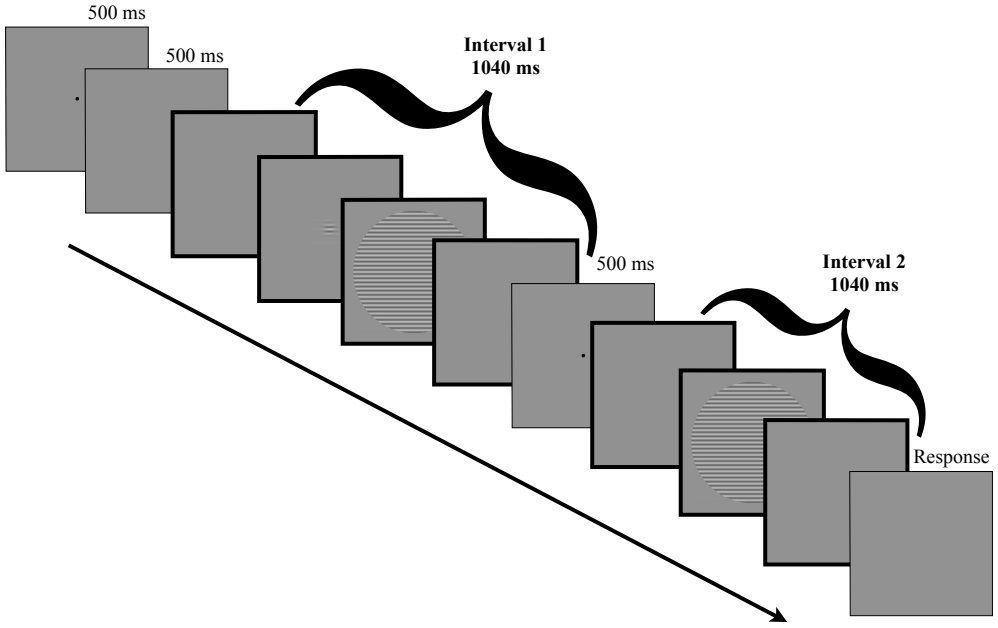


Figure 2.3: Procedure used in Experiments 1 and 3. Targets were presented in one of two sequential intervals (each 1040 ms); subjects indicated which of the two intervals contained the central target Gabor. In this example, the target (40 ms duration) is presented in interval 1, the mask type is a combination mask (100 ms duration), and the SOA is -40 ms. A central fixation point flickered for 500 ms before the first stimulus interval. After the 500 ms ISI, the second stimulus was displayed.

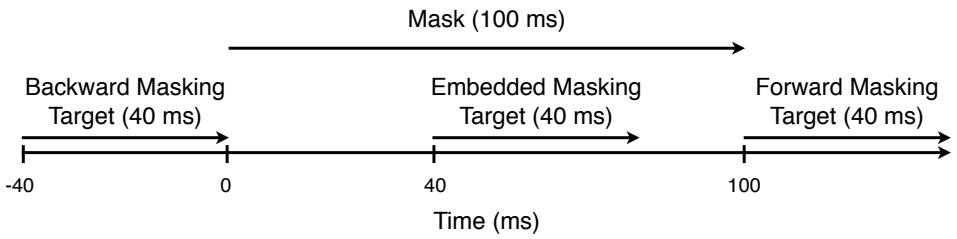


Figure 2.4: Timing parameters used in Experiments 1 and 3. The mask and target durations were 100 ms and 40 ms, respectively. The three target SOAs were -40 ms (backward masking), 40 ms (embedded masking), and 100 ms (forward masking).

the target and mask overlapped in time, and so we refer to this condition as the *embedded masking* condition. Finally, in the 100 ms SOA condition, the target appeared just after the offset of the mask, and therefore we refer to this SOA as the *forward masking* condition. In the no-mask control condition, the target onset occurred at the 0 ms time point (Figure 2.4). A 40 ms sound cue, in the form of a 1000 Hz tone, marked the mid-point of each stimulus interval.

There were 10 conditions in total: three mask types (center, surround, and combination) presented at each of the three SOAs (-40, 40, and 100 ms), plus a no-mask control condition. Subjects always completed the control condition

first. The presentation order for each mask type was randomized for each subject. All three SOA conditions were randomly intermixed for one mask type before proceeding to the next mask type. The entire experiment took approximately 1 hour and was completed in a single day of testing.

2.3.2 Results

Statistical analyses were performed using R (R Core Team, 2014). Inspection of the staircase data indicated that thresholds for two older subjects in the central mask condition exceeded the maximum displayable contrast. Data from those subjects therefore were not included in statistical analyses that included that condition.

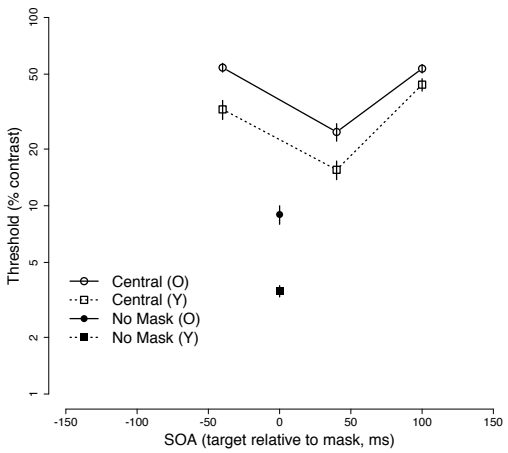
Thresholds for each masking condition are plotted as a function of SOA for both younger and older observers in Figure 2.5. To determine if our data from younger and older subjects followed the same patterns observed by Saarela and Herzog (2008), we analyzed the log-transformed thresholds from each age group separately using a 3 (SOA) $\times$ 3 (mask type) repeated-measures ANOVA (ANalysis Of VAriance). In younger subjects, the main effects of SOA ($F(2, 42) = 27.68$, $p < 0.001$) and mask type ($F(2, 42) = 235.3$, $p < 0.001$) were significant, as was the SOA $\times$ mask type interaction ($F(4, 84) = 11.08$, $p < 0.001$). Follow-up analyses of simple main effects indicated that differences among the three mask types were significant in the backward ($F(2, 42) = 39.95$, $p < 0.001$), embedded ($F(2, 42) = 45.62$, $p < 0.001$), and forward masking ($F(2, 42) = 277.70$, $p < 0.001$) conditions.

Similar results were obtained with older subjects: the main effects of SOA ($F(2, 38) = 12.72$, $p < 0.001$) and mask type ($F(2, 38) = 146.70$, $p < 0.001$) were significant, as was the SOA $\times$ mask type interaction ($F(4, 76) = 5.91$, $p < 0.001$). Furthermore, the simple main effect of mask type was significant in the backward ($F(2, 38) = 67.27$, $p < 0.001$), embedded ($F(2, 38) = 20.29$, $p < 0.001$), and forward masking ($F(2, 38) = 77.08$, $p < 0.001$) conditions.

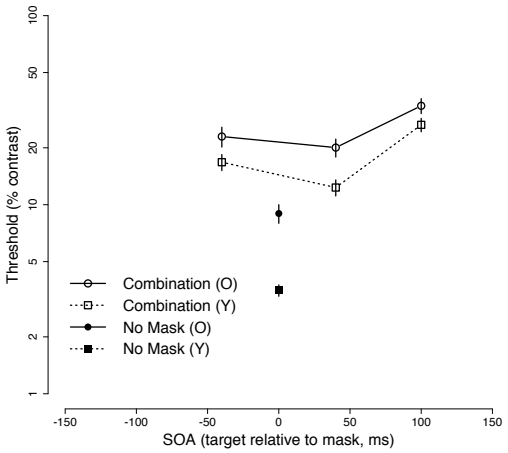
Hence, the patterns of masking obtained with younger and older subjects were qualitatively similar to the pattern obtained with younger subjects by Saarela and Herzog.

We next examined age differences. Thresholds in the no-mask condition were significantly higher in older than younger subjects ($t(1,40) = 5.49$, $p < 0.001$, one-tailed). Log-transformed thresholds in the central, combination, and surround mask conditions were submitted to separate 2 (age) $\times$ 3 (SOA) ANOVAs. For the central mask, there was a significant main effect of age ($F(1,40) = 18.82$, $p < 0.001$) and a significant main effect of SOA ($F(2,80) = 58.14$, $p < 0.001$). The age $\times$ SOA interaction was not significant ($F(2,80) = 2.62$, $p = 0.079$), though the age difference was slightly smaller in the forward masking (SOA=100 ms) condition than in the backward and overlay masking conditions. For the combination mask, the main effects of age ($F(1,40) = 10.06$, $p < 0.01$) and SOA ($F(2,80) = 23.46$, $p < 0.001$) were significant but the age $\times$ SOA interaction was not ($F(2,80) = 1.10$, $p = 0.34$). Finally, for the surround mask, the main effects of age ($F(1,40) = 27.35$, $p < 0.001$) and SOA ($F(2,80) = 6.31$, $p < 0.01$) were significant, but the age $\times$ SOA interaction was not ($F(2,80) = 0.96$, $p = 0.39$). Hence, in all three masking conditions, we found that thresholds in older adults were higher than thresholds in younger adults, but the age difference did not depend strongly on SOA.

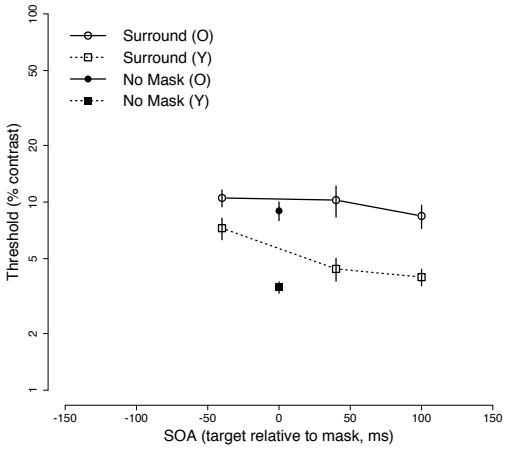
We next considered whether the strength of masking, defined as the ratio of thresholds measured in the masked and no-masked conditions, differed between age groups. Masking ratios for each masking condition are plotted as a function of SOA for younger and older adults separately in Figure 2.6. Log-transformed masking ratios were analyzed with a 2 (age) $\times$ 3 (mask type) $\times$ 3 (SOA) ANOVA. The main effect of age was significant ($F(1,40) = 12.85$, $p < 0.001$), reflecting the fact that masking ratios generally were lower in older than younger adults. The main effects of mask type ($F(2,80) = 373.28$, $p < 0.001$) and SOA ($F(2,80) = 39.46$, $p < 0.001$) also were significant, as was the mask type $\times$ SOA interaction ($F(4,160) = 15.11$, $p < 0.001$): on average, masking was greatest in the central mask condition and least in the surround



(a) Central masking thresholds.



(b) Combination masking thresholds.



(c) Surround masking thresholds.

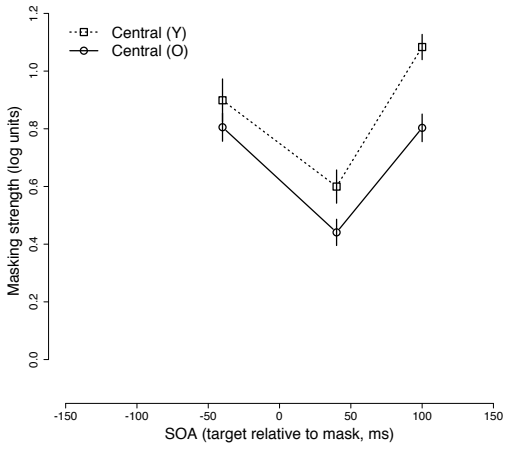
Figure 2.5: Masking thresholds plotted as a function of SOA in ms for younger (dashed lines with square data points) and older (solid lines with circular data points) observers. No-mask detection thresholds for both age groups are shown as single data points at the zero SOA time point. Error bars represent ± 1 SEM.

mask condition, but the differences among mask conditions varied with SOA. Finally, none of the interactions with age were significant (age × mask type: ($F(2, 80) = 2.28$, p = 0.11; age × SOA: $F(2, 80) = 1.45$, p = 0.24; age × mask type × SOA: $F(4, 160) = 1.39$, p = 0.24). Hence, the effects of mask type and SOA did not differ significantly between age groups, and age differences in masking strength did not vary significantly with mask type or SOA.

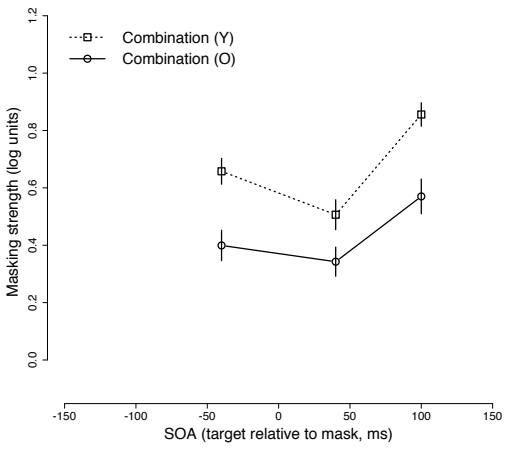
2.3.3 Discussion

The current results are similar to those obtained in younger adults by Saarela and Herzog (2008). Specifically, central and combination masks produced significant masking at all SOAs, although backward and forward masking was greater than embedded masking. In contrast, the surround mask produced very little masking at any SOA, but peaked slightly at the backward masking time point. Finally, the combination mask produced less backward masking than the central mask, which is consistent with Saarela and Herzog's idea that the surround portion of the combination mask inhibited the central portion of the mask at this time point. One difference between the current findings and those reported previously is that, unlike Saarela and Herzog, we found that the combination mask also produced less forward masking than the central mask. Despite this small difference, the current results obtained with younger subjects are in good qualitative agreement with those reported by Saarela and Herzog.

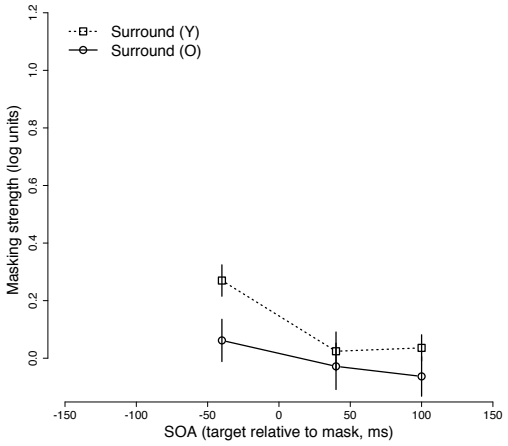
Petrov and McKee (2009) also measured the temporal effects of spatial suppression in younger adults for stimuli presented in the periphery rather than in the fovea. A surround mask was presented on both sides of a central fixation point, and subjects indicated which side contained the target in the center of the mask. They varied mask onset timing (i.e., sometimes the mask appeared before, simultaneously with, or after the target). Unlike our surround masking results and those of Saarela and Herzog, Petrov and McKee found that suppression was strongest when the surround and target appeared on the



(a) Central masking ratios.



(b) Combination masking ratios.



(c) Surround masking ratios.

Figure 2.6: Masking ratios plotted as a function of SOA in ms for younger (dashed lines with square data points) and older (solid lines with circular data points) observers. Error bars represent ±1 SEM.

screen simultaneously. However, Petrov et al. (2005) showed that surround suppression had a much stronger effect in the periphery than in the fovea. These results suggest that mechanisms of surround suppression are different in central and peripheral vision.

One explanation for why masking peaks at backward and forward masking time points is because at these SOAs, the target is masked by the sudden onset (backward masking) or offset (forward masking) of the mask. Transient bursts of neural activity have been shown to occur at spatiotemporal edges of stimuli (Macknik, 2006). In order for a target to be visible, these spatiotemporal edges must be present. Macknik explained that backward and forward masking inhibit these bursts, reducing target visibility. If this hypothesis is correct, then our results suggests that the inhibition of these bursts is similar in younger and older adults.

Older adults showed essentially the same pattern of masking as younger adults. The central mask produced more masking than the combination mask, and there was greater masking at the backward and forward masking time points than at the embedded time point. Overall, thresholds were significantly higher in older subjects for all mask types, a result that is consistent with previous research showing that older adults have impaired contrast sensitivity at medium and high spatial frequencies (Derefeldt et al., 1979; Elliott et al., 1990; Kline et al., 1983; Owsley et al., 1983; Tulunay-Keesey et al., 1988), but the temporal characteristics of masking did not differ significantly between age groups. If spatial suppression is responsible for reducing masking in the combination mask condition relative to the central mask condition, and if spatial suppression is altered by aging, then we would expect to find that the effects of mask type and/or SOA to differ between age groups. However, our analyses failed to find evidence that the effects of mask type or SOA differed between younger and older subjects. Our results therefore suggest that spatial suppression is not responsible for reducing masking in the combination mask condition, or that the mechanisms that produce such spatial suppression are unaffected by aging.

2.4 Experiment 2

2.4.1 Introduction

In Experiment 1, we found that masking strength, as indexed by the ratio of masked and unmasked thresholds, was lower in older than younger adults. However, this index of masking strength does not take into account differences in sensitivity for the mask, which may differ between older and younger subjects. Therefore, a control experiment was conducted to measure detection thresholds for the central, combination and surround masks and the no-mask condition in both age groups.

2.4.2 Methods

Participants

Nine younger (M = 18.9 years, range: 18 - 22, 8 females) and 9 older (M = 69.6 years, range: 62 - 81, 3 females) subjects were tested in this experiment. Table 2.1 shows the mean age and visual acuities (near and far) for both age groups, and MMSE and MoCA scores for older subjects. All scores were within normal ranges. Subjects were compensated for their time at a rate of $10/hour.

Apparatus, Stimuli, and Procedure

The target stimuli as well as each of the three types of masks described in Experiment 1 were presented in a 2-IFC detection experiment. As before, the viewing distance was 60 cm, and stimulus durations were 40 ms for the target and 100 ms for the central, combination and surround masks. Within each trial, a central fixation point flickered for 500 ms and, after a 500 ms

blank screen, was followed by two stimulus intervals. The fixation point also appeared on the screen during the 500 ms ISI. The stimulus had an equal chance of being presented in either interval and observers were required to determine whether a stimulus appeared in the first or second interval. A 600 Hz tone provided feedback after each incorrect trial. Stimulus contrast was manipulated by a two-down, one-up staircase to determine the contrast required to detect the stimulus interval correctly 71% of the time. As before, staircase step size was initially set to 0.25 log units, and reduced to 0.125, 0.05 and 0.025 log units after the second, fourth, and sixth staircase reversals, respectively. Each staircase comprised 50 trials, and threshold was defined as the mean of the last four reversals.

For each subject, the four conditions (target, central mask, combination mask, surround mask) were presented in one random order and then again in a different random order. For each condition, thresholds from the two blocks were averaged.

2.4.3 Results

Figure 2.7 illustrates the mask detection thresholds for younger and older observers. The log-transformed thresholds were analyzed with a 2 (age) $\times$ 4 (stimulus type) ANOVA, including the target and three mask stimuli. There was a significant main effect of age ($F(1, 16) = 44.96$, $p < 0.001$), indicating that thresholds were higher in older adults (older/younger mean threshold ratios: Target = 4.05; Central = 4.32; Surround = 5.12; Combination = 5.47). There also was a main effect of stimulus type ($F(3, 48) = 119.45$, $p < 0.001$): thresholds were highest for the target condition, followed by the central mask, and then the surround and combination masks. Finally, the age $\times$ stimulus type interaction was not significant ($F(3, 48) = 1.26$, $p = 0.30$), indicating that that the difference between age groups did not depend strongly on stimulus type.

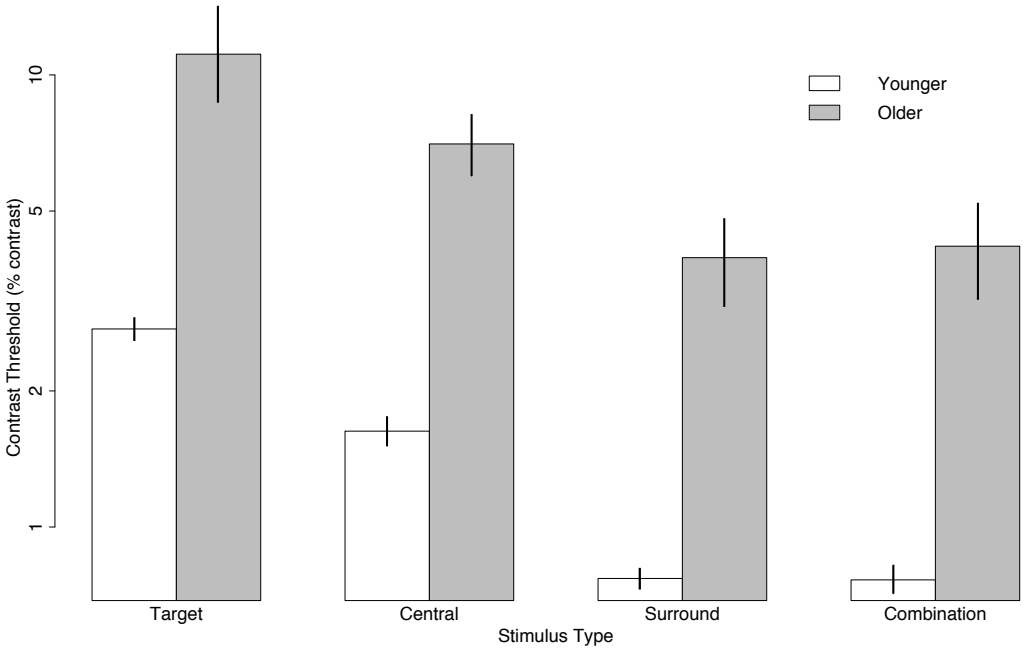


Figure 2.7: Target and mask detection thresholds for 9 younger (white bars) and 9 older (grey bars) observers. Error bars represent ±1 SEM.

