MOTION PERCEPTION AND AGING

THE EFFECTS OF AGING ON MOTION PERCEPTION IN HEALTHY OLDER ADULTS

By

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Abstract

The effects of aging on motion perception in healthy older adults

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Motion perception is required for nearly all aspects of daily living. It is fundamental to our ability to move within, and interact with, our dynamic environment. Previous work has shown that the ability to perceive a variety of different types of motion is significantly affected by increasing age. The programme of research described in this thesis further probes the complex effects of aging on motion perception using a number of different stimulus configurations and performance measures.

In order to relate psychophysical performance to neurophysiological recordings, we used two different notched-noise masking techniques to estimate the directional selectivity of masking in younger and older adults (Chapters 2 and 3). We found evidence to suggest that the directionally-selective mechanisms of older adults are more broadly tuned than their younger counterparts, which is consistent with the animal literature that links decreased neural inhibition with broader directional tuning. Behaviourally however, task-specific contrast sensitivity may play a role in explaining that result. We also uncovered a previously unobserved difference between horizontal and vertical motion perception which bears further study. In Chapters 4 and 5 we tested peripheral motion perception both under focused and divided attentional conditions. Older adults were impaired compared to younger adults when asked to make judgments about motion patterns in the peripheral vision field, but they were not differentially impaired under divided attention conditions. This has implications for the design and implementation of driver fitness testing, especially as it relates to the difficulty of the perceptual tasks used to assess a driver's competency.

The findings presented in this thesis paint a more complex picture of how increasing age impairs motion perception than previously described. Specifically, our observations show that age effects interact with stimulus contrast, attention, and motion direction, and these interactions each present an interesting avenue for further exploration.

Preface

This thesis comprises 6 chapters. Chapters 2-5, presenting the main research, were written collaboratively with my supervisors, Drs. Allison Sekuler and Patrick Bennett. Together we designed all the experiments and developed the research questions underlying them. Patrick Bennett programmed the template software for running a variety of experiments in our lab and I independently modified it as needed for my particular research. Most of the data collection was done by our research assistant, Donna Waxman, with occasional assistance from me or from undergraduate research assistants. The analyses, interpretation of the data, preparation of chapter drafts, and editing of the thesis chapters was done together with my supervisors.

No part of this thesis has been published elsewhere. Portions of Chapters 2-5 have been presented at Vision Science Society meetings (from 2008-2011 in Naples, Florida) and portions of Chapters Chapters 4 and 5 were presented at the 2009 Society for Neuroscience meeting in Chicago, Illinois.

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For my parents and for my brother,
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Chapter 1

Introduction

The 2007 Nobel Prize in Literature was awarded to Doris Lessing. She is quoted by The Sunday Times (London, May 1992) as saying,"The great secret that all old people share is that you really haven't changed in seventy or eighty years. Your body changes, but you don't change at all. And that, of course, causes great confusion". In some ways, this quote nicely encapsulates the societal relevance of this dissertation. The entire body shows age-related changes, and the brain itself is no exception. Some bodily changes are obvious; joint problems, sensory changes and even wrinkles can make themselves known through daily life. Less obvious though, are changes in the brains of older adults that can affect visual perception, and ultimately behaviour. The focus of this dissertation is these neural and perceptual changes and how they affect motion perception in older human adults. These are the sorts of changes that, as Ms. Lessing puts it, can cause confusion. When an impairment is invisible and cannot necessarily be diagnosed within a traditional medical framework, it can be difficult to convey its importance and severity.

Visual perception in general can be a difficult concept to explain. How do you convey the notion that what you see is not a direct representation of the light hitting your eyes, but rather, a complex interpretation of that light as its information is passed along a string of brain areas? Classic visual illusions, such as the Kanizsa Triangle, for instance (where you see a triangle created entirely from illusory contours), underscore this point perfectly; your brain fills in what it thinks your eyes should be seeing. Not only does the visual system conduct increasingly complex analyses of the visual input, but other neural systems (such as the motor or auditory systems) also tap into this information to guide our actions and contribute to perception.

Given the inherent difficulty of perception, imagine how it might change with age. We know that the population of Canada and the world is aging. The relative proportion of adults over the age of 65 is going to increase dramatically over the coming decades (StatisticsCanada, 2010). This presents a unique challenge to all aspects of society, but especially to the health care system. As age increases so does the incidence rate for many ailments and diseases. Changes in the memory and frontal areas of the brain can lead to cognitive impairments, even in the absence of disease (Andrews-Hanna et al., 2007), but changes in other parts of the brain can affect seemingly simpler processes, such as visual perception (Owsley, 2011). This dissertation describes a series of experiments that investigate age-related changes in motion perception, specifically for the skill of direction identification. The extent of these changes needs to be explored so as to better inform both the medical community and the public themselves.

Evolutionarily, motion perception is an ancient ability. Not only do we need to perceive the motion of objects or people around us, we also need to correctly understand and navigate our own self-motion through the world and use motion cues to maintain our balance and posture. Primitive creatures are typically able to sense motion (sometimes as movement of a light source) and respond to it by orienting or performing some other action (such as the flicking of a tongue in frogs to catch moving prey, (Goodale, 2011)). These simple responses have evolved into increasingly complex ones that now include, for human hockey goalies, actions such as catching a puck being shot towards them at over 100 km/h. In order to accurately respond to motion, creatures or individuals need to know the direction of motion of their target.

Before even considering visual perception at the neural level, let us first discuss the effect of age on the eyes and the early part of the visual pathway. Beginning in the eye, there is a decrease in the number of photoreceptors with age and changes in the distribution of rods and cones (Conn, 2006; Bonnel et al., 2003; Polidori et al., 1993). The lens also yellows, changing the quantity and quality of light hitting the retina. This, in turn, also leads to decreases in contrast sensitivity; older adults often need more contrast to make discriminations than younger adults do (Allen et al., 2010). Additionally, these optical changes together result in decreased acuity for older adults. Though a number of changes have been observed in this early part of the visual pathway, it seems that the next few stages are not particularly affected by aging. The optic nerve, lateral geniculate nucleus (LGN) and optic tract do not appear to show any age-related changes that affect perception or transmission (Spear, 1993). Once we reach the cortex, however, we once again begin to see the effects of age.

In some animals, such as rabbits, directional selectivity begins in the retina (Barlow and Hill, 1963), and recent work has been exploring the circuitry underpinning this retinal selectivity (Vaney and Sivyer, 2012). For other animals, including humans, directional selectivity begins in area V1, where neurons bringing visual information from the LGN meet the striate cortex. Here, directionally-selective cells each respond preferentially to certain directions (Hubel and Wiesel, 1959). This information is then passed on to higher, more upstream, visual cortical areas where it is combined with other afferent information to interpret complex visual motion (Orban, 2008; Goodale and Milner, 1992). It is this combination and interpretation of visual input that allows humans to see and interact with our rich, 3-dimensional moving world.

Work on older cats and primates has shown that directionally-selective cells in V1 and V2 have broader tuning - that is, they are not as preferentially sensitive to direction as cells in younger animals (Schmolesky et al., 2000; Yu et al., 2006). This kind of reduction in directional selectivity has also been found in area MT of primates (Liang et al., 2010). This has important consequences for motion perception in particular, as these types of cells are the ones that signal directional information to other areas of the brain and interpret incoming directional information. Additional changes in the aging cortex include increased overall noise and spontaneous activity (Hua et al., 2006; Wang et al., 2006; Yang et al., 2008) and decreased visual response latencies (Wang et al., 2005), both of which can affect the way the brain understands and acts upon all sensory input. The observed changes in tuning may be the result of changes in the inhibitory neurotransmitter system in the brains of older animals. This idea is supported by recent work observing decreases in GABA-ergic neurons in senescent cats (Hua et al., 2008) and showing that GABA agonists improve visual cortical function in senescent primates (Leventhal et al., 2003). Molecular investigations into neurotransmitter changes in older human brains have also revealed complex interactions between levels of different neurotransmitters (Williams et al., 2010; Pinto et al., 2010). While it is far from clear exactly how all of these chemical changes interact, specifically with respect to neural inhibition, they undoubtedly play a role in age-related changes in the cortex and can contribute to behavioural effects, such as surround suppression (Betts et al., 2005; Fu et al., 2010).

Changes to specific parts of the visual pathway result in perceptual changes but it is also worth noting that the functioning of the entire brain as a whole also shows changes with age. The functional network of interconnected brain areas that is involved in certain cognitive tasks reorganizes itself with age - the older brains use different areas of the brain to achieve the same results as younger adults (Davis et al., 2008; Bennett et al., 2001; Cabeza et al., 2002). One could imagine that if an older brain tried to recruit an already impaired perceptual area to aid in a complex cognitive task, then the performance deficit would be compounded and far more noticeable.

Compared to younger adults, older adults have different patterns of performance on motion perception tasks. They are impaired when asked to detect motion or to discriminate the direction of motion (Bennett et al., 2007; Billino et al., 2008; Gilmore et al., 1992; Porciatti et al., 1999; Snowden and Kavanagh, 2006; Tran et al., 1998) and have difficulty extracting information from optic flow (Atchley and Andersen, 1998). They are less able to perceive speed (Norman et al., 2003) and this likely contributes to their inability to accurately detect collisions (Andersen and Enriquez, 2006; Andersen et al., 2000; DeLucia et al., 2003) or judge times to collision when making street crossing decisions (Lobjois and Cavallo, 2007). They are less able to extract form information (Mckendrick et al., 2010) and perceive apparent motion (Roudaia et al., 2010) and this extends into perceiving point-light walkers (Pilz et al., 2010; Legault et al., 2009). Perceptual abilities and age can also interact with psychiatric and medical conditions (Golomb et al., 2009; Bidwell et al., 2006; Jackson and Owsley, 2003; Kavcic et al., 2010; Petroff et al., 1996).

We have learned a great deal about how motion perception changes with age, but we do not, by any means, have a complete picture of the age-related impairments. One of the goals of this dissertation, therefore, was to continue to explore the ways in which older adults demonstrate behavioural changes on a directional discrimination task. Do different paradigms reveal different sorts of deficits? How does performance on central and peripheral motion stimuli compare? Within the older adult population itself, does increasing age result in greater perceptual changes? A second goal of this dissertation was, in part, to see if we could find behavioural evidence for the broader directional tuning seen in neurophysiological work. Can we find evidence to suggest that older adults have more broadly tuned directionally-selective cells, and therefore poorer directional sensitivity, in a non-invasive laboratory setting?

1.1 Thesis Overview

By combining different psychophysical techniques (noise masking, threshold measures and accuracy measures) we are able to examine age-related motion perception from a number of differing viewpoints. The contribution of this thesis to the greater scientific community is a deeper understanding of age-related perceptual changes as well as a number of unique directions for future work. These results, in turn, may help form the basis for preventive or therapeutic measures for older adults, such as improved driver training as part of the relicensing process, which could have a tremendous impact on society.

This thesis is presented in six chapters: this introductory chapter, four chapters of experimental results and a final concluding chapter. Chapter 2 introduces us to the notion that age-related neuronal changes can be observed using behavioural perception tasks. We employed a masking paradigm to measure contrast motion discrimination thresholds. Older adults show evidence of broader directional tuning that appears to related to contrast sensitivity for moving patterns.

In Chapter 3 we again used a masking technique but altered the performance measure to eliminate the impact of age-related contrast sensitivity on masking strength. Here we again found evidence of broader directional tuning, suggesting that this result is not paradigm-specific. We also compared vertical and horizontal motion perception and found a difference in the pattern of deficits for our older adults. There appears to be something uniquely difficult about making vertical motion judgments, and these results were not likely due to eye movements during stimulus presentation.

In Chapters 4 and 5 we began to explore peripheral motion perception. In Chapter 4 we measured contrast thresholds for moving dot patterns presented within a large ring, or annulus. This moved the motion stimulus into the near visual periphery. Older adults were, again, impaired compared to younger adults.

Finally, in Chapter 5 we changed our response measure to accuracy and measured how motion perception changes with the addition of a central attentional task signal. When comparing performance on the focused and divided attention conditions we found that older adults were not differentially impaired when asked to divide their attention, but the cost of dividing attention was greater when signal coherence was higher and stimuli were in the left visual field.

At the beginning of this introduction a quote from Doris Lessing set the tone for this dissertation. Age-related changes may not always obvious, and so, they could very easily be misperceived. In our work with healthy, independent older adults we found meaningful age differences using very simple perceptual tasks. We found behavioural evidence of neural changes, as well as changes in behavioural performance in older adults that result in impaired motion perception. Motion perception deficits in older adults have the ability to dramatically impact the daily lives of all people, not just those who are impaired. By building on the results described in this dissertation, the research community will have a greater understanding of age-related perceptual changes, and medical professionals or policy makers may be able to devise ways to keep older adults and those who interact with them, safe and healthy for as long as possible.

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Chapter 2

The effect of aging on the bandwidths of directionally-selective mechanisms

Abstract

Psychophysical studies show that motion detection thresholds are elevated, and the accuracy of perceived direction is diminished, in older human subjects. Neurophysiological studies in older monkeys and cats also have shown that the bandwidth of directionally-selective cortical neurons widens with age. It is not known, however, if older human adults also show this age-related neuronal change. The current experiments examined this question by estimating the directional selectivity of masking in a group of younger adults and two groups of older adults using a notched-noise masking technique. Both Junior-Senior (60-70 years) and Senior-Senior ($>$ 70 years) adults had motion detection thresholds that were higher than thresholds in younger adults, and for both groups, the directional selectivity of masking was significantly broader than in Young ($<$ 30 years) adults. We conclude that human adults show age-related bandwidth changes in their directionally-selective mechanisms, mirroring recent animal results, and this difference may be related to contrast sensitivity for moving patterns, rather than age *per se*.

2.1 Introduction

It is well known that human biological and perceptual processes change with age, and the visual system is no exception (Owsley and McGwin, 2010; Faubert, 2002; Spear, 1993). For instance, several age-related changes that occur within the eye, such as the clouding of the lens, the thinning of the retina, the decrease in blood perfusion, and the loss of rod photoreceptors, can impact visual performance, especially in the peripheral visual field (Conn, 2006; Polidori et al., 1993; Bonnel et al., 2003). Less obvious though, is how physiological and anatomical changes that occur beyond the retina (e.g., the cortex) affect perception. The experiments described below use a behavioural psychophysical task to determine if such changes produce age-related changes in one aspect of visual perception, namely the perception of motion.

Many studies have shown that increasing age is associated with increased impairment in processing complex motion scenes, including judging times to collision (Andersen and Enriquez, 2006; Lobjois and Cavallo, 2007), extracting cues from optic flow information (Atchley and Andersen, 1998) or making judgments about biological walkers (Legault et al., 2009; Pilz et al., 2010; Kavcic et al., 2010). These impairments are found not only in complex tasks, but in simpler ones as well. Bennett et al. (2007), for example, showed that elderly participants were less able to detect coherent motion in random dot kinematograms. Adults over 70 years of age in particular were significantly less accurate at identifying the direction of motion, even when the motion was detected. In addition to subjective motion detection impairments, Tran et al. (1998) used optokinetic nystagmus (i.e., an objective measure of motion detection) and found age-related deteriorations with that measure as well. Other groups have found similar age-related impairments when subjects are asked to perceive and discriminate differences in speed (Norman et al., 2003), and Roudaia et al. (2010) found that spatial and temporal integration windows that underlie apparent motion were decreased in older adults.

