The Effect of Task Demand on Spatial Suppression and Summation in Motion and Orientation Discrimination: A Comparison of Young and Older Adults

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Yaffa Kizel

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5/9/2025
Date

DocuSigned by:
Chris Taylor
8C96C99C286D4CA...
Christopher P. Taylor, PhD
Graduate Faculty Advisor

DocuSigned by:
Sangeetha Metlapally
EF5BE7B05D3D4CA...
Sangeetha Metlapally, PhD
Thesis Committee Member

DocuSigned by:
Peter Bex
3E92398B601647F...
Peter J. Bex, PhD
Thesis Committee Member

Signed by:
Patrick Bennett
37379D195101406...
Patrick J. Bennett, PhD
Thesis Committee Member

5/9/2025
Date

DocuSigned by:
78A8AD972399447...
Thanasis Panorgias, MSc, PhD
Director of Graduate Studies

Abstract

THE EFFECT OF TASK DEMAND ON SPATIAL SUPPRESSION AND SUMMATION IN MOTION AND ORIENTATION DISCRIMINATION: A COMPARISON OF YOUNG AND OLDER ADULTS

Yaffa Kizel

New England College of Optometry, 2025

Purpose: Aging affects visual perception and performance in basic psychophysical tasks, including motion and orientation perception (Betts et al., 2005; Pilz et al., 2020). Previous research revealed a surprising result: older observers performed better than younger observers in a motion direction task when the stimuli were large and high contrast (Betts et al., 2005). However, recent work has complicated the simple story proposed 20 years ago (Schallmo et al., 2018). We aimed to explore the role of task demand on surround suppression and summation effects for motion and orientation discrimination in young and older adults to to help further elucidate underlying mechanisms for these age-related effects.

Methods: Duration thresholds were measured for discriminating motion (left/right) and orientation (±2° tilt from vertical) in 14 young (19-27 yrs) and 7 older (65-89 yrs) observers using Gabor stimuli (1 cpd) of varying in size ($2\sigma = 0.7°$ or 5°) and contrast (2% or 22.5%). The types of tasks were: 1) single-dimension stimuli and single responses (motion or orientation only); 2) dual-dimension stimuli (motion and orientation present) with certain single responses (respond to only motion or orientation); 3) dual-dimension stimuli with uncertain single responses (respond randomly to either motion or orientation); 4) dual-dimension stimuli with uncertain dual responses (respond to both motion and orientation, order randomized).

Results: Due to the limited recruitment of older participants (n=7), the aging comparisons presented are preliminary. Trends suggest reduced spatial suppression for high contrast motion stimuli with Older adults, consistent with prior work. The orientation discrimination task showed summation with larger and higher contrast stimuli for both age groups. When introducing response uncertainty and response order uncertainty, Young observers go from showing suppression with large, high contrast stimuli to summation, and Older observers show a very similar pattern to Young observers of summation for low and high contrast stimuli as it becomes larger. For Young observers, a task-dependent modulation occurred for motion stimuli: spatial suppression, characterized by threshold increases with size for high contrast stimuli, was observed under the Motion discrimination tasks with certain and uncertain responses. However, this pattern shifted to spatial summation (threshold decreases with size) for all other tasks.

Discussion: Task demands modulate spatial processing (suppression vs. summation) for motion perception in Young adults, even when using identical stimuli (i.e., the stimuli remain the same). Stimulus-driven interpretations of the original effect first noted by Tadin et al. (2003), whereby motion direction discrimination is more difficult with larger and higher contrast stimuli, have been proposed, but some of the data in this thesis question whether they are sufficient to characterize how the duration threshold changes with size and contrast for Motion and Orientation.

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Table of Contents

List of Figures

List of Tables

1. Introduction

1.1 The aging population and aging research

The proportion of senior adults is steadily increasing in the United States and many other countries due to rising life expectancy and low birth rates. Projections show that the population aged 60 years or older will likely double from 12% in 2015 to approximately 22% by 2050 (World Health Organization, 2023). Shifting demographics are a public health concern because age-related visual impairments and diseases are becoming more prevalent and increasingly affect the quality of life and independence of older adults (Owsley, 2011). Therefore, understanding the precise mechanisms underlying age-related changes in the visual system is critical for providing timely and evidence-based care.

The National Institute on Aging (NIA) does not recognize aging as a disease, but rather as a risk factor for many diseases. Most age-related research is funded by agencies other than the NIA (e.g., the National Heart, Lung, and Blood Institute, the National Cancer Institute), despite substantial age-associated risks that arise solely from the aging process. If the concern is not disease and treatment, what role does the basic research address when considering healthy aging?

Studying the healthy aging visual system in the absence of disease is a branch of visual development work. Researchers can acquire knowledge through experiments that explore how the visual system changes as a function of age, individual differences, and at a societal level. For an individual studied longitudinally, research into healthy aging can evaluate the lifestyle habits that super-agers (individuals whose health spans extend into their 80s and beyond with few signs of cognitive decline) use to achieve an exceptional health span or lifespan (Powell et al., 2023; Porto et al., 2016). On a broader societal level, characterizing visual performance in representative cross-sectional samples of healthy-aged observers could help develop guidance for the healthy senior population as a whole and improve quality of life longer into the lifespan by correlating lifestyle choices with subjective quality of life metrics, such as questionnaires. Identifying how these visual declines affect daily activities, such as mobility, driving, reading, and social interaction, can lead to better-informed policies and targeted resources to enhance the quality of life and autonomy of older adults.

1.2 Optical and physiological age-related changes in the visual system

A non-exhaustive list of age-related changes in visual performance includes decreased sensitivity and efficiency across various perceptual tasks, such as motion detection, orientation discrimination, contrast sensitivity, and spatial integration (Owsley, 2011; Andersen, 2012). Older observers experience optical changes to their visual system, such as lenticular sclerosis (loss of accommodative ability), loss of lens transparency due to cataract progression, and senile pupillary miosis. Calculations show that the retina of an individual aged 60 years receives approximately one-third as much light as that of individuals aged 20 years, with about two-thirds of the information loss due to pupillary meiosis and about one-third due to the increased opacity of the lens (Scialfa & Kline, 2007).

However, optical changes do not wholly explain age-related deficits in visual performance. If optical factors, such as reduced retinal illuminance from cataracts or pupillary miosis were the sole source of age-related deficits in visual performance, uniform declines in visual perception would occur regardless of the characteristics of visual stimulation and task demands. Age-related declines are notably stimulus-specific; they vary with stimulus size, contrast, orientation, and speed of motion, underscoring their neural rather than optical origin (Andersen et al., 2012). Additionally, research that controls for luminance differences between older and younger observers still demonstrates decreased performance among older adults, particularly in tasks involving motion direction discrimination and orientation detection (Betts et al., 2005, 2007; Bennett et al., 2007; Pilz et al., 2020).

Moreover, the observed declines in visual performance with aging cannot be attributed solely to general cognitive slowing or broad sensory deterioration. Structural brain imaging studies have revealed differential age-related effects across various brain regions. For example, while decreases in white matter volume occur predominantly in the prefrontal cortex, the area of the brain responsible for decision-making, attention, reasoning, and complex learning, similar structural declines are not typically observed in the visual cortex, the primary center of the brain responsible for processing visual information (Raz et al., 2004; Salat et al., 2005; Scialfa & Kline, 2007).

Raz et al. (2004) observed significant age-related reductions in prefrontal cortical volume and integrity of white matter tracts with magnetic resonance imaging (MRI), implicating regions involved in executive functioning and attentional control. However, visual cortex regions remained largely unaffected structurally by aging. Work by Salat et al. (2005) using diffusion tensor imaging (DTI) also demonstrated minimal changes in white matter integrity within temporal and posterior white matter, including the occipital areas, compared to significant deterioration in frontal regions of the brain. Although structural neuronal density and morphology changes within the visual cortex itself are minimal or inconclusive (Andersen et al., 2012; Spear, 1993), there is evidence that suggests functional changes at the neuronal level (Betts et al., 2005, 2007; Leventhal et al., 2003). Proposed mechanisms include alterations in synaptic organization, neurochemical composition, diminished intracortical inhibition, and demyelination in the visual pathway (Scialfa & Kline, 2007), which I will discuss further in subsequent sections of this thesis.

1.3 Aging and Spatial Vision

Spatial vision refers to the visual system's ability to detect, recognize, and interpret spatial relationships among visual stimuli, including position, shape, size, and orientation. Researchers and clinicians can assess spatial vision performance behaviorally via several different measures. For example, visual acuity is a standard and easy method that measures the smallest detail in a letter or optotype that can be resolved, usually involving a high-contrast target. The best achievable acuity for a human observer is 0.5 minutes of arc, but under normal conditions, it is about 1 minute of arc, corresponding to 20/20 acuity (Scialfa & Kline, 2007). Optometrists can often correct older adults to 20/20 acuity until their 60s, after which declining optical quality and decreasing photoreceptor density contribute to decreases in acuity (Scialfa & Kline, 2007).

Beyond acuity, measuring a contrast sensitivity function (CSF) provides a more comprehensive and predictive measure of visual performance. That being said, CSFs are typically measured by researchers in laboratory settings due to time constraints; however, see Hou et al. (2021) for an alternative perspective. A contrast sensitivity function is produced by measuring an observer's sensitivity to small differences in luminance for a range of spatial frequencies, from coarse to fine. The maximum contrast sensitivity for human observers is between three and five cycles per degree in photopic conditions. The high-frequency cutoff, which corresponds to visual acuity, is about 60 cycles per degree (Scialfa & Kline, 2007).

Older adults show systematic declines in contrast sensitivity, which are more noticeable for intermediate and high spatial frequencies. Low luminance conditions exacerbate these deficits, resulting in age-related deficits at low spatial frequencies as well. Classic studies on how contrast sensitivity changes with age show negligible changes up to 4 cycles per degree. Larger changes, increasing decade-by-decade from age 50 to 80, were observed when the target spatial frequencies exceeded 12 cycles/degree (Tulunay-Keesey et al., 1988; Elliott et al., 1990). The consensus is that age-related changes in high spatial frequency sensitivity are explained by optical factors, such as those mentioned above, and do not reflect changes in neural factors within the visual system (Tulunay-Keesey et al., 1988).

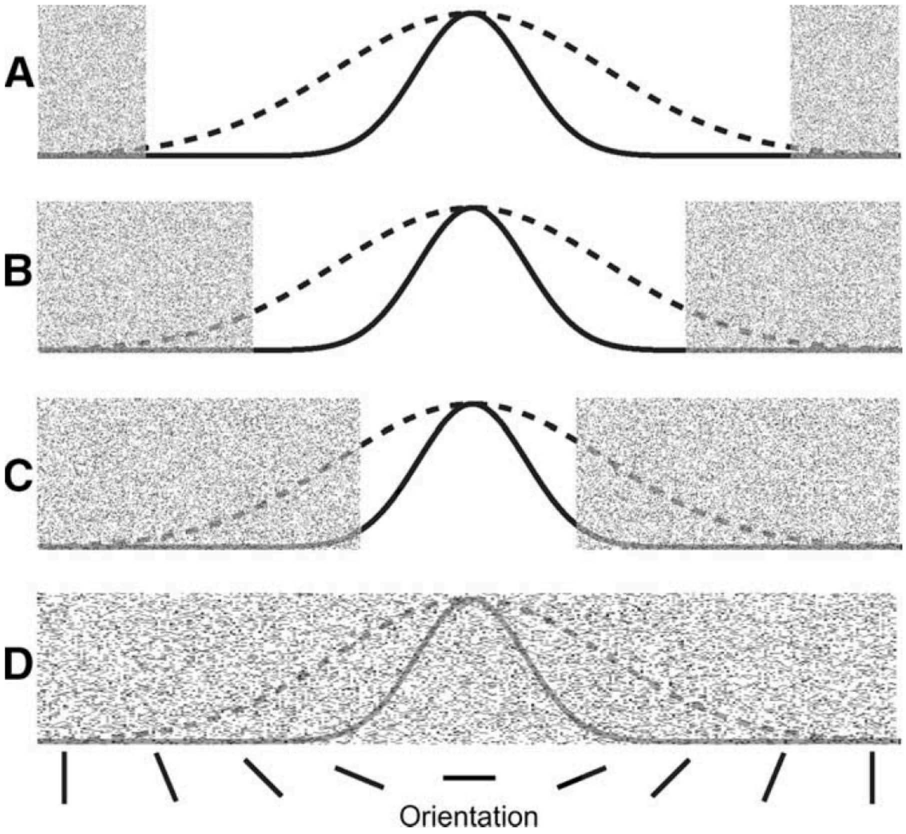

Figure 1: Illustration of the notched-noise masking paradigm adapted from the study by Govenlock et al. (2009). Each panel's solid and dashed lines demonstrate hypothetical orientation tuning functions of varying bandwidth. The orientation content of external noise is illustrated by the shaded regions. (A) Illustrates the orientation spectrum of noise that has been filtered with a wide notch filter centered on the horizontal orientation, which becomes progressively narrower in (B) and (C), and is zero in (D). Noise falling within the pass band of the orientation filters will increase response variability and lower the signal-to-noise ratio.