To demonstrate that there is still a main effect of age when the analysis is restricted to the mask conditions only, we conducted a 2 (age) × 3 (mask type) ANOVA with the no-mask target condition excluded. Like the previous analysis including the target condition, this analysis revealed a significant main effect of age ($F(1, 16) = 46.89$, $p < 0.001$) and mask type ($F(2, 32) = 77.33$, $p < 0.001$), but no age × mask type interaction ($F(2, 32) = 0.33$, $p = 0.72$)

2.4.4 Discussion

Although Saarela and Herzog (2008) did not measure mask detection thresholds, they did measure baseline target detection thresholds in younger adults

to be between 3 and 4% contrast. Therefore, our mean of 2.74% is in line with Saarela and Herzog's findings for younger adults. Furthermore, the larger the mask, the easier it was to detect at a lower contrast level. This pattern was found for both age groups, although older adults had higher detection thresholds overall. Perhaps older adults show higher detection thresholds than their younger counterparts because of the increased optical aberrations within the aging eye (Artal et al., 2003; Glasser and Campbell, 1998). The results from our mask detection experiment indicated that older observers were less sensitive to the mask as well as the target.

2.5 Experiment 3

2.5.1 Introduction

The results from Experiment 1 demonstrate that older adults show a similar spatiotemporal masking pattern (i.e., higher thresholds for the central than combination mask, and greater masking at backward and forward time points than at the embedded time point) to their younger counterparts, but the magnitude of masking, as indexed by the ratio of masked and unmasked thresholds, was lower in older adults. Experiment 2 demonstrated that detection thresholds for the various types of masks differed between younger and older adults.

This result suggests that the effective contrast of the masks used in Experiment 1 (i.e., mask contrasts divided by detection thresholds for each mask) likely differed between age groups. If masking strength depends on the effective mask contrast, then reduced masking in older subjects could simply reflect the fact that they are less sensitive to pattern contrast. One way to determine whether age differences in masking strength are caused by changes in effective mask contrast is to measure masking with a variety of mask contrasts. The effective contrast hypothesis predicts that the TvM (threshold-vs.-mask con-

trast) curves obtained from older and younger subjects can be superimposed by i) normalizing masked thresholds by dividing them by unmasked target detection threshold; and ii) normalizing mask contrasts by dividing them by mask detection thresholds. Experiment 3 tested this idea.

2.5.2 Methods

Embedded Central Condition

Eight younger ($M = 24.0$ years, range: 19 - 31, 3 females) and 8 older ($M = 72.8$ years, range: 61 - 81, 5 females) subjects were tested in this experiment. A small central mask was presented at six different contrast levels (0%, 5%, 10%, 20%, 40% and 60%) at the embedded masking time point (SOA = 40 ms). The apparatus and procedure used in this experiment were the same as those used in Experiment 1.

Embedded Combination Condition

Eleven younger ($M = 23.8$ years, range: 21 - 27, 7 females) and 10 older ($M = 68.7$ years, range: 63 - 73, 6 females) subjects were tested in this experiment, in which a large combination mask was presented at six different contrast levels (0%, 5%, 10%, 20%, 40% and 60%) at the embedded masking time point (SOA = 40 ms).

Backward Combination Condition

Eleven younger ($M = 24.1$ years, range: 18 - 32, 5 females) and 12 older ($M = 69.9$ years, range: 63 - 73, 6 females) subjects were tested in this experiment, in which a combination mask was presented at six different contrast levels (0%, 10%, 20%, 40%, 60%, and 80%) at the backward masking time

point (SOA = -40 ms).

Forward Combination Condition

Twelve younger (M = 24.2 years, range: 18 - 33, 5 females) and 9 older (M = 67.8 years, range: 63 - 72, 5 females) subjects participated. Mask contrast levels were identical to those used in the backward combination mask experiment (0%, 10%, 20%, 40%, 60%, and 80%), and the mask was presented at the forward masking time point (SOA = 100 ms).

2.5.3 Results

Embedded Central Condition

As in Experiment 1, isolated target detection thresholds (0% mask contrast) were significantly lower in younger ($M = 2.76\%$, $SEM = 0.09\%$) than older ($M = 9.15\%$, $SEM = 0.87\%$) adults ($t(14) = 7.32$, $p < 0.001$, one-tailed). The effect of threshold level as a function of central mask contrast (0%, 5%, 10%, 20%, 40%, and 60%) is illustrated for both age groups in Figure 2.8a. We found significant main effects of age ($F(1, 14) = 19.16$, $p < 0.001$) and mask contrast ($F(5, 70) = 20.80$, $p < 0.001$), and a significant age $\times$ mask contrast interaction ($F(5, 70) = 2.72$, $p < 0.05$). An analysis of the simple main effects revealed significant differences between the two age groups at 0% ($t(14) = 9.23$, $p < 0.001$) and 40% ($t(14) = 3.60$, $p < 0.01$) contrast. However, the age differences were not significant at 5% ($t(14) = 1.58$, $p = 0.14$), 10% ($t(14) = 0.39$, $p = 0.70$), 20% ($t(14) = 2.47$, $p = 0.03$), and 60% ($t(14) = 1.34$, $p = 0.21$) contrast.

To control for age differences in contrast sensitivity for the target and mask, we divided target detection thresholds in the masked conditions by threshold in the no-mask condition, and divided mask contrast by the mask

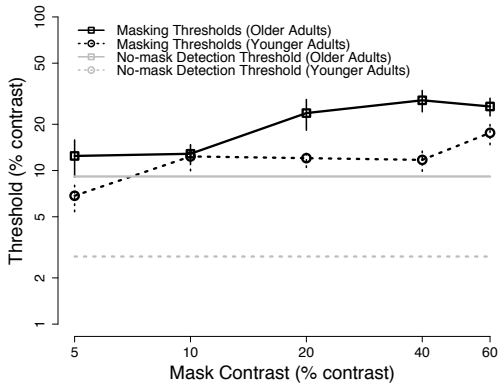
Table 2.2: Parameters of best-fitting power functions ($y = k \times x^p$) fit to normalized TvM functions.

Condition	Age	k (intercept)	p (slope)
Embedded Central	Younger	2.01	0.30
	Older	1.56	0.40
Embedded Combination	Younger	1.12	0.37
	Older	1.13	0.35
Backward Combination	Younger	0.66	0.57
	Older	1.57	0.51
Forward Combination	Younger	0.64	0.66
	Older	1.83	0.45

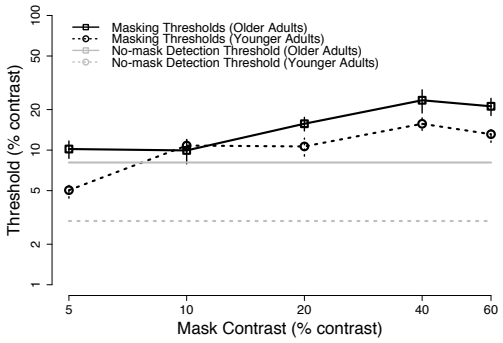
detection thresholds measured in Experiment 2. This type of normalization shifts the TvM functions in Figure 2.8a vertically and horizontally in the log-log plot. The normalized TvM functions are shown in Figure 2.9a. Note that the normalized TvM functions for older and younger adults appear to fall along a single line, and the best-fitting power functions computed for each group were very similar (see Table 2.2). These results suggest that, in this condition, a single function is sufficient to relate masking strength to effective mask contrast in younger and older adults.

Embedded Combination Condition

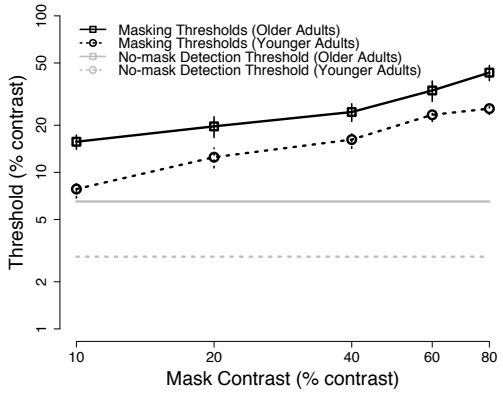
Baseline thresholds (0% mask contrast) were significantly lower in younger ($M = 2.97\%$, $SEM = 0.19\%$) than older ($M = 8.09\%$, $SEM = 1.19\%$) adults ($t(19) = 4.44$, $p < 0.001$, one-tailed). Figure 2.8b illustrates the detection thresholds as a function of mask contrast. A 2 (age) $\times$ 6 (mask contrast) ANOVA revealed significant main effects of age ($F(1, 19) = 7.90$, $p < 0.05$) and mask contrast ($F(5, 95) = 40.47$, $p < 0.001$), and a significant age $\times$ mask contrast interaction ($F(5, 95) = 5.81$, $p < 0.001$). Subsequent tests found a significant age difference at 0% ($t(19) = 6.47$, $p < 0.001$) and 5% ($t(19) =$



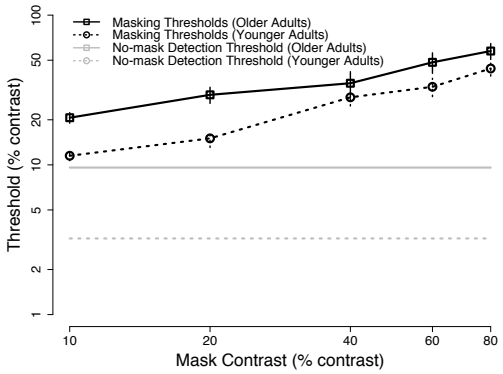
(a) Embedded central masking thresholds.



(b) Embedded combination masking thresholds.

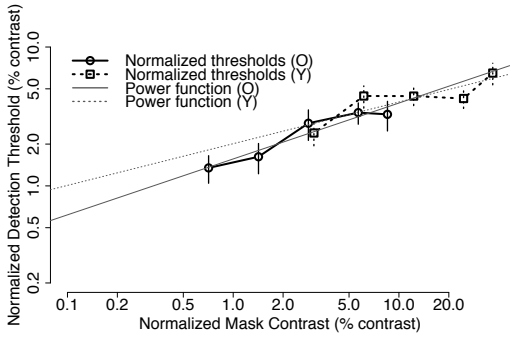


(c) Backward combination masking thresholds

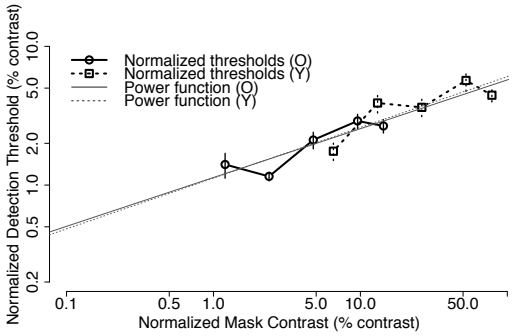


(d) Forward combination masking thresholds

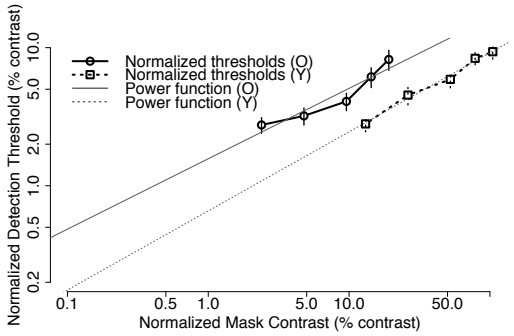
Figure 2.8: Masking thresholds plotted as a function of mask contrast for younger (dashed lines with circular data points) and older (solid lines with square data points) observers. The horizontal lines indicate thresholds in the no-mask condition. Error bars represent ±1 SEM. (a) Embedded central mask condition. (b) Embedded combination mask condition. (c) Backward combination mask condition. (d) Forward combination mask condition.



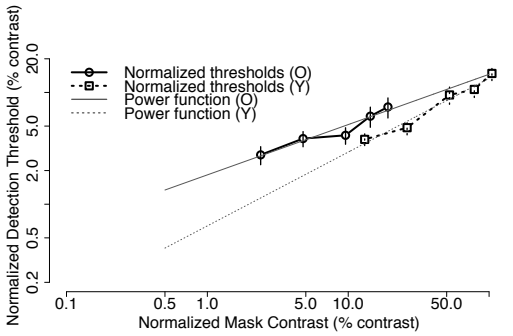
(a) Embedded central.



(b) Embedded combination.



(c) Backward combination.



(d) Forward combination.

Figure 2.9: Normalized thresholds plotted as a function of normalized mask contrast for younger (dashed lines with circular data points) and older (solid lines with square data points) observers. Thresholds were normalized by dividing thresholds obtained with masks by the threshold obtained in the no-mask condition. Mask contrast was normalized by dividing mask contrast by the mask detection thresholds measured in Experiment 2. Error bars represent ± 1 SEM. (a) Embedded central mask condition. (b) Embedded combination mask condition. (c) Backward combination mask condition. (d) Forward combination mask condition.

3.12, $p < 0.01$) contrast, but not at 10% ($t(19) = 0.88$, $p = 0.39$), 20% ($t(19) = 2.02$, $p = 0.06$), 40% ($t(19) = 1.41$, $p = 0.17$), or 60% ($t(19) = 1.69$, $p = 0.11$) contrast. The normalized TvM functions are shown in Figure 2.9b: To a first approximation, the functions from both groups fell along a single line, and the best-fitting power functions (see Table 2.2) for the two groups were similar. Hence, as was found in the Embedded Central Condition, the results suggest that a single function is sufficient to relate masking strength and effective mask contrast in older and younger adults.

Backward Combination Condition

Thresholds in the no-mask control condition were significantly lower in younger ($M = 2.89\%$, $SEM = 0.24\%$) than older ($M = 6.51\%$, $SEM = 0.91\%$) adults ($t(21) = 3.68$, $p < 0.001$, one-tailed). Thresholds as a function of combination mask contrast are presented in Figure 2.8c. A 2 (age) $\times$ 6 (mask contrast) ANOVA revealed significant main effects of age ($F(1, 21) = 18.24$, $p < 0.001$) and mask contrast ($F(5, 105) = 101.02$, $p < 0.001$); the age $\times$ mask contrast interaction was not significant ($F(5, 105) = 1.61$, $p = 0.16$). Normalized TvM functions are shown in Figure 2.9c. Interestingly, unlike what was found in the embedded conditions, normalizing thresholds and mask contrast did not eliminate age differences: although masking strength grew with effective contrasts at similar rates in the two age groups, normalized masking was significantly higher in older than younger adults at all levels of effective contrast. In other words, the slopes of the best-fitting power functions were similar, but the intercepts differed by more than a factor of two (Table 2.2). Therefore, even after detection thresholds were taken into account, there was still an age difference in the contrast required to detect a target when masked by a combination mask at the backward masking time point.

Forward Combination Condition

As in the other three conditions, thresholds in the no-mask condition were significantly lower in statistically different between younger ($M = 3.23\%$, $SEM = 0.23\%$) than older ($M = 9.59\%$, $SEM = 1.83\%$) adults ($t(19) = 3.99$, $p < 0.001$, one-tailed). Thresholds are plotted as a function of mask contrast in Figure 2.8d. A 2 (age) $\times$ 6 (mask contrast) ANOVA found significant main effects of age ($F(1, 19) = 18.59$, $p < 0.001$) and mask contrast ($F(5, 95) = 83.41$, $p < 0.001$), and a significant age $\times$ mask contrast interaction ($F(5, 95) = 3.16$, $p < 0.05$). Follow-up tests found significant age differences at 0% ($t(19) = 5.08$, $p < 0.001$), 10% ($t(19) = 4.38$, $p < 0.001$), and 20% ($t(19) = 3.53$, $p < 0.01$) contrast, but not at 40% ($t(19) = 0.47$, $p = 0.65$), 60% ($t(19) = 1.59$, $p = 0.13$) or 80% ($t(19) = 1.56$, $p = 0.13$) contrast. Normalized TvM functions shown in Figure 2.9d. Unlike the embedded conditions, and similar to what was found in the backward combination condition, normalized masking strength was higher in older than younger adults at all levels of effective mask contrasts, although the slope of the best-fitting power function was slightly lower in older subjects (Table 2.2).

2.5.4 Discussion

The main purpose of Experiment 3 was to determine if age differences in contrast sensitivity might explain some of the age effects found in Experiment 1. If age differences in masking (see Figure 2.6) reflected age differences in sensitivity to the mask and target contrast, rather than masking *per se*, we would expect that normalizing mask and target contrast using pattern detection thresholds would align the TvM curves from the two age groups. Inspection of normalized thresholds in Figure 2.9 show that we find this result in the embedded masking conditions, but not the forward and backward masking conditions. These results imply that age differences in contrast sensitivity cannot account for age differences in backward and forward masking.

Past studies have examined age differences in backward masking (Kline and Szafran, 1975; Kline and Birren, 1975; Walsh, 1976; Till and Franklin, 1981). In these studies, older adults required longer SOAs to escape the effects of masking than younger adults, implying that the effect of masking was greater in aging. These results are in agreement with our results from Experiment 1 where we found higher backward masking thresholds in older adults. In these past studies, however, mask contrast was not varied nor were masking thresholds divided by target detection thresholds to control for age differences.

The general shape of the normalized TvM functions for our embedded mask conditions are in good agreement with Legge and Foley (1980) who found that the effect of masking measured with small and large sine wave gratings at various contrast levels were well-fit by power functions. Legge and Foley measured contrast thresholds for detecting a target that was masked by a small (0.75 deg in diameter) and large (6 deg in diameter) overlay mask. Unlike our experiment, the mask and target in Legge and Foley's study always appeared on the display simultaneously for 200 ms (i.e., there was no manipulation of SOA). At high mask contrasts (3.2 to 51.2% contrast), they found that thresholds appeared to line up along a straight line when plotted in double logarithmic coordinates. Their best fitting power function for the mask when it was the same spatial frequency as the target (2%) had a slope of 0.672 for the small mask and 0.558 for the large mask. These slopes were greater than the slopes found for our embedded masking conditions (0.30 and 0.37 for the embedded central and embedded combination conditions, respectively). Slopes found in our backward and forward conditions, however, were similar to Legge and Foley (1980)'s power function slopes. Altogether, these findings imply that masking is stronger when the target appears at mask onset (forward and simultaneous masking) or offset (backward and simultaneous masking) as oppose to the target being embedded in mask presentation (embedded masking).

Our finding that masking is stronger at the spatiotemporal edges of stimuli is also consistent with the results of Macknik and Livingstone (1998) who found that the transient neural responses of V1 cells in rhesus monkeys that

normally occur at the onset and offset of a target stimulus were disrupted when a masking stimulus immediately preceded (forward masking) or followed (backward masking) the target. In both age groups, the rate at which masking increased with effective contrast was higher in the backward and forward masking conditions than in the embedded condition, but masking was higher in older adults at all effective contrasts. Therefore, our results suggest that the disruptive effect of a mask on transient neural responses that was found by Macknik and Livingstone may increase with aging.

2.6 General Discussion

The experiments presented here examined the spatial and temporal masking effects found in the aging visual system. The contrast threshold patterns found for younger adults in Experiment 1 were similar to the iso-oriented masking thresholds reported in Saarela and Herzog (2008)'s experiment. The effect of overlay masking was strongest overall and peaked at backward and forward masking time points, with central masking producing larger effects than combination masking. Strong masking effects at mask onset (Wilson and Kim, 1998; Yu and Levi, 1999) and offset (Snowden, 2001) using static stimuli have been previously reported. Saarela and Herzog's central and combination mask thresholds overlapped with each other at all time points except at backward masking where the effect of the combination mask weakened. They hypothesized that the surround portion of the combination mask reduced the strength of the central portion of the mask at this temporal offset. This result was interesting because the surround combined with a central mask (combination mask) produced effects when presented immediately after the target, however the surround mask on its own produced very little masking. Interestingly, in our study, we found spatial suppression with the combination mask at both backward and forward masking time points. This implies that both transient onset (Judge et al., 1980; Macknik and Livingstone, 1998; Schiller, 1968) and offset (Macknik and Livingstone, 1998; Macknik and Martinez-Conde, 2004)

responses are affected by surround modulation in younger adults.

We found that detection thresholds generally were higher in older than younger adults, but the effects of SOA and mask type were similar in the two age groups. These results are inconsistent with the hypothesis that i) that the low amount of masking found with a combination mask reflects the fact that a surround mask suppresses a center mask; and ii) that the center-surround suppressive mechanisms are less effective in the healthy aging brain. When we compared younger versus older thresholds for each of the 3 mask types separately in Experiment 1, we found that all of the analyses showed a main effect of age, but no age $\times$ SOA interaction. These age differences remained after thresholds were normalized by dividing each masked threshold by the no mask threshold. Based on the decreased spatial suppression in aging hypothesis, we hypothesized that older adults' thresholds for the central and combination masks would overlap with each other or at least be more similar to each other than in younger observers' data. This is because, for older observers, the surround portion of the combination mask would have less of a suppressive effect on the central portion of the mask. However, like the results for younger adults, combination mask thresholds for older adults were lower than central mask thresholds. Therefore, our results do not support the decreased spatial suppression in aging hypothesis.

Inconsistent results have been reported in the literature on aging and spatial suppression. For example, both Betts et al. (2005) and Karas and McKendrick (2012) tested older observers in a direction discrimination task measuring spatial suppression using dynamic stimuli. Betts et al. (2005) found reduced spatial suppression for older observers, while Karas and McKendrick (2012) found that older and younger observers had similar duration thresholds. The other experiment presented in Karas and McKendrick's 2012 paper was a perceived contrast task measuring spatial suppression in younger and older adults. The same subjects participated in both the direction discrimination task and the perceived contrast task. Karas and McKendrick (2012) found that older observers demonstrated *greater* spatial suppression than their younger

counterparts. Karas and McKendrick have also reported similar findings (i.e., older adults showing greater spatial suppression than younger adults) in other perceived contrast studies (Karas and McKendrick, 2009, 2011, 2015).

Since our results from Experiment 1 did not support the decreased spatial suppression in aging hypothesis, we conducted a mask contrast experiment (Experiment 2) to determine if overall contrast sensitivity changes in healthy aging could explain our results. Our results from Experiment 2 showed that older adults had higher detection thresholds for the mask types overall, and that they showed similar patterns across the mask types. In Experiment 3 we varied the mask contrast over a range of levels and plotted normalized target and masked contrast thresholds using our results from Experiment 2. We hypothesized that if increasing mask contrast led to similar younger and older normalized threshold by normalized mask contrast functions, then effective contrast would explain the main effect found in Experiment 1. We found that older observers' normalized threshold patterns only resembled those of younger participants for stimuli presented at the embedded masking time point. Therefore, changes in contrast may explain the age difference in the original spatial and temporal masking experiment when mask and target presentation overlap in time. However, stimuli presented at the backward and forward masking time points produced different normalized threshold patterns for younger and older adults. Older adults required more contrast to detect a target in the backward and forward combination masking conditions than younger adults. These results suggest that the effect of masking may become stronger in aging and that these age differences cannot be explained by differences in retinal contrast.