It generally is assumed that the discrimination of the direction of motion is ultimately limited by the directional tuning properties of visual neurons. From the pioneering work of Hubel and Wiesel (1962) we know that many neurons in primary visual cortex are directionally selective: they tend to respond better to some directions of movement than others. This pattern of selectivity continues into higher visual areas and has been studied extensively (see Orban, 2008, for a review). In both senescent monkeys and cats, directionally-selective neurons in early visual areas show broader tuning functions than their younger counterparts (Hua et al., 2006; Schmolesky et al., 2000; Yu et al., 2006). Electrophysiological results suggest that this broadening may be linked to a decrease in the functionality of inhibitory GABA-ergic mechanisms present in these elderly animals. For example, when a GABA agonist was applied to broadly tuned V1 cells in senescent monkeys, the senescent cells' tuning became narrower and resembled the tuning of neurons in younger monkeys (Leventhal et al., 2003). Additionally, at least in cats, it has been shown that there is a decrease in the overall density of GABA immuno-reactive neurons in V1 that occurs with age, and a reduction in the ratio of these neurons to the total number of neurons in V1 (Hua et al., 2008). Based on their psychophysical experiments documenting an age-related decrease in surround suppression of moving stimuli, Betts et al. (2005) suggested that the GABAergic system may be less effective in older humans as well, and Pinto et al. (2010) have found some evidence from analyses of post-mortem tissue consistent with that idea.

The results from Bennett et al. (2007) are consistent with a computational model that includes multiple directionally-selective channels with broader tuning and elevated noise in older subjects. The current experiments evaluated this idea by using notched-noise masking to estimate the behavioural directional tuning in younger and older observers. Notched masking has been used to measure the frequency selectivity of auditory filters (Patterson, 1976) and to estimate the orientation selectivity of visual filters (Govenlock et al., 2009). A similar type of masking paradigm also has been used to investigate detection thresholds in cyclopean (Cobo-Lewis and Yeh, 1994) and binocular vision (Henning and Wichmann, 2007). Using notched-noise masking, we will be able to estimate how age affects the properties of behavioural tuning functions in human adults. In a set of control experiments, we also examined the effect of mask contrast and of signal coherence on direction of motion discrimination.

2.1.1 Methods

Subjects

Three groups of subjects were recruited from the McMaster University community and the surrounding neighbourhoods: Young (Y, under 30 years old), Junior-Senior (JS, 60-70 years old) and Senior-Senior (SS, over 70 years old). Table 2.1 shows the mean age, near and far visual acuity, and contrast sensitivity (as measured by the Pelli-Robson sensitivity chart) for all three groups of subjects in all experiments. Mini-Mental

Table 2.1: Number of subjects, age, acuity, contrast sensitivity and Mini-Mental State Exam (MMSE) scores for all subjects in the three experiments.

Expt	group N (# females)	Age μ (σ)	Near acuity μ (σ)	Far acuity μ (σ)	Pelli-Robson μ (σ)	MMSE μ (σ)
2.1	10 Y (5)	21.0 (3.23)	1.46 (0.23)	1.37 (0.22)	1.95 (0.00)	N/A
	21 JS (10)	65.3 (2.08)	0.99 (0.21)	1.16 (0.19)	1.94 (0.03)	29.2 (1.21)
	22 SS (12)	74.5 (5.90)	0.97 (0.35)	0.97 (0.31)	1.88 (0.12)	29.1 (1.17)
2.2	6 Y (3)	23.3 (1.63)	1.56 (0.15)	1.55 (0.21)	1.95 (0.0)	N/A
Coherence	6 JS (3)	65.3 (2.88)	0.82 (0.30)	1.20 (0.26)	1.93 (0.06)	28.5 (1.38)
control	6 SS (3)	74.2 (1.33)	0.91 (0.22)	0.99 (0.44)	1.95 (0.00)	29.5 (0.84)
2.3	6 Y (3)	22.7 (3.50)	1.39 (0.16)	1.36 (0.17)	1.93 (0.06)	N/A
Contrast	6 JS (3)	65.0 (2.00)	0.91 (0.21)	1.17 (0.32)	1.95 (0.00)	29.2 (0.41)
control	6 SS (3)	73.8 (0.75)	0.93 (0.20)	1.03 (0.45)	1.95 (0.0)	28.8 (1.60)

State Exam (MMSE) scores are also included for older subjects. We also administered a questionnaire to ensure that all subjects had good health, visual or otherwise. All procedures were approved by the McMaster Ethics Review Board, and subjects were compensated for their time at a rate of \$10/hour.

Apparatus and Stimuli

The experiment was programmed in MatLab v7.4 (The Mathworks) using the Psychophysics and Video Toolbox (Brainard 1997; Pelli 1997) running on an Apple G4 PowerMac computer. The monitor had a resolution of 1280 × 1024 pixels and a refresh rate of 75 Hz. Average luminance was 30 cd/m^2. The room was dark, and the only light came from the display screen, which subtended 17.2 x 13.5 deg of visual angle when subjects were seated 114 cm away. Head position was maintained using a chin/forehead rest. Responses were made by pressing one of two keys on a standard QWERTY Macintosh keyboard.

In the centre of the screen was a fixation point. Five hundred drifting dots were displayed in an annulus that was centered on the fixation point and had inner and outer radii of 1 and 12 deg, respectively. Each square dot had a diameter of 6 pixels, subtended a visual angle of 0.08 deg, and drifted at a speed of 5 deg/sec. If a dot moved outside the annulus, or into the inner blank space, it was extinguished and replaced at a new random location within the annulus. Additionally, on every frame, 5% of the dots were extinguished and randomly re-positioned within the annulus.

Of the 500 total dots displayed, 25 (5%) were Signal dots, which moved coherently either to the right (0 deg) or to the left (180 deg), and 475 were Mask dots. The subject's task was to determine the direction of the Signal dots. The direction of each Mask dot was selected randomly from a distribution of directions that varied across conditions. The distribution of directions was created by filtering a uniform distribution (which spanned 360 deg) with two notches that were centered on 0 and 180 deg (Figure 2.1). Each notch had a full width of 2n deg: across conditions, 2n was 0, 10, 20, 30, 40, 50, 60, 80, 120, or 179 deg. These notch widths were chosen to sample the masking effect more frequently close to the direction of the Signal dot motion (i.e., 0 or 180 deg) where, presumably, the initial drop-off in selectivity would occur. The final value of 179 deg was chosen to create a situation in which Mask dots were moving essentially perpendicularly to the Signal dots. All dots were darker than the background luminance. Mask dots had a constant contrast of 0.4, but the contrast of Signal dots was varied across trials using the Quest staircase procedure (Watson and Pelli, 1983) to determine the contrast required to perform the task with an accuracy of 81%.

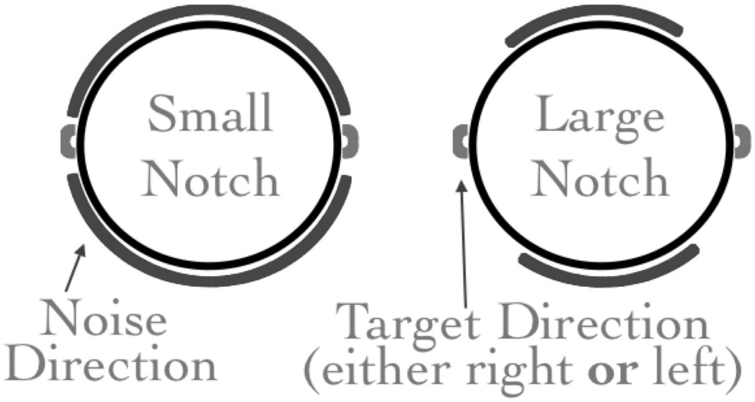

Figure 2.1: A schematic showing how the distribution of Mask dot directions would vary when the notch width was small (left) and large (right). In each figure, the entire 360 deg range of possible directions is represented by a black circle, the distribution of Mask dot directions is represented by large, dark grey semi-circles, and the distribution of Signal dot directions condition is represented by the small, light-grey crescents. On any single trial, the signal dot directions were centered on 0 deg *or* 180 deg.

Hypotheses

Suppose our subjects use directionally-selective mechanisms to determine the direction of motion of the Signal dots. In particular, we assume that subjects discriminate horizontal motion by comparing the responses of filters that respond maximally to motion in the directions of 0 and 180 deg. Adding random, uniformly distributed noise to the signal, as in the no-notch condition, would cause a reduction in sensitivity because the noise interferes with the channels required to determine the Signal's direction of motion (see the left-most panel of Figure 2.2). If we then created a notch in the noise mask, centered around the preferred direction of a given mechanism (as shown in the central panel of Figure 2.2), the bank of filters used to determine the direction of the motion stimulus would now be affected differentially by the noise. Those filters that responded preferentially to the directions within the notch would have a higher signal-to-noise ratio because there would be less noise within the range of directions to which they respond. As the size of the notch increased, the noise would eventually fall outside the channel's preferred region entirely (such as the right-most panel of Figure 2.2), resulting in maximal sensitivity to the original signal. If we plotted threshold as a function of increasing notch width, we ought to see a systematic decrease with increasing notch width (see the black line in Figure 2.3 for an illustration of this idea).

To make these hypotheses more concrete, let us suppose that we are looking at the response of a hypothetical individual directionally-selective mechanism that has a bandwidth of 20 deg and whose preferred response is to motion moving to the right (0 deg). This channel ought to respond maximally when presented with coherent motion moving to the right, but the addition of broadband directional noise will increase the variability of the channel's response and therefore reduce its sensitivity to rightward motion. If we created a notch in the noise stimulus that centered on the preferred direction (0 deg) and was 20 deg wide, then the variability of the channel's response would decrease and therefore it would become more sensitive to the presence of rightward motion. With this more specific example in mind, it is easier to see how changing the tuning properties of the channel itself would result in different patterns of results.

Let us now explore the differences that would result from mechanisms with different tuning properties. If older adults indeed have directionally-selective mechanisms that are more broadly tuned, creating a notch centered around the preferred direction would increase sensitivity and consequently reduce threshold, but the notch would have to be increased much more before it reached maximal sensitivity. Therefore, the function

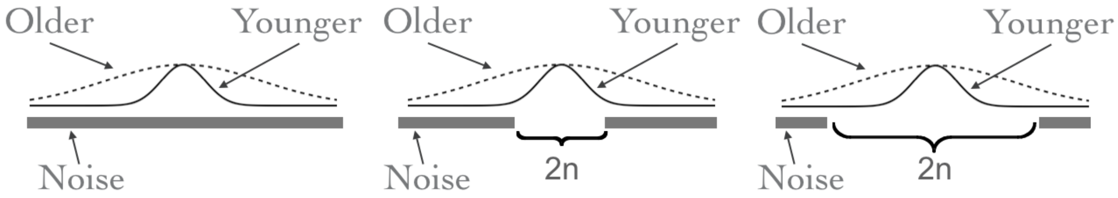

Figure 2.2: A schematic showing how hypothetical young and old directionally-selective mechanisms would be affected by, and interact with, the noise mask. The solid lines represent the tuning profile of the directionally-selective channel in a younger adult, and the dotted lines represent one in an older adult. The grey bar shows the directional bandwidth of the noise mask; as the notch (2n) increases, it interferes less with the preferred direction of the selective mechanism (i.e. the noise does not overlap with the peak of the tuning profile). The noise mask would affect older and younger adults differently because the tuning profiles of older adults are thought to be broader (i.e. the peak is not as defined). A channel with a broader tuning profile would still experience interference from the noise mask even when the notch is large.

relating threshold to notch width ought to have a shallower slope then the corresponding curve obtained with more selective channels (see Figure 2.3).

Another feature of Figure 2.3 is that the grey line is consistently higher than the black line, even at the asymptote, suggesting that older adults have lower overall sensitivity than younger adults regardless of their tuning properties. This result is expected because of the findings that the brains of older cats and primates shower higher rates of spontaneous activity (Hua et al., 2006; Yu et al., 2006) - this increased baseline noise will likely decrease sensitivity even under ideal conditions. For this reason, the schematic depicts the older adults' performance never reaching the same level as that of the younger adults. It is with these expectations in mind that we proceeded with this experiment.

Procedure

Each trial began with the fixation point briefly alternating between black and white to focus the subjects' attention. The fixation point then remained black and the moving dot fields appeared for 500 ms. Subjects were instructed to report the direction (right or left) of Signal dot motion after the dots are extinguished, by pressing the appropriate key on the keyboard. The next trial began 1 s after the response key was pressed.

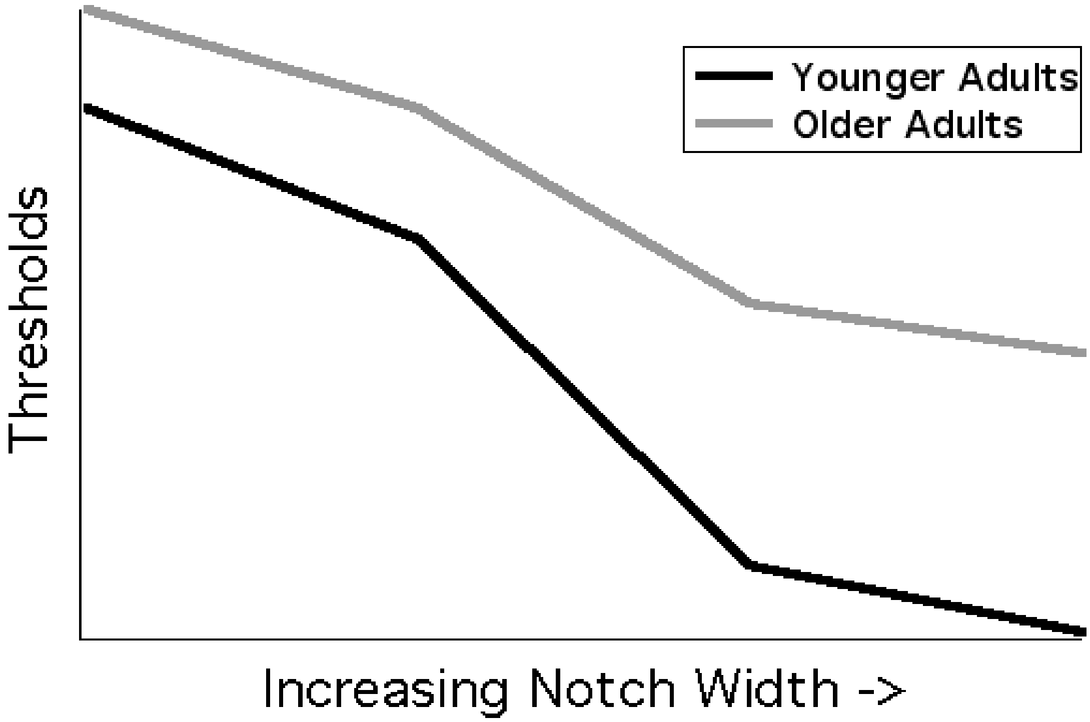

Figure 2.3: A schematic, for illustration purposes, showing how the threshold-vs-mask functions are expected to differ between younger and older adults. The black line represents younger adults and the grey line older adults. The x-axis shows increasing notch width and the y-axis represents thresholds (where lower values indicate better performance). Note that while we would expect the older adults to have overall higher thresholds, their function also shows a shallower slope as notch width increases. The younger adults are expected to have a much steeper drop early on, while the size of the notch is still relatively small. In contrast, the older adults are expected to have a much more gradual response to the increasing notch width. They would not exhibit as great a change in overall performance as a function of notch width.