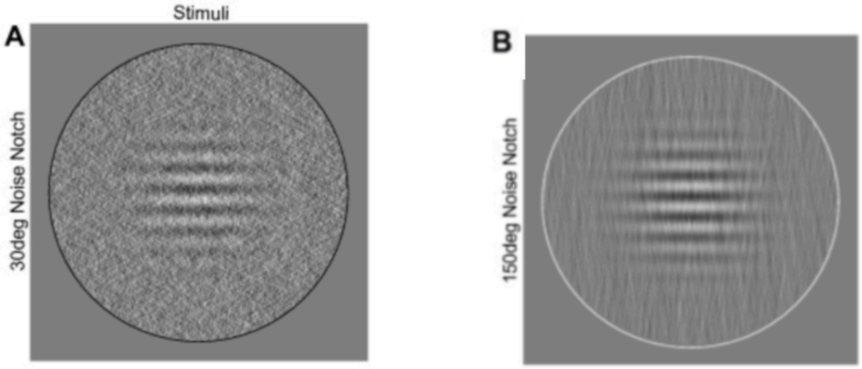

Figure 2: Notch-filtered noise stimuli adapted from the study by Govenlock et al. (2009). (A) demonstrates a stimulus constructed with a notch bandwidth of 30 degrees, while (B) demonstrates that of 150 degrees.

More recent research on spatial vision using advanced psychophysical techniques, such as notched-noise masking, have been used to assess the performance of young and old observers on a variety of visual tasks, such as the tuning of luminance and color in both the fovea and periphery, flicker detection and discrimination, and motion in random dot kinematograms (Beaudot & Mullen, 2005; Mullen & Losada, 1999; Smithson et al., 2009).

The two most relevant notched-noise masking studies relevant to this thesis are those by Govenlock et al. (2009; 2010). In two experiments, spatial frequency and orientation tuning was measured with a notched-filtered noise masking technique in both young and older observers. Notch-filtered noise-masking experiments utilize signal processing to selectively filter out a specific range of spatial frequencies or orientations from a broadband white noise masking.

When observers perform a detection task, the width of the notch filter is varied to find the minimum notch size that does not impair detection performance, known as the critical notch width. The critical notch width, a measure of channel bandwidth, is calculated by computing the half-width at half-height of a channel for a given contrast threshold elevation for a detection task. In two experiments that measured the critical notch width, Govenlock et al. (2009; 2010) found that critical notch width did not differ between younger and older participants for either spatial frequency or orientation. Thus, at the behavioral level, it was proposed that the tuning of spatial frequency and orientation channels is preserved in older observers.

Moreover, position acuity, measured with two-component sinusoidal gratings, is preserved with aging, even to levels of hyperacuity. This means that the limits of optics and cone density are exceeded due to neuronal pooling of photoreceptor information at higher levels of the visual system (Lakshminarayanan et al., 1995; Whitaker et al., 1992), although there are contrasting results found by Li et al. (2000), whereby vernier acuity increased with age. Hyperacuity tasks are telling because they can differentiate sensorineural changes from those due to optics in the eye (Scialfa & Kline, 2007). Finally, position discrimination mechanisms may also be preserved. The early spatial filters that discriminate relative spatial phase in two-component sinusoidal gratings were preserved in aged observers (Bennett et al., 2006).

While there is significant support for what is preserved in the aged spatial vision system, deficits become apparent when a visual task for older observers is made modestly more complex. Older observers’ performance is impaired relative to young observers on spatial vision tasks such as discriminating obliquely oriented stimuli, integrating contour information, figure-ground segmentation, and face identification (Casco et al., 2011; Pilz et al., 2020; Peven et al., 2019; Roudaia et al., 2008; McKendrick et al., 2013).

Of the work cited in the previous paragraph, a study by Pilz et al. (2020) contains a key finding that motivates the work presented here in this thesis. Pilz et al. (2020) compared the performance of older and younger observers on an orientation discrimination task with obliquely oriented Gabors. They performed two tasks to investigate whether old and young observers differed in their ability to discriminate (Experiment 1) or match (Experiment 2) the orientation of Gabor stimuli that were oriented across the entire range of orientation: horizontal (0 degrees), right-tilted oblique (45 degrees) vertical, and left-tilted (135 degrees).

In the first experiment of Pilz et al. (2020), observers did a two-interval forced-choice discrimination task. This involved the presentation of a low spatial-frequency Gabor presented for 300 ms, followed by a 100 ms noise mask and a 300 ms inter-stimulus interval, and then a second Gabor for 300 ms that differed in orientation. Randomly, in half the trials, the orientation of the second Gabor was presented at the same orientation or a different one, and observers were required to indicate which one matched the orientation of the previously presented stimulus.

In a second experiment, both younger and older observers performed a matching task where a Gabor was presented for 300 ms with a 100 ms noise mask, and then they adjusted a line to match the perceived orientation. In both experiments, orientation discrimination was worse at oblique orientations versus the cardinal axes (vertical and horizontal). Difficulty in discriminating oblique orientations is known as the oblique effect (Appelle, 1972). The oblique effect is well-known in the vision science literature, but the orientation-specific declines in orientation discrimination with aging were a novel contribution to the literature. The decline at oblique orientations is unlike other background results presented in this thesis (e.g., Govenlock, 2010), because older observers show deficits in their ability to discriminate orientation, however, *only* with oblique orientations.

1.4 Aging and temporal vision

Temporal vision is most commonly assessed using critical flicker frequency (CFF), the highest frequency at which a flickering light is perceived as steady, continuous light. The CFF is a measure of the temporal resolution of the visual system (Scialfa & Kline, 2007). Research has shown that the CFF tends to decline starting at around age 60 (Kaur et al., 2020; Del Romo et al., 2005). Decreases in CFF with age can lead to reductions in processing speed, and can largely be attributed to decreased retinal illumination resulting from reduced optical clarity and senile pupillary meiosis (Scialfa & Kline, 2007).

Deficits in motion perception with aging are seen in many other domains. Speed perception and time-to-collision (TTC) are often underestimated, which can have significant implications for vehicle accidents (Norman et al., 2003; Scialfa & Kline, 2007). Additionally, optic flow, which plays a crucial role in navigation and self-motion perception, becomes less reliable with age, potentially contributing to balance deficits and navigation difficulties (Warren et al., 2018). Biological motion perception, which allows humans to recognize movement patterns in living beings, also deteriorates in older individuals (Pilz et al., 2010).

A more comprehensive assessment of the visual system's temporal sensitivity involves the temporal contrast sensitivity function (tCSF), which is an extension of the contrast sensitivity function (CSF) and describes how well the visual system can detect luminance (contrast) changes at different temporal frequencies. The tCSF varies the depth of luminance change (contrast) of a small (2 to 5º) target sinusoidally around a mean luminance level over a range of frequencies (how fast a stimulus flickers) (Scialfa & Kline, 2007). With aging, temporal contrast sensitivity declines, particularly at higher temporal frequencies.. A leftward shift is also apparent towards lower frequencies, which indicates a decline in the speed of visual functioning (Scialfa & Kline, 2007). However, when controlling for retinal illumination, most of this age difference is eliminated, although there is likely still some contribution from reduced sensitivity of temporal visual channels and efficiency within the visual pathway (Scialfa & Kline, 2007).

In general, the detection and discrimination of motion tends to decline with older adults, particularly at near-threshold conditions. Differences between young and older visual systems are particularly evident when size and contrast are manipulated within motion direction discrimination tasks. Two phenomena critical to this thesis are outlined below: when young observers discriminate between leftward and rightward motion, low-contrast sine-wave gratings become easier to perceive as their size increases, reducing the time required to accurately determine direction—a phenomenon referred to as spatial summation (Tadin et al., 2003). Conversely, a larger stimulus size with high-contrast sinusoidal gratings results in longer discrimination times, indicating impaired performance as the stimulus grows larger (Tadin et al., 2003). This counterintuitive effect, termed spatial suppression, may arise due to inhibitory center-surround interactions mediated by inhibitory interneurons in the visual pathway (Angelucci & Bullier, 2003; Tadin, 2015). Inhibitory interneurons exhibit facilitative responses when low-contrast stimuli fall within their receptive fields, through a process known as summation. However, they produce inhibitory responses when high-contrast stimuli extend beyond their receptive fields, a phenomenon referred to as suppression (Liu et al., 2016: Sceniak et al., 1999).

Betts et al. (2005) found that older observers exhibited superior performance relative to younger observers when discriminating large, high-contrast motion stimuli—a counterintuitive finding given the robust evidence suggesting age-related declines across numerous visual functions (Owsley, 2011). Proposed physiological studies suggest that aging may selectively diminish inhibitory interactions that underlie spatial suppression due to reduced effectiveness, impaired signaling, or a decrease in the density of inhibitory interneurons (Karas & McKendrick, 2009; Yazdan et al., 2015). Thus, the reduced efficacy of spatial suppression mechanisms seen in older individuals makes them appear to perform "better" than younger individuals in the highly specific case of large, high-contrast motion stimuli. However, these age-related alterations in inhibitory spatial suppression mechanisms are largely detrimental as spatial suppression contributes to efficient visual perception by reducing neural noise and enhancing target salience within complex visual environments (Tadin, 2015). Furthermore, a reduction in spatial suppression could lead older adults to become more easily distracted by irrelevant stimuli, contributing to difficulties in tasks that require selective attention or the rapid processing of dynamic visual information (Andersen, 2012; Karas & McKendrick, 2009).

1.5 Visual cognition and suppression/inhibition

By design, researchers investigating age-related changes in suppression using visual psychophysics have minimized the influence of higher-level factors, such as visual working memory, attention, and response uncertainty. Thus, while they have explored the limits of vision, they have done so by ignoring the fact that similar performance can be achieved by different, and perhaps suboptimal, mechanisms that are useful in daily life but not in the lab (Tadin & Blake, 2005). The section below will briefly describe evidence for declines in aging involving more demanding tasks than those used in basic spatial or temporal vision.

1.6 Effects of aging on visual cognition tasks

Older adults generally exhibit reduced performance compared to the young in visual cognition tasks, particularly when selective or divided attention is required (Grady, 2012). Older observers experience greater difficulty filtering irrelevant stimuli, as demonstrated by increased susceptibility to interference in tasks such as the well-known Stroop and Flanker paradigms (West & Alain, 2000; Zhu et al., 2010). The Stroop task measures inhibitory control by requiring participants to name the ink color of a word while suppressing word reading. Older adults typically show greater interference effects than younger adults (Spieler et al., 1996). Similarly, the Flanker task, which involves identifying a central target among distracting flankers, reveals heightened distractibility and slower responses among older adults compared to younger participants (Maylor & Lavie, 1998).

Go/No-Go paradigms show older adults exhibit deficits in response inhibition compared to younger individuals. These tasks require participants to execute a motor response (Go trials) while inhibiting it when a specific No-Go stimulus appears. Older adults exhibit increased commission errors, indicating age-related declines in response control and flexibility (Maillet et al., 2020). The findings across a broad range of cognitive neuroscience tasks with older observers align with broader evidence indicating reduced prefrontal cortical efficiency in aging, which plays a crucial role in inhibitory control and response suppression (Falkenstein et al., 2002).

Task complexity further accentuates age-related differences in visual attention and inhibition. Older adults can perform comparably to younger observers in simple, single-task scenarios. However, dual-tasks require multiple responses to a single stimulus, which can be challenging for older adults. Dual tasks involve dividing and sustaining attention or operating under task demands that exceed those used in basic visual tasks, simultaneously across multiple stimuli or tasks (Künstler et al., 2018).

1.7. The attentional inhibition hypothesis

As described earlier, Govenlock et al. (2009) used a basic psychophysical task to measure the orientation channel bandwidth via notched-noise masking. Orientation selectivity requires task-irrelevant orientations to be suppressed or filtered out of a neural circuit's response. Govenlock et al. (2009) failed to show an increase in orientation tuning bandwidths with increasing age, and older observers performed at a level consistent with that of younger observers. To explain the lack of age differences, the authors proposed two hypotheses to explain their findings.