References

Andersen, G. J., Ni, R., Jan 2008. Aging and visual processing: declines in spatial not temporal integration. Vision Res 48 (1), 109–18.

Artal, P., Guirao, A., Berrio, E., Piers, P., Norrby, S., 2003. Optical aberrations and the aging eye. Int Ophthalmol Clin 43 (2), 63–77.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2009. Spatial characteristics of center-surround antagonism in younger and older adults. J Vis 9 (1), 25.1–15.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., Feb 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–6.

Billino, J., Bremmer, F., Gegenfurtner, K. R., May 2008. Differential aging of motion processing mechanisms: evidence against general perceptual decline. Vision Res 48 (10), 1254–61.

Blakemore, C., Tobin, E. A., 1972. Lateral inhibition between orientation detectors in the cat's visual cortex. Exp Brain Res 15 (4), 439–40.

Brainard, D. H., 1997. The psychophysics toolbox. Spat Vis 10 (4), 433–6.

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), 1985–98.

Cavanaugh, J. R., Bair, W., Movshon, J. A., Nov 2002. Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. J Neurophysiol 88 (5), 2530–46.

Chan, Y. M., Battista, J., McKendrick, A. M., 2012. Aging effects on collinear facilitation. J Vis 12 (6), 21.

Churan, J., Richard, A. G., Pack, C. C., 2009. Interaction of spatial and temporal factors in psychophysical estimates of surround suppression. J Vis 9 (4), 15.1–15.

Derefeldt, G., Lennerstrand, G., Lundh, B., Aug 1979. Age variations in normal human contrast sensitivity. Acta Ophthalmol (Copenh) 57 (4), 679–90.

Derrington, A. M., Henning, G. B., 1989. Some observations on the masking effects of two-dimensional stimuli. Vision Res 29 (2), 241–6.

Elliott, D., Whitaker, D., MacVeigh, D., 1990. Neural contribution to spatiotemporal contrast sensitivity decline in healthy ageing eyes. Vision Res 30 (4), 541–7.

Foley, J. M., Jun 1994. Human luminance pattern-vision mechanisms: masking experiments require a new model. J Opt Soc Am A Opt Image Sci Vis 11 (6), 1710–9.

Folstein, M. F., Folstein, S. E., McHugh, P. R., Nov 1975. Mini-mental state. a practical method for grading the cognitive state of patients for the clinician. J Psychiatr Res 12 (3), 189–98.

Fries, W., Albus, K., Creutzfeldt, O. D., 1977. Effects of interacting visual patterns on single cell responses in cats striate cortex. Vision Res 17 (9), 1001–8.

Glass, J. M., Jun 2007. Visual function and cognitive aging: differential role of contrast sensitivity in verbal versus spatial tasks. Psychol Aging 22 (2), 233–8.

Glasser, A., Campbell, M. C., Jan 1998. Presbyopia and the optical changes in the human crystalline lens with age. Vision Res 38 (2), 209–29.

Jones, H. E., Grieve, K. L., Wang, W., Sillito, A. M., Oct 2001. Surround suppression in primate V1. J Neurophysiol 86 (4), 2011–28.

Judge, S. J., Wurtz, R. H., Richmond, B. J., Apr 1980. Vision during saccadic eye movements. i. visual interactions in striate cortex. J Neurophysiol 43 (4), 1133–55.

Karas, R., McKendrick, A. M., 2009. Aging alters surround modulation of perceived contrast. J Vis 9 (5), 11.1–9.

Karas, R., McKendrick, A. M., Nov 2011. Increased surround modulation of perceived contrast in the elderly. Optom Vis Sci 88 (11), 1298–308.

Karas, R., McKendrick, A. M., 2012. Age related changes to perceptual surround suppression of moving stimuli. Seeing Perceiving 25 (5), 409–24.

Karas, R., McKendrick, A. M., Mar 2015. Contrast and stimulus duration dependence of perceptual surround suppression in older adults. Vision Res.

Kline, D. W., Birren, J. E., Sep 1975. Age differences in backward dichoptic masking. Exp Aging Res 1 (1), 17–25.

Kline, D. W., Schieber, F., Abusamra, L. C., Coyne, A. C., 1983. Age, the eye, and visual channels: Contrast sensitivity and response speed. Journal of Gerontology 38 (211-216).

Kline, D. W., Szafran, J., May 1975. Age differences in backward monoptic visual noise masking. J Gerontol 30 (3), 307–11.

Legge, G. E., Foley, J. M., Dec 1980. Contrast masking in human vision. J Opt Soc Am 70 (12), 1458–71.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., Ma, Y., May 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–5.

Macknik, S., Martinez-Conde, S., Jun. 2004. The spatial and temporal effects of lateral inhibitory networks and their relevance to the visibility of spatiotemporal edges. Neurocomputing 58, 775–782.

Macknik, S. L., 2006. Visual masking approaches to visual awareness. Prog Brain Res 155, 177–215.

Macknik, S. L., Livingstone, M. S., Jun 1998. Neuronal correlates of visibility and invisibility in the primate visual system. Nat Neurosci 1 (2), 144–9.

Maffei, L., Fiorentini, A., 1976. The unresponsive regions of visual cortical receptive fields. Vision Res 16 (10), 1131–9.

McGeer, P. L., McGeer, E. G., Jan 1976. Enzymes associated with the metabolism of catecholamines, acetylcholine and gaba in human controls and patients with parkinson's disease and huntington's chorea. J Neurochem 26 (1), 65–76.

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., Chertkow, H., Apr 2005. The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. J Am Geriatr Soc 53 (4), 695–9.

Nelson, J. I., Frost, B. J., Jan 1978. Orientation-selective inhibition from beyond the classic visual receptive field. Brain Res 139 (2), 359–65.

Olzak, L. A., Laurinen, P. I., Dec 1999. Multiple gain control processes in contrast-contrast phenomena. Vision Res 39 (24), 3983–7.

Owsley, C., Sekuler, R., Siemsen, D., 1983. Contrast sensitivity throughout adulthood. Vision Res 23 (7), 689–99.

Pelli, D., Robson, J., Wilkins, A., 1988. The design of a new letter chart for measuring contrast sensitivity. Clinical Vision Sciences 2 (3), 187–&.

Pelli, D. G., 1997. The videotoolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10 (4), 437–42.

Petrov, Y., Carandini, M., McKee, S., Sep 2005. Two distinct mechanisms of suppression in human vision. J Neurosci 25 (38), 8704–7.

Petrov, Y., McKee, S. P., 2009. The time course of contrast masking reveals two distinct mechanisms of human surround suppression. J Vis 9 (1), 21.1–11.

Pinto, J. G. A., Hornby, K. R., Jones, D. G., Murphy, K. M., 2010. Developmental changes in GABAergic mechanisms in human visual cortex across the lifespan. Front Cell Neurosci 4, 16.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
URL http://www.R-project.org/

Ross, J., Speed, H. D., Oct 1991. Contrast adaptation and contrast masking in human vision. Proc Biol Sci 246 (1315), 61–9.

Saarela, T. P., Herzog, M. H., 2008. Time-course and surround modulation of contrast masking in human vision. J Vis 8 (3), 23.1–10.

Saarela, T. P., Herzog, M. H., 2009. Size tuning and contextual modulation of backward contrast masking. J Vis 9 (11), 21.1–12.

Schiller, P. H., Jul 1968. Single unit analysis of backward visual masking and metacontrast in the cat lateral geniculate nucleus. Vision Res 8 (7), 855–66.

Sekuler, R., Sekuler, A. B., 2000. Oxford Textbook of Geriatric Medicine, 2nd Edition. No. pp. 874-880. Oxford University Press, New York.

Sengpiel, F., Sen, A., Blakemore, C., Sep 1997. Characteristics of surround inhibition in cat area 17. Exp Brain Res 116 (2), 216–28.

Snowden, R. J., Jul 2001. Contrast gain mechanism or transient channel? why the effects of a background pattern alter over time. Vision Res 41 (15), 1879–83.

Snowden, R. J., Hammett, S. T., Jun 1998. The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. Vision Res 38 (13), 1935–45.

Tadin, D., Lappin, J. S., Gilroy, L. A., Blake, R., Jul 2003. Perceptual consequences of centre-surround antagonism in visual motion processing. Nature 424 (6946), 312–5.

Till, R. E., Franklin, L. D., Mar 1981. On the locus of age differences in visual information processing. J Gerontol 36 (2), 200–10.

Tulunay-Keesey, U., Ver Hoeve, J. N., Terkla-McGrane, C., Dec 1988. Threshold and suprathreshold spatiotemporal response throughout adulthood. J Opt Soc Am A 5 (12), 2191–200.

Walsh, D. A., Mar 1976. Age differences in central perceptual processing: a dichoptic backward masking investigation. J Gerontol 31 (2), 178–85.

Webb, B. S., Dhruv, N. T., Solomon, S. G., Tailby, C., Lennie, P., Dec 2005. Early and late mechanisms of surround suppression in striate cortex of macaque. J Neurosci 25 (50), 11666–75.

Wilson, H. R., Kim, J., Sep 1998. Dynamics of a divisive gain control in human vision. Vision Res 38 (18), 2735–41.

Xing, J., Heeger, D. J., 2000. Center-surround interactions in foveal and peripheral vision. Vision Res 40 (22), 3065–72.

Yu, C., Klein, S. A., Levi, D. M., 2001. Surround modulation of perceived contrast and the role of brightness induction. J Vis 1 (1), 18–31.

Yu, C., Levi, D. M., Jun 1999. The time course of psychophysical end-stopping. Vision Res 39 (12), 2063–73.

Chapter 3

The effect of aging on spatial suppression in a perceived speed task

3.1 Abstract

In younger adults, direction discrimination for high-contrast patterns becomes more difficult as stimulus size increases (Tadin et al., 2003). Betts et al. (2005, 2009) found that this effect, known a spatial suppression, diminished significantly in older adults. They hypothesized that this behavioural finding occurred as a result of decreased GABAergic inhibition in the aging visual system (Leventhal et al., 2003). van der Smagt et al. (2010) found evidence for spatial suppression in younger adults using a task that measured the perceived speed, rather than the direction, of drifting gratings. They reported that perceived speed increased with stimulus size at low contrast, but decreased with increasing size at high contrast. The experiments in this chapter examined whether the effects of spatial suppression on speed judgments are reduced in

older adults. In Experiment 1, 14 younger and 13 older subjects compared the speed of a reference grating drifting at a speed of 1 cps that varied in size (small and large) and contrast (low and high) across conditions to the speed of a test grating that drifted at a speed determined by the method of constant stimuli and whose size (small) and contrast (medium) were fixed. We replicated van der Smagt et al.'s spatial suppressive effect found at high contrast in younger observers. However, we did not find an effect of stimulus size at low contrast. Surprisingly, older adults showed the same pattern as younger adults at both contrast levels. In Experiment 2, we tested 13 younger and 10 older adults and increased the speed of the reference grating to 4 cps. We found similar results for both age groups. These findings are not consistent with the hypothesis that spatial suppression in tasks with dynamic stimuli is reduced in aging.

3.2 General Introduction

Aging has been shown to impair performance in many visual psychophysical tasks, including tasks that measure motion perception (Ball and Sekuler, 1986; Anderson and Atchley, 1995; Atchley and Anderson, 1998; Norman et al., 2003; Raghuram et al., 2005; Snowden and Kavanagh, 2006; Tran et al., 1998; Bennett et al., 2007; Roudaia et al., 2010; Betts et al., 2012), but Betts et al. (2005) found a conspicuous counter-example to this general trend. Betts et al. asked younger and older observers to indicate the direction of a horizontally-drifting grating. They manipulated the size and contrast of the drifting stimulus and measured the duration required to accurately identify the grating's direction. For low-contrast gratings, they found that both age groups needed less time to discriminate motion direction for large rather than small gratings. Tadin et al. (2003) had already reported this spatial summation effect in younger subjects and proposed that the low-contrast surround might be facilitating detection in the central portion of the stimulus through summation. However, for high-contrast gratings, Tadin et al. (2003) and Betts et al. (2005) found

that younger observers required longer durations to discriminate the direction for larger rather than smaller moving stimuli. Tadin et al. (2003) suggested that this spatial suppression effect occurred because the large, high-contrast surround of the stimulus suppressed the neural response to the center stimulus. Interestingly, performance for older adults did not change as much as it did for the younger adults as stimulus size increased (Betts et al., 2005). Indeed, the stimulus duration required to accurately discriminate the direction of large, high-contrast gratings was shorter in older than younger adults. Betts et al. argued that their findings suggested that spatial suppression was reduced with aging.

Effects that are similar to those obtained by Betts et al. (2005) with older adults also have been found in patients with SCZ (Tadin et al., 2006) and MDD (Golomb et al., 2009). In both clinical studies, patients and controls were assessed with Tadin et al. (2003)'s direction discrimination task, and patient populations showed less of an effect of size for high-contrast gratings than control observers. As with older observers, these results were taken as evidence for decreased spatial suppression in the clinical populations.

The behavioural results found in Betts et al. (2005) are consistent with physiological evidence which suggests that inhibitory mechanisms in the visual cortex decline with age (Leventhal et al., 2003). Leventhal et al. showed that most older primate V1 neurons responded equally well to all orientations and directions of a visual stimulus. However, once the inhibitory neurotransmitter GABA, or the GABA agonist muscimol, was injected into these cells, the orientation- and direction-selective responses of most of these cells increased significantly and resembled results from younger monkeys. Fu et al. (2010) measured responses of V1 neurons in younger and older primates to both central and surround stimuli and found that older V1 cells showed reduced suppression indices. Taken together, these studies suggest that the deterioration of GABA-mediated inhibitory mechanisms may contribute to reduced cortical functioning in older observers, including decreased spatial suppression.

It is important to note that previous reports on spatial suppression and aging have reached opposing conclusions regarding whether spatial suppression increases or decreases in healthy older observers. For example, Karas and McKendrick (2009) measured the perceived contrast of *static* textured visual patterns in younger and older subjects. They manipulated the size and contrast of their stimuli and asked observers to indicate which of the two intervals contained the stimulus with the higher contrast. Stimulus duration was 500 ms. They measured PSE (point-of-subjective equality), which was defined as the contrast of the test stimulus where the reference stimulus subjectively appeared the same, and found that while both age groups showed spatial suppression, older observers showed greater spatial suppression.

The same research group conducted another perceived contrast experiment, but this time using *static* sine wave grating stimuli (Karas and McKendrick, 2011). In their experiment, they presented sinusoidal gratings and observers were asked to indicate which of the two intervals contained the central stimulus that appeared higher in contrast. The first interval contained the reference stimulus, which was always small but varied in contrast, while the second interval contained the test stimulus, which was made up of a small stimulus always presented at 70% contrast. Within the test interval, the central stimulus was presented alone or simultaneously with a surround stimulus at 40% contrast. Both intervals were 500 ms in duration. They measured the PSE to correctly match the contrast of the reference to the test stimulus. Older observers demonstrated greater shifts in their PSE, indicative of greater spatial suppression.

The same authors conducted two experiments investigating spatial suppression in aging using *dynamic* stimuli: a perceived contrast experiment and a direction discrimination experiment (Karas and McKendrick, 2012). Their perceived contrast experiment was similar to their experiments from Karas and McKendrick (2011), except the central portion of the test stimulus was always presented at 40% contrast and on a given trial the stimuli drifted randomly either leftwards or rightwards. Stimulus duration was 500 ms. Their findings

were similar to their 2011 results as they found that although both age groups demonstrated spatial suppression, the effects was greater in older adults.

In Karas and McKendrick (2012)'s motion direction discrimination experiment, observers to were asked to indicate the direction of a drifting sinusoidal grating with a button press. Their task replicated the high contrast condition in the motion direction studies described in Tadin et al. (2003) and Betts et al. (2005). Karas and McKendrick varied the size of the stimulus and kept the contrast high. Within each interval, the stimulus would either drift leftwards or rightwards. They measured the duration required to correctly discriminate the motion direction of the stimulus. Karas and McKendrick found that at the smallest size, older adults had longer duration thresholds than younger adults. With increasing size, both age groups demonstrated longer duration thresholds, indicative of spatial suppression. However, at the largest stimulus size, older adults had lower duration thresholds than younger adults. Therefore, the net effect of spatial suppression was weaker in older adults. This pattern is qualitatively similar to what was reported in Betts et al. (2005), however their older adults showed even less spatial suppression than Karas and McKendrick's results. Unlike Betts et al. (2005), the analysis of the suppression indices (representing the log difference in duration threshold between each size condition and the smallest stimulus) did not reveal a main effect of age nor an interaction between age and size in Karas and McKendrick (2012). Therefore, although older adults showed a trend for slightly reduced spatial suppression in their dynamic direction discrimination task, Karas and McKendrick concluded that older adults performed similarly to younger adults.

More recently, Karas and McKendrick (2015) conducted another perceived contrast experiment using *static* sinusoidal gratings. The first interval always contained a small stimulus that varied in contrast, and the second interval contained a central patch surrounded by an annulus. Within the second interval, the center and surround were presented at three different contrasts that varied separately, resulting in nine center-surround conditions. They conducted this experiment at stimulus durations of both 100 ms and 500 ms. They found that

when the surround was higher in contrast than the center stimulus, there was spatial suppression for both age groups but a greater effect in older observers. Furthermore, although the effect of spatial suppression increased for both age groups at the shorter stimulus duration, it remained greater for older observers. In all of their perceived contrast studies using both static and dynamic stimuli at various stimulus durations, this research group has found that older observers consistently demonstrate greater spatial suppression than younger observers (Karas and McKendrick, 2009, 2011, 2012, 2015). In their direction discrimination study, they found a similar pattern to Betts et al. (2005) in that older adults demonstrated a trend for less spatial suppression, but the age effect was not statistically significant (Karas and McKendrick, 2012).

In Experiment 1 in Chapter 2, we did not find an age effect in spatial suppression using static masking stimuli. We had hypothesized that if older adults had less spatial suppression like in Betts et al. (2005), then their thresholds for the combination mask at backward and forward masking time points would be similar to the central mask because the surround portion of the combination mask would not reduce the strength of the central portion of the mask. However, we found that thresholds in the older adult group for the combination mask were similar to those of the central mask (Figure 2.5). Therefore, the pattern of results in spatial suppression experiments is not entirely consistent.

Tadin et al. (2011) showed that there might be something special about moving, not static, stimuli. Using TMS, Tadin et al. (2011) showed that disrupting area MT improved performance in a direction discrimination task for younger adults in the large, high-contrast condition resembling the behavioural results found for older adults in Betts et al. (2005)'s study. Interestingly, they found that when V1 was disrupted using TMS, performance did not change. Therefore, Tadin et al. (2011)'s experiment shows that there is a direct relationship between area MT and spatial suppression using dynamic gratings. Their finding is interesting because neural activity in area MT/V5 has been shown to be highly correlated with the perception of moving stimuli (Newsome et al., 1989; Culham et al., 2001).

The motion task that Tadin et al. (2003), Betts et al. (2005) and Karas and McKendrick (2012) used was a direction discrimination task. If the reduced inhibition with aging hypothesis holds true for the motion processing system, then the age-related reduction in spatial suppression should extend to other motion discrimination/perception tasks. If inhibition does not influence spatial suppressive effects equally in all motion tasks, then we would not necessarily expect less suppression with aging, which is more similar to what was found by Karas and McKendrick (2012) in their dynamic perceived contrast experiment where they found greater spatial suppression in older adults. One example of an alternative motion task is to judge the speed of drifting gratings, rather than their direction. Many studies have demonstrated that performance in perceived speed tasks is greatly affected by motion in the surround (Norman et al., 1996; Tynan and Sekuler, 1975; Loomis and Nakayama, 1973). One study in particular manipulated the size and contrast of a drifting grating, similar to what Tadin et al. (2003), Betts et al. (2005) and Karas and McKendrick (2012) did in their direction discrimination task. van der Smagt et al. (2010) conducted an experiment that examined the effects of contrast and size on perceived speed. Their experiments used a 2-IFC procedure. On each trial, subjects saw two drifting sine wave gratings presented in two successive intervals. The first interval contained the reference grating, which consisted of a central patch that was either presented in isolation or surrounded by an annulus. The center and surround stimuli always had the same speed (1 cps), motion direction (which varied randomly across trials), and contrast (ranging from 1.4% to 66.4%). The second interval contained the test grating, which had the same size, spatial frequency, and direction as the central patch, but had a fixed contrast of 38%. The subject's task was to say whether the reference (interval 1) or test (interval 2) grating appeared to have the greater speed. The speed of the test grating was varied across trials using a 1-up/1-down staircase procedure to estimate the PSE, which was defined as the speed that caused subjects to say that the test grating had the greater speed on 50% of the trials. A PSE of 1 cps indicated that perceived speeds of the test and reference gratings were equivalent when their physical speeds were the same,

and therefore any differences in stimulus size (i.e., no surround or surround conditions) and/or contrast (low and high contrast conditions) did not affect the perceived speed of the central patch. PSEs less than or greater than 1 indicated that the the size and/or contrast of the reference grating led the observer to perceive the test stimulus as moving slower or faster, respectively. van der Smagt et al. found that perceived speed decreased when a surround was added to a high-contrast grating, and perceived speed increased when a surround was added to a low-contrast grating (Figure 3.1). These results are analogous to the spatial summation (low contrast) and spatial suppression (high contrast) effects found for younger observers reported by Tadin et al. (2003) and Betts et al. (2005) in a direction discrimination task.

Previous studies have shown that older observers have difficulty discriminating differences in speed. Norman et al. (2003) and Snowden and Kavanagh (2006) reported that speed discrimination thresholds in older observers are higher than they are in younger subjects across a wide range of speeds and stimulus durations; Raghuram et al. (2005) also found higher speed discrimination thresholds in older adults, but only for short stimulus durations. However, specific center-surround effects on speed perception in aging have not been studied. It is important to understand these effects because accurate speed perception is essential for mobility in daily life. To avoid accidents, like bumping into another person or a car accident, it is important to make accurate judgements about our own speed as well as the speed of the environment. Since the human lifespan is dramatically increasing and the number of senior citizens will increase by a factor of 1.5 within the next 30 years (Statistics Canada, 2014), it is imperative that we understand speed perception changes in aging or else the incidence of car accidents may increase. It has already been established, in the Fatality Analysis Reporting System (FARS), that there has been a steady increase in the number of severe car accidents (including fatalities) for older drivers beginning at age 60 (Evans, 2004).