The first 34 subjects in this study completed 40 trials in each condition; the remaining subjects completed 50 trials per condition[1]. Preliminary analyses failed to reveal any differences between these groups of subjects, and therefore the two groups were combined for subsequent analyses. There were 10 conditions, each using a different notch width, which were block-randomized. Subjects completed two sessions of 10 conditions each on separate days.

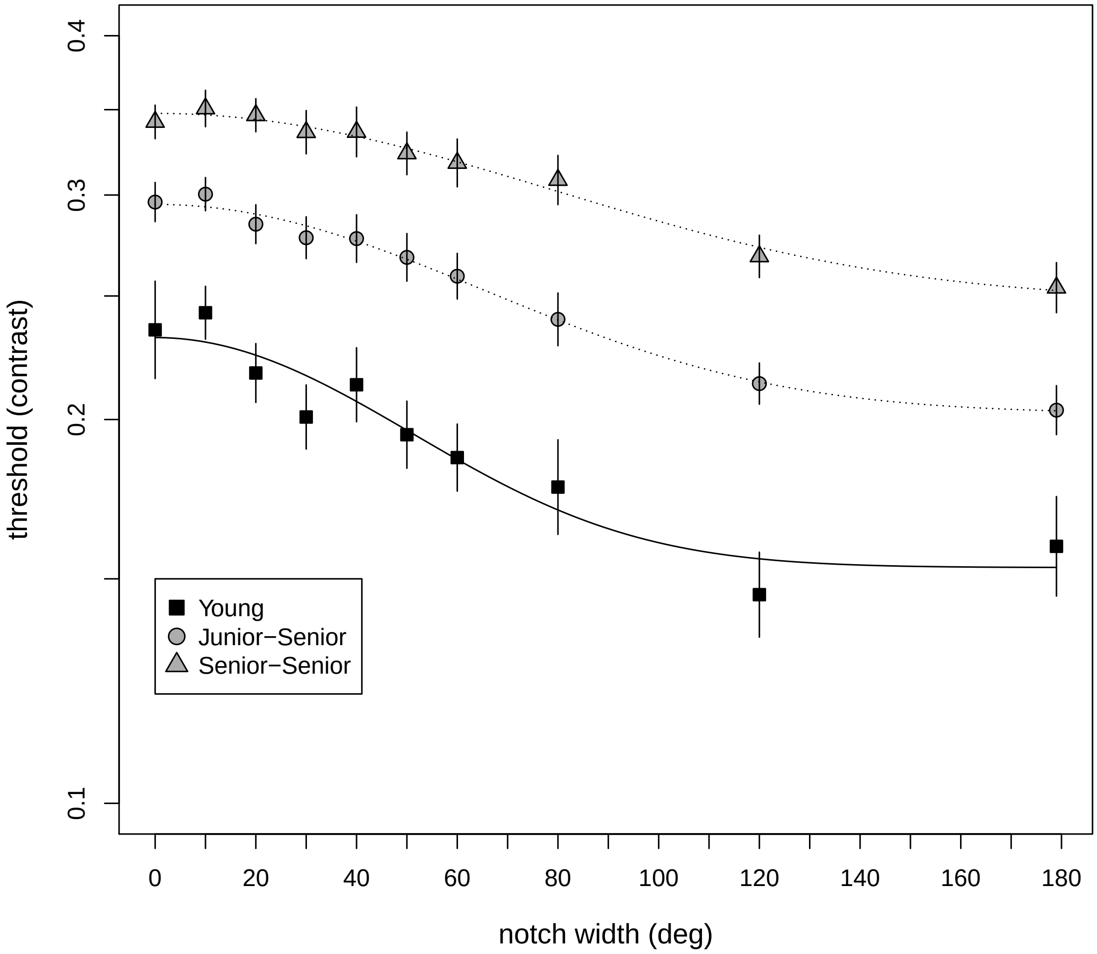

Figure 2.4: A graph showing contrast thresholds obtained as a function of notch width for each of our groups. The points represent mean thresholds and the lines represent best-fitting versions of Equation 2.1. The error bars represent ±1 SEM.

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[1] The number of trials was increased to see if thresholds could be determined more accurately, but the additional trials failed to have any statistically significant effect.

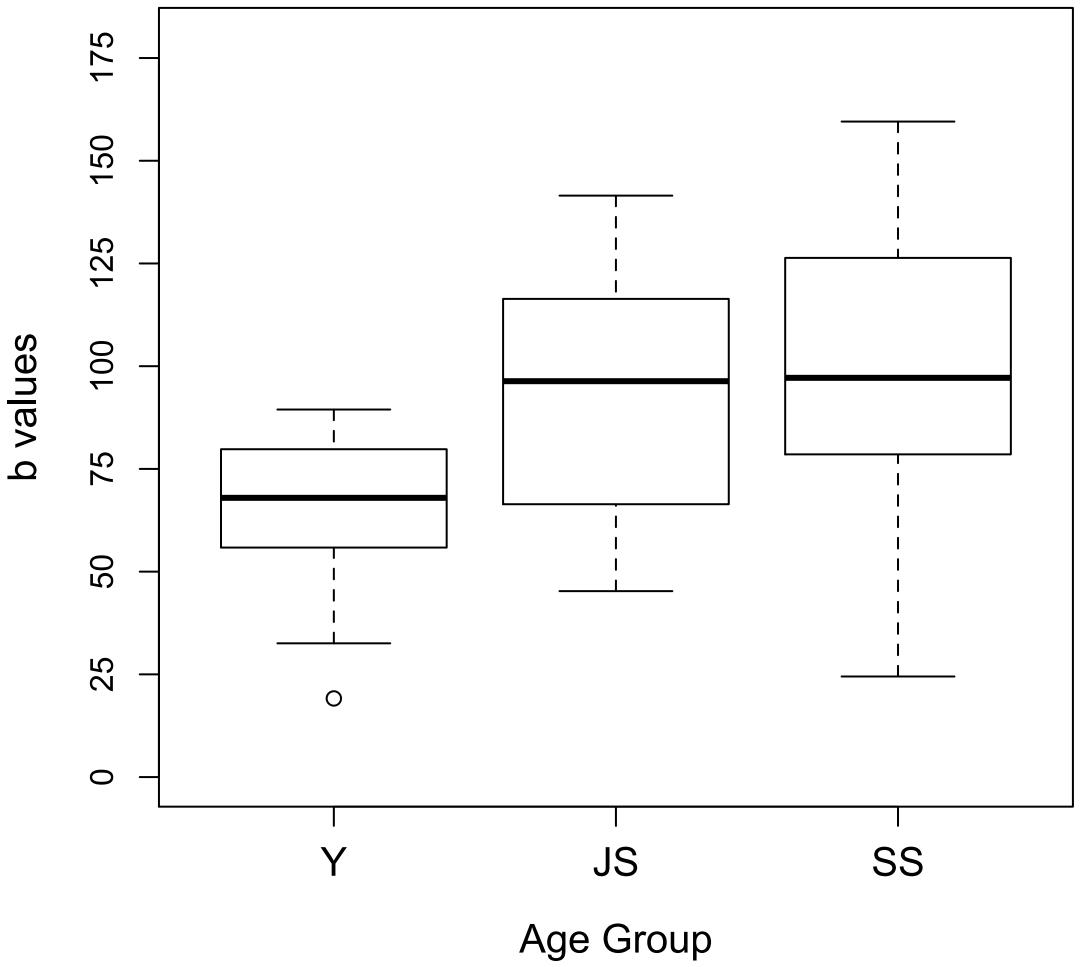

Figure 2.5: A boxplot of b values estimated by fitting Equation 2.1 to data from individual subjects in Experiment 2.1. Higher values of b correspond to shallower masking functions. The lower and upper edges of the box represent the 25th and 75th percentile, respectively, and the band in the middle of the box is the 50th percentile. The extent of the whiskers represents 1.5 times the interquartile-range with points lying outside this range (outliers) shown as circles.

2.1.2 Results

All of the analyses were done using R version 2.13.1 (Team, 2011) on valid threshold values[2]. Contrast thresholds for each notch value were estimated for each subject in each session, and values were averaged across sessions. Average thresholds for each of the three age groups (Y, JS, SS) are shown in Figure 2.4. An ANOVA computed on log-transformed thresholds using R's nlme package (Pinheiro et al., 2011) revealed a significant main effect of notch width ($F(9, 447) = 74.6$, $p < 0.001$) and age ($F(2, 50) = 32.2$, $p < 0.001$), and a notch width x age interaction ($F(18, 447) = 1.7$, $p < 0.05$). These results suggest that thresholds decreased as a function of notch width, older adults had higher thresholds overall compared to younger adults, and the effect of notch width on threshold varied across age groups.

Inspection of Figure 2.4 suggests that the slope of the threshold-vs.-notch function varied across age groups. To test this idea, data from individual subjects were fit with the exponential function

$$y = k + a * \exp\left(-(x/b)^2\right) \tag{2.1}$$

where k is the lower asymptote, a is the difference between the lower asymptote and the maximum value, and b governs the rate of decline from $(a + k)$ to k. Our parameter of interest is b, which is related inversely to the rate of decline, and is our index of the selectivity of direction channels. If our hypothesis is correct, and directionally-selective mechanisms are more broadly tuned in older adults, then thresholds in older adults should decline more slowly with increasing notch width, and therefore b should be larger in older subjects. The fitted values of b generally were consistent with this hypothesis (Figure 2.5). An ANOVA on the b values revealed that a significant effect of group ($F(2, 48) = 5.17$, $p = 0.009$), and planned comparisons found that values in the Y group differed from those in the JS and SS groups ($F(1, 48) = 9.98$, $p = 0.003$), but that the two older groups did not differ from each other ($F(1, 48) = 0.36$, $p = 0.55$).

To determine if the other best-fitting parameters of Equation 2.1 differed significantly across age groups, we used a percentile bootstrap procedure (Efron and Tibshirani, 1993) to calculate 95% confidence intervals for each equation parameter for each age group. The procedure for this analysis begins by generating a bootstrap sample of subjects for each

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[2] Occasionally subjects produced invalid threshold values by failing to respond accurately to a sufficient number of trials. In these instances, the staircase procedure was not able to calculate their thresholds given the number of trials and staircase reversals. Invalid thresholds were removed from the analyses.

age group by randomly selecting, with replacement, subjects from the original data set. For each bootstrapped sample, we then calculate the average threshold for each notch width. Equation 2.1 is then fit to the bootstrapped averages, and the values of the equation parameters are saved. These steps are repeated 999 times, which yields just as many sets of parameters for each age group. For each bootstrapped parameter, we then sort the generated values and select the values that define the percentile bootstrap 95% confidence interval. This is done by finding the values that mark the boundaries of the lower and upper 2.5% of the entire set of values (which, in turn, then defines the 95% confidence interval). Tables 2.2 - 2.4 show the confidence intervals; the 50% value corresponds to the median. Groups differ when the highest value for one group is lower than than lowest value for another, in other words, when the confidence intervals do not overlap. These intervals indicate there were age differences for parameters k and b, but not a. These results are consistent with the hypothesis that directionally-selective mechanisms are more broadly tuned in older adults than in young adults.

	2.5%	50%	97.5%
Y	0.13	0.15	0.18
JS	0.19	0.20	0.22
SS	0.23	0.25	0.27

Table 2.2: Bootstrapped confidence intervals for parameter k

	2.5%	50%	97.5%
Y	0.07	0.08	0.10
JS	0.08	0.09	0.10
SS	0.08	0.10	0.12

Table 2.3: Bootstrapped confidence intervals for parameter a

	2.5%	50%	97.5%
Y	44.57	64.62	77.43
JS	71.79	84.07	97.51
SS	87.97	102.19	122.21

Table 2.4: Bootstrapped confidence intervals for parameter b

In summary, the results of this first experiment suggest that the differential effect of changing notch width on performance in this direction discrimination task may be due to broader directionally-selective mechanisms in older adults.

2.2 Signal Coherence

Experiment 2.2 was designed to examine the effect of increasing the coherence of the signal on the the directional selectivity of masking. The apparatus and general procedure for Experiment 2.2 were identical to those of Experiment 2.1 except that the current experiment used a signal consisting of 25, 50 or 100 signal dots within a constant total 500 stimulus dots. To reduce testing time, thresholds were measured with only four notch widths of 0, 30, 90 and 179 deg. Mask contrast was 0.4, and all other details of the stimuli were the same as those in Experiment 2.1. Thresholds for each of the three signal levels were obtained in a single experimental session, and each subject completed three experimental sessions. Information about the subjects is reported in Table 2.1.

2.2.1 Results

Thresholds measured with each level of signal coherence are plotted as a function of notch width in Figure 2.6 (A-C). For each subject, the linear trend of threshold across notch width was defined as 180 times the slope of a regression fit to the log-transformed thresholds. This value corresponds to the change in threshold that is associated with an increase of notch width from 0 to 180 deg. Thresholds were well-fit by a straight line: the median value of R^2 was at least 0.75 for all age groups and conditions. The values were averaged across subjects, and the means are plotted in Figure 2.6 (D).