The first explanation involves the selective recruitment of neurons tuned to a narrow range of orientations. Thus, older adults maintain youthful orientation tuning by relying on a reduced subset of visual neurons that remain selective in old age. The selective recruitment hypothesis posits that aging may not degrade all visual neurons equally, and that a subset must retain their precision (i.e., narrow channel bandwidths), enabling older individuals to perceive orientation with youthful accuracy. In higher level terms, the age-associated changes in task performance that are thought to reflect a decline in neural inhibition, such as those discussed above (e.g., the Go/No Go paradigm), may be the result of age-dependent recalibration to preserve basic visual abilities such as orientation selectivity, but at the cost of a loss of sensitivity.

A second hypothesis proposed by Govenlock et al. (2009) is that the aging visual system actively compensates for any loss in neural selectivity by using attention or other top-down processes. The authors proposed that the aging brain may utilize neural processing from areas downstream from the primary visual cortex or feedback from downstream visual processing areas to preserve orientation selectivity, a concept referred to as the attentional inhibition hypothesis. Brain imaging work using positron emission tomography (PET) supports the attentional inhibition hypothesis (e.g., Bennett et al., 2001) by demonstrating that higher-level areas of the brain, beyond V1, are utilized by older observers when performing a simple, low-level, and minimally demanding visual task.

1.8 Animal Models of Age-Related Visual Decline

The attentional inhibition hypothesis has face validity because, unlike work with awake behaving humans, animal research on orientation selectivity has found age-related declines in performance. The key difference with these animal models is that neural recordings were made in anesthetized monkeys, rather than awake and behaving animals, which precludes the use of cognitive, attentional, or feedback mechanisms as compensatory processes. For example, Leventhal et al. (2003) investigated neuronal responses in anesthetized macaque monkeys and showed that older monkeys had broadened orientation neural tuning curves, indicating reduced neuronal selectivity among older animals. Specifically, orientation-selective neurons in older macaques responded less distinctly to preferred orientations, suggesting diminished neural precision in encoding visual stimuli without top-down modulation. Additionally, Schmolesky et al. (2000) found that aging in anesthetized rhesus monkeys reduced the selectivity of visual neurons and slowed their overall responsiveness to visual stimuli. These studies highlight a fundamental impairment in the efficiency and accuracy of visual processing at the neuronal level for orientation processing.

Moreover, animal studies suggest that age-related visual deficits are associated with anatomical and physiological changes in cortical neurons. Hua et al. (2006) demonstrated structural changes, including dendritic spine loss and reduced synaptic density in the visual cortex of older macaques, potentially disrupting the synaptic communication required for precise orientation selectivity. Peters et al. (1997) provided further evidence that myelin sheaths deteriorate significantly in the visual cortices of aged primates, contributing to slower and less coordinated neuronal signaling, which in turn reduces neural specificity. In addition to structural deterioration, elevated neuronal noise decreases orientation selectivity. Yang et al. (2009) reported higher spontaneous neuronal activity in older monkeys, suggesting a reduction in the signal-to-noise ratio in the aging brain. Increased spontaneous neural firing reduces the precision of orientation (mainly controlled by regions in V1) and motion (mainly controlled by the middle temporal area, MT) signals because neurons less reliably transmit orientation or direction, and downstream neurons would require a longer integration time to achieve a signal-to-noise ratio equivalent to that of younger animals. Altogether, anesthetized animal studies provide evidence that aging inherently diminishes orientation selectivity at the neuronal level through a combination of structural degeneration, reduced neural responsiveness, and elevated noise (Hua et al., 2006; Leventhal et al., 2003; Peters et al., 1997; Schmolesky et al., 2000; Yang et al., 2009).

2. Aims and an introduction to the experimental design

The present study aims to investigate the role of increased cognitive load and attention on observer performance with a motion direction and orientation discrimination task, and to compare these findings between younger and older observers. Firstly, we designed this experiment to include a partial replication of previous studies of spatial suppression (e.g., Tadin et al., 2003; Betts et al., 2005) with a reduced number of sizes and contrasts. Moreover, in their previous work, Betts et al. (2005) employed a staircase method to measure the duration threshold (McDougal, 1904), which is the stimulus duration (in seconds) required to correctly distinguish leftward from rightward motion in a sine-wave grating. Because we did not find an example of previous work that used a duration threshold measure to quantify orientation thresholds in older and younger observers, we measured duration thresholds to assess near-threshold orientation discrimination (±2 deg). This component of the experimental design is a conceptual replication of the study by Pilz et al. (2020), but instead measures observer performance using a duration threshold. Note that duration threshold is a perceptual measure based on how long the stimulus is displayed on the screen, and differs from reaction time which is directly influenced by motor abilities that tend to decline with age (Johari et al., 2018). Also note that this makes the experiment self-paced, as observers can respond to stimuli at their own speed; however, to reduce fatigue and the potential for inaccuracies due to a delay in responses, participants were instructed to go as quickly and accurately as possible.

Next, we aimed to assess whether changing the task demands would alter spatial summation and suppression in younger and older observers. We created stimuli that either moved leftward or rightward *and* were oriented either +2 degrees or -2 degrees off vertical to create stimuli that varied on two stimulus dimensions trial-to-trial. Combining two stimulus dimensions enables us to adjust the task demand for our younger or older observers by simply altering the task (i.e., responding to either motion, orientation, or both) while keeping the stimulus constant.

Before designing the experiment, we piloted the orientation discrimination task and the dual task in three non-naive observers to ensure that the orientation task was less difficult, measured by duration thresholds, than the motion task. Pilot testing showed that the orientation task would not be challenging for younger or older observers and is thus predicted not to interfere with a change in the strategy in the motion discrimination task. And yet, when including the orientation task as an uncertain response task (where the observer is randomly assigned a single stimulus dimension to respond to) or in the dual task (where the observer is required to respond to both stimulus dimensions in a randomized order), they are required to encode both stimulus dimensions because they are needed to generate a correct response under uncertainty and two correct responses in the dual response task.

3. Methods

3.1. Recruitment, setting, and subjects

Our goal for recruitment was 20 younger and 20 older subjects, based on work by Betts at al. (2005); however, due to logistical limitations explained in subsequent sections of this paper, this was not achieved. Ultimately, 14 young subjects and 7 older subjects were recruited for this study. The young group was defined as those aged 19 to 27 years, and the old group was defined as those 65 and above. Inclusion criteria were as follows: no history of ocular surgery (except cataract surgery), no diagnosis of age-related macular degeneration, glaucoma, or significant retinal disease, no current use of ocular medications (excluding artificial tears), and near visual acuity better than 20/25. Subjects were recruited via email. Recruitment posters were also placed at New England College of Optometry (NECO) clinics and on the NECO Research Interest webpage.

3.2. Preliminary testing

Testing was performed over two to three sessions spanning no more than two weeks, as done in the study by Betts et al. (2005). The study was divided into several sessions to minimize participant fatigue, with each session lasting approximately 1.5 to 2 hours in duration. Sessions were scheduled based on participants' availability and ideal performance times, determined by responses to the morningness-eveningness questionnaire, which consists of 19 items scored on a scale with assigned point values to assess when individuals are most alert and active throughout their day. This validated questionnaire records an individual's self-reported waking hours and their "peak" time, which is when they feel like they perform at their best. The scoring ranges from evening to morning type (Shahid et al., 2012).

On the first day of the study, informed consent was obtained. Each participant completed a brief demographic questionnaire, the Morningness-Eveningness Questionnaire, near visual acuity using a Sloan ETDRS format near vision chart, ocular biometry with the Haag-Streit Lenstar 900 (Haag-Streit, Bern, Switzerland), and autorefraction with the Topcon KR-1W wavefront analyzer (Topcon, Tokyo, Japan). The demographic questionnaire included basic demographic information, the date of the last eye exam, a history of ocular disease, the approximate age at which glasses were prescribed, a family history of refractive error, and an estimated time spent asleep and awake.

Data collected from the Haag-Streit Lenstar 900 included axial length, lens thickness, and anterior/posterior chamber depth. Older participants also completed the Montreal Cognitive Assessment (MoCA), a screening test for cognitive impairment scored out of 30. The MoCA assesses cognitive domains, including memory, attention, visuospatial skills, and executive functioning. A score of 25 or lower indicates cognitive impairment, while a score of 26 or higher indicates normal cognition (Nasreddine et al., 2005). All participants received an honorarium of $30 per session.

Figure 3: The Vpixx 12-bit monitor (ViewPixx, Montreal, Canada) used to present the stimuli.

3.3. Apparatus and stimulus parameters

Participants were seated 57 cm from a computer display. Their head was stabilized with a chin-forehead rest. The only illumination in the room came from a Vpixx 12-bit computer monitor (Montreal, Canada) with an average luminance of 40 cd/m^2 (See *Figure 3*). The monitor's refresh rate was 120 Hz. A Linux computer using MatLab (2022a) and the Psychophysics and VideoToolboxes (Brainard, 1997; Kleiner et al., 2008; Pelli, 1997) were used to generate a Gabor patch with a spatial frequency of 1 cyc/deg that varied in contrast

(2% or 22.5%) and size (0.7° or 5°). These parameters were selected from prior work (Betts et al., 2005), based on the criteria for measuring the minimum size and contrast pairs required to observe a spatial suppression effect. Moreover, 1 cyc/deg was selected as testing was performed at an intermediate distance (57 cm), and this low spatial frequency would allow for older presbyopic participants to resolve the stimulus regardless of if correction was worn. Older observers were given the option of whether or not to wear correction based on their preference. Responses were collected via a playstation-style game controller, and feedback was provided after each trial with a high-pitched beep indicating a correct response and a low-pitched beep indicating an incorrect response.

3.4. Stimuli and Tasks

Before beginning the psychophysical portion of the study, a set of instructions outlining the stimulus and required responses was recited to the participant, and any questions were answered. Additionally, before each block of trials, the subject was verbally informed of the specific stimulus and response required for that block. Each participant was also given a practice set of above-threshold trials before completing each block for the first time, where a minimum of 75% correct was necessary to ensure understanding of the stimulus and task.

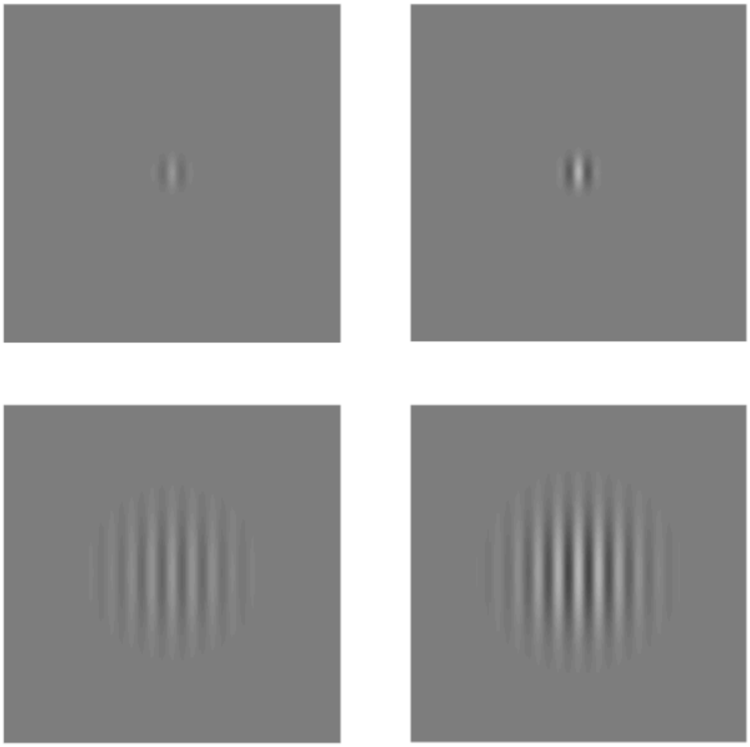

Figure 4: Sample of vertical Gabor stimuli used in the single-dimension motion task. Top left is small and low contrast. Top right is small and high contrast. Bottom left is large and low contrast. Bottom right is large and high contrast. For demonstration purposes, low contrast in this figure is set to 8% and high contrast is set at 45%.

Duration thresholds for two contrasts (2% and 22.5%) at two sizes ($2\sigma = 0.7$ and 5 degrees) were measured for six different tasks (See *Figure 4*). The terminology used in this thesis is as follows: a single-dimension *stimulus* is one where, from trial to trial within a block, **either** the direction of motion or orientation is changed. As explained previously, these are partial replications of Betts et al. (2005) for motion and a conceptual replication of

Pilz et al. (2020). For a single-dimension stimulus, the observer is certain of the stimulus dimension to respond to on each trial. When the data from these tasks are presented, it will be a single-dimensional task with certain responses labeled as *Motion* or *Orientation;* these labels, along with all others, are listed in Table 1.