In the current set of experiments, we set out to determine whether or not older adults would show spatial summation and spatial suppression in a

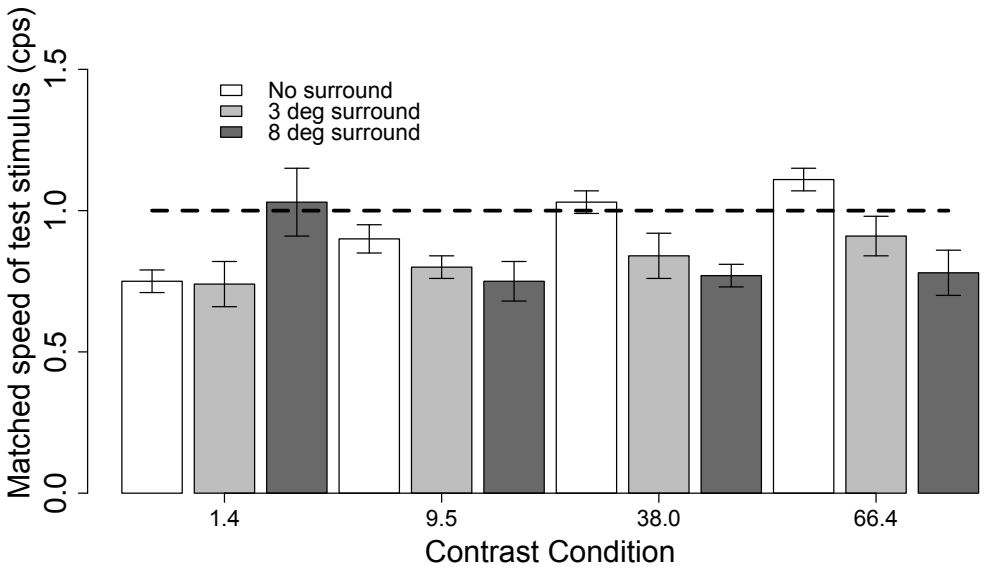


Figure 3.1: Replotted from Figure 2 in van der Smagt et al. (2010). PSEs (speeds of the test stimulus, (38% contrast, no surround) when matched to that of the reference stimulus) for all contrast/size combinations, averaged across 9 observers. Error bars depict ±1 SEM. The horizontal dashed line represents the reference speed (1 cps).

perceived speed discrimination task. We measured perceived speed for drifting gratings in younger and older observers and varied contrast and size. We predicted that if spatial suppression is reduced in older adults in motion tasks, then older adults should show less spatial suppression at high contrast than their younger counterparts.

3.3 Experiment 1

3.3.1 Introduction

Observers compared the speed of the central patch of a moving grating (i.e., the reference stimulus) shown in one stimulus interval to the speed of the test grating shown in another stimulus interval. Our goal was to replicate van der Smagt et al. (2010), and to determine whether surround interactions, as estimated by PSEs for speed, varied as a function of age across the adult lifespan.

3.3.2 Participants

Fourteen younger (M = 22.0 years; range: 17 – 28, 8 female) and 13 older (M = 68.8 years; range: 62 – 77, 7 female) adults participated in the current experiment. Subjects received $10/hour for their time. Before being tested, all subjects completed a written informed consent form. The SLOAN Two Sided ETDRS Near Point Test as well as the 4 m 2000 Series Revised ETDRS chart were used to measure near and far visual acuity, respectively. Contrast sensitivity was measured using the Pelli-Robson Contrast Sensitivity Test (Pelli et al., 1988). All subjects tested in this experiment had normal to corrected-to-normal visual acuity and contrast sensitivity, and did not have visual disorders or abnormalities. Older subjects were screened for general cognitive abilities with the MMSE (Folstein et al., 1975) as well as the MoCA (Nasreddine et al.,

2005). Demographic information for all subjects in Experiments 1 and 2 are summarized in Table 3.1.

3.3.3 Apparatus

Psychophysics and Video Toolboxes (version 3.0.8) software (Brainard, 1997; Pelli, 1997) were used to program the experiment in the MATLAB (version 7.9) environment which ran on a Macintosh G5 computer. Stimuli were displayed on a 21-inch Sony Trinitron CRT monitor (model GDM-F520) with a spatial resolution of 1280 × 1024 pixels (pixel size = 0.014 deg) and a refresh rate of 100 Hz. The display was the sole source of light in the testing room, and had an average luminance of 65 cd/m^2. Stimuli were viewed binocularly from a distance of 57 cm, and the display subtended 36.19 × 28.99 deg. A chin/forehead rest was used to stabilize head position. All responses were collected with a standard QWERTY Macintosh keyboard. The duration of the entire experiment was about 1 hour, including breaks between blocks.

3.3.4 Stimuli and Procedure

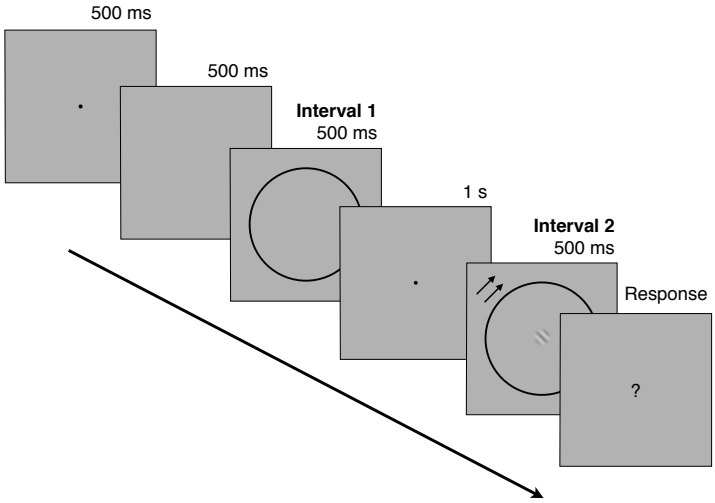
Each subject completed a short contrast detection experiment, followed by a perceived speed experiment. Figure 3.2 illustrates the experimental procedure for each portion of the experiment. The stimulus parameters used in this experiment were chosen to match those used in van der Smagt et al. (2010) so that a comparison of the results could be made more easily.

Detection Task

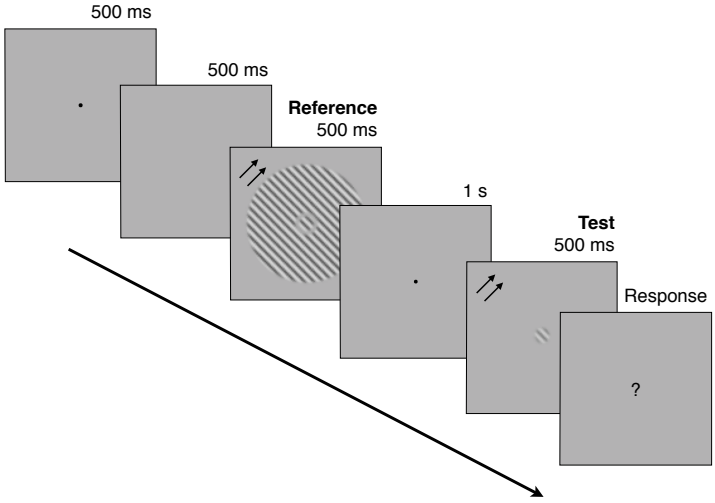
In the 2-IFC detection task, subjects were instructed to identify the interval containing a small (3 deg in diameter) drifting stimulus. The edges of the stimuli were smoothed using a normal cumulative distribution function (σ =

Table 3.1: Experiment, number of subjects, age, decimal near acuity, decimal far acuity, MMSE and MoCA scores for older subjects. Values in parentheses are standard deviations.

Experiment	Subjects (N)	Age (μ,σ)	Near Acuity (μ,σ)	Far Acuity (μ,σ)	MMSE (μ,σ)	MoCA (μ,σ)
1	14 younger	22.0 (2.9)	1.37 (0.26)	1.39 (0.24)		
	13 older	68.8 (4.6)	0.95 (0.23)	1.00 (0.20)	29.07 (0.73)	26.92 (1.71)
2	13 younger	21.8 (2.4)	1.37 (0.22)	1.28 (0.25)		
	10 older	69.7 (5.1)	1.10 (0.27)	1.10 (0.17)	28.90 (1.20)	27.20 (1.87)



(a) Detection Task.



(b) Perceived Speed Task.

Figure 3.2: (a) Example of one trial from the detection experiment. In this example the first interval was blank, followed by an ISI and the second interval containing the stimulus. (b) Example of one trial from the perceived speed experiment. The reference stimulus was always presented in interval 1 and the test stimulus was always presented in interval 2. The stimulus intervals were separated by an ISI.

32 pixels). The 2 cpd grating drifted within the circular window at a speed of 1 cps. Stimulus orientation, and therefore the direction of motion (which was perpendicular to the orientation) was randomized for every trial. A flashing fixation point was displayed in the center of the screen for 500 ms, followed by a blank screen for 500 ms. The stimulus was displayed either in interval 1 or 2 for a duration of 500 ms. Each stimulus interval coincided with the presentation of a thin, high-contrast circle (22.04 deg in diameter) in the center of the display; the circle served to reduce the subject's uncertainty about the temporal extent of each interval. The two intervals were separated by a 1 s ISI, consisting of a fixation point presented in the center of the otherwise blank screen. Stimulus contrast was varied across trials with two interleaved 2-down/1-up staircases, which converge on the contrast needed to obtain 70% correct responses. Auditory feedback was provided after every trial to indicate whether the subject's response was correct (1200 Hz tone) or incorrect (600 Hz tone). The experiment ended after each staircase reached 50 trials or 14 reversals. Thresholds were calculated by taking an average of the last 4 reversals for each staircase and then averaging those values. The detection experiment lasted 5-10 minutes.

Perceived Speed Task

The perceived speed task began after a short break following the detection task. The procedure is illustrated in Figure 3.2b. Each trial began with the presentation of a flashing fixation point for 500 ms, followed by a 500 ms presentation of a blank screen. Next, the reference stimulus was presented for 500 ms, followed by a 1 s ISI that contained only a central fixation point, followed by a 500 ms presentation of the test stimulus. The observer was instructed to indicate whether the reference (interval 1) or test (interval 2) stimulus appeared to be drifting at a faster pace by pressing the left or right key, respectively, on a computer keyboard. No auditory feedback was provided since this was a task measuring subjective perception. The 2 cpd circular sine

wave gratings drifted at a speed of 1 cps. Orientation varied randomly across trials.

The reference and test stimuli were always presented in the first and second stimulus interval, respectively. Stimulus size (3 and 18.37 deg in diameter) and contrast (low and high contrast, see below) varied for the reference stimulus only. Reference speed was kept constant at 1 cps. The edges between the center (3 deg in diameter) and surround (18.37 deg in diameter) portions of the stimulus were smoothed using a cumulative normal function, which resulted in a small gap that was similar in size to the one used by van der Smagt et al. (2010).

The low and high contrast values used for each subject were, respectively, 2 and 40 times their individual detection thresholds. The four contrast/size blocks (low contrast/small, low contrast/large, high contrast/small, high contrast/large) were presented in a randomized order. The test stimulus was always small (3 deg) and the contrast was set to 8.94 times each individual's detection threshold value[1].

The direction of motion (and orientation) of the grating was randomized for every trial, but the reference and test directions were identical within a single trial. The method of constant stimuli was used to vary the speed of the test stimulus. Nine speeds (0.4, 0.5, 0.63, 0.8, 1, 1.26, 1.58, 2, and 2.5 cps) were presented in a random order 12 times each. Psychometric functions were fit to the data from each individual subject to estimate the PSE, which corresponded to the test speed that was perceptually equivalent to the reference speed (1 cps). A PSE greater than 1 indicated that the reference stimulus appeared to move faster than its physical speed of 1 cps, whereas a PSE less than 1 indicated that the reference stimulus appeared to move slower than 1 cps. PSEs were determined by sorting the test speeds from slowest to fastest, calculating the proportion of "test perceived faster than reference" responses at

[1]Using a multiplier of 8.94 results in a test contrast that is midway between the low and high reference contrasts when all three contrasts are expressed on a log scale.

each test speed, fitting a Weibull function to these data, and then estimating the 50% point on the psychometric function.

3.3.5 Results

Contrast detection thresholds and PSEs were estimated using MATLAB, and statistical analyses (t-tests and ANOVAs) were performed using R (R Core Team, 2014). As expected, detection thresholds for younger ($M = 0.57\%$, $SEM = 0.03\%$) and older ($M = 0.81\%$, $SEM = 0.03\%$) adults differed significantly ($t(1, 25) = 4.99$, $p < 0.001$).

Because detection thresholds were used to calculate the low and high contrast values used in the perceived speed experiment, low contrast values ranged between 0.8% and 1.8% for younger adults and 1.4% and 2.2% for older adults whereas high contrast values ranged between 16% and 36% for younger adults and 28% and 44% for older adults. Test contrast values ranged between 3.59% and 8.08% for younger adults and 6.29% and 9.89% for older adults.

Results from the perceived speed experiment are summarized in Figure 3.3. The PSEs were analyzed with a 2 (age) $\times$ 2 (contrast) $\times$ 2 (size) split-plot ANOVA, with age as the between-subjects variable and contrast and size as the within-subjects variables. The analysis revealed a main effect of size ($F(1, 25) = 21.56$, $p < 0.01$), indicating that, in both age groups, PSEs were lower for larger reference stimuli than smaller reference stimuli. The size $\times$ contrast ($F(1, 25) = 9.59$, $p < 0.01$) interaction was significant. An analysis of the simple main effects of size demonstrated that the effect of size was significant at the high reference contrast condition ($F(1, 26) = 29.59$, $p < 0.001$) but not at the low reference contrast condition ($F(1, 26) = 2.34$, $p = 0.14$). The remaining effects and interactions were not significant. There was no main effect of contrast ($F(1, 25) = 0.79$, $p = 0.38$). In addition, there was no main effect of age ($F(1, 25) = 0.16$, $p = 0.70$), indicating that the results between younger and older adults were similar. The age $\times$ size

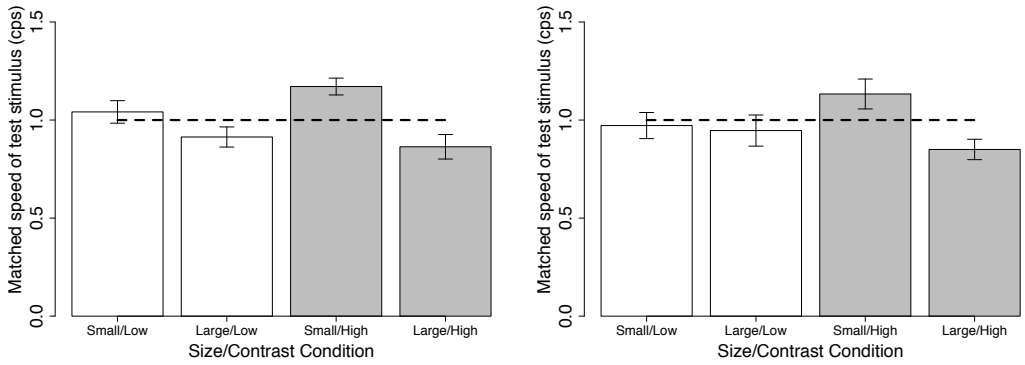
($F(1, 25) = 0.62$, $p = 0.44$), age × contrast ($F(1, 25) = 0.01$, $p = 0.93$), and age × size × contrast ($F(1, 25) = 0.31$, $p = 0.58$) interactions were not significant.

A separate age × size ANOVA at high contrast was conducted to determine if the amount of spatial suppression differed between the two age groups. The analysis revealed a significant main effect of size ($F(1, 25) = 28.50$, $p < 0.001$), indicating that PSEs were lower for the larger size. The analysis, however, did not reveal a main effect of age ($F(1, 25) = 0.17$, $p = 0.69$) or a significant age × size interaction ($F(1, 25) = 0.05$, $p = 0.83$). Taken together, these results suggest that both age groups showed similar levels of spatial suppression at high-contrast.

We also conducted an age × size ANOVA at low contrast and found no main effect of age ($F(1, 25) = 0.06$, $p = 0.81$), size ($F(1, 25) = 2.34$, $p = 0.14$), or an age × size interaction ($F(1, 25) = 0.99$, $p = 0.33$), indicating that there was no summation or suppression at low contrast for either age group and PSEs were similar between the age groups.

3.3.6 Discussion

We investigated the influence of center-surround mechanisms in speed perception. Our results did not fully replicate those from van der Smagt et al. (2010)'s experiment with younger adults at a slow reference speed. Whereas van der Smagt et al. found center-surround effects consistent with Tadin et al. (2003) (i.e., spatial summation at low contrast and spatial suppression at high contrast), our younger adults showed spatial suppression at high contrast but no effect of size at low contrast (i.e., neither summation nor suppression at low contrast). We also found that the effects of size and contrast did not differ significantly between younger and older adults.



(a) Younger Adults.

(b) Older Adults.

Figure 3.3: Experiment 1 PSEs for all contrast/size combinations at the 1 cps reference speed for 14 younger observers and 13 older observers. The dashed lines indicate a PSE of 1.

3.4 Experiment 2

3.4.1 Introduction

Previous studies investigating spatial suppression have shown different effects as stimulus speed increases. van der Smagt et al. (2010) found that increasing the velocity of the reference stimulus improved perceived speed performance for small, high-contrast stimuli (i.e., the matched speed of the test stimulus was closer to the true stimulus speed when the reference speed increased). However, they found that the effect of the surround decreased with increasing stimulus speed. Like van der Smagt et al., Lappin et al. (2009) found that performance improved with increasing stimulus speed in their direction discrimination task measuring duration thresholds in younger adults. However, unlike van der Smagt et al., Lappin et al. found that as speed increased, the effect of spatial suppression increased. They varied the size of their stim-

uli at high contrast and found that although duration thresholds decreased for both small and large stimuli as speed increased, the difference between the two sizes was larger at faster velocities. Betts et al. (2009) conducted a similar experiment to Lappin et al. and measured duration thresholds for a direction discrimination task in both younger and older adults. Like Lappin et al., they found that performance improved overall with increasing speed and that the effect of spatial suppression increased with increasing speed for younger adults. However, thresholds for older adults showed the opposite result: reduced spatial suppression at higher speeds.

Given our hypothesis that spatial suppression is reduced in aging in motion tasks, and the finding that increasing speed improves performance in older adults at high contrast (Betts et al., 2009), we wanted to determine if increasing the reference speed in our perceived speed experiment would result in less spatial suppression in older than younger adults. Therefore, in Experiment 2 we increased the speed of the reference stimulus.

3.4.2 Methods

In Experiment 2, the speed of the 2 cpd reference stimulus was set to 4 cps. The nine speeds used to determine the PSEs were set to 1.6, 2, 2.52, 3.2, 4, 5.04, 6.32, 8, and 10 cps. Other than those speed changes, the stimuli and procedures did not vary from those used in Experiment 1. A different set of thirteen younger ($M = 21.8$ years; range: 19–28, 10 female) and 10 older ($M = 69.7$ years; range: 61–78, 4 female) adults participated in this experiment (see Table 3.1).

3.4.3 Results

Detection thresholds for younger ($M = 0.35\%$, $SEM = 0.02\%$) and older adults ($M = 0.64\%$, $SEM = 0.03\%$) were significantly different in Experiment

2 ($t(1, 21) = 8.10$, $p < 0.001$). However, these detection thresholds were significantly lower than the thresholds measured in Experiment 1 (at a slower speed) for both younger ($t(1, 25) = 5.33$, $p < 0.001$) and older ($t(1, 21) = 3.78$, $p < 0.01$) adults, indicating that it was easier for subjects to detect a stimulus drifting at a faster than slower speed.

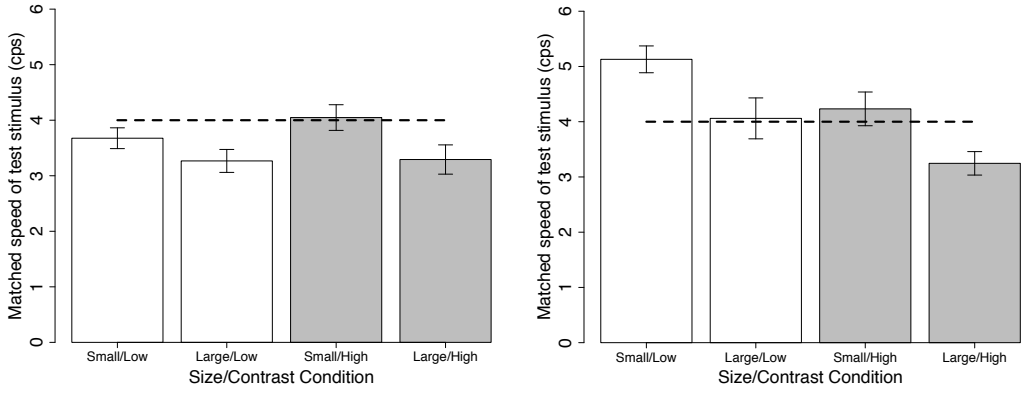
Contrast values used in the discrimination experiment were set for individual subjects based on their detection thresholds. Low contrast values, calculated by multiplying detection thresholds by a factor of 2, ranged between 0.6% and 1.2% for younger adults and 1.2% and 1.4% for older adults. High contrast values, calculated by multiplying detection thresholds by a factor of 40, ranged between 12% and 24% for younger adults and 20% and 28% for older adults. Finally, test contrast, calculated by multiplying detection thresholds by a factor of 8.94, ranged between 2.69% and 5.39% for younger adults and 4.49% and 6.29% for older adults.