The condition using 25 signal dots was a replication of Experiment 2.1 and therefore we first analyzed results from that condition separately: An ANOVA on log-transformed thresholds revealed significant main effects of age ($F(2, 15) = 15.3$, $p < 0.001$) and notch width ($F(3, 45) = 56.3$, $p < 0.0001$), as well as a significant age x notch width interaction ($F(6, 45) = 2.6$, $p = 0.03$). Inspection of 2.6 (D) indicates that the linear trend varied significantly across groups ($F(2, 15) = 8.84$, $p = 0.003$), and was closer to zero (i.e., the threshold-vs.-notch width function was significantly shallower) in the SS group than the other two groups. Hence, the results in the 25 signal dots condition replicated the results

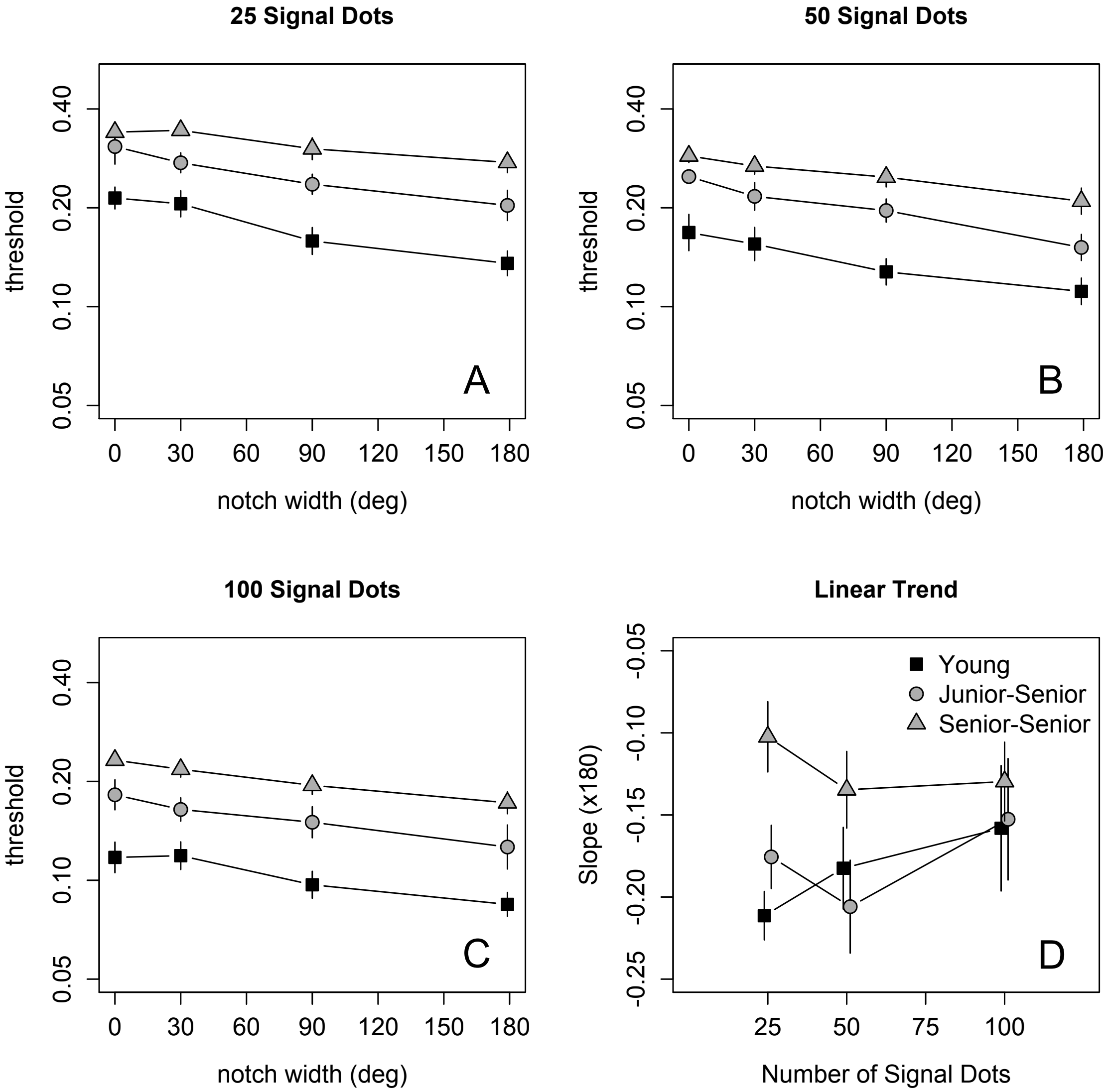


Figure 2.6: Contrast thresholds plotted as a function of notch width for conditions that used 25 (A), 50 (B), and 100 (C) signal dots. The linear trend of the threshold-vs.-notch width function for each subject was defined as 180 times the slope of the regression line fit to the log-transformed thresholds; this value corresponds to the linear change in threshold (in log units) that is associated with a 180 deg increase in notch width. The average values are shown in panel D. Error bars represent ±1 SEM.

of Experiment 2.1.

To determine if the age x notch width interaction depended on signal coherence, log-transformed thresholds from all conditions were combined and analyzed with a 3 (age group) x 4 (notch width) x 3 (signal coherence) ANOVA. The main effects of age group ($F(2, 15) = 16.24$, $p < 0.001$), notch width ($F(3, 45) = 106.3$, $p < 0.0001$), and coherence ($F(2, 30) = 243$, $p < 0.0001$) were significant, as was the age x notch width interaction ($F(6, 45) = 2.33$, $p = 0.05$). All other interactions were not significant ($F < 1$ and $p > 0.5$ in every case). The results of the ANOVA suggest that thresholds generally were higher in older adults, that thresholds decreased as a function of notch width, and that the age difference varied with notch width. Crucially, the age x notch width x coherence interaction was not significant ($F(12, 90) = 0.61$, $p = 0.82$), suggesting that the age x notch width interaction did not vary significantly with the number of signal dots. Nevertheless, the data in Figure 2.6 suggest that the age difference in the slope of the threshold-vs.-notch width curves became smaller as the number of signal dots was increased from 25 to 100. To provide a more powerful test of this hypothesis, we combined the Y and JS groups and then compared the linear trends in the combined group to the linear trends in the SS group using a 2 (group) x 3 (coherence) ANOVA. The main effect of group was significant ($F(1, 16) = 6.00$, $p = 0.026$), indicating that that the magnitude of the linear trend was smaller in the SS group. However, the main effect of coherence ($F(12, 32) = 0.76$, $p = 0.48$) and the group x coherence interaction ($F(2, 32) = 1.56$, $p = 0.23$) were not significant. Hence, we failed to find evidence that the group difference in linear trend varied significantly with the number of signal dots, though admittedly, this failure to find a significant interaction may be due to the relatively small size of our samples. As it stands though, this failure to find significance suggests to us that the masking selectivity differences we have observed were not due to task difficulty (since increasing coherence reduced task difficulty).

2.3 Mask Contrast

It is known that older adults have poorer contrast sensitivity than their younger counterparts (Allen et al., 2010; Bennett et al., 1999; Sekuler et al., 1982). Experiment 2.3 was undertaken to examine the possibility that age differences in the directional selectivity of masking were due to decreased contrast sensitivity in the elderly.

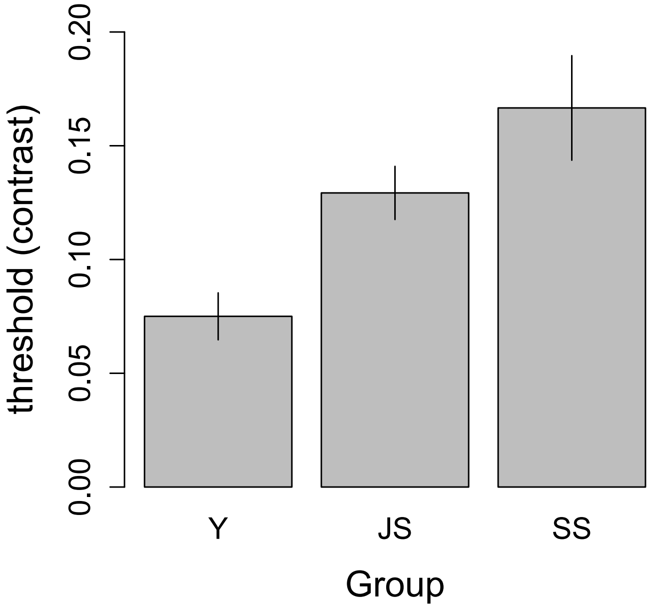


Figure 2.7: Thresholds measured with mask dot contrast set to zero. Tukey HSD tests revealed that thresholds in the Y group were significantly lower than in the JS and SS groups, but that the JS and SS groups did not differ from each other. Error bars represent ±1 SEM.

The apparatus and general procedure for Experiments 2.3 were identical to those of Experiment 2.1. Subjects were required to make a judgment about whether the Signal dots were moving to the right or to the left. Unlike Experiment 2.1, Mask dot contrast was 0, 0.1, 0.2, and 0.4 in separate conditions. As this change alone would have quadrupled the time required to complete the experiment, as in Experiment 2.2, only notch widths of 0, 30, 90 and 179 deg were used. All other details of the stimuli were the same as in Experiment 2.1. Thresholds for each of the four notch levels were obtained at each of the four contrast levels in one experimental session, and each subject completed three experimental sessions. Information about the subjects is reported in Table 2.1.

2.3.1 Results

Thresholds obtained with mask contrast set to zero are shown in Figure 2.7. Tukey HSD tests performed on log-transformed thresholds revealed that thresholds in the Y group were significantly lower than thresholds in the JS (difference = 0.25, $p_{adj} = 0.007$) and SS (difference = 0.35, $p_{adj} < 0.001$) groups, but that the JS and SS groups did not differ from each other (difference = 0.10, $p_{adj} = 0.33$).

Thresholds measured with mask contrasts of 0.1, 0.2, and 0.4 are shown in Figure 2.8. To a first approximation, log-thresholds were a linear function of log-contrast, and the threshold-vs.-contrast functions in the three age groups were nearly parallel for each notch width. To increase the power of our statistical tests for between-group differences, data from the JS and SS groups were combined into a single group, and log-transformed thresholds were then analyzed with a 2 (group) x 4 (notch width) x 3 (contrast) ANOVA. The results of the ANOVA are shown in Table 2.5. The main effects of group, notch width, and contrast were significant. Examination of Figure 2.8 indicates that the main effects reflect the fact that i) thresholds were higher in older adults than younger adults; ii) thresholds increased as a function of contrast; and iii) thresholds decreased with increasing notch width.

The ANOVA also found that the group x notch width and notch width x contrast interactions were significant. The group x notch width interaction indicates that the difference between age groups depended on notch width, and a comparison of panels A and D in Figure 2.8 reveals that group differences were slightly larger when the notch width was 179 deg than when it was 0 deg. The significant notch width x contrast interaction reflects the fact that the effect of notch width on threshold was larger at

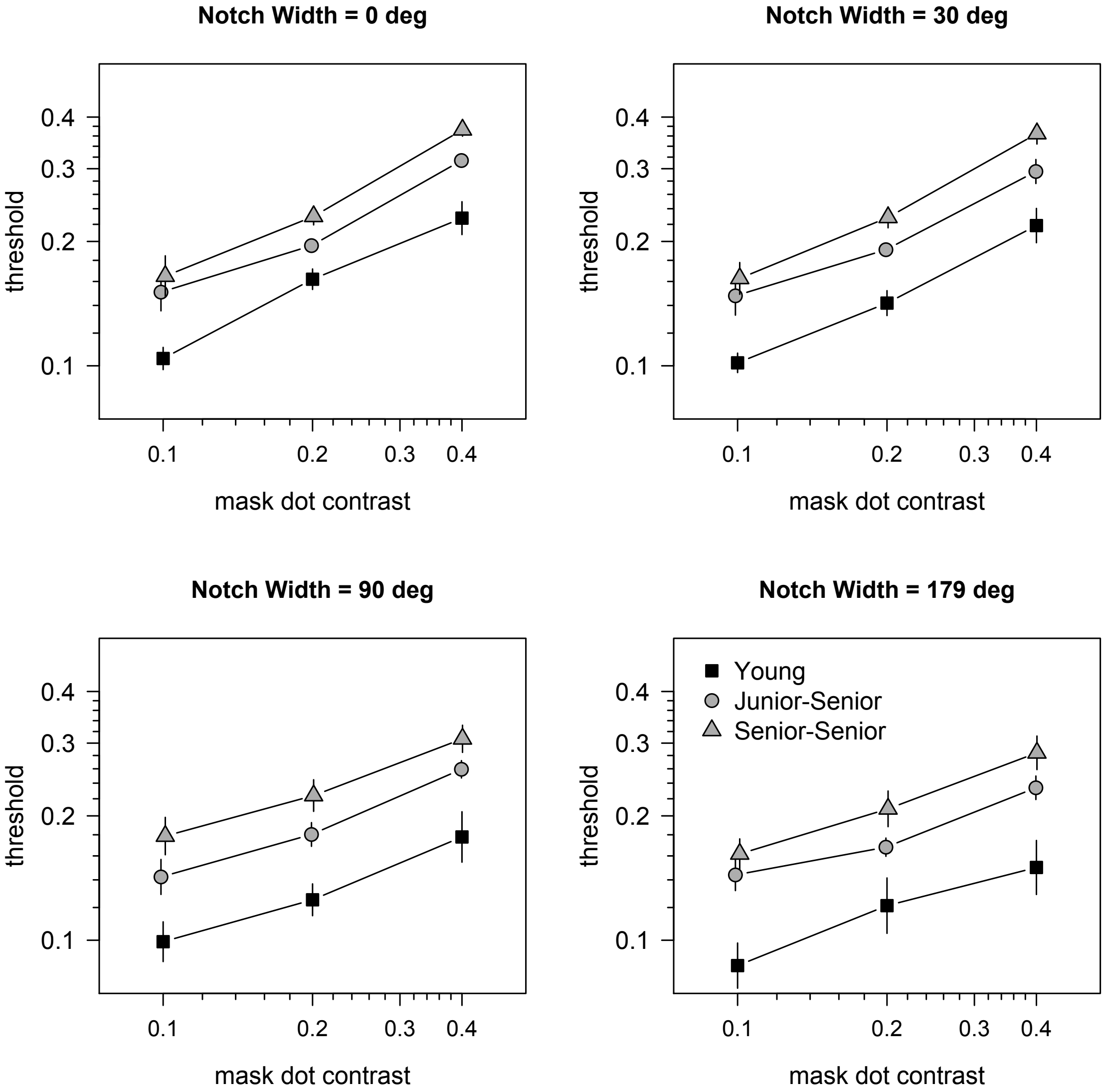


Figure 2.8: Thresholds measured with mask dot contrasts of 0.1, 0.2, and 0.4 and notch widths of 0, 30, 90, and 179 deg. Error bars represent ±1 SEM.

higher contrasts. This point is illustrated more clearly in Figure 2.9, which plots the linear trend of log-transformed threshold across notch width for each mask dot contrast: the linear trend increased (i.e., the threshold-vs.-notch function became steeper) with increasing contrast, and the effect of contrast was similar for each age group. Figure 2.9 also shows that the magnitude of the linear trend was smaller (i.e., the threshold-vs.-notch function was shallower) in older subjects, and that the age difference was similar across mask contrasts. This observation is consistent with the results of the ANOVA, which failed to find a significant three-way interaction between group, notch width, and contrast.

	SS	df	Error SS	Error df	F	p
Group	1.74	1	1.358	16	20.46	0.00035
Notch	0.26	3	0.138	48	30.36	< 0.0001
Contrast	2.66	2	0.177	32	240	< 0.0001
Group × Notch	0.03	3	0.138	48	3.48	0.0229
Group × Contrast	0.01	2	0.177	32	0.95	0.396
Notch × Contrast	0.07	6	0.103	96	11.58	< 0.0001
Group × Notch × Contrast	0.01	6	0.103	96	1.18	0.324

Table 2.5: Results of ANOVA performed on log-transformed thresholds displayed in Figure 2.8. Data from the JS and SS groups were combined, and therefore the Group factor compared younger and older subjects.