Task	**Stimulus**	**Response Uncertainty**	**Response Order Uncertainty**
Motion	Motion: Left/Right Orientation: 0	**None**	**None**
Orientation	Motion: 0 Orientation: +/- 2 deg	**None**	**None**
Dual-Dimension Motion	**Motion: Left/Right** **Orientation: +/- 2 deg**	**None**	**None**
Dual-Dimension Orientation	**Motion: Left/Right** **Orientation: +/- 2 deg**	**None**	**None**
Motion Uncertain Response	**Motion: Left/Right** **Orientation: +/- 2 deg**	**Yes**	**None**
Orientation Uncertain Response	**Motion: Left/Right** **Orientation: +/- 2 deg**	**Yes**	**None**
Dual Response Uncertain Order	**Motion: Left/Right** **Orientation: +/- 2 deg**	**Partial** - Certain that 2 responses are required	**Yes** - Second response in **VSTWM**

Table 1: Stimuli and task requirements for all tasks and their corresponding response and response order uncertainty. Note that the Motion Uncertain Response and Orientation Uncertain Response tasks were simultaneously run with the same block of trials, but with two staircases operating for half the total trials. Also note that the Dual-Dimension Motion, Dual-Dimension Orientation, Motion Uncertain Response, Orientation Uncertain Response, and Dual Response Uncertain Order tasks use the same visual stimulus and only differ in their task response requirements. Also note VSTWM, is an acronym for visual short-term working memory. VTSWM is required to to briefly store and manipulate visual

representations, which is critical for processing visual information and guiding subsequent actions (Menegaux et al., 2020)

Dual-dimension stimuli contain **both** changes in motion direction and orientation from trial to trial. The observer could, via instruction, either be certain or uncertain of the dimension that they must respond to achieve a correct response. In other words, the task demand was different for the same stimuli.

The dual-dimension stimuli were combined with four different responses to create four tasks. Firstly, a *certain single-response* task involved having the observer consistently respond to one and only one stimulus dimension (i.e., orientation OR motion) on each trial for an entire block. An u*ncertain single-response* task involved having the observer respond to **either** the direction of motion or orientation of the stimulus, with the response dimension randomly selected on each trial. The *uncertain dual-response* task required the observer to respond to **both** motion and orientation. However, observers were uncertain about the order in which they would be responding (motion first and orientation second, or orientation first and motion second). See Figure 5 for a depiction of examples of dual-dimension stimuli.

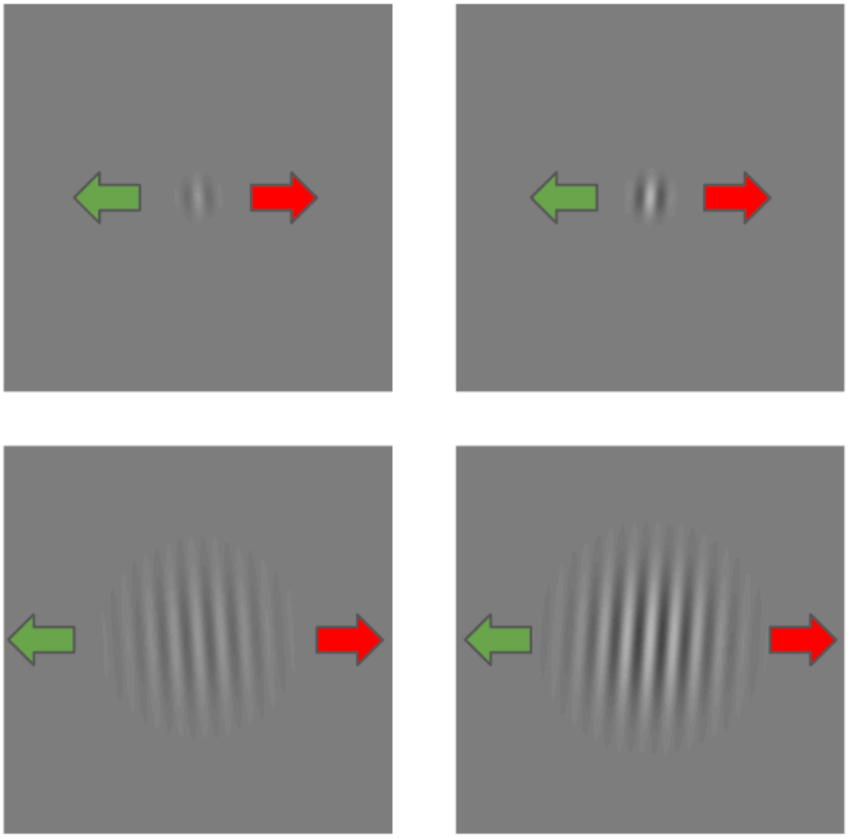

Figure 5: Sample of dual-dimension Gabor stimuli. The top left is small and low contrast, tilted to the left. The top right is small and high contrast, tilted to the right. The bottom left is large and low contrast, tilted to the left. On the bottom right is large and high contrast, tilted to the right. For demonstration purposes, the low contrast in this figure is set to 8%, the high contrast to 45%. Tilt remains at ±2 degrees. Also, for demonstration purposes, red arrows indicate rightward motion and green arrows indicate leftward motion. Dual-dimension stimuli can present in any random combination of small or large, low or high contrast, and tilt to the left or right for any given trial.

3.5. Experimental design

A block consisted of 150 trials for each of the six tasks. The first task included a block that replicated those used in Betts et al. (2005), in which the observer reported whether a vertical grating was moving to the left or right. In the second block of trials, participants were asked to discriminate the orientation of a stationary Gabor, either tilted to the left or right by ±2 ° away from vertical, conceptually replicating the study by Pilz et al. (2020). These are the first and second single-dimension discrimination tasks, respectively.

Two tasks used dual-dimension stimuli with certain single responses (the tasks were done in a random order). Here, the stimulus contained both motion and orientation, and the observer consistently responded to only one stimulus dimension for the entire block of trials. That is, observers reported the direction of stimulus motion (either rightward or leftward) or stimulus orientation (either to the right or left of the vertical axis). The stimulus dimension that participants responded to was indicated by the word “motion” in black font or “tilt” in white font which appeared at the top of the display. Participants were also verbally informed of the required response before commencing the trial block.

Two tasks used dual-dimension stimuli and uncertain responses. One task involved an uncertain *single* response: a stimulus containing both motion and orientation was displayed on each trial, and responses were to a single, randomly selected stimulus dimension. Observers were uncertain whether to respond to motion or orientation until the prompt appeared after the stimulus was removed. Finally, a task involved an uncertain *dual* response to a dual-dimension stimulus. This meant that observers were instructed to report the stimulus's motion direction and orientation in a randomly selected order once the stimulus was removed. The order of these responses was again indicated at the top of the screen with either the word “motion” or “tilt”. Each participant completed every task twice.

4. Results

4.1. Aging Results

Due to logistical challenges in recruiting healthy individuals aged 65 and older, our sample consists of seven older observers during the data collection phase of this project. Admittedly, our small sample of older observers is a major limitation for interpreting aging results. Thus, this section will describe the results qualitatively by analyzing graphical presentations and general trends in the data, especially those related to hypotheses that can be justified by prior research, and more specifically, interactions between size and contrast.

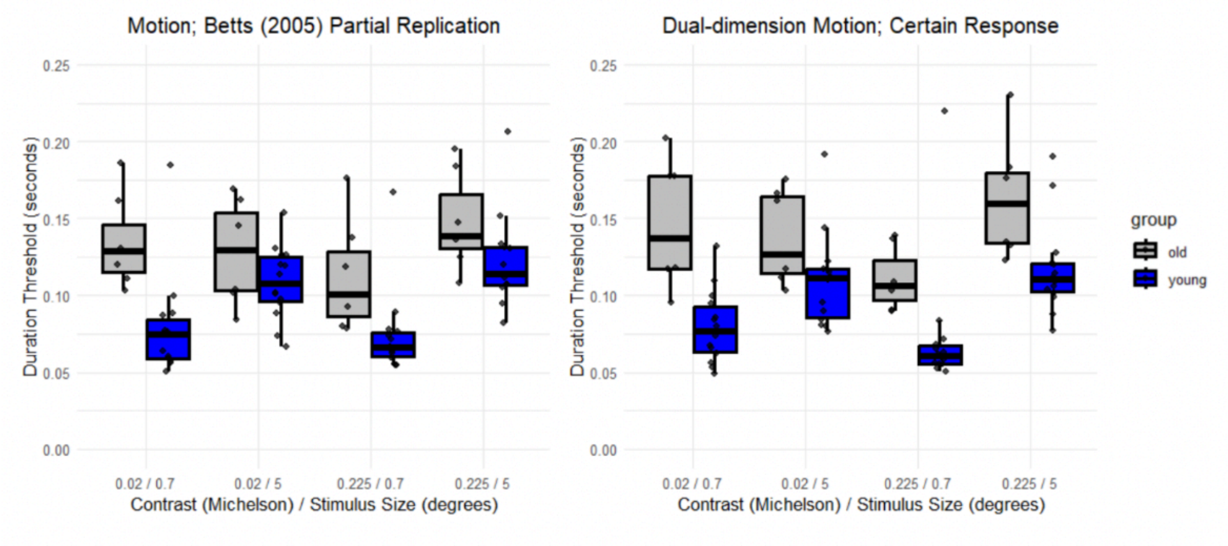

Figure 6. Tukey box-plots for the partial replication of Betts et al. (2005) are on the left, and the new dual-dimension stimulus with certain responses for motion is on the right. Each point represents the individual observer's duration threshold, averaged across two staircase runs. Specifically, the panel on the left displays the data with a vertically oriented Gabor (following Betts et al., 2005). The panel on the right shows the data from the dual-dimensional stimulus, where motion discrimination was performed with the Gabor tilted (+/- 2 degrees) off the vertical axis.

Spatial suppression is indicated when the duration threshold increases when comparing a contrast by size interaction, while summation is indicated when there is a decrease in duration threshold. Figure 6 demonstrates that for the Motion task, the pattern of duration thresholds for the partial replication of the Betts et al. (2005) paper is broadly consistent with the data we observed. There is no evidence of spatial suppression with high-contrast (22.5%) stimuli for Older observers. Curiously, the data from the Younger observers, using both low- and high-contrast stimuli, appear to exhibit a suppression effect with increasing size.

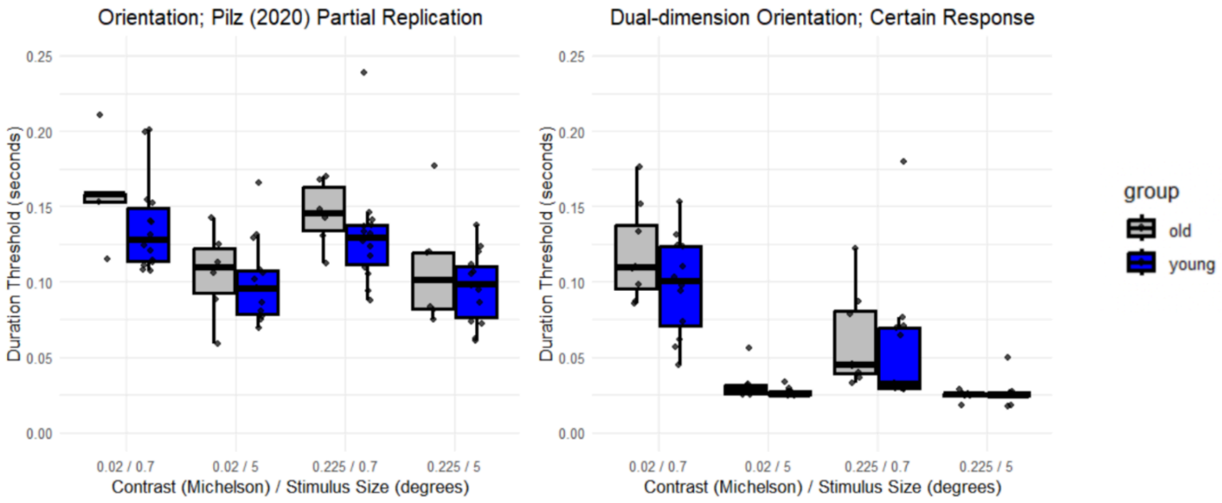

Figure 7: Tukey box-plots for the conceptual replication of Pilz et al. (2020) are on the left, which contain stimuli only tilted (+/- 2 degrees) off the vertical axis without motion. Tukey box-plots for the dual-dimension stimulus, which was both moving and tilted, with certain responses for orientation are on the right.