The PSE results are illustrated in Figure 3.4. A 2 (age) $\times$ 2 (contrast) $\times$ 2 (size) split-plot ANOVA revealed a significant main effect of size ($F(1, 21) = 65.64$, $p < 0.001$), similar to what was found in Experiment 1, indicating that PSEs were lower for larger stimuli. There was a main effect of age ($F(1, 21) = 4.33$, $p < 0.05$), but no main effect of contrast ($F(1, 21) = 2.39$, $p = 0.14$). The age $\times$ size ($F(1, 21) = 5.31$, $p < 0.05$) interaction was significant. A closer look at the simple main effects revealed significant differences between the small and large-sized conditions in younger ($F(1, 12) = 19.28$, $p < 0.001$) and older adults ($F(1, 9) = 56.37$, $p < 0.001$), but the difference appeared to be larger in the older age group. In addition, the age $\times$ contrast ($F(1, 21) = 9.69$, $p < 0.01$) interaction was significant. The simple main effects analysis showed a significant difference between the low and high contrast conditions in older ($F(1, 9) = 7.96$, $p < 0.05$), but not younger adults ($F(1, 12) = 1.15$, $p = 0.30$). The size $\times$ contrast ($F(1, 21) = 0.71$, $p = 0.41$) and the age $\times$ size $\times$ contrast ($F(1, 21) = 1.26$, $p = 0.27$) interactions were not significant.

To determine if there were different amounts of spatial suppression for

each age group, we conducted an age × size ANOVA at high contrast. Like in Experiment 1, we found a significant main effect of size ($F(1, 21) = 93.83$, $p < 0.001$), but no main effect of age ($F(1, 21) = 0.04$, $p = 0.85$) or a significant age × size interaction ($F(1, 21) = 1.67$, $p = 0.21$). These results imply that both age groups demonstrated similar levels of spatial suppression at high-contrast.

An age × size ANOVA at low contrast revealed a significant main effect of age ($F(1, 21) = 13.08$, $p < 0.01$), with older adults having higher PSEs. The main effect of size was also significant ($F(1, 21) = 16.98$, $p < 0.001$), with larger stimuli having lower PSEs overall. Finally, the size × age interaction nearly reached significance ($F(1, 21) = 3.76$, $p = 0.07$). We conducted t-tests to investigate this interaction and found that there was no significant difference between the small and large sizes for younger observers ($t(1, 24) = 1.47$, $p = 0.16$). However, there was significant suppression at low contrast in older observers ($t(1, 18) = 2.41$, $p < 0.05$).



(a) Younger Adults.

(b) Older Adults.

Figure 3.4: Experiment 2 PSEs for all contrast/size combinations at the 4 cps reference speed for 13 younger observers and 10 older observers. The dashed lines indicate a PSE of 4.

3.4.4 Discussion

van der Smagt et al. (2010) found that, at high contrast, the strength of spatial suppression was reduced when the reference speed increased. Given the reduced spatial suppression hypothesis in aging, we wanted to determine whether or not there would be less suppression in our older than younger subjects when the stimulus speed increased.

In Experiment 2, we increased the speed of the reference grating from 1 cps to 4 cps. Unlike what we found in Experiment 1, in Experiment 2 we found a significant main effect of age: PSEs were higher overall for older than younger adults, meaning that the perceived speed was faster for older adults. Additionally, we found a significant age $\times$ size interaction in the current experiment. This finding was driven by the larger PSE difference between the small and large-sized stimuli for older adults. The age $\times$ contrast interaction was also significant, driven by the larger difference between the low contrast and high contrast stimuli in older adults. On average, older adults had higher PSEs in the low contrast, small stimulus condition than their younger counterparts. This result demonstrates that low contrast, small stimuli drifting at a fast speed appear to be drifting even faster for older adults.

A comparison of the results in Experiments 1 and 2 shows that, like van der Smagt et al. (2010), we found that increasing stimulus speed brought PSEs closer to the true, physically equivalent speed for small, high-contrast stimuli in both age groups, a result that supports the idea that perceived speed becomes more veridical with increasing speed (van der Smagt et al., 2010; Betts et al., 2009; Lappin et al., 2009).

To determine if increasing the velocity of the reference stimulus improved perceived speed, we compared the results for the small, high-contrast condition in younger observers between Experiments 1 and 2. Our t-test revealed a significant difference, ($t(1, 25) = 12.69$, $p < 0.001$), replicating van der Smagt et al. (2010)'s finding.

To understand the changes in suppression with increasing speed, we compared the results of Experiment 1 and 2 by conducting a 2 (experiment) $\times$ 2 (age) $\times$ 2 (contrast) $\times$ 2 (size) ANOVA. There was a significant main effect of experiment ($F(1, 42) = 346.42$, $p < 0.001$), with PSEs in Experiment 2 being higher overall than in Experiment 1. The main effect of age nearly reached significance ($F(1, 42) = 3.46$, $p = 0.07$), indicating that older PSEs were higher than younger PSEs overall, driven mostly from the older group's small, low-contrast results in Experiment 2. There was a main effect of size ($F(1, 42) = 80.58$, $p < 0.001$), with large sizes having lower PSEs than small sizes overall. The following interactions reached significance or near significance: experiment $\times$ age interaction ($F(1, 42) = 5.16$, $p < 0.05$), experiment $\times$ size interaction ($F(1, 42) = 31.08$, $p < 0.001$), experiment $\times$ size $\times$ age interaction ($F(1, 42) = 4.09$, $p < 0.05$), experiment $\times$ contrast interaction ($F(1, 42) = 3.24$, $p = 0.08$), contrast $\times$ age interaction ($F(1, 42) = 8.60$, $p < 0.01$), experiment $\times$ contrast $\times$ age interaction ($F(1, 42) = 9.11$, $p < 0.01$). All other effects did not reach significance.

For the low contrast conditions, there was no significant difference between the two sizes in younger adults at the slow or fast speed. van der Smagt et al. (2010) had reported that at low contrast, younger adults showed spatial summation at the slow speed, but no effect at high contrast. Older observers demonstrated no effect of the surround at the slower speed, like our younger observers, but did show suppression at the high speed.

To determine if there were changes in the amount of spatial suppression for each age group at high contrast between each experiment, we conducted a 2 (experiment) $\times$ 2 (age) $\times$ 2 (size) ANOVA at high contrast. We found a significant main effect of experiment ($F(1, 42) = 204.47$, $p < 0.001$), indicating that PSEs were generally higher in Experiment 2 than 1. The main effect of size reached significance ($F(1, 42) = 119.10$, $p < 0.001$), suggesting that PSEs for the larger size were lower than PSEs for the smaller size. There was a significant experiment $\times$ size interaction ($F(1, 42) = 32.25$, $p < 0.001$). We investigated this interaction by analyzing simple main effects and found

that there were significant differences between small and large sized stimuli at high contrast in Experiment 1 ($t(1, 52) = 5.07$, $p < 0.001$) and Experiment 2 ($t(1, 44) = 3.41$, $p < 0.01$), indicating that both age groups showed spatial suppression at both speeds. To determine which experiment yielded greater spatial suppression, we calculated PSE ratios by dividing the PSE value at the small size by the PSE value at the large size. Experiment 1 mean PSE values were 1.15 at the small size and 0.86 at the large size. In Experiment 2, mean PSE values were 4.13 at the small size and 3.27 at the large size. Therefore, PSE ratios were 1.34 for Experiment 1 and 1.26 for Experiment 2. Therefore, there was significantly greater suppression overall in Experiment 1 than 2, indicating that, like the younger observers in van der Smagt et al. (2010), our younger observers demonstrated less spatial suppression at the faster speed. We had predicted that older adults would show even *less* spatial suppression than younger adults. Instead we found that older adults showed less spatial suppression in the higher speed experiment, similar to what was found in younger subjects. Therefore, we did not find evidence for reduced spatial suppression in aging when stimulus speed is increased.

3.5 General Discussion

In this chapter, we set out to determine if the center-surround antagonistic patterns found for younger and older adults in Betts et al. (2005)'s direction discrimination experiment would be found in a speed perception task. We conducted van der Smagt et al. (2010)'s speed discrimination experiment that varied the contrast and size of stimuli on a set of younger and older adults. van der Smagt et al. found that younger adults showed spatial summation at low contrast and spatial suppression at high contrast. Additionally, when the speed of the reference stimulus increased, they showed no effect of the surround at low contrast and less suppression at high contrast.

Before we measured speed perception, we measured detection thresholds

to use the values to normalize the contrast levels in the speed discrimination experiment. We did this to make sure that each subject was able to detect the stimulus. Our detection threshold results for our drifting 2 cpd stimulus were as expected based on Owsley et al. (1983)'s finding that contrast sensitivity declines in aging for medium to high spatial frequencies ($>$ 1 cpd). The older adults required a higher contrast to detect the small drifting grating. When we increased the speed of the stimuli in Experiment 2, detection thresholds were lower than they were in Experiment 1 for both age groups, indicating that it may be easier to detect a faster stimulus.

In our perceived speed task in Experiment 1, we did not find strong spatial summation at the low contrast condition in younger subjects: perceived speed was approximately equal to physical speed (i.e., 1 cps) for both small and large stimuli (Figure 3.3). When the speed increased in Experiment 2, there was still no evidence for summation or suppression at the low contrast condition for younger observers. Although van der Smagt et al. found strong spatial summation for the 8 deg surround, they did not find significant summation for the 3 deg surround. Older adults, like their younger counterparts, showed no summation at the low contrast condition when the speed was slow in Experiment 1. When the speed increased in Experiment 2, however, older subjects demonstrated spatial suppression.

At the high contrast condition at the slow speed, we found spatial suppression in both younger and older adults: adding a surround to a high contrast stimulus slows down perceived speed. This effect may have occurred because the presence of a surround decreases the perceived contrast of the center (Snowden and Hammett, 1998; Takeuchi and De Valois, 2000), which would decrease the perceived speed of the center. Additionally, Xiao et al. (1998) measured MT/V5 neurons in monkeys and found that they showed strong surround inhibition that did not vary across a broad range of speeds. Their finding suggests that there is a physiological relationship between a moving surround and surround suppression in the neuron. Therefore, this could explain why it was more difficult for our subjects to perceive the central speed of a stimulus when

it was surrounded by a moving large, high-contrast stimulus.

When the speed increased, we found reduced spatial suppression at high contrast for younger adults. This result confirmed van der Smagt et al. (2010)'s finding that the magnitude of spatial suppression was reduced at the faster speed for younger subjects. We had expected, based on our hypothesis that spatial suppression is reduced in aging in tasks with dynamic stimuli and Betts et al. (2009)'s result showing that increasing the speed improved performance for older subjects at high contrast, that older adults would show a greater reduction in spatial suppression than their younger counterparts. We found that although older adults showed reduced spatial suppression in the high contrast condition when the speed increased, supporting Betts et al. (2009)'s finding, they showed the same amount of reduced spatial suppression as the younger adults.

One potential explanation for our failure to obtain summation effects in the low contrast conditions like van der Smagt et al. (2010) is that we used the method of constant stimuli rather than the adaptive staircase method. In the method of constant stimuli, the speed levels of the test stimulus are presented randomly whereas in the staircase method the speed level of the test stimulus relies on previous responses and converges on near-PSE values. In other words, the variability in stimulus speeds across trials likely was greater in our experiments than in van der Smagt et al.'s study, particularly near the end of an experimental session, and perhaps this stimulus variability affects PSEs.

Another reason why we might not have replicated van der Smagt et al. (2010)'s results at low contrast is because we used detection thresholds to normalize the contrast levels in the speed discrimination experiment rather than setting the contrast to 1.4% like they did. However, we believe that this explanation cannot account for our findings: Prior to conducting the experiments presented in this chapter, we conducted a pilot direction discrimination study using identical stimuli to the ones used in Experiment 1, except that stimulus

contrast was set to 1.4% and 66.4%. We found that most of the older subjects were unable to complete the experiment because they could not detect the low contrast stimulus. Therefore, in a second pilot study, we doubled the contrast used in the low contrast condition to 2.8% and found – as in the current experiments – that younger and older adults showed suppression at both low and high contrast, implying that 2.8% contrast was too high to exhibit summation. It is for this reason that we decided to use multiples of the individual detection thresholds to set the low and high contrast values. It ensured that the low contrast stimulus was as low as it could be while still being detectable. Our low contrast levels ranged from 0.8% and 1.8% in younger adults. However, since these values are very similar to van der Smagt et al.'s contrast of 1.4%, the lack of spatial summation found in our younger subjects cannot be fully explained by differences in the way in which the low contrast value was set. In summary, we do not believe that fixing the low contrast to the value used by van der Smagt et al. would have changed our results in the low contrast condition.

We do believe, however, that fixing the high contrast value to the value used by van der Smagt et al. may have changed our results in the high contrast condition. Since we calculated contrast levels based on detection threshold for each subject individually, and older adults require higher contrast levels, this means that the contrast levels set for our older subjects were higher than they were for younger subjects. In all of the previously discussed speed discrimination in aging experiments, the contrast levels were set to the same level for both younger and older subjects. Therefore, our older subjects were just as able to detect the low contrast stimulus as their younger counterparts, and this might explain why we did not find a reduced age effect.

Perhaps we did not find reduced spatial suppression in aging when the reference was drifting at a faster speed because our stimuli were drifting on the screen for a relatively long duration (500 ms). The behavioural age effect reported in the study by Betts et al. (2005) measuring direction discrimination thresholds was found using much more briefly presented drifting stimuli (<

100 ms). In addition, some of the literature on aging and speed discrimination have supported the idea that age differences might be larger with shorter stimuli. For example, Raghuram et al. (2005) found that age differences in speed perception disappeared when the stimulus duration increased from 500 to 1000 ms. Subjects were told to focus on a central fixation point while oppositely drifting stimuli were presented in square apertures on the left and right. Their task was to determine which of the two stimuli was moving faster. Two consecutive correct responses were necessary to reduce the speed difference between the two gratings, while two consecutive incorrect responses were required to increase the speed difference between the two gratings. All stimuli were 40% contrast and 1.5 deg in diameter (similar to our high contrast/small size condition). When the stimulus duration was 500 ms, they found that older subjects performed worse in the task. They attributed their results to differences in temporal integration of speed with aging. They found that when the stimulus duration increased to 1000 ms, the age effect disappeared. However, Norman et al. (2003) found that speed perception gets worse with age at even unlimited stimulus durations. They found age differences in a speed perception task with narrow bands of dots moving at 3 different speeds. Even after training, older adults continued to show higher thresholds than younger adults overall. This study shows us that age differences still persist after long durations.

Physiological results also support the idea that spatial suppression in aging might occur in studies using briefly presented stimuli. For example, surround suppressed cells in MT/V5 are more strongly modulated by motion direction for briefly presented small stimuli, and performance deteriorates with increasing size (Churan et al., 2008). Churan et al. suggested that behavioural spatial suppression may occur because the outputs from MT/V5 neurons provide relatively little information about large, briefly-presented stimuli. Therefore, perhaps there would be reduced spatial suppression in aging if we were to shorten the stimulus duration in the perceived speed task.

References

Anderson, G. J., Atchley, P., 1995. Age-related differences in the detection of three-dimensional surfaces from optic flow. Psychology and Aging 10, 650–658.

Atchley, P., Anderson, G. J., 1998. The effect of age, retinal eccentricity, and speed on the detection of optic flow components. Psychology and Aging 13 (2), 297–308.

Ball, K., Sekuler, R., Mar 1986. Improving visual perception in older observers. J Gerontol 41 (2), 176–82.

Bennett, P. J., Sekuler, R., Sekuler, A. B., Mar 2007. The effects of aging on motion detection and direction identification. Vision Res 47 (6), 799–809.

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2009. Spatial characteristics of center-surround antagonism in younger and older adults. J Vis 9 (1), 25.1–15.

Betts, L. R., Sekuler, A. B., Bennett, P. J., Jan 2012. Spatial characteristics of motion-sensitive mechanisms change with age and stimulus spatial frequency. Vision Res 53 (1), 1–14.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., Feb 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–6.

Brainard, D. H., 1997. The psychophysics toolbox. Spat Vis 10 (4), 433–6.

Churan, J., Khawaja, F. A., Tsui, J. M. G., Pack, C. C., Nov 2008. Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT. Curr Biol 18 (22), R1051–2.

Culham, J., He, S., Dukelow, S., Verstraten, F. A., Apr 2001. Visual motion and the human brain: what has neuroimaging told us? Acta Psychol (Amst) 107 (1-3), 69–94.

Evans, L., 2004. Traffic safety. Science Serving Society, Bloomfield Hills, MI.

Folstein, M. F., Folstein, S. E., McHugh, P. R., Nov 1975. Mini-mental state. a practical method for grading the cognitive state of patients for the clinician. J Psychiatr Res 12 (3), 189–98.

Fu, Y., Wang, X. S., Wang, Y. C., Zhang, J., Liang, Z., Zhou, Y. F., Ma, Y. Y., Aug 2010. The effects of aging on the strength of surround suppression of receptive field of v1 cells in monkeys. Neuroscience 169 (2), 874–81.

Golomb, J. D., McDavitt, J. R. B., Ruf, B. M., Chen, J. I., Saricicek, A., Maloney, K. H., Hu, J., Chun, M. M., Bhagwagar, Z., Jul 2009. Enhanced visual motion perception in major depressive disorder. J Neurosci 29 (28), 9072–7.

Karas, R., McKendrick, A. M., 2009. Aging alters surround modulation of perceived contrast. J Vis 9 (5), 11.1–9.

Karas, R., McKendrick, A. M., Nov 2011. Increased surround modulation of perceived contrast in the elderly. Optom Vis Sci 88 (11), 1298–308.

Karas, R., McKendrick, A. M., 2012. Age related changes to perceptual surround suppression of moving stimuli. Seeing Perceiving 25 (5), 409–24.

Karas, R., McKendrick, A. M., Mar 2015. Contrast and stimulus duration dependence of perceptual surround suppression in older adults. Vision Res.

Lappin, J. S., Tadin, D., Nyquist, J. B., Corn, A. L., 2009. Spatial and temporal limits of motion perception across variations in speed, eccentricity, and low vision. J Vis 9 (1), 30.1–14.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., Ma, Y., May 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–5.

Loomis, J. M., Nakayama, K., 1973. A velocity analogue of brightness contrast. Perception 2 (4), 425–7.

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., Chertkow, H., Apr 2005. The montreal cognitive assessment, moca: a brief screening tool for mild cognitive impairment. J Am Geriatr Soc 53 (4), 695–9.

Newsome, W. T., Britten, K. H., Movshon, J. A., 1989. Neuronal correlates of a perceptual decision. Nature 341 (6237), 52–54.

Norman, H. P., Norman, J. F., Todd, J. T., Lindsey, D. T., 1996. Spatial interactions in perceived speed. Perception 25 (7), 815–30.

Norman, J. F., Ross, H. E., Hawkes, L. M., Long, J. R., 2003. Aging and the perception of speed. Perception 32 (1), 85–96.

Owsley, C., Sekuler, R., Siemsen, D., 1983. Contrast sensitivity throughout adulthood. Vision Res 23 (7), 689–99.

Pelli, D., Robson, J., Wilkins, A., 1988. The design of a new letter chart for measuring contrast sensitivity. Clinical Vision Sciences 2 (3), 187–&.

Pelli, D. G., 1997. The videotoolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10 (4), 437–42.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
URL http://www.R-project.org/

Raghuram, A., Lakshminarayanan, V., Khanna, R., Oct 2005. Psychophysical estimation of speed discrimination. ii. aging effects. J Opt Soc Am A Opt Image Sci Vis 22 (10), 2269–80.

Roudaia, E., Bennett, P. J., Sekuler, A. B., Pilz, K. S., 2010. Spatiotemporal properties of apparent motion perception and aging. J Vis 10 (14), 5.

Snowden, R. J., Hammett, S. T., Jun 1998. The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. Vision Res 38 (13), 1935–45.

Snowden, R. J., Kavanagh, E., 2006. Motion perception in the ageing visual system: minimum motion, motion coherence, and speed discrimination thresholds. Perception 35 (1), 9–24.

Statistics Canada, Sept 2014. Population projections for Canada, Provinces and Territories, 2013 to 2063.
URL http://www.statcan.gc.ca/pub/91-520-x/2014001/tbl/tbl2.4-eng.htm

Tadin, D., Kim, J., Doop, M. L., Gibson, C., Lappin, J. S., Blake, R., Park, S., Nov 2006. Weakened center-surround interactions in visual motion processing in schizophrenia. J Neurosci 26 (44), 11403–12.

Tadin, D., Lappin, J. S., Gilroy, L. A., Blake, R., Jul 2003. Perceptual consequences of centre-surround antagonism in visual motion processing. Nature 424 (6946), 312–5.

Tadin, D., Silvanto, J., Pascual-Leone, A., Battelli, L., Jan 2011. Improved motion perception and impaired spatial suppression following disruption of cortical area MT/V5. J Neurosci 31 (4), 1279–1283.

Takeuchi, T., De Valois, K. K., 2000. Modulation of perceived contrast by a moving surround. Vision Res 40 (20), 2697–709.

Tran, D. B., Silverman, S. E., Zimmerman, K., Feldon, S. E., Apr 1998. Age-related deterioration of motion perception and detection. Graefes Arch Clin Exp Ophthalmol 236 (4), 269–73.

Tynan, P., Sekuler, R., Nov 1975. Simultaneous motion contrast: velocity, sensitivity and depth response. Vision Res 15 (11), 1231–8.

van der Smagt, M. J., Verstraten, F. A. J., Paffen, C. L. E., Aug 2010. Center-surround effects on perceived speed. Vision Res 50 (18), 1900–4.

Xiao, D. K., Raiguel, S., Marcar, V., Orban, G. A., May 1998. Influence of stimulus speed upon the antagonistic surrounds of area MT/V5 neurons. Neuroreport 9 (7), 1321–6.