Older subjects were less sensitive to signal contrast in the no-mask condition (Figure 2.7) and presumably also were less sensitive to the mask dot contrast. We found that the slope of the threshold-vs.-notch width function increased with increasing contrast (Figure 2.9), which implies that lowering sensitivity to mask contrast ought to reduce the slope of the masking function. To what extent are age differences in the slope of the threshold-vs.-notch width function due to age differences in contrast sensitivity? One way of evaluating this hypothesis would be to normalize motion discrimination thresholds by dividing masked thresholds by threshold in the no-mask condition. However, the linear trend was calculated using log-transformed thresholds, and therefore would not be affected by this divisive normalization. Another strategy would be to plot the linear trend measured for each subject against each subject's no-mask threshold. If the age differences in masking were due to differences in baseline contrast sensitivity, then the linear trend and baseline threshold ought to be correlated significantly, and the form

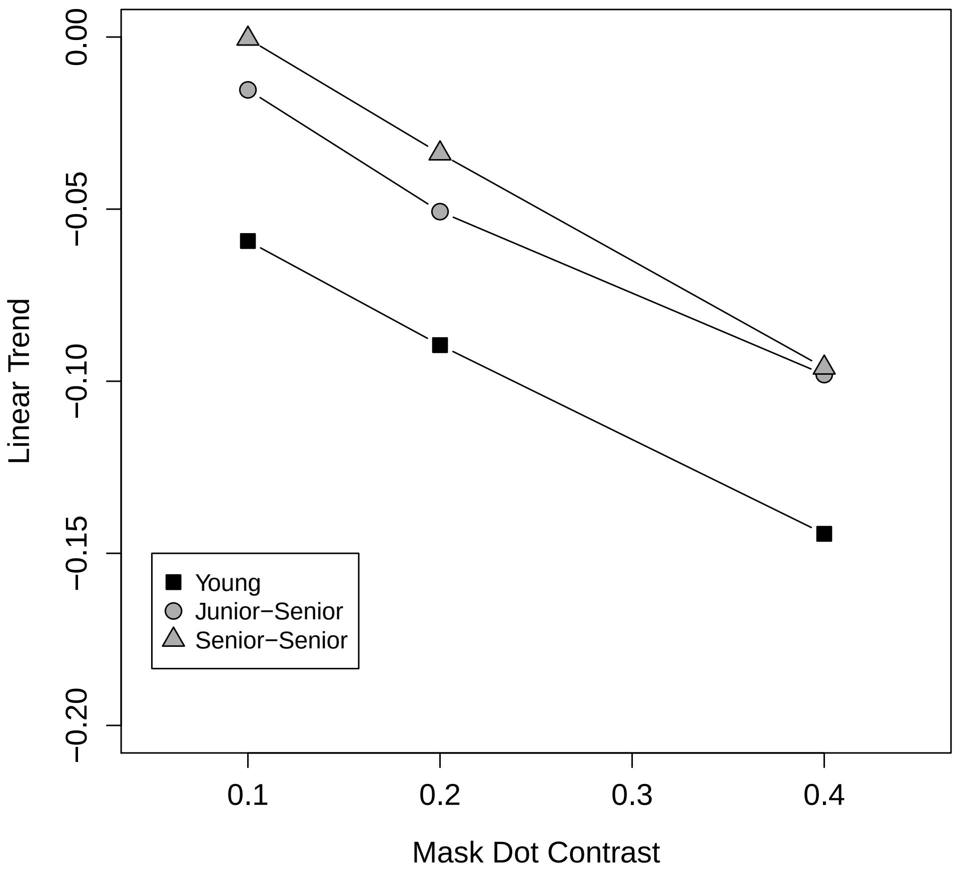


Figure 2.9: Linear trends estimated for the log-threshold vs. notch width functions for each age group and mask contrast. The linear trend becomes increasingly negative (i.e. the functions become increasingly steep) as mask dot contrast increases. However, the differences between the age groups remain approximately constant across contrast values.

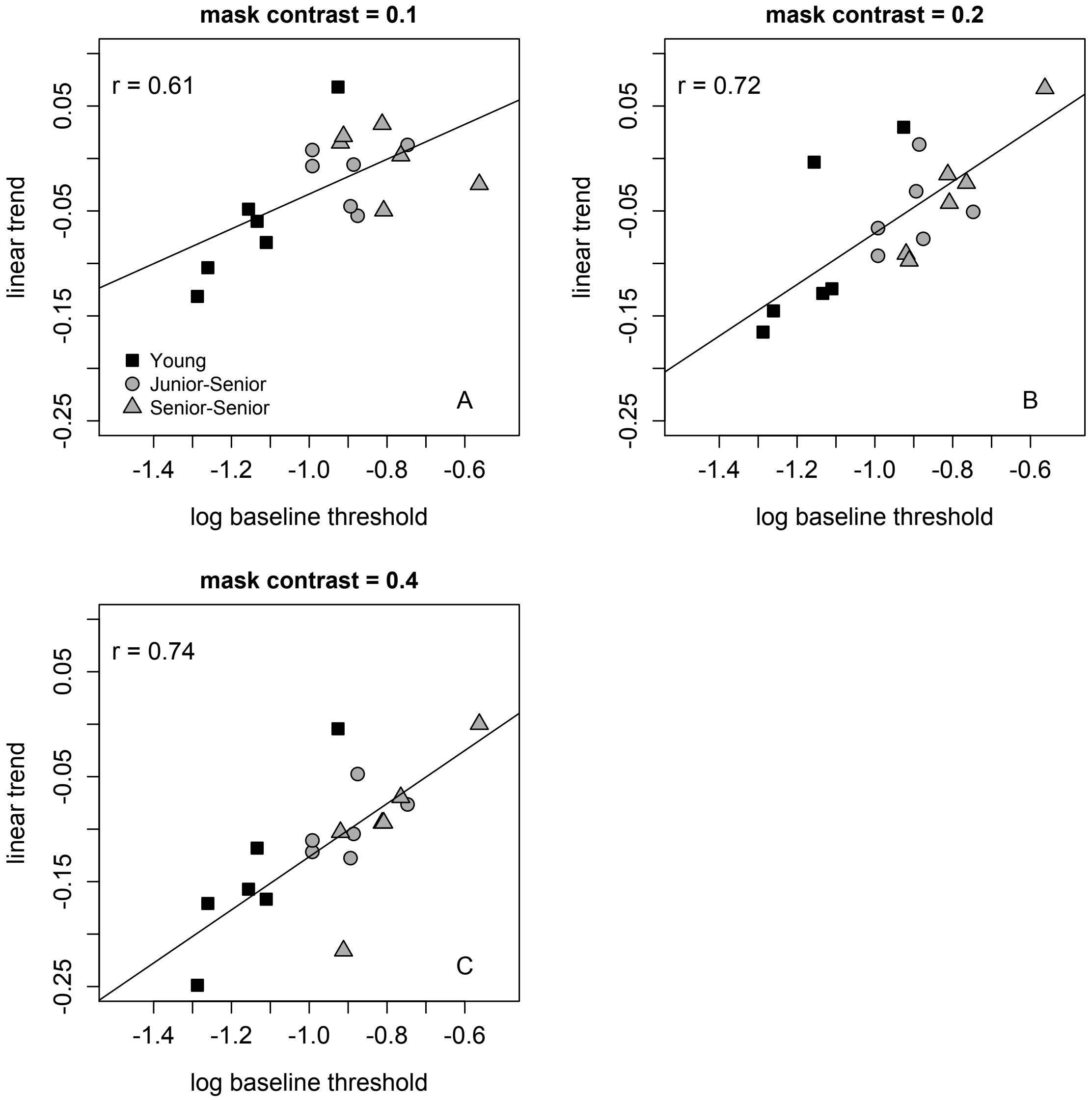


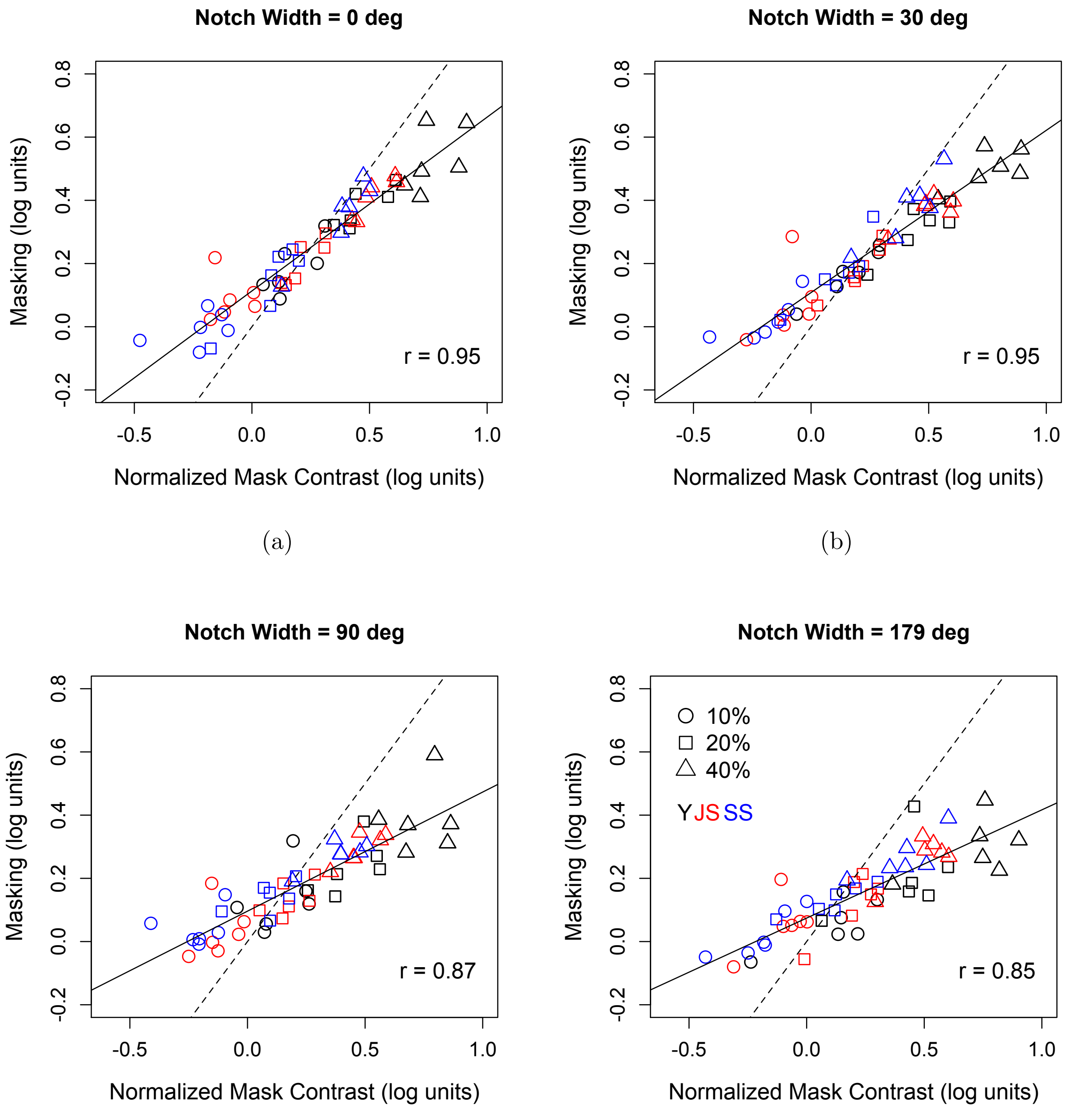
Figure 2.10: Scatter plots that illustrate the relation between the slope of the threshold-vs.-notch width function and detection threshold for an unmasked stimulus. Log-transformed threshold in the zero-contrast mask condition is plotted on the horizontal axis, and the linear trend of log-transformed threshold across notch width is plotted on the vertical axis. Each symbol represents the results of one subject. Results obtained with mask dot contrasts of 0.1, 0.2, and 0.4 are shown in panels A, B, and C, respectively. The solid line in each panel is the best-fitting (least-squares) regression line fit to the data. For each mask contrast, the linear trend of the threshold-vs.-notch width function is significantly correlated with baseline threshold ($p < 0.001$ in all cases). Furthermore, the association between the linear trend and baseline threshold does not appear to differ significantly across age groups.

of the association between the two variables should be the same in each age group. Scatter plots that illustrate the relation between the slope of the threshold-vs.-notch width function and detection threshold for an unmasked stimulus are shown in Figure 2.10. In each mask contrast condition, the correlation between linear trend magnitude and baseline threshold was significant, and the association between the two variables did not appear to differ across age groups. Finally, Figure 2.11 shows masking plotted as a function of normalized mask contrast, which was defined as the $\log_{10}$ difference between mask contrast (i.e., 0.1, 0.2, or 0.4) and baseline threshold measured in the no-mask condition. Notice that, for each notch width, the data from all three age groups are well described by a single function, which again suggests that age differences in masking can be accounted for by age differences in contrast sensitivity for the target and the mask.

These analyses suggest that age differences in the steepness of the masking function are accounted for by age differences in contrast sensitivity. However, it is important to note that age differences in motion masking were not correlated with Pelli-Robson contrast sensitivity, which did not differ between groups (see Table 2.1). Thus, the variable that accounts for the age differences is not *absolute* contrast sensitivity. Rather, it is contrast sensitivity for the stimulus used in our task that accounts for the observed age differences in masking.

2.4 Discussion

In these experiments, we used a notched-masking technique to examine the tuning properties of directionally-selective mechanisms in older human adults. We had subjects discriminate the direction of motion of Signal dots that were embedded in randomly moving Mask dots. We restricted the motion of the Mask dots by creating a notch, centered around 0 and 180 deg on each trial in order to determine a tuning function for the directionally-selective mechanism responsible for discriminating horizontal motion. Our principal finding in Experiment 2.1 is that both groups of older adults (JS and SS) were less sensitive to motion direction in general and showed evidence of broader tuning. This broadening is in line with what would be predicted based on recent neurophysiological findings in senescent monkeys and cats (Hua et al., 2006; Schmolesky et al., 2000; Yu et al., 2006). In two control experiments that manipulated mask contrast and signal coherence levels we attempted to replicate our results and determine the possible causes of this age-related tuning difference. In Experiment 2.2 we replicated the main findings from



(a)

(b)

(c)

(d)

Figure 2.11: Masking plotted as a function of normalized mask contrast. Masking was defined as the $\log_{10}$ difference between thresholds obtained with a mask and threshold obtained in the no mask condition. Normalized contrast was defined as the $\log_{10}$ difference between mask contrast (i.e., 10%, 20%, or 40%) and threshold in the no-mask condition. Each point represents the data from a single subject in the Y (black), JS (red), or SS (blue) group. The solid line in each panel represents the regression line; the dashed line represents the line $y = x$.