Figure 7 (left panel) shows that the findings of this study generally replicate Pilz et al. (2020). There is a trend of Older observers generally exhibiting more suppression (with longer duration thresholds) than Young observers, particularly for low- and high-contrast small stimuli. However, the small sample size of Older observers precludes us from making any claims towards significance. Figure 7 (right panel) shows that for large stimuli in the dual-dimension certain response condition, both Older and Younger observers are near our minimum displayable durations. Still, no observers had threshold estimates at the floor. For both Old and Young observers, there was a summation effect: at both low and high stimulus contrasts, duration thresholds decreased with increasing stimulus size. While this trend is also observed with the replication of Pilz (2020), it is much more apparent in the certain dual-dimension orientation task. This difference between tasks may be attributed to a practice effect, as the tasks were only partially randomized, and the Dual-Dimension Orientation task was always completed after the Pilz et al. (2020) replication.

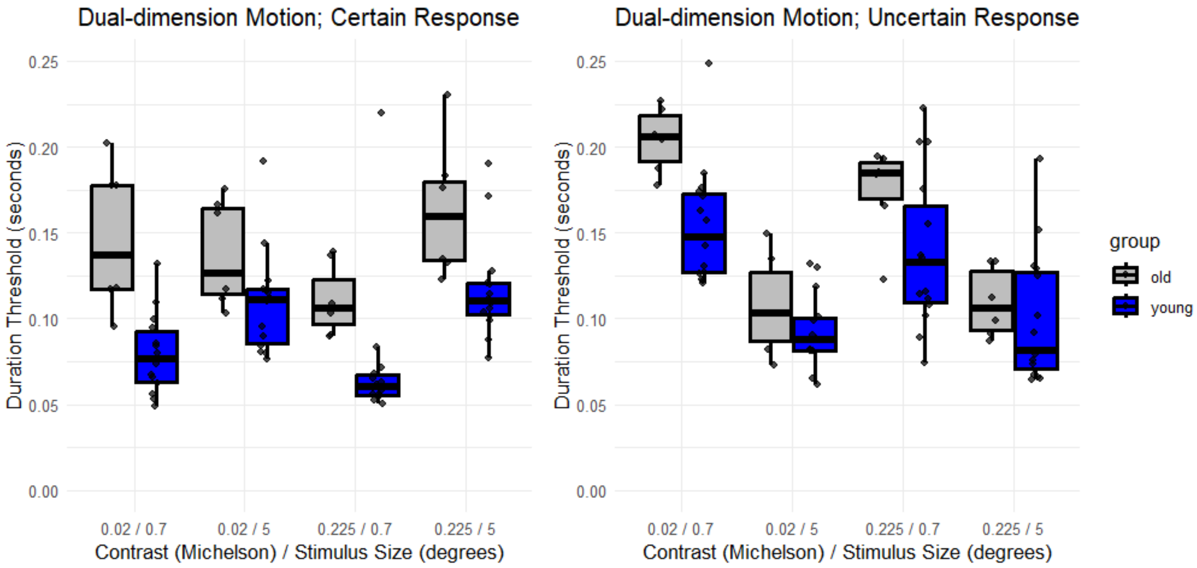

Figure 8: Tukey box-plots for the dual dimension stimulus with certain responses for motion on the left. On the right are Tukey box-plots for the dual dimension stimulus with uncertain responses, with duration thresholds determined by a staircase controlled by only motion responses.

Examining Figure 8 (left panel), the effect of age on duration thresholds in the Dual-Dimension Certain Response Motion task is similar irrespective of the contrast and size of the stimulus: Old observers had higher duration thresholds compared to Young observers in all conditions. However, with the introduction of uncertainty (right panel), the age difference varied across conditions. Specifically, summation in the low and high-contrast conditions was greater in Older observers, so duration thresholds measured with large stimuli were similar in the two age groups. This intriguing finding is different from that found by Betts et al. (2005), where, in general, evidence of summation for Young observers was not found with any high contrast stimuli. We will return to these ideas in the discussion of the GABA Hypothesis and the Contrast Gain Hypothesis.

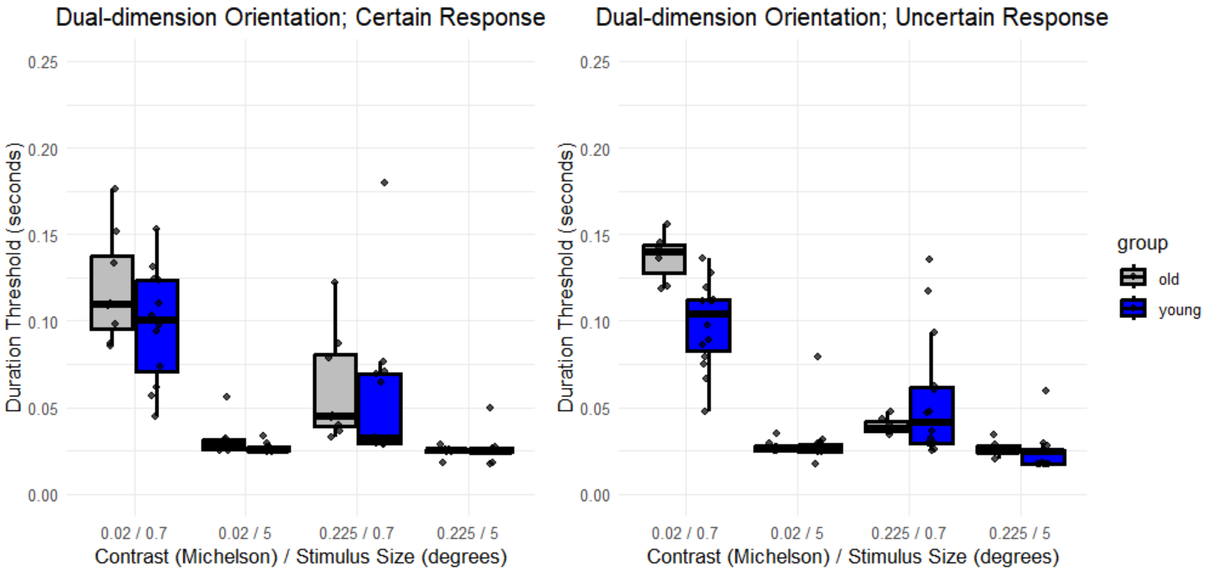

Figure 9: Tukey box-plots for the dual dimension stimulus with certain responses for orientation on the left. On the right are Tukey box plots for the dual-dimension stimulus with

uncertain responses, with duration thresholds determined by a staircase controlled by only orientation responses.

Looking at figure 9 (left panel), when examining dual dimension stimuli with certain orientation responses, as well as dual dimension stimuli with uncertain responses, the effects follow the same trends as the replication of Pilz et al. (2020). With large stimuli, both Young and Older observers are near our minimum displayable durations. Generally, increased or equivalent summation is observed when comparing the Young group to the Older group.

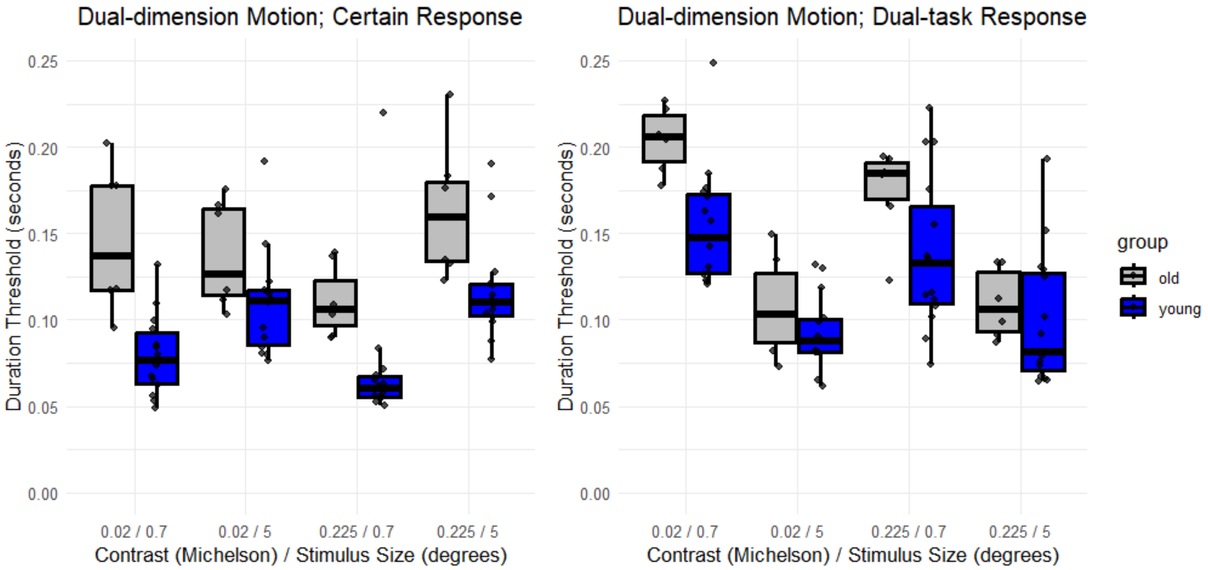

Figure 10: The left panel is the identical data from the right panel from Fig.6 – the stimulus in this task was a +/- 2 deg oriented grating that moved either left or right. As the text describes, observers were instructed to only respond left/right to the motion of the stimulus on each trial, and from their responses, a motion duration threshold was obtained. The data in

the right panel also show motion duration responses with the same stimuli, but observers also had to report the stimulus orientation either before or after reporting the motion direction (report order uncertainty).

Lastly, when examining figure 10 (left panel), we again see that older observers generally perform the same irrespective of stimulus size and contrast with the Dual-Dimension Motion task. Younger observers generally exhibit suppression with increasing size in the Dual-Dimension Motion task. Interestingly, with the Dual-Dimension Dual-Task, Older observers show stark summation for larger stimuli, and Young observers go from showing suppression to summation with larger stimuli. Younger observers also tend to perform better than Older observers for all stimuli and tasks.

4.2. Young Observers

We investigated age-related changes in basic spatial and visual processing with marginally increased task demands. The effects of age were not analyzed in detail because the size of our Older sample (n=7) was too small. However, the data set collected from Young subjects reveals a curious result given the background literature cited above. The Young results relate to work on monkeys by Pack et al., 2005. The link between spatial suppression and neural inhibition relies upon a logical leap from psychophysics to single-cell neural recordings in MT. Evidence exists that demonstrates a contrast dependence in area MT of awake behaving monkeys (Pack et al., 2005), where neurons exhibit an increased spike rate for large, low-contrast stimuli compared to large, high-contrast stimuli (See *Figure 11*).

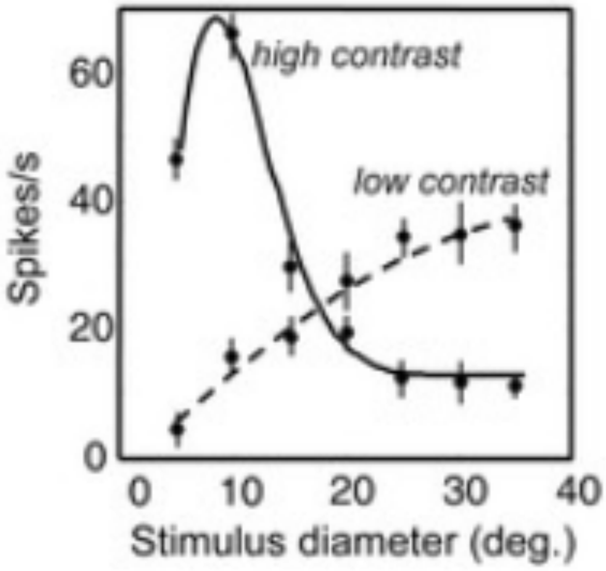

Figure 11: Stimulus diameter in degrees for a random dot kinematogram (RDK) stimulus versus spikes per second for a single representative neuron in area MT for high-contrast (solid line) and low-contrast (dashed line) RDK stimuli, adapted from Pack et al. (2005).