Chapter 4

The effect of aging on spatial suppression in a motion step task

4.1 Abstract

Direction discrimination for younger adults becomes more difficult as high-contrast stimuli increase in size and as low-contrast stimuli decrease in size (Tadin et al., 2003). However, although older adults show spatial summation at low contrast, they demonstrate decreased spatial suppression at high contrast (Betts et al., 2005). It has been hypothesized that this behavioural finding occurs as a result of decreased GABAergic inhibition in the aging visual system (Leventhal et al., 2003), but it is unclear whether the finding extends to other tasks. For example, we did not find evidence for reduced spatial suppression in older adults in our spatiotemporal masking experiment (Chapter 2) or in our perceived speed experiment (Chapter 3). In addition, it has been shown that while older adults demonstrate greater spatial suppression in perceived

contrast tasks (Karas and McKendrick, 2009, 2011, 2012, 2015), they show a trend for slightly reduced spatial suppression in a dynamic direction discrimination task (Karas and McKendrick, 2012). Churan et al. (2009) described results from a motion step task consistent with summation at low contrast and suppression at high contrast for younger subjects, providing us with an opportunity to examine the effects of aging in another paradigm using brief motion stimuli. In Experiment 1, we tested 21 younger and 19 older adults in this task. A vertically-oriented 0.5 cpd Gabor stimulus remained static in the center of the screen for 40 ms, and then, after a brief motion step, the phase-shifted Gabor was presented for another 40 ms. A 1-up/2-down staircase manipulated the size of the phase shift (1-89 deg) required to correctly determine the motion direction. There were four blocks, one for each combination of contrast (low and high) and size (3.65 and 14.15 deg). Older subjects, but not younger subjects, exhibited spatial summation in the low contrast condition, and both age groups exhibited spatial suppression in the high contrast condition. In Experiment 2, we tested a different group of 19 younger and 14 older adults. We added a smaller size condition (1.82 deg) and found spatial summation at low contrast and spatial suppression at high contrast in both age groups. We did not find evidence to suggest that the magnitude of spatial suppression differed between younger and older adults.

4.2 Introduction

Betts et al. (2005) used a task described by Tadin et al. (2003) to measure the shortest stimulus duration at which younger and older adults could accurately discriminate the direction of drifting sine wave gratings that varied in size and contrast. When stimulus contrast was low, Betts et al. found that duration thresholds in both age groups decreased as stimulus size increased: in other words, both older and younger observers exhibited spatial summation. At high contrasts, Betts et al. replicated previous reports that duration thresholds in younger adults increased with increasing stimulus size (Golomb

et al., 2009; Lappin et al., 2009; Seitz et al., 2008; Tadin et al., 2006; Tadin and Lappin, 2005; Tadin et al., 2003); however, this so-called spatial suppression effect was significantly reduced in older adults, leading to the surprising result that duration thresholds for large, high-contrast stimuli actually were lower in older observers. Reduced spatial suppression, which also has been found in patients with MDD and SCZ (Golomb et al., 2009; Tadin et al., 2006), may be linked to changes in cortical inhibitory circuits that have been found in the senescent brain (Leventhal et al., 2003) and in clinical populations (Sanacora et al., 1999, 2004; Yoon et al., 2010).

Other studies investigating the effects of spatial suppression in aging have reported inconsistent results. For example, in experiments that measured center-surround effects on the perceived contrast of static and dynamic patterns, Karas and McKendrick (2009, 2011, 2012, 2015) found that spatial suppression was significantly greater in older adults than younger adults. However, in an experiment that used the same direction discrimination task used by Betts et al., Karas and McKendrick found that suppression was slightly less, though not significantly so, in older than younger adults. In addition, we did not find evidence for reduced spatial suppression in our spatiotemporal masking experiments (Chapter 2) or in our experiments that measured center-surround interactions on perceived speed (Chapter 3). These contradicting findings make sense, however, when you consider that surround suppressed cells in the MT/V5 area are more strongly modulated by motion direction stimuli that are presented for very brief durations (<40 ms) (Churan et al., 2008). Churan et al. presented briefly moving Gabor stimuli to surround-suppressed and non-surround-suppressed MT cells in primates. They measured neural responses to these brief stimuli and found that the surround-suppressed cells were more strongly tuned to stimulus motion direction than the non-suppressed cells. This important finding suggests that the behavioural age differences in psychophysical tasks investigating spatial suppression may only be revealed when the stimulus presentation is very brief.

For this reason, we were interested in psychophysical studies looking at

spatial suppression using stimuli that undergo very brief spatial displacements (Tadin et al., 2003; Churan et al., 2009). These experiments used a two-frame stimulus that consisted of two, sequentially-presented static sine wave gratings that differed only in spatial phase. Hence, the "motion" consisted solely of a very brief spatial displacement. Observers were then asked to indicate the direction of the phase shift. In these studies, younger adults showed the classic spatial summation pattern at low contrast, and the spatial suppression pattern at high contrast (Figure 4.1). In other words, performance improved with increasing size for low contrast stimuli (spatial summation), and decreased with increasing size for high contrast stimuli (spatial suppression).

Thus, we set out to determine whether or not older adults would show reduced spatial suppression in a series of brief motion tasks modeled after Churan et al. (2009). In Experiment 1, we presented phase shift discrimination thresholds using two different stimulus sizes and contrasts. In Experiment 2, we added a smaller sized stimulus condition. If the reduced spatial suppression in aging hypothesis holds true for brief motion onsets, then older adults should show less spatial suppression when the stimulus presentation is brief versus in other studies using extended durations.

4.3 Methods

4.3.1 Participants

Twenty-one younger (M = 21.9 years; range: 18 – 29, 12 female) and 19 older (M = 70.6 years; range: 63 – 80, 9 female) adults participated in Experiment 1. A different set of 19 younger (M = 23.2 years; range: 18 – 32, 13 female) and 14 older (M = 70.2 years; range: 64 – 82, 6 female) adults participated in Experiment 2. Since both low and high contrast levels used in the phase step task were normalized for each subject by computing a multiple of each individual's contrast detection threshold from the detection task, subjects

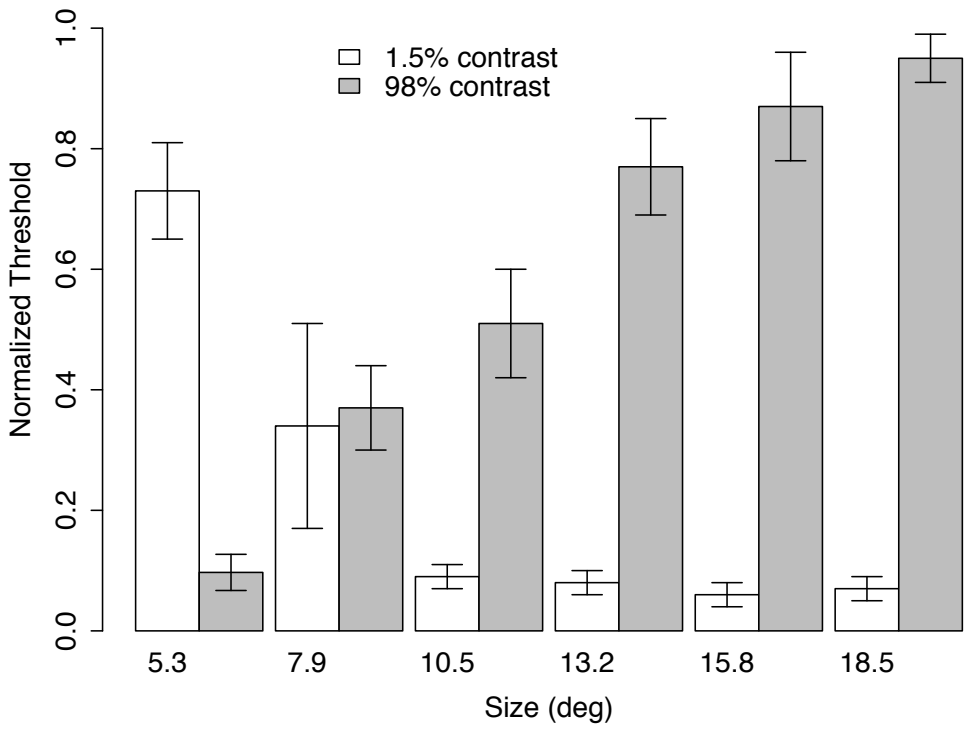


Figure 4.1: Figure replotted from Figure 2B in Churan et al. (2009). Normalized thresholds were calculated to make the trends for each subject independent of their individual performance in motion discrimination. Normalized thresholds (Tnorm = (T - Tmin) / (Tmax - Tmin), where Tmin and Tmax represent the minimal and maximal thresholds obtained from each subject on any condition in Churan et al.'s Experiment 1) were calculated for each of the four subjects. The average of these normalized thresholds are shown in this figure. Low contrast gratings (1.5% contrast) are shown as white bars and high contrast gratings (98% contrast) are shown as gray bars. There were six stimulus size conditions (5.3, 7.9, 10.5, 13.2, 15.8, and 18.5 deg). Performance improved for low-contrast gratings (thresholds decreased) and worsened for high-contrast gratings (thresholds increased) as stimulus size increased. Error bars depict ±1 SEM.

were excluded from the analysis if their high contrast level was greater than 100%. Additionally, subjects were excluded if they failed to obtain thresholds in at least one condition. Most of the poor thresholds were in the large, high-contrast condition in both Experiments 1 and 2, suggesting that this condition was more difficult for observers than the other conditions. Only one failed threshold was in the medium, high contrast condition. Seven younger and seven older subjects were excluded from Experiment 1, and nine younger and two older subjects were excluded from Experiment 2. Near and far visual acuity were measured using the SLOAN Two Sided ETDRS Near Point Test and the 4 Meter 2000 Series Revised ETDRS chart, respectively. The Pelli-Robson Contrast Sensitivity Test (Pelli et al., 1988) was used to measure contrast sensitivity. All subjects had normal or corrected-to-normal vision. The older subjects completed the MMSE (Folstein et al., 1975) as well as the MoCA (Nasreddine et al., 2005) tests to screen for general cognitive ability. Informed consent was obtained from each subject prior to testing. Subjects were compensated at a rate of $10/hour for their time. Participant demographics are summarized in Table 4.1.

4.3.2 Apparatus

All stimuli were generated on a Macintosh G5 computer and displayed on a 21-inch Sony Trinitron CRT monitor (model GDM-F520) with a spatial resolution of 1280 × 1024 pixels (pixel size = 0.014 deg) and a refresh rate of 100 Hz. Participants viewed the stimuli binocularly from a distance of 57 cm, using a chin/forehead rest to stabilize head position. All responses were collected using a standard Macintosh keyboard. The display screen subtended a visual angle of 36.19 × 28.99 deg and was the sole source of light in the testing room (average luminance of 65 cd/m^2). Psychophysics and Video Toolboxes (version 3.0.8) software (Brainard, 1997; Pelli, 1997) were used to program the experiment in the MATLAB (version 7.9) environment.

Table 4.1: Experiment, number of subjects, age, decimal near acuity, decimal far acuity, MMSE and MoCA scores for older subjects. Values in parentheses are standard deviations.

Experiment	Subjects (N)	Age (μ,σ)	Near Acuity (μ,σ)	Far Acuity (μ,σ)	MMSE (μ,σ)	MoCA (μ,σ)
1	21 younger	21.9 (3.4)	1.45 (0.23)	1.36 (0.33)		
	19 older	70.8 (5.1)	0.99 (0.15)	1.07 (0.14)	29.16 (0.77)	27.21 (2.44)
2	19 younger	23.2 (3.4)	1.38 (0.24)	1.39 (0.24)		
	14 older	70.2 (5.4)	1.00 (0.22)	1.03 (0.22)	28.86 (1.10)	26.21 (2.49)

4.3.3 Stimuli and Procedure

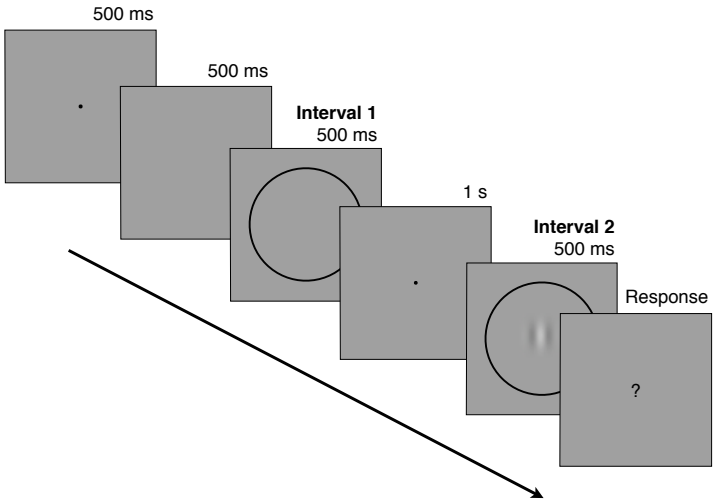
All subjects ran in a contrast detection experiment followed by a perceived direction experiment. The duration of the entire experimental session was about 1 hour, including breaks between blocks.

4.3.4 Detection Task

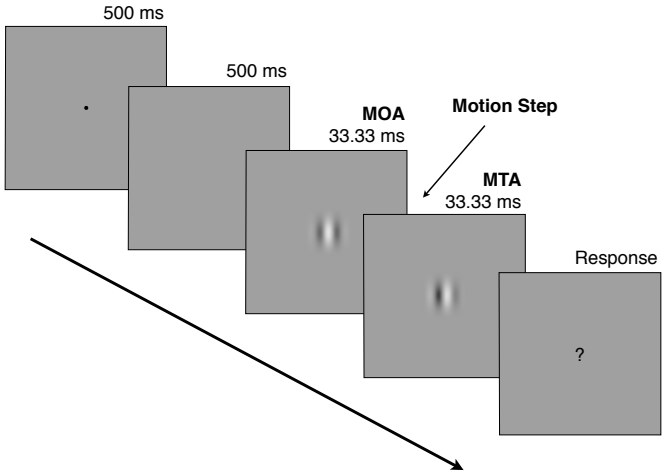
A contrast detection task was conducted prior to the direction discrimination task to ensure that the contrast values set were normalized for each subject. Subjects were instructed to determine which of the two stimulus intervals contained a vertically-oriented 0.5 cpd static Gabor patch that was presented at a duration of 40 ms. In Experiment 1 the size was set to the medium size (3.65 deg) and in Experiment 2 the size was set to the small size (1.82 deg). The time course of one trial is presented in Figure 4.2a. At the start of each trial, a flashing fixation point was presented in the center of the screen for 500 ms. Following a blank screen (500 ms), each interval was presented for 500 ms with an ISI of 1 s in between. During each stimulus interval, circular cues were presented on the screen to indicate the start and finish of each stimulus interval. Detection threshold data was collected using two 1-up/2-down interleaving adaptive staircases. Only negative auditory feedback, in the form of a 600 Hz tone, was provided on incorrect trials. This experiment terminated after the subject completed 50 trials or the staircases reached 15 reversals. This portion of the experiment took approximately 10 minutes to complete.

4.3.5 Phase Step Task

After a short break, the phase step task began. The procedure is shown in Figure 4.2b. Each trial began with a flashing fixation point (500 ms), fol-



(a) Detection Task.



(b) Phase Step Discrimination Task.

Figure 4.2: (a) Example of one trial from the detection experiment. In this example the first interval is blank, followed by an ISI and the second interval containing the stimulus. (b) Example of one trial from the phase step experiment. In this example the first interval contains the medium-sized, high-contrast Gabor, followed by an ISI and the second interval containing the medium-sized, high-contrast Gabor with its phase shifted rightwards.

lowed by a blank screen (500 ms). A vertically-oriented 0.5 cpd Gabor patch was displayed for 33.33 ms (2 frames; frame rate = 60 fps) before and after the horizontal motion step at low or high contrast. In Experiment 1, only the medium (3.65 deg) and large (14.15 deg) sizes were presented; and in Experiment 2 the small (1.82 deg), medium (3.65 deg) and large (14.15 deg) sizes were presented. We defined the period between the appearance of the stimulus and before the motion step as the MOA (motion onset asynchrony), and the period after the motion step up until the stimulus disappeared as the MTA (motion termination asynchrony). Subjects were asked to discriminate the direction of the horizontal motion step (i.e., did the motion appear to be moving leftwards (left key) or rightwards (right key)?). Auditory feedback (600 Hz tone) was given for incorrect trials only.

The low and high contrast levels were normalized for each subject by multiplying each individual's contrast detection threshold by 1.5 for the low contrast conditions, and by 11 and 30 times for the high contrast conditions in Experiments 1 and 2, respectively. Each block consisted of one contrast and one size level. The order of the size/contrast blocks was randomized for each subject.

The direction of the motion step was randomized for every trial. A 1-up/2-down staircase was used to vary the phase step between 1 and 89 deg. The staircase procedure was terminated after the subject reached 60 trials or 15 reversals. This experiment took approximately 50 minutes to complete.

4.4 Results

4.4.1 Analysis

Contrast detection and phase step thresholds were taken as the average of the last 4 staircase reversals. All statistical analyses (t-tests and ANOVAs) were performed using R (R Core Team, 2014).

4.4.2 Experiment 1

The first experiment was conducted to determine how size and contrast affect motion discrimination for very brief stimulus presentations. Detection thresholds for a medium-sized Gabor (3.65 deg), shown in Figure 4.3, were significantly higher in older adults ($M = 2.76\%$, $SEM = 0.15\%$) than younger adults ($M = 2.38\%$, $SEM = 0.14\%$; $t(1, 24) = 1.82$, $p < 0.05$, one-tailed). A t-test on the detection thresholds for all subjects, including the seven younger and seven older subjects excluded in the current experiment, yielded similar results. Individual detection thresholds were multiplied by specific constants to set the low (1.5 times) and high (30 times) contrast levels for the phase step task. Low contrast values ranged between 2.4-4.8% for younger adults and 2.4-5.0% for older adults, and high contrast values ranged between 48-96% for younger adults and 48-99% for older adults.

Figure 4.4 shows the performance of younger and older adults for low contrast (white bars) and high contrast (gray bars) Gabors across the different stimulus sizes. For younger subjects, thresholds increased with stimulus size in both the low- and high-contrast condition, although the effect of size was greater in the high-contrast condition. For older subjects, thresholds decreased with increasing size in the low-contrast condition, but increased with size in the high-contrast condition. These trends were evaluated with a 2 (age) $\times$ 2 (contrast) $\times$ 2 (size) ANOVA on phase step thresholds, which treated age as a between-subjects factor and contrast and size as within-subjects factors. The analysis revealed significant main effects of size ($F(1, 24) = 42.79$, $p < 0.001$) and contrast ($F(1, 24) = 80.57$, $p < 0.001$). There was no main effect of age ($F(1, 24) = 0.24$, $p = 0.63$). The age $\times$ size interaction was significant ($F(1, 24) = 6.86$, $p < 0.05$). An analysis of the simple main effects revealed a significant difference between the medium and large sizes in younger ($t(1, 27) = 4.96$, $p < 0.001$) and a nearly significant difference between those sizes in older ($t(1, 23) = 1.89$, $p = 0.07$) adults. Additionally, the size $\times$ contrast ($F(1, 24) = 52.85$, $p < 0.001$) interaction was significant, with a significant

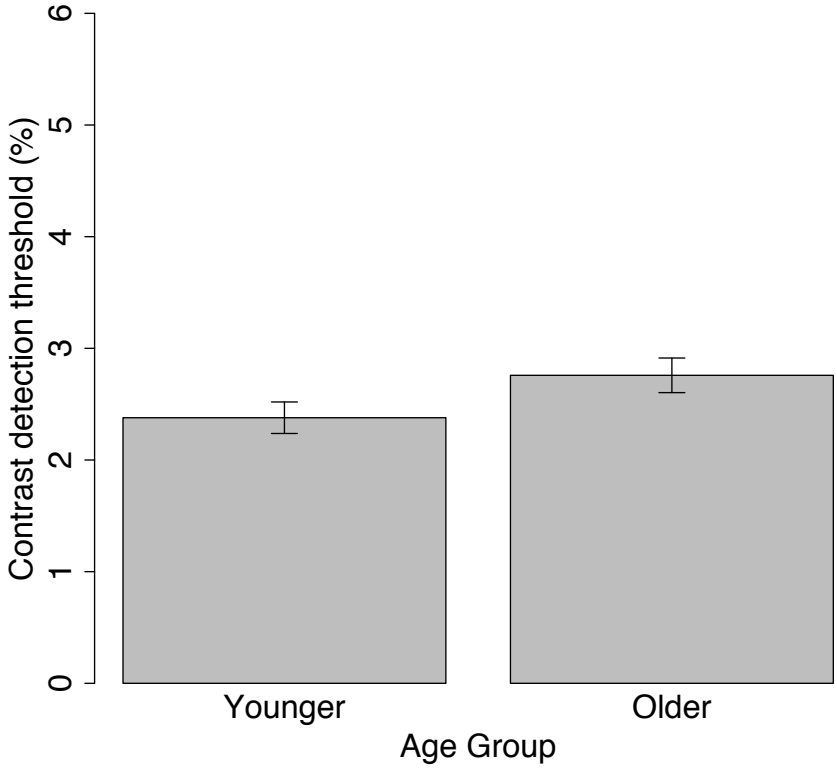


Figure 4.3: Mean detection thresholds for 14 younger and 12 older subjects in Experiment 1 for a medium-sized (3.65 deg) Gabor patch. Error bars represent ±1 SEM.

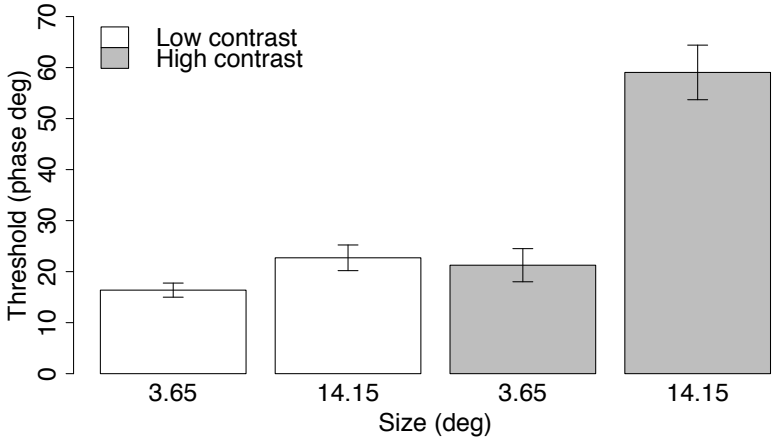
difference between medium and large sizes at high contrast ($t(1, 25) = 7.51$, $p < 0.001$) but not at low contrast ($t(1, 25) = 0.12$, $p = 0.91$). The age $\times$ size $\times$ contrast interaction did not reach significance ($F(1, 24) = 0.10$, p = 0.76). Our analyses using the data from all subjects, including the excluded younger and older adults, revealed similar results.