Experiment 2.1 and demonstrated that the age differences we observed were not due to challenges related to extracting the signal from our stimulus. In Experiment 2.3 we found that while older adults showed significantly higher contrast thresholds on the no-mask condition, the age differences in the steepness of the masking function can be accounted for by age differences in contrast sensitivity. The interesting point from this analysis, however, is that contrast sensitivity as measured by the Pelli-Robson test does not differ between age groups. It appears that the task-specific contrast sensitivity accounts for the age-related masking differences. Taken together these results support the idea that aging results in impairments in direction identification that may have, at least in part, a neural basis, such as broader tuning of the directionally-selective mechanisms. These age-related changes in performance do not rely solely on changes in *absolute* contrast sensitivity or to a subject's ability to extract the signal from surrounding noise.

The impact of contrast sensitivity on our results relates to the work done by Allen et al. (2010). They measured global motion coherence thresholds for translational, radial or rotational motion patterns at different contrast levels in both younger and older adults. They found that the differences in performance were characterized by a lateral shift of the threshold vs contrast function along the horizontal axis. Older adults required twice the dot contrast level to reach asymptotic performance compared to younger adults, and so the age-related deficits were driven primarily by impairments in contrast sensitivity. Overall, this findings matches ours, highlighting the importance of contrast sensitivity to performance on motion perception tasks, but Allen et al. (2010) did not evaluate contrast sensitivity independently as we did. It would be interesting to see if in their participant population Pelli-Robson contrast sensitivity either differed between groups, or was correlated with performance on the motion task.

There has been some suggestion that the broader tuning seen in the visual cortical neurons of older animals is due to changes in intra-cortical inhibitory circuits. Tuning is thought to be the result of inter-cortical inhibition: GABA-mediated mechanisms are responsible for neural response properties in cat and monkey visual cortex (Leventhal et al., 2003). In human psychophysical experiments, there also has been some suggestion that impairments in inhibitory mechanisms are responsible for certain age-related changes in behaviour (Betts et al., 2005). By using large, high contrast motion stimuli, Betts et al. (2005) showed a counterintuitive improvement in performance for older adults (related to surround suppression) that they believe was linked to age-related inhibitory changes noted in animal physiology (Hua et al., 2008; Leventhal et al., 2003). This idea has received support from a recent study where TMS was used to disrupt area MT/V5 in humans (and consequently, the inhibitory activity in that part of the cortex), resulting in improved perception of large, high-contrast moving patterns (Tadin et al., 2011). In this context, our current results also could be explained by a decrease in inhibitory control. If there is decreased inhibition in human visual cortex, it could de-tune directionally-selective mechanisms and cause the impairments we see in our results. While aging and TMS undoubtedly differ in the way they affect the visual cortex, the similarities in the results of studies suggest that there is a connection between the underlying neural mechanisms responsible; increases in tuning and changes in surround suppression may both be linked to changes in intra-cortical inhibitory processes, and subsequently, to observed perceptual effects that emerge with age.

The type of stimulus used also seems to have an effect on the observed age-related changes in human adults. When examining orientation tuning, neither Govenlock et al. (2009) nor Delahunt et al. (2008) found evidence of broader tuning in older humans, even though such a result has been seen in animal neurophysiology (Leventhal et al., 2003). This was also the case when investigating spatial frequency tuning (Govenlock et al., 2010). By contrast, Wilson et al. (2011) have found evidence of increased tuning bandwidth for face orientation in older human adults using face stimuli. What might cause this difference in orientation tuning results? As described above, an emerging hypothesis is that there are changes in intra-cortical inhibitory mechanisms with age. These could include changes in neuronal tuning and surround suppression, among other as of yet unknown effects. It may be the case that the significant effects of these changes only emerge when using stimuli that require higher levels of neural processing (in either the dorsal or ventral pathways). This could explain why simple orientation tuning (that relies on V1, such as Govenlock et al. (2009)) does not show age-related changes, but orientation tuning within the context of higher-order, complex stimuli (such as the faces used in Wilson et al. (2011)) does. While the locus of specific neuronal changes may be found as early as V1, as suggested by Hua et al. (2006), perceptual effects may not be seen until these local impairments are pooled to make higher-order perceptual decisions. It has been shown in primates that the perception of stimuli such as ours is highly correlated with neural activity in area MT (Newsome et al., 1989). The advent of functional neuroimaging has also revealed that area MT consistently responds to a variety of dynamic stimuli, including random dot patterns (see Culham et al., 2001, for a review). Thus, while the perceptual response to our stimuli obviously includes information pooled from early visual areas (like V1), this same response also requires additional processing that may be further affected by aging. This idea is supported by Faubert (2002) who argues that it may by the complexity of the processing that results in age-related differences, rather than the specific attribute being evaluated. His argument is supported by recent work from his group that showed that when using motion stimuli that were spatio-temporally identical, age differences only emerged for the more complex, second-order stimulus, not the simpler, first-order one (Habak and Faubert, 2000). Perhaps it is through this notion that our own contrast analyses in Experiment 2.3 make sense; absolute contrast sensitivity, measured in a simple, static setting, does not affect the masking selectivity, but dynamically measured contrast sensitivity increases the complexity to a point that is reveals a different kind of deficit and impacts directional tuning.

When examining their results several groups have found that older women perform worse than their male counterparts when using correlated motion stimuli (Gilmore et al., 1992), optic flow stimuli (Atchley and Andersen, 1998) or making collision judgments (DeLucia et al., 2003). Although this difference between older men and women is not always found when using motion stimuli (Billino et al., 2008; Tran et al., 1998), when it does occur it is nearly always that case that women are worse than men, even when it is found in younger subjects (Kaiser et al., 1985). Work by Conlon and Herkes (2008) also found an age and gender interaction with a global motion task, but not with a global form or rapid sequence processing task. They argue that the level of perceptual difficulty of a task, particularly as it relates to extracting a signal from noise, may be contributing to this gender difference. Global form tasks often require the extraction of a signal from noise, but a coherent motion task (which is a dynamic rather than a static stimulus and requires extraction of signal from noise) may increase the perceptual difficulty to a point that reveals gender differences. Given these previous results, we examined gender differences in our main experiment (Experiment 2.1) and found that women had higher thresholds (and therefore poorer performance), but only in the SS group ($F(1, 218) = 10.03$, $p < 0.002$). The smaller number of subjects in Experiments 2.2 and 2.3 precludes a similar analysis, but perhaps older females are more affected by factors such as mask contrast or signal coherence since they make the task more perceptually difficult, as discussed above.

Since we found a gender difference only in the SS group, it is worth discussing how to categorize age groups. Dividing our groups into JS and SS groups using the age of 70 as our splitting point had a basis in the literature (Bennett et al., 2007) but not all aging work has found that there is something special about the age of 70; in fact, McBain et al. (2010) tested participants over a broad range of ages and found that visual motion performance began to significantly decline between the 51-60 and 61-70 age groups, a full decade earlier than what we tested. By contrast, Billino et al. (2008) also tested over a broad age range but found gradual changes with age rather than a decisive point of change, and Tran et al. (1998) found a linear relationship between age and motion perception, again with no specific point of age-related change. In general, most aging studies tend to lump older adults together rather than divide them into 'older' and 'younger' seniors. There is a great deal of variability in most subject populations, but particularly in the elderly, both neurophysiologically (ex. Raz et al. (2010)) and perceptually (ex. Block et al. (1998)). This makes it difficult to determine if and where an age cutoff should be placed. Thus, an interesting future avenue of research would be to investigate the role of the age cut-off in determining average subject results, perhaps by re-evaluating existing data with different age group or inclusion criteria.

The results of these experiments contribute to our understanding of age-related neural changes in human adults. By attempting to relate animal neurophysiology and human psychophysics, we bridge different disciplines and find linkages between disparate areas of work. Understanding age-related perceptual changes will be crucial as the population continues to age.

2.5 Acknowledgements

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Chapter 3

The effect of age on motion perception for vertical and horizontal judgments

Abstract

It has been shown that older adults are impaired in a variety of motion perception tasks when compared to younger subjects. The cause of this impairment is unknown, but it is possible that older adults are exhibiting the perceptual consequences of a broadening of their directionally-selective cortical neurons. This hypothesis is supported by recent neurophysiological work that has found bandwidth changes in these neurons in older cats and monkeys. The current experiments examined this hypothesis by evaluating the masking functions of younger and older adults for both horizontal and vertical direction discriminations using a notched-noise masking technique. The results suggest that older adults (both Junior-Seniors, 60-70 years old, and Senior-Seniors, over 70 years old) differ from younger subjects (under 30 years old), especially at larger mask offsets and when making vertical motion judgments. The results from a control experiment which varied the duration of the stimulus suggest that these findings are not likely due to eye movements. The conclusion from this work is that older human adults show perceptual changes consistent with the hypothesis that directionally-selective mechanisms broaden with age.

3.1 Introduction

Older adults show impaired motion sensitivity and direction identification (Bennett et al., 2007), which, when combined with age-related changes in visual acuity, can have meaningful effects on their ability to perceive motion in daily life, for instance, when driving (Owsley and McGwin, 2010). Older adults also show impairments when asked to discriminate the speed of simple motion patterns (Norman et al., 2003), and they perform poorly when using motion cues to make complex timing judgments, such as when crossing the street (Lobjois and Cavallo, 2007). What might lead to diminished motion perception in older adults? One possibility is that the neurons that code information about motion respond differently in older brains than in younger brains. In fact, neurophysiological work in animals has shown that the directionally-selective neurons in the early visual areas of cats and primates are more broadly tuned than those of younger animals (Hua et al., 2006; Schmolesky et al., 2000; Yu et al., 2006). In effect, these neurons are less selective to any one specific direction of motion, which could lead to decreased discrimination abilities. If this broadening is occurring in older adult humans as well, it could help explain the observed, behavioural age-related deficits in motion perception.

In Chapter 2, we used notched noise masking to derive masking functions (in this case, defined by contrast thresholds as a function of notch width) for younger and older subjects. Using this technique, we found evidence to suggest that directionally-selective mechanisms may be more broadly tuned in older adults although the broader channels may be linked to reduced contrast sensitivity for moving patterns rather than age *per se.*. This chapter outlines an extension of our work from Chapter 2. Using the principle of notched noise masking, we attempted to estimate the bandwidth of the directionally tuned mechanisms used to perceive motion, but we made two important changes to the stimuli from Chapter 2. First, rather than measuring thresholds by adjusting stimulus contrast, we fixed dot contrast at a high value and measured thresholds by adjusting the percentage of dots that moved coherently. This new procedure reduces the likelihood that any observed age differences could be due to differences in contrast sensitivity (Allen et al., 2010). The second important change from the experiments in Chapter 2 is the nature of the noise mask. For the experiments described in this chapter we used a noise mask that had a narrower directional bandwidth and a different spatial configuration. These changes allowed us to see if our directional tuning findings were limited to the specific stimulus parameters used in Chapter 2, or if they generalized to other stimuli.

3.2 Methods

3.2.1 Subjects

Subjects were recruited from the McMaster University community and the surrounding areas. Subjects were split into three age groups: Young (Y; under 30 years old), Junior-Seniors (JS; 60-70 years old), and Senior-Seniors (SS; over 70 years old). Table 3.1 shows the mean age, near and far visual acuity, and contrast sensitivity (as measured by the Pelli-Robson sensitivity chart) for all three groups of subjects. Mini-Mental State Exam (MMSE) scores are also included for older subjects. We administered a questionnaire to ensure that all subjects had good visual and general health. All procedures were approved by the McMaster Ethics Review Board, and subjects were compensated for their time.

Table 3.1: Number of subjects, age, acuity, contrast sensitivity and Mini-Mental State Exam (MMSE) scores for all subjects. The MMSE was not administered to the Y subjects. Values are presented as means with the standard deviation in parentheses.

N by group (# females)	Age (μ, σ)	Near acuity (μ, σ)	Far acuity (μ, σ)	Pelli-Robson (μ, σ)	MMSE (μ, σ)
18 Y (9)	22.7 (3.2)	1.46 (0.23)	1.41 (0.25)	1.94(0.04)	N/A
16 JS (8)	66.0 (2.4)	1.03 (0.27)	1.19 (0.22)	1.90 (0.09)	28.8 (1.4)
16 SS (9)	74.4 (3.3)	.095 (0.18)	0.99 (0.16)	1.90 (0.09)	28.9 (1.3)

Apparatus and Stimuli

The experiment was run on a Macintosh computer (OSX 10.6.2) using the Matlab environment (v. 7.9.0.529, The Mathworks) and the Psychophysics and Video Toolbox (v. 3.0.8, Brainard 1997; Pelli 1997) The monitor had a resolution of 1280 × 1024 pixels and a frame rate of 100 Hz. Subjects viewed the display binocularly from a viewing distance of 57 cm; viewing position was stabilized by a forehead/chin rest. There was no light in the room other than that coming from the experimental monitor. The average luminance of the display during the experiment was $30.4 cd/m^2$.