Pack et al. (2005) claim that monkey neural recordings were consistent with a task whilst their neural activity was being recorded. Before going briefly into our results for Young observers, we note that the link between physiology and psychophysics is quite weak. First of all, in Pack et al. (2005) monkeys were merely watching the motion stimulus and were not required to do a task. That being said, on their own, the data from Pack et al. (2005) are a beautiful example of awake behaving monkey physiology. For their neural recordings, the pattern of findings can be summarized in Figure 11, where spike rate (spikes/second recorded from an individual neuron) is on the y-axis and spatial extent of the random dot kinematogram (RDK) stimulus is on the x-axis. For high-contrast random dots (solid line), such as black on a grey background or white on a grey background, as the size of the RDK stimulus increases from 5 to 10 degrees in diameter, there is approximately a ⅓ rd increase in firing rate. When the spatial extent of the RDK is increased further, from 10 to 15 degrees, the firing rate drops to nearly ½ of that at 5 degrees, and beyond 20 degrees there is a baseline level of response that is independent of stimulus size. Also in Figure 11, we can see what Pack et al. (2005) observed with a low contrast RDK stimulus (dashed line). A low contrast stimulus is one where the dots of the random dot motion stimulus are closer to a mean background grey and have either a positive or negative contrast polarity. Unlike the high contrast stimulus, the spike rate of a neuron increases with increasing stimulus size from around baseline until it saturates at around a size of 25 degrees.

The data in Figure 11 are from MT neurons in the dorsal pathway. Note that we observed a result consistent with spatial summation for high-contrast large stimuli using a psychophysical duration threshold measure. The generalizability of these neurophysiological results to all perceptual tasks may not apply, especially a task like orientation discrimination that is likely subserved by mechanisms in V1 or down the ventral stream, and it is unlikely that data from MT will hold.

Shifting gears back toward the data presented in this thesis, the reader is encouraged to examine the blue box plots (Young data) and compare the duration threshold data from the dual-dimension stimulus with certain responses for motion and the dual-dimension stimulus with uncertain motion responses (Figure 8). Note that the stimulus remained the same in both conditions and the task merely differs in uncertainty: in the certain task, the response is always to the direction of motion, and in the uncertain task, the response is randomly either to motion (Figure 8, right panel) or to orientation (Figure 9, right panel). In figure 8., one can see that high contrast and low contrast motion duration thresholds *increase* with increasing size when the observer is certain of their response, indicating that spatial suppression is present. However, they *decrease* with *increasing* size when the observer faces response *uncertainty,* suggesting spatial summation.

Examining Figure 12, we see that for both low (0.02%) and high (22.5%) contrast stimuli, only the tasks that required the observer to make a motion response with certainty (whether in the Motion task or a Dual-Dimension Motion task) exhibit a result consistent with spatial suppression. Recall from the methods section that, except for the tasks involving single-dimension stimuli (motion or orientation only), the stimulus remained the same in all tasks, and only the task responses required change. Approximately half the trials in the Dual-Dimension Certain Motion Response Task were *exactly* the same as those for the Dual-Dimension Certain and Uncertain Response Motion Tasks. In other words, we applied a *task-based intervention* to elicit a change in surround suppression and summation effects, similar to unblindable pharmaceutical interventions (e.g., Schallmo et al., 2018) discussed later in this thesis.

We defined two quantities:

$$\Delta\tau_{\text{size}} = DT_{\text{large}} - DT_{\text{small}} \qquad [Y1]$$

$$\Delta\tau_{\text{contrast}} = DT_{\text{high}} - DT_{\text{low}} \qquad [Y2]$$

where $\Delta\tau_{\text{size}}$ is the difference between an observer's duration threshold (DT) for large and small (0.7 and 5 degrees), and $\Delta\tau_{\text{contrast}}$ is the difference in duration threshold between high and low contrast patterns. Note that $\Delta\tau_{\text{size}}$ can be computed at both our low (2%) and high (22.5%) contrast and $\Delta\tau_{\text{contrast}}$ for our small ($2\sigma = 0.7$ degrees) and large ($2\sigma = 5$ degrees). Note that applying equation Y1 allows us to look at the effect of contrast, task, and their interaction, whereas applying equation Y2 allows us to look at the effect of stimulus size, task, and their interaction.

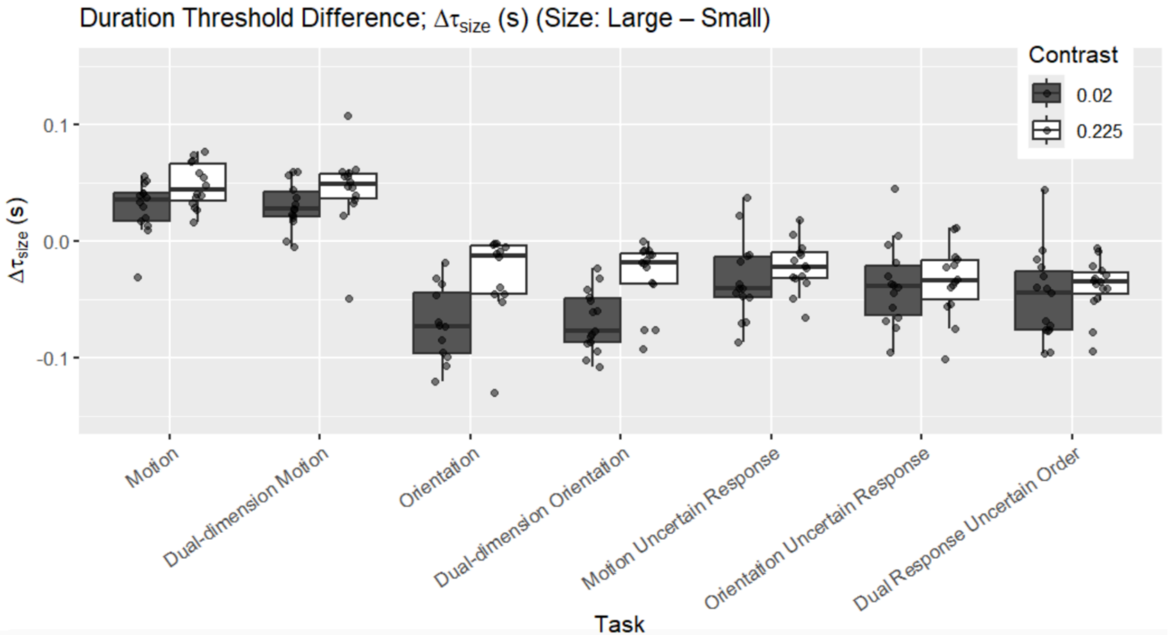

Figure 12: A jittered box-plot of $\Delta\tau_{\text{size}}$ in seconds versus task type for Young subjects only. The data are depicted in grey for low contrast ($c = 0.02$) and in white for high contrast ($c = 0.225$). Note that positive values of $\Delta\tau$ indicate spatial suppression, and negative values indicate summation.

Computing a repeated measures ANOVA in R with package `ez` (Lawrence, 2016) shows there were main effects of Task ($F(6,91) = 44.23$, $p < 0.001$, $\eta^2G = 0.624$) and Contrast ($F(1,91) = 25.09$, $p < 0.001$, $\eta^2G = 0.106$), and a marginal but non-significant interaction between Task and Contrast ($F(6,91) = 2.08$, $p = 0.063$, $\eta^2G = 0.056$). The ANOVA here is run as a protective test with the null-hypothesis that there is no difference. The ANOVA does not tell us where $\Delta\tau_{\text{size}}$ differs by task, which is our key question of interest; thus, we move on to pairwise comparisons.

Following Fig. 12, we will highlight a few task comparisons with $\Delta\tau_{\text{size}}$, specifically for tasks that used motion as a stimulus dimension. To minimize the number of statistics in the text, unstandardized effect sizes and their 95% confidence intervals are reported. The effect sizes are generally large (Cohen's $d > 1.99$), and all *p*-values are less than a conventional alpha. All the details of the statistical comparisons in the Appendix (Table YR1).

For both low and high contrast stimuli, $\Delta\tau_{\text{size}}$ is greater for the Motion Certain Response Task than the Motion Uncertain Response Task. For low contrast, $\Delta\tau_{\text{size}}$ was 60.2 ms (95% CI: 42.7 – 77.8 ms) longer in the Motion Certain Response than in the Motion Uncertain Response, and for high contrast, $\Delta\tau_{\text{size}}$ was 67.2 ms (95% CI: 47.7 – 86.8 ms) longer. Counterintuitively, if an observer was certain that they had to make a left/right response to a moving grating, regardless of its size, their duration threshold was greater than if they were uncertain whether they were to respond to the direction of motion or the orientation of the Gabor. In short, the classic surround suppression effect observed by Tadin

(2003) is absent when another task-relevant stimulus dimension, in this case orientation, is introduced.

However, there is a stimulus difference between the Motion Certain and Motion Uncertain Response tasks, which could be a potential confound. That is, the Motion Certain task is vertical, whereas the Motion Uncertain Response task is slightly off vertical, thus requiring the observer to attend to four different directions of motion. Thus, it is worthwhile to compare the Dual-Dimension Motion Task and the Motion Uncertain Response Task because in these two tasks, the stimulus set is the same and only the task demands differ. We found that $\Delta\tau_{\text{size}}$ for the Dual-Dimension Motion was larger than for the Motion Uncertain Response for both low and high contrast stimuli (low, 58.4 ms, 95% CI: 34.5 – 82.2 ms; high, 60.1 ms, 95% CI: 38.3 – 83.5 ms). Thus, controlling for the potential stimulus confound, we again find that merely the presence of uncertainty in the stimulus dimension that the observer must attend to *abolishes* any evidence of surround suppression. If the surround suppression observed in this task was truly reflective of the activity of neurons in MT (Pack et al., 2005), then this result is puzzling, as the orientation bandwidth of neurons in MT is surely greater than +/- 2 degrees.

Lastly, we turn to the Dual Response Uncertain Order task. For both low and high contrast stimuli, when comparing Dual-dimension Motion to Dual Response Uncertain Order, we again find that adding a small VSTWM load also *abolishes* a spatial suppression effect (low, 76.4 ms, 95% CI: 44.6 – 108 ms; high, 76.4 ms, 95% CI: 58.8 – 94.1 ms). Again, the classic spatial suppression is *abolished*.

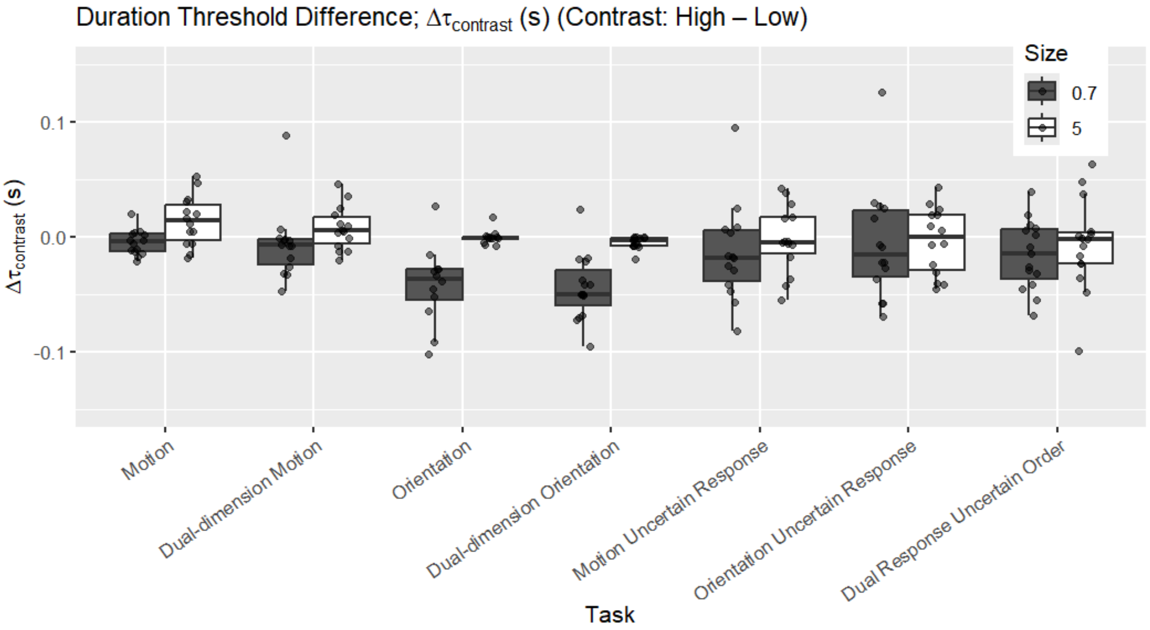

Figure 13: A jittered box-plot of $\Delta\tau_{\text{contrast}}$ in seconds versus task type for Young subjects only. The large ($2\sigma = 5$ degrees) and small ($2\sigma = 0.7$ degrees) data are depicted separately in the grey and white boxplots. Note that positive values of $\Delta\tau_{\text{size}}$ indicate spatial suppression and negative values indicate summation.