To investigate the effect of age on spatial suppression, we analyzed the high contrast thresholds in a 2 (age) $\times$ 2 (size) ANOVA. Although we found a main effect of size ($F(1, 24) = 58.24$, $p < 0.001$), there was no main effect of age ($F(1, 24) = 0.02$, $p = 0.9$) or an age $\times$ size interaction ($F(1, 24) = 1.81$, $p = 0.19$).

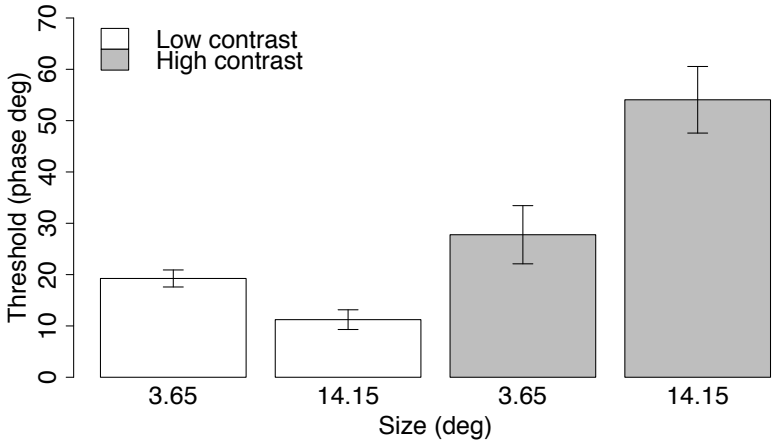
Our analyses suggest that both age groups exhibited spatial suppression at high contrast, but that only older subjects exhibited spatial summation at low contrast. The latter result is consistent with the findings of Betts et al. (2005), who reported that spatial summation in their direction discrimination task was greater in older than younger adults. However, unlike Betts et al., we did not find that spatial suppression was reduced in older subjects. One potentially important difference between Betts et al. and the current experiment is that the previous study measured suppression with a larger range of stimulus sizes. To examine whether age differences in spatial suppression in the current task depend significantly on the range of stimulus size, we conducted a second experiment that added a smaller stimulus.

4.4.3 Experiment 2

For Experiment 2, we added a third stimulus size (1.82 deg). Detection thresholds were higher in older ($M = 4.92\%$, $SEM = 0.37\%$) than younger ($M = 4.28\%$, $SEM = 0.48\%$) subjects (Figure 4.5), though the difference was not statistically significant ($t(1, 20) = 1.07$, $p = 0.15$, one-tailed). A *t*-test on data from all subjects, including the nine younger and two older excluded subjects, revealed similar detection threshold results. In the phase-



(a) Younger subjects.



(b) Older subjects.

Figure 4.4: Results from the phase shift task in Experiment 1. Mean performance of 14 younger subjects and 12 older subjects for low contrast (white bars) and high contrast (gray bars) Gabor stimuli at different stimulus sizes. Error bars represent ±1 SEM.

step discrimination task, low and high contrast levels were set to 1.5 and 11 times the detection threshold, respectively. Low contrast values ranged between 4.4-11.6% for younger adults and 4.5-9.9% for older adults. High contrast values ranged between 31.9-84.7% for younger adults and 33.0-72.6% for older adults.

The results from the phase shift discrimination task are shown in Figure 4.6. Discrimination thresholds in younger adults exhibited spatial summation at low contrast and spatial suppression at high contrast, in agreement with Churan et al. (2009). At low contrast, thresholds were highest for the medium-sized stimulus and lowest at the largest size in younger adults, creating an inverted-U-shaped function (Figure 4.6a). Discrimination thresholds for older adults also exhibited spatial summation at low contrast and spatial suppression at high contrast (Figure 4.6b).

We conducted a 2 (age) $\times$ 2 (contrast) $\times$ 3 (size) split-plot ANOVA on the phase step thresholds. There was a significant main effect of size ($F(2, 40) = 25.46$, $p < 0.001$) and contrast ($F(1, 20) = 13.25$, $p < 0.001$). The main effect of age was not significant ($F(1, 20) = 0.02$, $p = 0.90$). The two-way interaction between size and contrast was significant ($F(2, 40) = 17.70$, $p < 0.001$), the age $\times$ size interaction nearly reached significance ($F(2, 40) = 3.06$, $p = 0.06$), and the age $\times$ size $\times$ contrast interaction was not significant ($F(2, 40) = 0.16$, $p = 0.85$). An analysis including data from excluded subjects yielded similar results.

The size $\times$ contrast interaction was analyzed by combining the two age groups and comparing the low- and high-contrast conditions at each size with separate t-tests. The difference was significant in the small ($t(1, 21) = 4.50$, $p < 0.001$) and large ($t(1, 21) = 5.62$, $p < 0.001$) condition, but not the medium size condition ($t(1, 21) = 1.11$, $p = 0.28$).

Given the relatively low power of our experiment we thought it was appropriate to analyze the age $\times$ size interaction using one-way ANOVAs to compare the three size conditions within each age group. In younger adults,

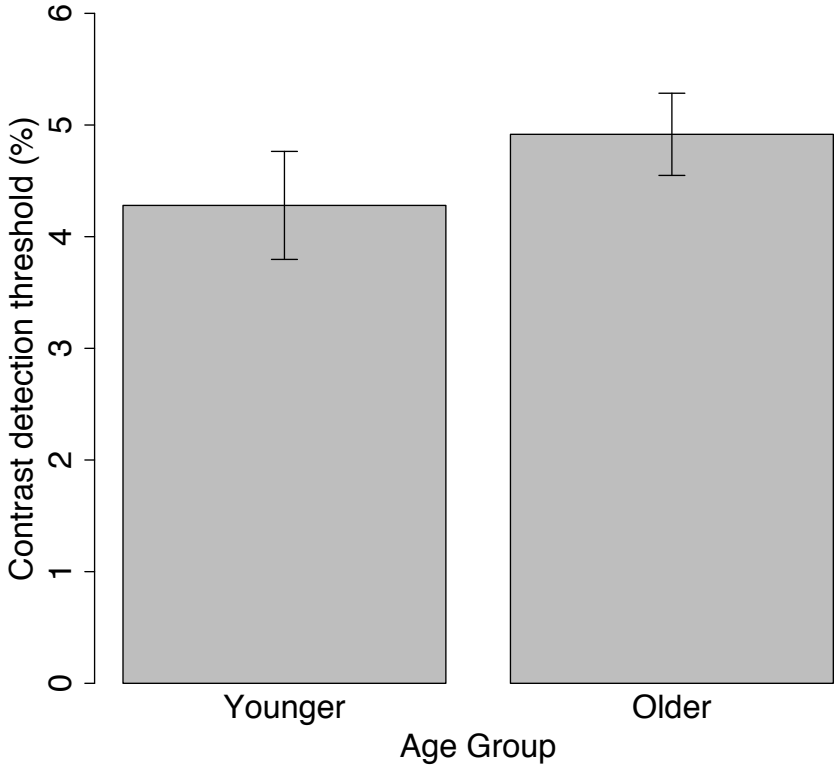


Figure 4.5: Mean detection thresholds for 10 younger and 12 older subjects in Experiment 2 for a small-sized (1.82 deg) Gabor patch. Error bars represent ±1 SEM.

the effect of size was significant ($F(2, 18) = 28.76$, $p < 0.001$), and follow-up tests revealed that thresholds differed between the small and large condition ($t(1, 19) = 4.64$, $p < 0.001$) and medium and large conditions ($t(1, 19) = 4.39$, $p < 0.001$). In older subjects, the effect of size was significant ($F(2, 22) = 5.47$, $p < 0.05$). Thresholds differed between the small and large condition ($t(1, 23) = 2.15$, $p < 0.05$) and medium and large conditions ($t(1, 23) = 2.12$, $p < 0.05$).

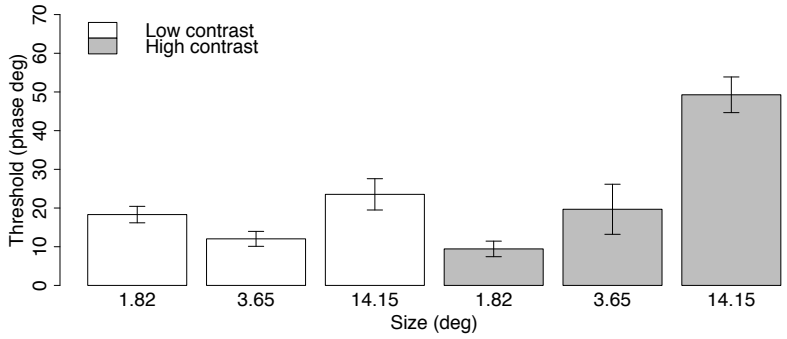
To investigate the age differences in spatial suppression at high contrast, we analyzed the high contrast threshold results in a 2 (age) $\times$ 3 (size) ANOVA. There was a significant main effect of size ($F(2, 40) = 32.80$, $p < 0.001$), but no main effect of age ($F(1, 20) = 0.01$, $p = 0.94$). The age $\times$ size interaction did not reach significance ($F(2, 40) = 1.13$, $p = 0.33$).

We also analyzed the low contrast threshold results in a 2 (age) $\times$ 3 (size) ANOVA. We did not find a significant effect of age ($F(1, 40) = 0.11$, $p = 0.75$) or size ($F(2, 40) = 1.35$, $p = 0.27$), and the age $\times$ size interaction did not reach significance ($F(2, 40) = 2.05$, $p = 0.14$).

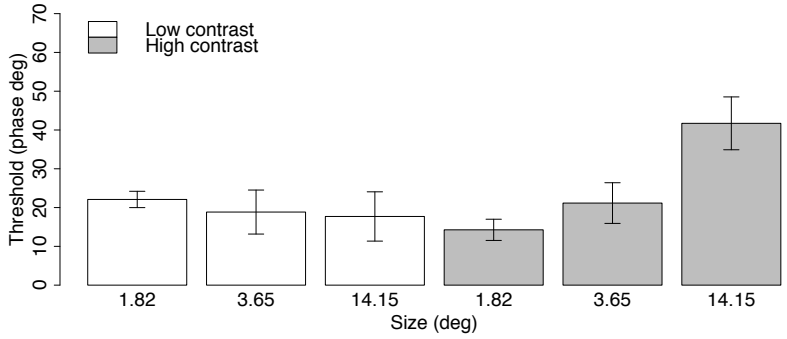
4.5 General Discussion

In this experiment, we studied the effects of age on spatial summation and suppression using a phase-step direction discrimination task. We found that younger adults showed the classic pattern of spatial summation at low contrast and spatial suppression at high contrast found in previous studies (Tadin et al., 2003; Betts et al., 2005; Golomb et al., 2009; Tadin et al., 2006; van der Smagt et al., 2010).

Thresholds measured in older adults also exhibited spatial summation at low contrast and spatial suppression at high contrast. At low contrast, our analyses did not indicate that spatial summation was different between the age groups. However, younger adults showed higher thresholds in the medium than both the small and large-sized conditions, while older adults showed a decrease



(a) Younger subjects.



(b) Older subjects.

Figure 4.6: Results from the phase shift task in Experiment 2. Mean performance of 10 younger subjects and 12 older subjects for low contrast (white bars) and high contrast (gray bars) Gabor stimuli at different stimulus sizes. Error bars represent ±1 SEM.

in threshold between the small and medium-sized conditions. This finding indicates that older adults may show slightly greater summation than younger adults, consistent with Betts et al. (2005)'s finding of increased summation in seniors.

At high contrast, we did not find significant evidence to suggest that the effect of spatial suppression was different between the two age groups. However, the difference between thresholds in the small and large-sized conditions was smaller in older than younger adults, suggesting that there might be less spatial suppression in older adults. This trend is also consistent with Betts et al.'s finding that spatial suppression decreases in aging. However, in Betts et al.'s study the suppressive effect in older adults was very small, whereas in our study the strength of suppression was still strong in seniors. Perhaps this inconsistency between our results and those of Betts et al. was due to the slight differences in the ways in which the stimuli were presented.

Tadin et al. (2003) and Betts et al. (2005) each conducted a direction discrimination experiment. In these experiments, a stimulus moved continuously on the screen in one direction until the subject pressed a button to indicate the direction of movement (i.e., leftwards or rightwards). Our direction discrimination experiments presented in Chapter 3 were also continuous, as a stimulus drifted continuously on the display for 500 ms. In Tadin et al. (2003)'s paper, in addition to presenting findings from their direction discrimination experiment using continuous stimuli, these authors also described their phase shift experiment. In both Tadin et al., Churan et al. (2009), and the experiments presented in the current chapter (Chapter 4), the stimulus motion comprised of a single brief phase step. In all of these experiments, the size and contrast of the stimuli were varied to measure spatial summation and suppression. Therefore, the major differences between these continuous and brief direction discrimination tasks were due to temporal rather than spatial factors.

The effects of spatial summation and suppression have been explained by both the sudden onset of a stimulus (stimulus transient) and by the onset

of stimulus motion (motion transient). Typically, the stimulus transient and motion transient have been considered identical because many spatial summation and suppression tasks present a continuously drifting grating (i.e., the stimulus and motion onsets occur simultaneously). However, in our experiments presented in the current chapter (Chapter 4), as well as the brief phase step experiments presented by Tadin et al. and Churan et al., the stimulus transient and motion transient were separate events.

When a static stimulus appears abruptly, it induces a transient response in V1 neurons that declines quickly (<100 ms) (Müller et al., 2001; Maunsell et al., 1990). Similarly, an abrupt moving stimulus prompts a transient response in MT/V5 surround suppressed neurons (Churan et al., 2008). This brief stimulus onset transient acts as a forward mask and interferes with the ability to detect the subsequent motion direction. Masking is a well known phenomenon in which the presence of of one stimulus (mask) reduces the sensitivity to another stimulus (target) (Breitmeyer and Öğmen, 2006). In Saarela and Herzog (2008) and Chapter 2, masking effects were shown to be strongest when a central (small mask that overlays the target) or combination (central-plus-surround annulus) mask appeared immediately before (forward masking) and after (backward masking) the target. When Churan et al. (2009) extended the duration of the MOA and MTA, subsequently separating the stimulus onset and offsets from the motion step, they found that the effect of contrast and size disappeared. They attributed this attenuation to the disappearance of forward and backward masking effects.

In the continuous (Tadin et al., 2003; Betts et al., 2005) and brief (Tadin et al., 2003; Churan et al., 2009) experiments, younger subjects demonstrated spatial summation at low contrast and spatial suppression at high contrast. In the experiments we presented in Chapter 3 using continuously moving stimuli, our younger subjects did not demonstrate any spatial suppression at low contrast, but did show spatial suppression at high contrast. Results from younger subjects in the current chapter (Chapter 4) using a brief phase step showed some evidence for spatial summation at low contrast and strong spatial sup-

pression at high contrast. Additionally, healthy younger adults have demonstrated spatial summation at low contrast and spatial suppression at high contrast in other behavioural studies varying the size and contrast of stimuli (Tadin et al., 2006; Golomb et al., 2009; van der Smagt et al., 2010; Karas and McKendrick, 2012). Taken together, younger adults tend to demonstrate spatial summation at low contrast and spatial suppression at high contrast when the stimuli are presented either continuously (Tadin et al., 2003; Betts et al., 2005; Tadin et al., 2006; Golomb et al., 2009; van der Smagt et al., 2010; Karas and McKendrick, 2012) or briefly (Tadin et al., 2003; Churan et al., 2009). Therefore, younger adults are sensitive to the spatial (size and contrast) and temporal (stimulus transient) effects of the stimulus.

In continuous motion and brief motion experiments looking at aging and spatial suppression, older adults have shown different behavioural effects. In Betts et al. (2005), the stimulus duration was less than 100 ms and older adults showed less spatial suppression than younger adults. Although our results from the current chapter (Chapter 4) along with Karas and McKendrick (2012)'s results did not show significant age effects using direction discrimination tasks with brief durations, these results did show a trend towards older adults demonstrating less spatial suppression than younger adults. In contrast, in spatial suppression studies with stimuli being presented for longer durations, increased spatial suppression has been observed in older adults. For example, in Chapter 3, both age groups showed similar spatial suppression at a slow speed, and when the speed increased, both age groups continued to show spatial suppression. Although we did not find significant age differences in spatial suppression at the higher speed, the results indicated that there might be a trend for greater suppression in older adults. In addition, Karas and McKendrick (2009, 2011, 2012, 2015) have found that older adults demonstrate greater spatial suppression than younger adults in perceived contrast tasks where the stimuli are displayed for 500 ms. Therefore, there appears to be less spatial suppression in older adults when the stimulus is presented for brief durations and greater spatial suppression in older adults when the stimulus is

presented for longer durations.

At brief stimulus durations, older adults might be less sensitive to the stimulus transient. Therefore, there might be a smaller cortical transient response when the stimulus appears on the screen for a brief duration in older adults, which explains why they showed a trend for less suppression than younger adults. Another possible explanation for less spatial suppression in aging at brief durations is that spatial suppression has been found to disappear at very low speeds (Lappin et al., 2009), although this is not what was found in the perceived speed experiments reported in van der Smagt et al. (2010) or Chapter 3. Perhaps older adults require faster speeds to show greater spatial suppression in experiments with brief stimuli because in our phase step experiment (Chapter 4), the motion occurred in a single step so it appeared faster than in the continuous experiment where the same motion occurred over a longer duration (Chapter 3).

References

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., Feb 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–6.

Brainard, D. H., 1997. The psychophysics toolbox. Spat Vis 10 (4), 433–6.

Breitmeyer, B. G., Öğmen, H., 2006. Visual masking: time slices through conscious and unconscious vision, 2nd Edition. Vol. no. 41. Oxford University Press, Oxford.
URL http://www.loc.gov/catdir/toc/ecip063/2005031831.html

Churan, J., Khawaja, F. A., Tsui, J. M. G., Pack, C. C., Nov 2008. Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT. Curr Biol 18 (22), R1051–2.

Churan, J., Richard, A. G., Pack, C. C., 2009. Interaction of spatial and temporal factors in psychophysical estimates of surround suppression. J Vis 9 (4), 15.1–15.

Folstein, M. F., Folstein, S. E., McHugh, P. R., Nov 1975. Mini-mental state. a practical method for grading the cognitive state of patients for the clinician. J Psychiatr Res 12 (3), 189–98.

Golomb, J. D., McDavitt, J. R. B., Ruf, B. M., Chen, J. I., Saricicek, A., Maloney, K. H., Hu, J., Chun, M. M., Bhagwagar, Z., Jul 2009. Enhanced visual motion perception in major depressive disorder. J Neurosci 29 (28), 9072–7.

Karas, R., McKendrick, A. M., 2009. Aging alters surround modulation of perceived contrast. J Vis 9 (5), 11.1–9.

Karas, R., McKendrick, A. M., Nov 2011. Increased surround modulation of perceived contrast in the elderly. Optom Vis Sci 88 (11), 1298–308.

Karas, R., McKendrick, A. M., 2012. Age related changes to perceptual surround suppression of moving stimuli. Seeing Perceiving 25 (5), 409–24.

Karas, R., McKendrick, A. M., Mar 2015. Contrast and stimulus duration dependence of perceptual surround suppression in older adults. Vision Res.

Lappin, J. S., Tadin, D., Nyquist, J. B., Corn, A. L., 2009. Spatial and temporal limits of motion perception across variations in speed, eccentricity, and low vision. J Vis 9 (1), 30.1–14.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., Ma, Y., May 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–5.

Maunsell, J. H., Nealey, T. A., DePriest, D. D., Oct 1990. Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. J Neurosci 10 (10), 3323–34.

Müller, J. R., Metha, A. B., Krauskopf, J., Lennie, P., Sep 2001. Information conveyed by onset transients in responses of striate cortical neurons. J Neurosci 21 (17), 6978–90.

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., Chertkow, H., Apr 2005. The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. J Am Geriatr Soc 53 (4), 695–9.

Pelli, D., Robson, J., Wilkins, A., 1988. The design of a new letter chart for measuring contrast sensitivity. Clinical Vision Sciences 2 (3), 187–&.

Pelli, D. G., 1997. The videotoolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10 (4), 437–42.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
URL http://www.R-project.org/

Saarela, T. P., Herzog, M. H., 2008. Time-course and surround modulation of contrast masking in human vision. J Vis 8 (3), 23.1–10.

Sanacora, G., Gueorguieva, R., Epperson, C. N., Wu, Y.-T., Appel, M., Rothman, D. L., Krystal, J. H., Mason, G. F., Jul 2004. Subtype-specific alterations of gamma-aminobutyric acid and glutamate in patients with major depression. Arch Gen Psychiatry 61 (7), 705–13.

Sanacora, G., Mason, G. F., Rothman, D. L., Behar, K. L., Hyder, F., Petroff, O. A., Berman, R. M., Charney, D. S., Krystal, J. H., Nov 1999. Reduced cortical gamma-aminobutyric acid levels in depressed patients determined by proton magnetic resonance spectroscopy. Arch Gen Psychiatry 56 (11), 1043–7.

Seitz, A. R., Pilly, P. K., Pack, C. C., Oct 2008. Interactions between contrast and spatial displacement in visual motion processing. Curr Biol 18 (19), R904–6.

Tadin, D., Kim, J., Doop, M. L., Gibson, C., Lappin, J. S., Blake, R., Park, S., Nov 2006. Weakened center-surround interactions in visual motion processing in schizophrenia. J Neurosci 26 (44), 11403–12.

Tadin, D., Lappin, J. S., Jul 2005. Optimal size for perceiving motion decreases with contrast. Vision Res 45 (16), 2059–64.

Tadin, D., Lappin, J. S., Gilroy, L. A., Blake, R., Jul 2003. Perceptual consequences of centre-surround antagonism in visual motion processing. Nature 424 (6946), 312–5.

van der Smagt, M. J., Verstraten, F. A. J., Paffen, C. L. E., Aug 2010. Center-surround effects on perceived speed. Vision Res 50 (18), 1900–4.

Yoon, J. H., Maddock, R. J., Rokem, A., Silver, M. A., Minzenberg, M. J., Ragland, J. D., Carter, C. S., Mar 2010. GABA concentration is reduced in visual cortex in schizophrenia and correlates with orientation-specific surround suppression. J Neurosci 30 (10), 3777–81.