Subjects were presented with 400 circular black dots, measuring 0.02 deg in diameter

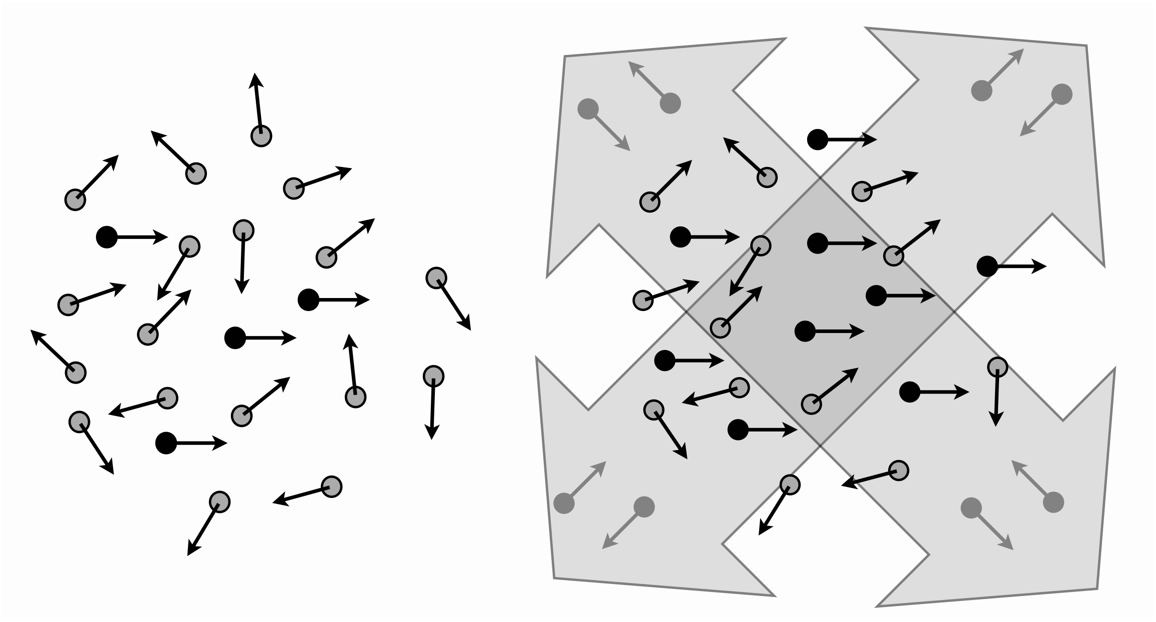


Figure 3.1: A schematic of our stimuli. The left and right panels illustrate the no-mask and mask conditions, respectively. In both panels, dots with black arrows represent the direction of motion of Target dots, with the subset of those dots depicted by the solid black circles representing the subset of coherently moving Target dots (in this case, moving to the right). In the right panel, the grey arrows indicate possible directions of motion of the 100 Mask dots. The angle between the two bands of Mask dots was varied to adjust the mask direction offset. Note that the mask dots were positioned anywhere within the display, not only within the arrows; it was their direction, not their position, that was restricted.

with a contrast of 0.8, moving at 5 deg/sec. 300 dots were Target dots and the remaining 100 were Mask dots. All dots moved within an annulus whose outer edge had a radius of 6 deg and whose inner edge had a radius of 1 deg. Some proportion of Target dots moved in random directions, and the remaining Target dots moved coherently along a horizontal (i.e., 0 or 180 deg) or vertical (i.e., 90 or 270 deg) trajectory. Figure 3.1 depicts a schematic of the horizontal target direction, for both the no-mask and mask conditions. The directions of the Mask dots fell within two 10 deg bands of directions that were centered around the target direction by $\pm\theta$ deg (the large grey arrows in Figure 3.1). Each 10 deg band contained equal numbers of dots moving in opposite directions, so that the 100 mask dots had no net horizontal or vertical motion. For this experiment, θ was ±5, ±30, ±60, or ±90 deg. So, for example, if the direction of Target motion was 0 deg and θ was 5 deg, the directions of the noise bands would range from 25-35 deg and 325-335 deg. There also was a no-mask condition in which the contrast of the mask dots was set to zero (illustrated on the lefthand side of Figure 3.1). The stimulus was displayed for 500 ms.

3.2.2 Procedure

The subjects' task was to determine if the target dots were moving to the right or the left (for horizontal target direction trials) or up or down (for vertical target direction trials). Subjects were instructed to look at a fixation point, which was presented 100 ms before stimulus onset and remained visible for the entire 500 ms stimulus duration. Subjects made un-speeded responses using a button press and received auditory feedback following incorrect responses. The next trial started automatically 1 s after subjects made their response. Two practice trials for each mask direction offset (i.e. value of θ) began each session, and subjects had the option to receive more practice trials if they felt uncomfortable with the task (but this option was exercised by only a few subjects).

Vertical and horizontal target motions were presented in two separate blocks. Within each block, five mask conditions (i.e. four values of θ producing mask direction offsets plus a no-mask condition) were randomly inter-mixed. For each mask condition, two interleaved, 3-down, 1-up staircases adjusted the proportion of coherently-moving Target dots and threshold was defined as the mean of the last six reversal points. There were 80 trials per each of the five mask conditions within a block (for a total of 400 trials per block), with a inter-trial interval of 1 s. Subjects completed two blocks of the vertical target motion trials and two blocks of the horizontal motion trials within a session, and each session lasted approximately one hour.

3.3 Results

3.3.1 Thresholds

For each subject, the two thresholds obtained for each mask offset were averaged. An ANOVA on log-transformed thresholds in the no-mask condition yielded significant main effects of age group ($F(2, 47) = 10$, $p < 0.001$) and target direction ($F(1, 47) = 20.3$, $p < 0.001$). The age group x target direction interaction approached significance ($F(2, 47) = 3.08$, $p = 0.055$). Analyzing the effect of age group for the horizontal and vertical target directions separately, we again found significant effects of age for both target directions (horizontal: $F(2, 47) = 6.35$, $p < 0.01$; vertical: $F(2, 47) = 10.2$, $p < 0.001$). Tukey HSD comparisons revealed that the pattern of differences varied with target direction: only the SS differed from the Y group in the horizontal direction (Figure 3.2), but both the JS and SS groups from Y subjects for the vertical target direction (Figure 3.3).

Additional analyses showed that target direction affected thresholds for the JS ($F(1, 15) = 24$, $p < 0.001$) and SS ($F(1, 15) = 5.24$, $p < 0.05$) groups, but not the Y group ($F(1, 17) = 1.45$, $p = 0.24$). To see if the effect of target direction differed between the two older groups, the ANOVA was performed using only the JS and SS groups. Here, we found a significant age group x target direction interaction ($F(1, 30) = 4.67$, $p < 0.05$), suggesting the effect of the target direction was different for the JS and SS groups. Inspection of Figures 3.2 and 3.3 shows that target orientation had a much greater effect on thresholds in the JS group.

Our analyses of the no-mask condition demonstrate that discrimination thresholds were higher in older adults compared to younger ones, but the difference depended on the direction of the target motion. Both groups of older subjects showed higher thresholds than the Y group for vertical target motion, but only the SS group showed the same increase for horizontal motion. This result suggests that the SS group has a greater overall motion perception deficit than the JS group. Target motion did not appear to affect the Y group.

Log-transformed thresholds in the masked conditions were analyzed with a 3 (group)

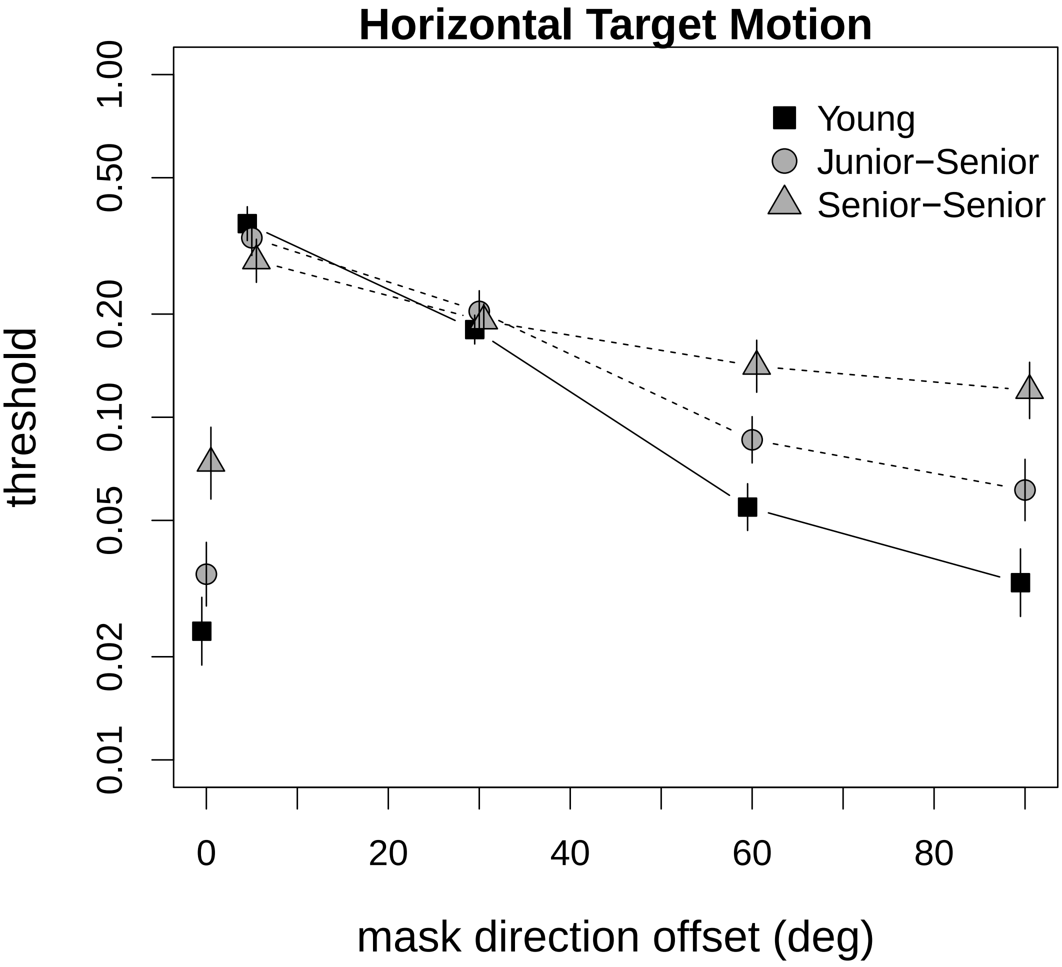


Figure 3.2: Coherence thresholds as a function of mask direction offset for the Horizontal target direction condition. The zero degree mask offset value represents trials where there was no mask, and error bars represent ±1 SEM. Note the higher values (poorer sensitivity) for the SS group as represented by the grey triangles.

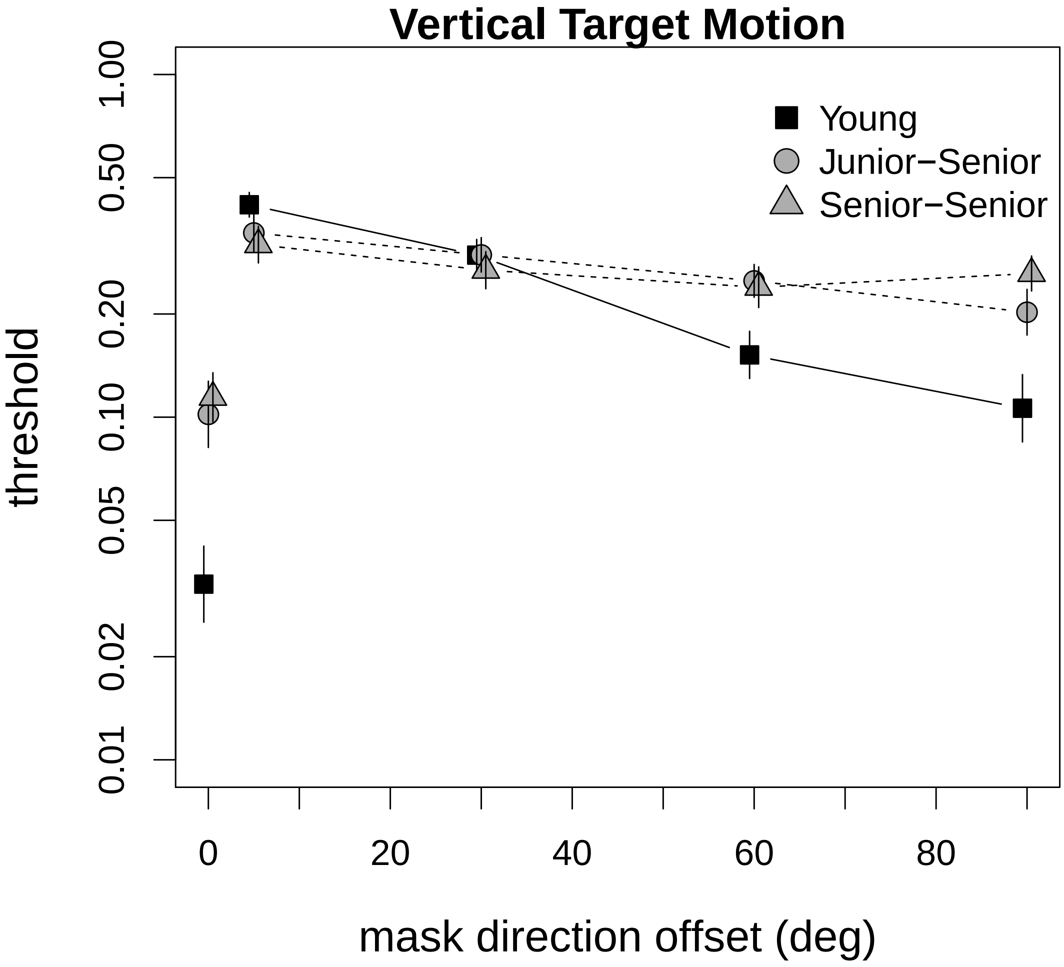


Figure 3.3: Coherence thresholds as a function of mask direction offset for the Vertical target direction condition. The zero degree mask offset value represents trials where there was no mask, and error bars represent ±1 SEM. Notice how much lower the thresholds are for the Y group (depicted by black squares), especially in the two highest mask offset values.

x 4 (mask direction offset) x 2 (target direction) ANOVA. The main effects of age group ($F(2, 47) = 3.86$, $p < 0.05$), target direction ($F(1, 47) = 78.32$, $p < 0.001$) and mask offset ($F(3, 141) = 110.09$, $p < 0.001$) were significant. The interactions between age group and mask direction interaction ($F(6, 141) = 13.27$, $p < 0.001$), and between target direction and mask offset ($F(3, 141) = 39.58$, $p < 0.001$) also were significant. Unlike the no-mask condition, neither the group x target direction interaction nor the group x target direction x mask offset interaction were significant.

Since the interaction between age group and mask offset was significant, we analyzed the effect of age group at each mask direction after averaging thresholds across horizontal and vertical target directions. At both the 5 and 30 deg mask direction offsets, there was no main effect of age. However, the effect of age group was significant for both the 60 deg ($F(2, 47) = 6.44$, $p < 0.01$) and 90 deg ($F(2, 47) = 9.59$, $p < 0.001$) offsets values, respectively and Tukey HSD comparisons revealed that, at both offsets, the JS and SS groups differed from the Y group, but not from each other. This difference from the Y group can be seen in Figure 3.2, and is even more apparent in Figure 3.3.

We also calculated the main effect of target direction at each mask offset. The effect of target motion was significant for the 30 ($t(49) = -4.55$, $p < 0.001$), 60 ($t(49) = -6.41$, $p < 0.001$) and 90 degree ($t(49) = -5.81$, $p < 0.001$) offset values; the effect of target motion at the 5 degree mask offset value was not significant ($t(47) = -1.46$, $p = 0.15$). Our analyses of thresholds for masked conditions suggest that all the age groups were similarly affected by small mask offsets, but increasing the mask offset resulted in an age effect.

3.3.2 Masking

Thresholds were used to calculate the strength of masking, which was defined as the log difference between thresholds obtained with a mask and the threshold obtained in the no-mask condition. Masking strength is plotted as a function of mask direction offsets in Figures 3.4 and 3.5. An ANOVA on the log-transformed masking values revealed significant main effects of age group ($F(2, 47) = 12.64$, $p < 0.001$) and mask offset ($F(3, 141) = 110.09$, $p < 0.001$). The age group x target direction ($F(2, 47) = 4.7$, $p < 0.05$) and mask offset x target direction ($F(3, 141) = 39.58$, $p < 0.001$) interactions were both significant. Perhaps most importantly, the age group x mask offset interaction was significant ($F(6, 141) = 13.27$, $p < 0.001$), suggesting that the effect of mask offset on masking strength varied across age groups. The group x mask offset x target direction interaction was not significant ($F(6, 141) = 1.53$, $p = 0.17$).