Figure 13 shows $\Delta\tau_{\text{contrast}}$ for both large and small stimuli. Computing a repeated measures ANOVA in R with package `ez` (Lawerence, 2016) shows there were main effects of Task ($F(6,91) = 3.06$, $p < 0.001$, $\eta^2G = 0.105$) and Stimulus Size ($F(1,91) = 25.09$, $p < 0.001$, $\eta^2G = 0.105$), and a marginal but non-significant interaction between Task and Contrast ($F(6,91) = 2.08$, $p = 0.063$, $\eta^2G = 0.0541$,). The ANOVA is run as a protective test and the null-hypothesis is that there is no difference. It does not tell us where $\Delta\tau_{\text{contrast}}$ differs by task, which is our key question of interest.

From Figure 13, we have two tasks of interest to compute pairwise comparisons on, listed in Table in the Appendix (Table YR2). If we compare Orientation Certain Response with Orientation Uncertain Response, we see that $\Delta\tau_{\text{contrast}}$ is -39.4 ms (95% CI: -74.9 ms – -3.8 ms), which indicates that observers had duration thresholds that were longer in low contrast when the stimulus size was small, indicating summation. The reader is encouraged to compare Tables YR1 and YR2 and note that unlike for the pairwise comparisons for $\Delta\tau_{\text{size}}$, the effect sizes are smaller for $\Delta\tau_{\text{contrast}}$ (now $|d| < 1$) and are negative to indicate that these comparisons of interest reflect our interest in spatial summation.

Disappointingly, none of the other planned pairwise comparison with 2-tailed tests were near a traditional alpha cut-off, but there is perhaps a trend in the Orientation Certain Response versus the Orientation Uncertain Response at the small size ($\Delta\tau_{\text{contrast}} = -22.9$ ms, 95% CI: -6.12 ms – 3.2 ms). Neither of the large sizes (5 degrees) were significant.

5. Discussion

5.1. Limitations

The greatest limitation of this study was the small sample size of older individuals. Our recruitment efforts, which included email, posters in the NECO clinics, and posting on the NECO Research website, did not reach or inspire a community of healthy and willing older adults 65 and over to participate in our research study. A different recruitment approach could have been more successful, such as directly reaching out to communities of healthy seniors at community centers or living facilities.

As is common in the aging and vision subfield, we employed a “two-group” strategy, defining upper and lower age-limit bounds to categorize our groups of Young and Old observers. Age cut-offs are defined by the investigators. The rationale for setting our upper limits on Young participants is to avoid middle-aged participants with incipient presbyopia by setting the upper bound of Young in the mid-to-late 30s. Defining the Old group cut-off is motivated by social norms, and the youngest age at which there is a consensus that the label “senior” applies – the standard retirement age of 65. However, given the resources available at NECO, which would enable us to measure lens thickness and accommodation, a modified recruitment strategy of collecting a stratified sample (e.g., aiming for an N of at least 10 observers per decade) is possible, allowing us to recruit healthy participants of any age. Because age is not a discrete variable, this approach is intuitive and easily addressed statistically by moving away from methods such as ANOVAs and t-tests to linear modeling. Although the findings of this study can only be assessed qualitatively in this thesis, altering our recruitment approach to remove age restrictions may be a promising future direction for further investigation.

Furthermore, a limitation of this (ongoing) study is that neither the Young nor the Older participants are truly naive; they are merely naive about the experimental hypotheses. Young participants were recruited from the NECO student population, and therefore had been familiarized with Gabors and suppression/summation effects through the course material. Over half of the older observers consisted of NECO faculty, whose expertise lies in vision science and clinical optometry, and thus, they are not naive observers either. Although participants were not debriefed on the study until its completion in the final session, their performance may have been influenced by their prior knowledge of vision science and psychophysics.

Lastly, this thesis, particularly our interpretation of the results, relies on some of the assumptions of the standard model of spatial vision which posits a quasi-independent processing of visual features via separate channels—in our case, specifically motion and orientation (Graham, 1989; Carandini & Heeger, 2012). According to the standard channel-based model, visual stimuli are analyzed along different dimensions, each processed largely independently through specialized neural populations that exhibit selective sensitivity to distinct features such as motion direction or stimulus orientation.

5.2 What Versus Where?

A fundamental heuristic widely recognized within neuroscience literature is the functional dichotomy between the dorsal (or 'where') pathway and the ventral (or 'what') pathway, as described by Goodale and Milner (1992). The dorsal stream, originating primarily from magnocellular layers and extending towards the parietal cortex, is largely responsible for spatial location, movement, and visually guided actions. Conversely, the ventral stream, primarily associated with parvocellular layers projecting to the temporal cortex, specializes in detailed visual processing, including object identification, color perception, and form perception. This concept provides a simple framework for this study, in which the motion task generally activates the dorsal pathway, and the orientation task activates the ventral pathway.

However, despite clear anatomical and functional distinctions between the dorsal and ventral pathways, there is noteworthy evidence demonstrating overlap and integration between motion and orientation signals at early cortical stages, particularly in the primary visual cortex (V1). Neurons within V1 exhibit responsiveness to both stimulus orientation and motion direction, thereby serving as initial points of convergence between these seemingly distinct visual pathways (Hubel & Wiesel, 1968; Movshon & Newsome, 1996). For example, electrophysiological recordings have shown that individual neurons in V1 can jointly encode information regarding both orientation and the direction of stimulus motion (Pack et al., 2003). Thus, while our experimental design and theoretical assumptions operate under the premise that motion and orientation discrimination pathways function largely independently, it is worthwhile to acknowledge the potential for interaction and overlap between these dimensions, particularly at initial cortical processing stages. Such considerations may have implications for interpreting the results of our study, especially for the tasks with uncertainty and dual tasks, as these separate dimensions may not be completely independent and may instead share neural resources. A lack of independence suggests that motion and orientation may interact at early cortical stages, which could lead to interference or competition between tasks (Pashler, 1994; Wickens, 2002).

Moreover, the concept of what and where pathways, and their development and degeneration across the lifespan, can provide some context for our findings. During visual development in the early years of life, visual abilities and behavior are thought to be processed by the ventral stream and emerge before those of the dorsal stream (Daw et al., 2006). Is there a connection between early visual development and the normal processes of aging? Visual abilities that develop later in life are more vulnerable to age-related changes and become impaired earlier in the aging process than those developed earlier, as they are often less robust and require more complex visual processing (Baltes et al., 1997). One way to describe the tendency for late-developing visual abilities to be vulnerable compared to those that develop early is the "last in, first out" or LIFO hypothesis. It is plausible that visual abilities largely mediated by the dorsal pathway—such as global motion processing and spatial suppression—are particularly vulnerable to age-related decline due to their later maturation and greater reliance on precise inhibitory control.

Spatial suppression plays an important role in contrast sensitivity and segmentation of objects from background, which is critical for everyday tasks including navigation through an environment, and object detection, such as while driving or playing sports. Of particular relevance to the quality of life in older adults is the association of temporally varying stimuli and motion with the rate of falling among older adults (Saftari et al., 2018). Falls are not only deleterious to the quality of life of aged individuals from the injuries they suffer, but falling has a powerful association with death in adults aged 65 and over (Kakara et al., 2023). It is possible that this LIFO hypothesis can rationalize the weakened inhibitory mechanisms which mediate surround suppression in motion processing, and why these dorsal mechanisms are first to deteriorate to deleterious levels compared to ventral mechanisms such as orientation. A possible explanation proposed to explain these age-related changes in surround suppression is a decrease in inhibitory neurotransmitters, which will be discussed in the section below.

5.3. The GABA hypothesis

One hypothesis proposed in aging literature, supported by experiments in aging monkeys, suggests that the inhibitory neurotransmitter gamma-aminobutyric acid (GABA) influences the tuning properties of neurons encoding motion and orientation (Leventhal et al., 2003). According to the GABA hypothesis, the reduced inhibitory signaling associated with aging leads neurons in visual cortical areas to exhibit decreased selectivity, impacting motion perception and spatial suppression effects (Betts et al., 2005; Schmolesky et al., 2000). Leventhal et al. (2003) directly investigated this hypothesis by administering pharmacological agents targeting GABA receptors in the primary visual cortex (V1) of monkeys. Specifically, they administered muscimol, a GABA-A receptor agonist. They found significantly improved orientation and direction selectivity in older monkeys, restoring neuronal tuning curves to levels comparable to those observed in younger monkeys. Conversely, the administration of bicuculline, a GABA-A receptor antagonist, resulted in diminished neuronal selectivity, with notably weaker effects in older monkeys compared to young monkeys, indicating age-related deficits in GABAergic inhibition. These findings suggest that age-related reductions in GABAergic inhibition may underlie the decreased neuronal selectivity for both motion direction and orientation (Leventhal et al., 2003). Consequently, older individuals might exhibit impaired visual performance, such as reduced spatial suppression, due to broader and less distinct neuronal tuning curves.

Additional support from animal studies further emphasizes the role of diminished inhibitory processes with aging in shaping visual processing deficits (Hua et al., 2008; Schmolesky et al., 2000). For instance, Hua et al. (2008) demonstrated that visual cortical neurons in aged cats exhibit decreased orientation and direction selectivity attributable to reduced GABAergic inhibitory neurotransmission, resulting in broader tuning curves and diminished visual acuity. Similarly, Schmolesky et al. (2000) reported significant reductions in inhibitory synaptic inputs to cortical neurons in older monkeys, specifically showing fewer and less effective GABAergic synapses. As a result, older monkeys had broader neuronal tuning, reduced signal-to-noise ratios, and consequent impairments in tasks such as orientation discrimination and motion detection.

Human studies utilizing Magnetic Resonance Spectroscopy (MRS) have provided indirect support for this hypothesis, demonstrating that reduced cortical GABA concentrations correlate with impairments in various visual tasks, including orientation discrimination and motion perception (Pitchaimuthu et al., 2017; Chadnova et al., 2019). For example, Pitchaimuthu et al. (2017) observed that lower GABA levels in visual cortex regions were associated with decreased performance on orientation discrimination tasks in older adults, suggesting a link between neurotransmitter levels and perceptual capabilities. Similarly, Chadnova et al. (2019) demonstrated that reduced GABA concentrations correlated significantly with diminished motion perception accuracy, further supporting the connection between inhibitory neurotransmission and declines in visual function in aging populations. These converging lines of evidence support the hypothesis that the age-related decline in inhibitory neurotransmission, particularly involving GABA, contributes significantly to the observed deficits in motion and orientation perception in older adults.

5.4. The Contrast Gain Hypothesis

Schallmo et al. (2018) provide a compelling argument for a simpler explanation of spatial suppression and summation effects observed in human visual motion perception. Rather than invoking physiological excitatory or inhibitory mechanisms, the authors proposed that divisive normalization can explain the data on summation and suppression. Divisive normalization is well-specified computationally, but an intuitive sense of the computation is as follows. Suppose we assume that a given neuron's activity is divided by a factor related to the summed activity of surrounding neurons. In that case, the visual system utilizes the neural activity as an ensemble to normalize the output based on the strength of the input, thereby maximizing its dynamic range in response to the visual stimulus. In other words, divisive normalization allows the visual system to optimize information transmission to subsequent processing mechanisms across different stimulus conditions.

Schallmo et al. (2018) conducted a comprehensive set of experiments using psychophysics, functional magnetic resonance imaging (fMRI), pharmacology, and magnetic resonance spectroscopy (MRS) to support their hypothesis. Most relevant to this thesis are the results of the pharmacological intervention study. The benzodiazepine lorazepam, which acts as a GABA receptor agonist, was administered to humans who were required to perform a task identical to our Motion task. In a crossover design with a washout period, observers then performed the task after taking a placebo. However, it should be noted that the dosage of lorazepam was 1.5 mg, which is minimally therapeutic, if at all (Ghiasi et al. 2023).

The authors proposed that if suppression depends on GABA-mediated inhibition, then increasing GABA signalling (e.g., pharmacologically) should correspond with increased duration thresholds, particularly for large stimuli where suppression is greatest. However, the study's results revealed that increasing inhibition with lorazepam did not lead to stronger suppression; in fact, lorazepam administration led to weaker spatial suppression compared to the placebo. Firstly, lorazepam increased thresholds across all conditions to varying degrees. Secondly, the effect of lorazepam was stronger for smaller stimuli at both low and high contrast, reducing the difference in thresholds between smaller and larger stimuli. This indicates a decrease in spatial suppression, which is the opposite of what would be expected if the underlying mechanism involved GABA-mediated neural inhibition. Additionally, MRS measurements of GABA in the visual cortex did not show a significant correlation with suppression strength.