Chapter 5

General Discussion

5.1 Literature Review

The goal of the current research program was to investigate spatial suppression mechanisms in the healthy aging brain. The hypothesis that spatial suppression is reduced in the senescent brain comes from previous literature on behavioural and physiological changes in aging as well as spatial suppression mechanisms. Betts et al. (2005) found that older adults required less time to discriminate the direction of a large, high-contrast moving stimulus than younger adults. In their task, subjects were asked to indicate the direction of a drifting grating that varied in size and contrast. The size manipulation was included in order to tap into surround inhibitory mechanisms. Older adults were less influenced by the surround portion of the larger stimulus than their younger counterparts. Betts et al. concluded that spatial suppression decreases in aging. In a later study, Betts et al. (2009) extended their original findings and conducted the direction discrimination study using various spatial frequency (0.5 to 4 cpd) and speed (2 to 8 dps) conditions. Across these conditions, Betts et al. found that older adults consistently showed reduced spatial suppression. Betts et al. explained their findings as behavioural evi-

dence for reduced cortical inhibitory function (GABA) in the aging brain. The results presented in all of the experimental chapters (Chapters 2, 3, and 4) are inconsistent with the hypothesis that there is a *general* deterioration of spatial suppression mechanisms in senescence.

There has been evidence supporting the idea that GABA concentration is reduced in aging. For example, Leventhal et al. (2003) measured individual V1 cell responses in both older and younger primates before and after GABA was administered electrophoretically. Prior to GABA administration, older V1 cells generally responded equally well to all orientations and directions of a stimulus. However, after GABA administration, a greater percentage of the older V1 cells responded more strongly to specific stimulus orientations. Since the younger primate cells were strongly tuned without the administration of GABA, Leventhal et al. concluded that GABA levels deteriorate in V1 with age and this deterioration is directly linked to orientation tuning. Pinto et al. (2010, 2015) also provided evidence supporting the idea that GABA may decrease in the aging human brain. They found that the expression of the GABAergic markers, GAD65 (Pinto et al., 2010) and Gephyrin (Pinto et al., 2010, 2015), were significantly reduced in older adults compared to younger adults. Lower levels of these GABAergic markers may indicate that there are lower levels of GABA in aging.

Additionally, Petroff et al. (1996) measured occipital GABA levels in epileptic seizure patients and found that their levels were lower than the healthy control group. A separate study found that older adults ($>$ 60 years) were more likely to experience a seizure than younger adults (Tallis et al., 1991). Therefore, since older adults experience seizures more than younger adults, and people who experience seizures have lower levels of GABA, these findings provide indirect evidence suggesting that GABA levels may decrease in aging. A different set of studies also provided evidence to suggest that GABA levels may decrease in the aging brain. Sandberg et al. (2014) found that occipital GABA levels decreased as scores measuring cognitive failures increased, suggesting that there is a correlation between low GABA levels and a greater

incidence of cognitive failures as measured by an established CFQ (Broadbent et al., 1982). Furthermore, the prevalence of cognitive impairment (including mild cognitive impairment (MCI)) has been shown to increase with age (Graham et al., 1997). Since GABA decreases in adults who experience greater cognitive failures, and the prevalence of cognitive failures increases with age, there might be lower levels of GABA in older adults. These studies all provide indirect evidence that GABA may be reduced in the aging human brain and lower levels of GABA have been shown to be correlated with reduced educed efficacy of spatial suppression.

There is some neurophysiological evidence to support the relationship between reduced GABA and reduced surround suppression in aging. Fu et al. (2010) found that V1 cells in older monkeys showed reduced suppression indices compared to the V1 cells of younger monkeys when presented with central and central-plus-surround stimuli. Therefore, taken together with the results from Leventhal et al. (2003), these studies suggest that reduced GABA levels in older primates may contribute to reduced surround suppression.

Other studies have shown a relationship between reduced behavioural spatial suppression and low GABA levels in different special populations. For example, Golomb et al. (2009) found that patients with MDD demonstrated less spatial suppression in the direction discrimination task originally described in Tadin et al. (2003). Sanacora et al. (1999, 2004) found that patients with depression had lower levels of occipital GABA. Similarly, Tadin et al. (2006) found that patients with SCZ had reduced spatial suppression in the direction discrimination task and Yoon et al. (2010) found that SCZ patients had lower levels of occipital GABA. These studies suggest that there is a relationship between the reduced efficacy of GABA-mediated inhibitory mechanisms and decreased behavioural spatial suppression.

Taken together, these studies suggest that if older adults show generalized reduced spatial suppression, they likely have reduced GABA levels. However, reduced spatial suppression has not been found in all studies investigating be-

havioural spatial suppression in older adults. For example, Karas and McKendrick conducted a series of behavioural spatial suppression experiments in older adults and did not find reduced spatial suppression in aging. In their first study, Karas and McKendrick (2009) conducted a perceived contrast task using *static* stimuli. In this task, they measured PSE, determining the contrast of the test stimulus where the reference stimulus appeared the same for each subject. Stimuli appeared on the display for 500 ms. They hypothesized that older adults would show reduced spatial suppression, based on Betts et al. (2005)'s findings. However, they found that both age groups showed spatial suppression at high contrast, and the magnitude was greater in older adults. They suggested that a decrease in perceptual brightness induction in aging might explain their results.

Karas and McKendrick (2011) ran another perceived contrast task, but presented *static* sine wave gratings. They asked observers to indicate which of the 500 ms intervals contained the higher contrast stimulus. They manipulated the size and contrast of the stimuli. Their results were similar to what they had found previously; older adults demonstrated greater spatial suppression than younger adults.

Karas and McKendrick (2012) conducted two different spatial suppression experiments in younger and older adults: a contrast discrimination experiment and a direction discrimination experiment. In both experiments, the sine wave stimuli were *dynamic*. In the contrast discrimination study, stimuli were presented on the display for 500 ms. Karas and McKendrick found that older adults demonstrated greater spatial suppression than younger adults, much like what they found in Karas and McKendrick (2009) and Karas and McKendrick (2011), except this time the stimuli were drifting. In their direction discrimination study, they only presented stimuli at high contrast and asked subjects to indicate the direction of the drifting stimulus, similar to the high contrast condition in Tadin et al. (2003) and Betts et al. (2005). They measured duration thresholds and found that both age groups' thresholds were longer when the stimulus size was larger than smaller, indicative of

spatial suppression. However, the net effect of spatial suppression was slightly reduced in older adults, although the difference was not statistically significant. Therefore, Karas and McKendrick (2012)'s results showed a trend for less suppression in aging, like Betts et al..

In their latest paper, Karas and McKendrick (2015) conducted a contrast discrimination study using *static* stimuli and varied the contrast of the center and surround portions of the stimuli. They conducted the same experiment using both 500 and 100 ms stimulus durations. They found that when the surround was higher in contrast than the center, both age groups showed spatial suppression with older adults showing a greater effect at both stimulus durations. The effect of spatial suppression increased for both age groups at the shorter stimulus duration. Overall, these authors have found that older adults consistently demonstrate greater spatial suppression in perceived contrast tasks where the stimuli are static or dynamic and appear on the display for 500 ms (Karas and McKendrick, 2009, 2011, 2012, 2015). When stimulus durations are much more brief, Karas and McKendrick (2012) have shown a trend for reduced spatial suppression in aging, like Betts et al. (2005).

5.2 Summary of Findings

The results presented in this dissertation do not support the hypothesis that spatial suppression deteriorates in older adults. In Experiment 1 of Chapter 2, we investigated spatiotemporal masking effects by presenting static Gabor stimuli in a masking paradigm using Saarela and Herzog (2008)'s task. In our study, subjects were instructed to detect which interval contained the central target stimulus in a 2-IFC task. We presented a mask stimulus in each stimulus interval. There were three different types of mask stimuli: a central mask (which covered the visible spatial extent of the target), a surround mask (which covered the large spatial extent of the screen) and a combination mask (i.e., the central and surround masks combined together). In addition, we ma-

nipulated the presentation timing of the mask. The mask was presented either before the target (backward masking), after the target (forward masking), or the mask and target presentation overlapped in time (embedded masking). We found that older and younger observers showed similar masking strength patterns. Both age groups demonstrated greater masking at the backward and forward masking time points than at the embedded masking time point. In addition, masking was strongest for the central mask followed by the combination mask, and there was minimal masking for the surround mask. We found that older observers had higher thresholds than younger observers overall. To control for age differences, we calculated masking ratios by dividing masked thresholds by no-mask thresholds and found a main effect of age with older adults showing lower masking ratios than younger adults. However, the masking ratio did not take into account individual mask thresholds in the absence of the target. To determine if there was an age difference in both mask detection thresholds and target detection thresholds, we measured detection thresholds for each mask type and the target in both younger and older adults (Experiment 2). We found only a main effect of age with older adults having higher thresholds overall. Therefore, we concluded that the ability to detect the target and mask did not explain the main effect of age found in our masking ratio results from Experiment 1. Finally, we measured target detection thresholds as a function of mask contrast to determine if the age-related differences found for mask ratios were simply due to age-related differences in effective contrast (Experiment 3). We found that normalized masking thresholds increased at a similar rate for both age groups once contrast differences in aging were normalized for the embedded masking conditions only. This finding indicated that effective contrast explained the main effect of age for mask ratios found between the age groups at the embedded masking time point. However, masking was stronger for older adults in the backward and forward masking conditions indicating that effective contrast could not explain the main effect of age found at these time points.

Because Betts et al. (2005) found the age-related spatial suppression effect

with moving rather than static stimuli, Chapter 3 explored whether we would see a reduction in spatial suppression for older relative to younger observers in a different motion task. The motion task we chose was one that focused on the speed of motion, rather than the direction and was based on the perceived speed task used in van der Smagt et al. (2010). The drifting stimuli were displayed for 500 ms. We found that older adults showed a similar pattern as younger adults at low and high contrast in Experiment 1. Both age groups showed no effect between the small and large sized stimuli at low contrast. At high contrast, both age groups demonstrated spatial suppression. When the speed increased in Experiment 2 at low contrast, older adults showed suppression while younger adults showed no effect as stimulus size increased. At high contrast, both age groups demonstrated similar levels of spatial suppression. These results demonstrate that an age-related decrease in spatial suppression does not appear to be a general property in motion perception.

In Betts et al. (2005)'s study the stimuli were displayed on the screen for brief periods of time (40-100 ms), but in our experiments in Chapter 3, the drifting stimuli were displayed for 500 ms. Churan et al. (2008) reported that surround suppressed cells in area MT/V5 of primates were more strongly modulated by motion direction stimuli presented for very brief durations (<40 ms). Churan et al. had found that surround suppressed cells showed stronger tuning to motion direction than non-suppressed cells. These results imply that we might only find behavioural age differences in tasks investigating suppression if the stimuli are displayed for very brief durations. Given this idea, in Chapter 4, we conducted a series of spatial suppression experiments using static stimuli to induce brief motion. These experiments were based on Experiment 1 from Churan et al. (2009). In these experiments, a static stimulus was presented briefly (33 ms), followed by a briefly presented second static stimulus (33 ms) with a different phase. Subjects were then asked to indicate the direction of the motion step. We found that both age groups demonstrated spatial suppression at high contrast. Although there was no age difference in the magnitude of spatial suppression found at high contrast, there was a trend showing less

spatial suppression in older adults. It is important to note that while we found a trend for reduced spatial suppression in older adults in our phase step study with brief stimuli, older adults still showed strong spatial suppression, while in Betts et al. (2005) the effect of suppression was very minimal in older adults.

5.3 Future Directions

Based on the findings from the current dissertation, it would be useful to further explore the behavioural effects of spatial suppression in the aging brain as well as the neural basis for suppression to determine where and under what circumstances the changes occur. This section describes ideas for future experiments.

Currently, evidence supporting a strong relationship between decreased visual cortical GABA and reduced spatial suppression in older adults are indirect. We know that there is indirect evidence supporting the idea that there is a lower concentration of GABA in area V1 of older humans (Leventhal et al., 2003; Pinto et al., 2010) and that reduced GABA is correlated with both reduced behavioural spatial suppression (Golomb et al., 2009; Sanacora et al., 1999, 2004; Tadin et al., 2006; Yoon et al., 2010) and suppression indices of V1 cells (Fu et al., 2010). We also know that, based on the results presented in this dissertation as well as other studies investigating the effects of spatial suppression in aging, that older adults tend to show reduced spatial suppression in tasks with brief stimuli. Given these findings, it would be ideal to measure both visual cortical GABA levels as well as behavioural spatial suppression with both brief and longer duration stimuli in the same group of younger and older subjects. Then it would be possible to determine whether or not GABA levels are correlated with brief behavioural spatial suppression.

It would also be important to measure GABA concentrations in visual areas V1 and MT/V5 separately because studies have shown that spatial suppres-

sion effects between these areas are different. For example, Tadin et al. (2011) had found that applying TMS on area MT/V5 prior to Tadin et al. (2003)'s direction discrimination experiment disrupted behavioural spatial suppression in younger, but not older adults. When TMS was applied to V1, performance did not vary in either age group from the no TMS condition. Based on these results, Tadin et al. concluded that there is a direct relationship between area MT/V5 and surround suppression. In addition, Churan et al. (2008) found that surround suppressed neurons in MT/V5 of primates responded more strongly to brief stimuli, supporting the link between area MT/V5, spatial suppression, and briefly presented stimuli. Based on these results, we predict that GABA levels will be reduced in both visual areas MT/V5 and V1 older adults and that the link between MT/V5 and behavioural spatial suppression will be stronger than the link between V1 and behavioural spatial suppression. We also predict that older adults will show reduced spatial suppression in tasks targeting spatial suppression using brief stimulus durations.

One way of measuring GABA levels directly in humans is to localize specific areas in the visual cortex and then acquire GABA data using the MEGA-PRESS (MEscher-GArwood Point REsolved SpectroScopy) pulse sequence in MRS. This is the method that was used to correlate GABA levels with spatial suppression in other special populations (Sanacora et al., 1999, 2004; Yoon et al., 2010).

To test our hypothesis, it would be ideal to run a variety of behavioural spatial suppression tasks on the same group of subjects. For example, the direction discrimination task (Tadin et al., 2003; Betts et al., 2005), the speed discrimination task (van der Smagt et al. (2010), Chapter 3), and the phase step task (Churan et al. (2009), Chapter 4). Since we found that older adults demonstrated a trend for reduced spatial suppression in a task with briefly presented stimuli (Chapter 4), it would be interesting to conduct older and younger observers in more tasks with very brief stimulus durations. For example, in our spatiotemporal masking studies presented in Chapter 2, the target and mask were always presented for 40 and 100 ms, respectively. Perhaps if

the stimulus duration were shorter, we would find more evidence for reduced spatial suppression in older adults (i.e., their central and combination masking thresholds would be very similar). In addition, in Chapter 3, our stimuli were drifting on the display for 500 ms and we did not find evidence for reduced spatial suppression in aging. It would be interesting to conduct this experiment at a shorter stimulus duration. Finally, if we were to vary the stimulus duration of both the MOA and the MTA of the phase step task we utilized in Chapter 4, we expect that both age groups would show greater spatial suppression with decreasing stimulus duration, but that perhaps the functions would look different. More specifically, we would expect that younger adults' thresholds would vary more with stimulus duration, while for older adults, the slope would be more shallow. As the stimulus durations increase above 100 ms, we expect that thresholds for both younger and older adults would be more similar because the stimulus duration would no longer be considered brief. Overall, we expect that when the stimulus duration is very brief, older adults will show reduced spatial suppression.

Although it is important to quantify actual GABA concentration in the aging visual cortex and correlate it with behavioural performance in a variety of spatial suppression tasks, it is also necessary to determine the direct link between spatial suppression and cortical inhibition in the aging human brain. We can do this by administering GABA agonists and antagonists in the form of a pill to human subjects. These drugs increase and decrease, respectively, action at the GABA receptor. When these drugs are administered directly to V1 neurons, they alter the tuning properties of V1 cells. For example, Leventhal et al. (2003) administered a GABA antagonist to V1 cells in younger monkeys and found that the magnitude of orientation selectivity decreased. They also showed that a GABA agonist sharpened V1 orientation tuning for older primates. This evidence suggests that GABA levels affect V1 tuning properties in animal models. However, we do not know if increasing GABA concentration via drug administration can tune visual cortical neurons in older adults and alter spatial suppressive mechanisms. Therefore, direction

discrimination thresholds can be measured after a GABA agonist drug is administered to older participants and a GABA antagonist drug is administered to younger participants. The optimal choice for a drug would be one with as few side effects as possible and that targets the correct visual cortical area. If the GABA antagonist reduces the efficacy of inhibitory mechanisms, and GABA levels are related to psychophysical spatial suppression, then we would expect the performance of younger observers to match that of the older observers: i.e., their duration thresholds for a large, high-contrast stimulus would improve. Alternatively, we predict that a GABAergic agonist would enhance behavioural spatial suppression in older observers. Once this causal connection is made in the aging population, it may be possible to develop treatments for natural declines in visual processing that occur with aging.

References

Betts, L. R., Sekuler, A. B., Bennett, P. J., 2009. Spatial characteristics of center-surround antagonism in younger and older adults. J Vis 9 (1), 25.1–15.

Betts, L. R., Taylor, C. P., Sekuler, A. B., Bennett, P. J., Feb 2005. Aging reduces center-surround antagonism in visual motion processing. Neuron 45 (3), 361–6.

Broadbent, D. E., Cooper, P. F., FitzGerald, P., Parkes, K. R., Feb 1982. The Cognitive Failures Questionnaire (CFQ) and its correlates. Br J Clin Psychol 21 (Pt 1), 1–16.

Churan, J., Khawaja, F. A., Tsui, J. M. G., Pack, C. C., Nov 2008. Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT. Curr Biol 18 (22), R1051–2.

Churan, J., Richard, A. G., Pack, C. C., 2009. Interaction of spatial and

temporal factors in psychophysical estimates of surround suppression. J Vis 9 (4), 15.1–15.

Fu, Y., Wang, X. S., Wang, Y. C., Zhang, J., Liang, Z., Zhou, Y. F., Ma, Y. Y., Aug 2010. The effects of aging on the strength of surround suppression of receptive field of v1 cells in monkeys. Neuroscience 169 (2), 874–81.

Golomb, J. D., McDavitt, J. R. B., Ruf, B. M., Chen, J. I., Saricicek, A., Maloney, K. H., Hu, J., Chun, M. M., Bhagwagar, Z., Jul 2009. Enhanced visual motion perception in major depressive disorder. J Neurosci 29 (28), 9072–7.

Graham, J. E., Rockwood, K., Beattie, B. L., Eastwood, R., Gauthier, S., Tuokko, H., McDowell, I., Jun 1997. Prevalence and severity of cognitive impairment with and without dementia in an elderly population. Lancet 349 (9068), 1793–6.

Karas, R., McKendrick, A. M., 2009. Aging alters surround modulation of perceived contrast. J Vis 9 (5), 11.1–9.

Karas, R., McKendrick, A. M., Nov 2011. Increased surround modulation of perceived contrast in the elderly. Optom Vis Sci 88 (11), 1298–308.

Karas, R., McKendrick, A. M., 2012. Age related changes to perceptual surround suppression of moving stimuli. Seeing Perceiving 25 (5), 409–24.

Karas, R., McKendrick, A. M., Mar 2015. Contrast and stimulus duration dependence of perceptual surround suppression in older adults. Vision Res.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., Ma, Y., May 2003. GABA and its agonists improved visual cortical function in senescent monkeys. Science 300 (5620), 812–5.

Petroff, O. A., Rothman, D. L., Behar, K. L., Mattson, R. H., Dec 1996. Low brain GABA level is associated with poor seizure control. Ann Neurol 40 (6), 908–11.

Pinto, J. G. A., Hornby, K. R., Jones, D. G., Murphy, K. M., 2010. Developmental changes in GABAergic mechanisms in human visual cortex across the lifespan. Front Cell Neurosci 4, 16.

Pinto, J. G. A., Jones, D. G., Williams, C. K., Murphy, K. M., 2015. Characterizing synaptic protein development in human visual cortex enables alignment of synaptic age with rat visual cortex. Front Neural Circuits 9, 3.

Saarela, T. P., Herzog, M. H., 2008. Time-course and surround modulation of contrast masking in human vision. J Vis 8 (3), 23.1–10.

Sanacora, G., Gueorguieva, R., Epperson, C. N., Wu, Y.-T., Appel, M., Rothman, D. L., Krystal, J. H., Mason, G. F., Jul 2004. Subtype-specific alterations of gamma-aminobutyric acid and glutamate in patients with major depression. Arch Gen Psychiatry 61 (7), 705–13.

Sanacora, G., Mason, G. F., Rothman, D. L., Behar, K. L., Hyder, F., Petroff, O. A., Berman, R. M., Charney, D. S., Krystal, J. H., Nov 1999. Reduced cortical gamma-aminobutyric acid levels in depressed patients determined by proton magnetic resonance spectroscopy. Arch Gen Psychiatry 56 (11), 1043–7.

Sandberg, K., Blicher, J. U., Dong, M. Y., Rees, G., Near, J., Kanai, R., Feb 2014. Occipital GABA correlates with cognitive failures in daily life. Neuroimage 87, 55–60.

Tadin, D., Kim, J., Doop, M. L., Gibson, C., Lappin, J. S., Blake, R., Park, S., Nov 2006. Weakened center-surround interactions in visual motion processing in schizophrenia. J Neurosci 26 (44), 11403–12.

Tadin, D., Lappin, J. S., Gilroy, L. A., Blake, R., Jul 2003. Perceptual consequences of centre-surround antagonism in visual motion processing. Nature 424 (6946), 312–5.

Tadin, D., Silvanto, J., Pascual-Leone, A., Battelli, L., Jan 2011. Improved motion perception and impaired spatial suppression following disruption of cortical area MT/V5. J Neurosci 31 (4), 1279–1283.

Tallis, R., Hall, G., Craig, I., Dean, A., Nov 1991. How common are epileptic seizures in old age? Age Ageing 20 (6), 442–8.

van der Smagt, M. J., Verstraten, F. A. J., Paffen, C. L. E., Aug 2010. Center-surround effects on perceived speed. Vision Res 50 (18), 1900–4.

Yoon, J. H., Maddock, R. J., Rokem, A., Silver, M. A., Minzenberg, M. J., Ragland, J. D., Carter, C. S., Mar 2010. GABA concentration is reduced in visual cortex in schizophrenia and correlates with orientation-specific surround suppression. J Neurosci 30 (10), 3777–81.