Schallmo et al. (2018) propose that a normalization model is a good fit for the suppression data. In particular, higher thresholds for smaller stimuli after administering lorazepam may be explained by the normalization model, which reduces the strength of the input, or in other words, reduces the contrast gain. Lowering contrast gain would raise thresholds for small stimuli but have little effect for large stimuli, so it is proposed that the effect of lorazepam reducing spatial suppression is more consistent with reduced contrast gain. This effect likely localizes to brain regions relevant to motion perception, particularly region MT.

Digging into the details of the normalization model described above, it is worthwhile to illustrate how it works. This is a direct application of a model that has been established in the literature (Reynolds & Heeger, 2009). It defines two functions, labelled E and S, which are multi-variable functions that describe a term known as the drive for excitation and suppression:

$$E(x,\theta,c) = e(x_{w_e},\theta_{w_e}) * N(x,\theta,c) \qquad \text{[S1]}$$

$$S(x,\theta,c) = e(w_{w_s},\theta_{w_s}) * E(x,\theta,c) \qquad \text{[S2]}$$

The variables are as follows: x is the spatial extent of the stimulus. In our methods, our measure of x is 2σ, based on the Gaussian envelope. θ is a parameter for orientation, which with our stimulus represents orientation within a range of ±2 degrees. Variable c represents the contrast of the stimulus. The function N is called a neural image and represents a population response to a given input stimulus. Functions S and E are two-dimensional Gaussians that represent the selectivity (or tuning width; see our Figure 1 for a one-dimensional example) for excitation and suppression.

How does one use Equations 1 and 2 to obtain a threshold? To do this, the quantity R, or response rate, which can be thought of as a neuron or ensemble of neurons firing at some number of spikes per unit of time, is computed from outputs of the excitatory E and inhibitory S functions defined in equations 1 and 2 with parameters x, θ, and c selected from our stimulus parameters to obtain:

$$R = \frac{E}{S+\sigma} \qquad \text{[S3]}$$

E and S are defined as above, but σ is not to be confused with our parameter for size constant; it is referred to as the semi-saturation constant, which is a free parameter in the model expressed in arbitrary units, and is a scalar value. The semi-saturation constant influences how the neural response (R) saturates as the input contrast increases.

Schallmo et al. (2018) used values of $\sigma = 0.0002$ or $\sigma = 0.0001$ in their work. To compute a duration threshold level of responding *T,* the model requires two additional steps, as shown in the Equations below. The predicted threshold *T* depends on the ratio of the maximum response rate (R) and a criterion level β. The criterion level β is a free parameter in arbitrary units; Schallmo allows it to vary based on the input contrast, *c*.

That gives us the equation:

$$T = \frac{\beta(c)}{max(R)} \qquad \text{[S4]}$$

Equations 1–4 now provide us with a curve-fitting procedure, as they represent the optimal values for the parameters that describe the data based on our stimuli[1]. We could use the values of the stimulus contrast and the size of the stimulus used in our experiments as inputs; however, this modeling is beyond the scope of this thesis[2].

Note that Schallmo et al. (2018) employed a pharmacological intervention using lorazepam, a benzodiazepine drug and GABA-A receptor agonist, to investigate its influence on spatial suppression mechanisms. They reported that, contrary to what was hypothesized, lorazepam administration did not significantly alter the overall pattern of spatial suppression effects. The hypothesis was rooted in the premise that spatial suppression fundamentally depends upon GABA-mediated inhibitory processes, and so enhancing GABAergic

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[1] However, a methodological flaw is that Schallmo et al., 2018 used the square-root of stimulus contrast as an input to their model when testing the effect of lorazepam, which adds a free parameter to the model and essentially assumes contrast gain explains their effect before fitting. They justify this decision because duration thresholds were longer across all conditions when administered lorazepam versus a placebo, see their Fig. 4 panel D. However, focusing on their data in Fig. 4 suggests that slope of the stimulus size versus duration threshold differs between the subjects administered lorazepam versus a placebo at 98% contrast. Of course, we tested neither lorazepam nor 98% contrast.

[2] However, a table of parameters fit for the model are shown in the appendix. The values all hover around 100 and never approach the 0.85 assumed by Schallmo for lorazepam.

inhibition pharmacologically should have heightened duration thresholds, especially for larger, high-contrast stimuli where spatial suppression is typically pronounced.

Our experimental intervention differs methodologically, as we introduced cognitive uncertainty—specifically, response uncertainty and response order uncertainty—as the modulatory factor rather than pharmacological manipulation. Despite this difference, both interventions aim to modulate inhibitory processing mechanisms underlying spatial suppression. Schallmo et al. (2018) modelled their GABAergic manipulation mathematically, suggesting that the effect of lorazepam could be represented through a reduction in input contrast or overall signal strength (contrast gain), effectively mimicking diminished stimulus intensity. This conceptualization posits that increased inhibitory action through lorazepam paradoxically results in reduced neural responsiveness, analogous to decreasing input contrast.

However, applying this analogy to our uncertainty manipulations presents a theoretical challenge. Increasing cognitive uncertainty via task demand would intuitively seem more consistent with adding noise rather than reducing the strength of the visual signal itself. Thus, while lorazepam acts pharmacologically at a neuronal receptor level to reduce effective signal strength, our cognitive uncertainty intervention potentially introduces variability or noise at a perceptual decision-making or attentional stage, rather than directly altering neural responsiveness to contrast. Further computational modeling studies, particularly those employing a signal detection or noise-integration framework, could clarify whether the cognitive uncertainty we imposed aligns more closely with changes in contrast gain or with increases in internal noise.

5.5. Conclusion and Future Directions

Our findings demonstrate that a minor modification to the stimulus used by Tadin et al. (2003)—specifically, invoking response uncertainty and response order uncertainty via a Visual Short-Term Working Memory (VSTWM) load—abolishes the classic spatial suppression effect. This indicates that uncertainty manipulations, such as those presented in this study, can modulate spatial suppression and summation. Moreover, response uncertainty and response order uncertainty were found to decrease spatial suppression in larger stimuli and make older observers perform similarly to younger observers for motion tasks (see Figures 8 and 10).

These results align with broader literature suggesting that cognitive factors, including uncertainty and attentional load, can influence early visual processing. For instance, studies have shown that increased cognitive load can modulate early stages of visual perception, affecting tasks such as contrast detection and motion discrimination (Lavie, 2005; Forster & Lavie, 2008). Studies by Lavie (2005) and Forster and Lavie (2008) propose that increasing cognitive or perceptual load can paradoxically enhance selective attention by reducing processing capacity available for distractors. These studies demonstrated that under higher cognitive load, observers become less susceptible to distraction by irrelevant stimuli, thereby modulating perceptual and attentional performance. This explanation from a cognitive neuroscience perspective can help explain how introducing cognitive uncertainty in our study reduced spatial suppression and improved older adults' visual processing performance.

Considering future directions, if uncertainty can make “old look like young,” then counterintuitively, perhaps adding an irrelevant task could improve older adults' ability to learn new information and skills. For example, older individuals often have a harder time learning and remembering new routes. By integrating an irrelevant secondary task while learning a new route, such as counting pedestrians or identifying building types while navigating, this may generate uncertainty and boost their performance. Similarly, older individuals often struggle with technology; performing an irrelevant task such as switching between font sizes or display modes may similarly enhance their performance. Future studies can explore the role of combining a simple task simultaneously with a more complicated main task to examine older observers’ performance relative to young individuals.

Moreover, this study’s findings may be applied even within the NECO population. It is becoming increasingly evident that our student body is under increased cognitive load, with concerns of anxiety before proficiencies and exams, and an inability to filter information to focus on relevant details. Exploring the impact of anxiety on performance can be studied in the lab, perhaps even using a fast version employing adaptive methods (Bergsma et al., 2007; Watson, 2017; Skerswetat et al., 2024) or possibly via web-browser platforms (De Leeuw, 2015), given that high-refresh rate monitors (>100 Hz) are common. Given that other non-sensory factors seem to correlate with spatial suppression (Melnick et al., 2013), perhaps a validated anxiety questionnaire (Baker et al., 2015), such as the Anxiety Symptoms Questionnaire (ASQ), could correlate with suppression/summation measures with or without uncertainty, after statistically controlling for baseline personality traits.

Overall, this study demonstrates a link between behavior and spatial suppression and summation. By simply introducing increased cognitive demand, we observe significant shifts in the performance of young and older individuals. These findings underscore the importance of considering cognitive factors, such as uncertainty and attentional load, in the study of visual perception and aging. Future research exploring these interactions, may help to develop interventions that leverage cognitive strategies to mitigate age-related declines in visual processing.

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Appendix

Table M1: Subject demographics and preliminary testing scores

Subject	Sex	Age	Morningness-eveningness score	MoCA score
1	F	23	32	N/A
2	M	24	70	N/A
3	F	27	53	N/A
4	M	25	47	N/A
5	F	24	66	N/A
6	F	23	50	N/A
7	F	22	27	N/A
8	F	24	71	N/A
9	F	25	40	N/A
10	F	22	36	N/A
11	M	25	37	N/A
12	F	26	23	N/A
13	F	27	59	N/A
14	F	23	46	N/A
15	M	76	77	26
16	M	75	68	27
17	M	65	58	27
18	M	86	66	26
19	F	77	80	27
20	M	68	62	26
21	M	65	49	28

Table YR1: Pairwise comparisons for Figure 12 $\Delta\tau_{\text{size}}$

Contrast	Task 1	Task 2	N Pairs	t	df	p (raw)	Mean Diff (s)	CI Low (s)	CI High (s)	d (effsize)
0.02	Motion	Motion Uncertain Response	13	7.492	12	0.0000	0.0602	0.0427	0.0778	1.987
0.02	Dual-dimension Motion	Motion Uncertain Response	13	5.328	12	0.0002	0.0584	0.0345	0.0822	2.125
0.02	Motion	Dual Response Uncertain Order	13	9.057	12	0.0000	0.0779	0.0591	0.0966	2.217
0.02	Dual-dimension Motion	Dual Response Uncertain Order	13	5.269	12	0.0002	0.0760	0.0446	0.1074	2.573
0.225	Motion	Motion Uncertain Response	13	7.481	12	0.0000	0.0672	0.0477	0.0868	3.299
0.225	Dual-dimension Motion	Motion Uncertain Response	13	5.863	12	0.0001	0.0609	0.0383	0.0835	2.357
0.225	Motion	Dual Response Uncertain Order	13	11.637	12	0.0000	0.0828	0.0673	0.0983	4.073
0.225	Dual-dimension Motion	Dual Response Uncertain Order	13	9.421	12	0.0000	0.0764	0.0588	0.0941	2.934

Table YR2 - Pairwise comparisons for Figure 13 $\Delta\tau_{\text{contrast}}$

Stim Size	Task 1	Task 2	t	df	p	Mean Diff (s)	CI Low (s)	CI High (s)	d (effsize)
0.7	Dual-dimension Orientation	Orientation Uncertain Response	-2.414	12	0.0327	-0.0394	-0.0749	-0.0038	-0.968
0.7	Orientation	Orientation Uncertain Response	-1.984	11	0.0727	-0.0290	-0.0612	0.0032	-0.871
5	Dual-dimension Orientation	Orientation Uncertain Response	-0.413	12	0.6869	-0.0032	-0.0202	0.0137	-0.128
5	Orientation	Orientation Uncertain Response	0.578	11	0.5747	0.0051	-0.0142	0.0243	0.273

Table M2 : Reynolds & Heeger Model Fits to the Model proposed by Schallmo et al., 2018

Condition	**Criterion beta(k)**	**Response Scalar A**	**Semi-saturation (sigma)**	**Excitatory width (xw_e)**	**Suppressive width (xw_s)**
Motion	5.690	94.329	1e-06	0.3449	1.483
Dual-Dimension Motion	5.625303	93.448915	0.000244	0.362383	1.626283
Orientation	1.654	106.835	7.1e-05	339.971	339.971
Dual-Dimension Orientation	1.642	107.186	7.6e-05	325.964	325.964
Motion Uncertain Response	4.848	91.904	1.6e-05	204.644	204.644
Orientation Uncertain Response	4.866	91.442	1.5e-05	211.231	211.231
Dual Response Uncertain Order	5.018	90.181	2e-05	212.785	212.785