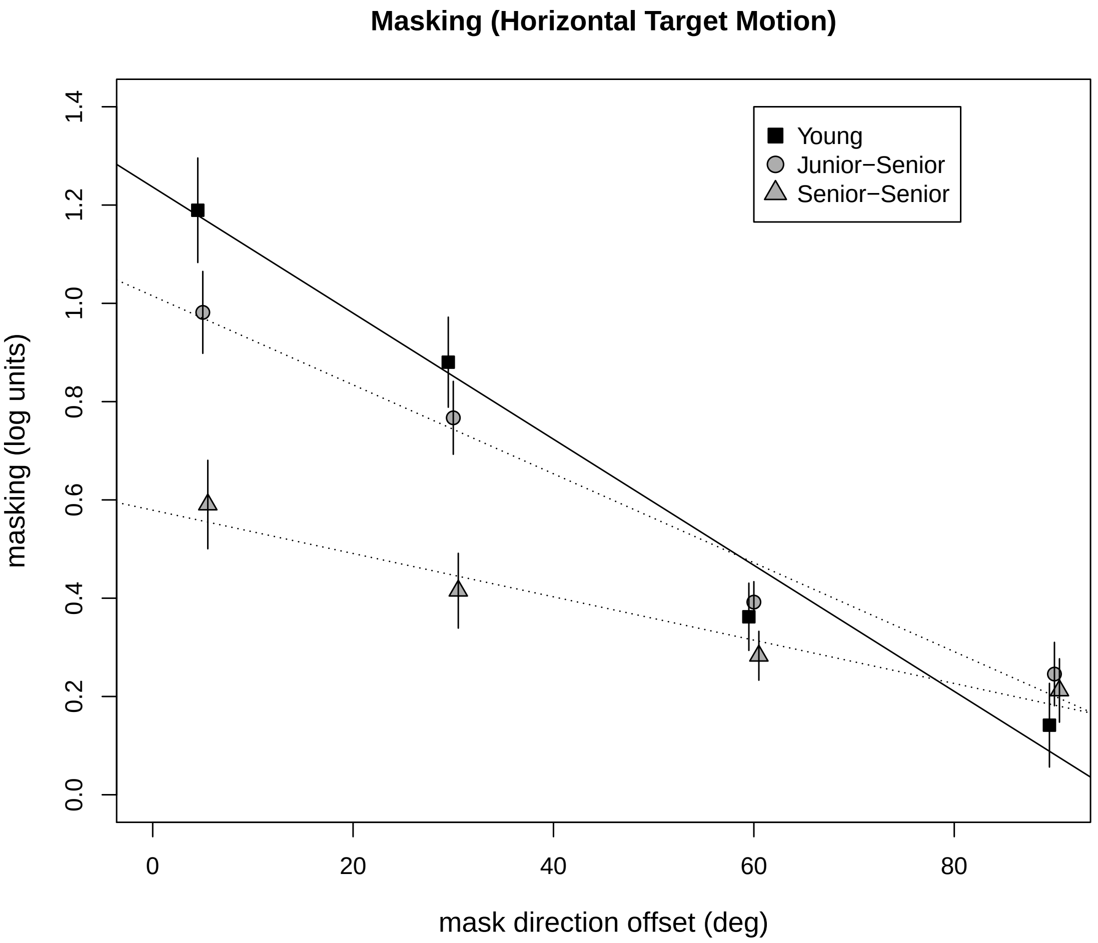


Figure 3.4: Masking strength in log units as a function of mask direction offset for the Horizontal target direction condition. Straight lines are the regression lines fit to each age group separately and error bars represent ±1 SEM. The SS group (grey triangles) can be seen to exhibit decreased masking effects compared to the other two groups.

The log masking functions were approximately linear, so we analyzed the shape of the masking functions with a linear trend analysis. The linear trend differed across age groups ($F(2, 47) = 16.21$, $p < 0.001$) and target directions ($F(1, 47) = 52.71$, $p < 0.001$), but the age group x target direction interaction was not significant ($F(2, 47) = 1.54$, $p = 0.22$). The lack of a significant interaction means that the age difference in linear trend did not differ significantly between horizontal and vertical target motions.

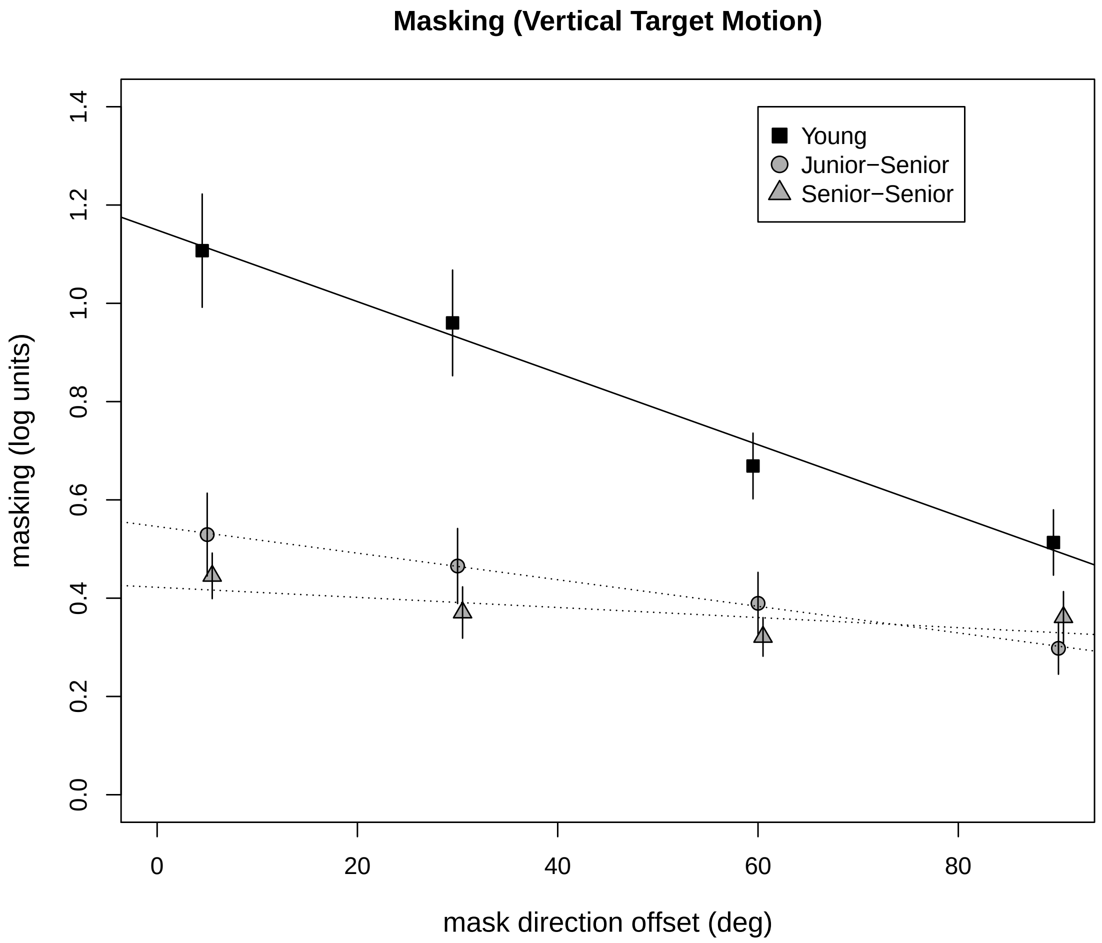


Figure 3.5: Masking strength in log units as a function of mask direction offset for the Vertical target direction condition. Straight lines are the regression lines fit to each age group separately and error bars represent ±1 SEM. Notably, here the JS and SS groups are showing almost the same pattern of results, one quite different from the Y group.

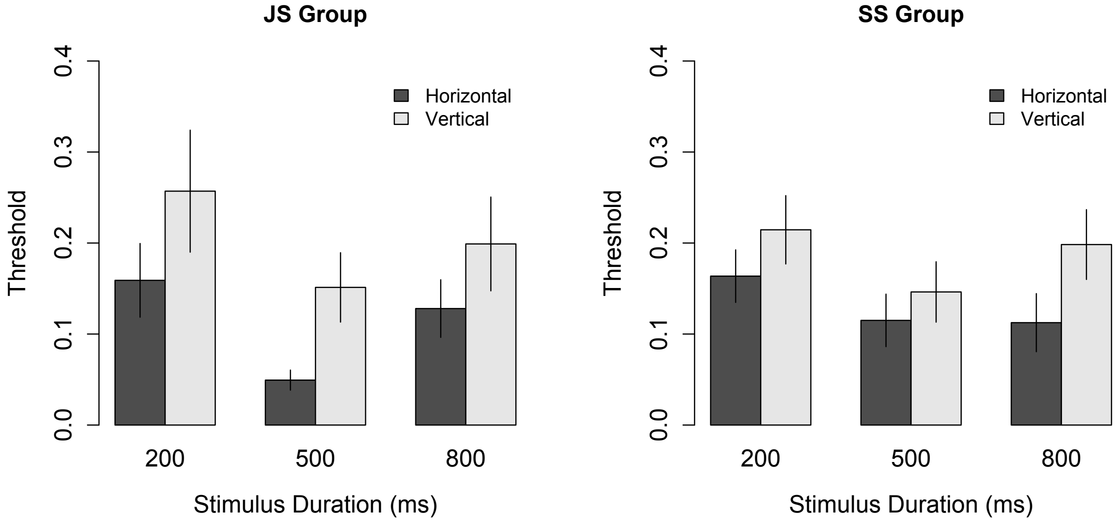
The main effect of target direction reflected the fact that masking functions for all three age groups were less steep in the vertical target motion condition. To better understand the main effect of age, we averaged the linear trend scores for each subject across target directions and then used Tukey HSD tests to compare the resulting average scores. The result was that the two older groups (JS and SS) differed from the Y group, but did not differ from each other. The steeper linear trend in younger subjects reflected the fact that masking was greater in younger subjects in conditions when the mask direction offset was small (Figures 3.4 and 3.5). Furthermore, this difference in masking was the result of younger subjects having significantly lower thresholds than older subjects in the no-mask condition, rather than having higher thresholds in the masked conditions (Figures 3.2 and 3.3).

3.4 Duration Control Experiment

It is known that older adults show longer saccade latencies (Carter et al., 1983), as well as impaired smooth pursuit behaviours (Kanayama et al., 1994) and impaired ocular following (Kolarik et al., 2010). The stimulus duration used in our experiment (500 ms) was long enough to allow subjects to move their eyes, and therefore age differences in eye movements may have contributed to age differences in motion detection thresholds. As a preliminary investigation of the role of eye movements in our task, we re-ran the experiment with a shorter stimulus duration (to reduce the possibility of eye movements) and a longer stimulus duration (to allow more time for eye movements). We tested only older adults (the JS and SS groups) because we were not interested in age-related eye movement differences, *per se*. Rather, we were specifically interested to see if the pattern of results we observed was due to some extraneous factor, such as eye movements. For this reason, the Y group was not run in this control.

3.4.1 Procedure

The procedure for these controls was nearly identical to the one used in Experiment 3.1. Stimulus duration was 200 and 800 ms in, respectively, the short and long duration conditions, rather than the 500 ms duration used in the original experiment. In the short duration conditions, thresholds were measured with all of the mask offsets used in Experiment 3.1; in the long duration condition, thresholds were measured with mask direction offsets of ±5 deg and ±90 deg and in a no-mask condition. In the short duration condition, there were 10 subjects in the JS group (mean age = 63.1) and 11 subjects in the SS group (mean age = 76.5). In the long duration condition, there were 10 subjects in the JS group (mean age = 62.4) and 12 subjects in the SS group (mean age = 75.8). No subject was tested with more than one duration (i.e., each experiment used different subjects).



(a) (b)

Figure 3.6: Thresholds measured in the no-mask condition in JS (a) and SS (b) groups with stimulus durations of 200, 500, and 800 ms. Data in the 500 ms condition is from Experiment 3.1. Error bars represent ±1 SEM.

3.4.2 Results

Thresholds in the no-mask condition are shown in Figure 3.6. For comparison, Figure 3.6 includes thresholds from the JS and SS groups in Experiment 3.1, which used a stimulus duration of 500 ms. A 2 (age group) x 2 (target direction) x 3 (stimulus duration) ANOVA performed on log-transformed thresholds revealed a significant main effect of stimulus duration ($F(2, 69) = 5.34$, $p = 0.007$); planned comparisons found that thresholds in the 200 ms condition were higher than the 500 and 800 ms conditions ($F(1, 69) = 7.97$, $p = 0.006$) but that thresholds in the 500 and 800 ms conditions did not differ from each other ($F(1, 69) = 2.70$, $p = 0.105$). There was a main effect of target direction ($F(1, 69) = 58.5$, $p < 0.0001$), demonstrating that thresholds were higher in the vertical target motion condition. Inspection of Figure 3.6 suggests that the effect of stimulus duration on thresholds obtained with horizontal motion was greater in the JS group, but the group x duration x target direction interaction did not reach conventional levels of statistical significance ($F(2, 69) = 2.94$, $p = 0.6$). The main effect of age group ($F(1, 69) = 1.36$, $p = 0.25$) and all two-way interactions with age group ($F \geq 1.80$ and $p \geq 0.184$ in each case) were not significant.

Thresholds measured in conditions using mask direction offsets of 5 and 90 deg are shown in Figure 3.7, which also includes thresholds obtained with a stimulus duration of 500 ms in Experiment 3.1. Inspection of Figure 3.7 suggests that thresholds generally were lower when the mask direction offset was 90 deg than when it was 0 deg, but that the effect of mask offset was smaller for i) vertical target motion compared to horizontal target motion; ii) the 200 ms stimulus duration compared to durations of 500 and 800 ms; and iii) the SS group compared to the JS group.

These observations were evaluated with a 2 (age group) x 2 (mask direction offset) x 2 (target direction) x 3 (stimulus duration) ANOVA performed on log-transformed thresholds. As expected, the ANOVA revealed a significant main effect of mask direction offset ($F(1, 69) = 123$, $p < 0.0001$) and significant two-way interactions between offset and target direction ($F(1, 69) = 51.2$, $p < 0.0001$), stimulus duration ($F(2, 69) = 8.87$, $p < 0.001$), and age group ($F(1, 69) = 11.26$, $p = 0.0013$). The significant target direction x mask offset interaction, illustrated in Figure 3.8a, means that the difference between thresholds in the 0 and 90 deg offset conditions was larger for horizontal target motion than vertical motion. Furthermore, the ANOVA found that the target direction x mask offset interaction did not vary significantly across stimulus durations ($F(2, 69) = 2.39$, $p = 0.10$) or age groups ($F(1, 69) = 1.47$, $p = 0.23$). The duration x mask offset interaction, illustrated in Figure 3.8b, shows that the effect of mask offset was smaller when the stimulus duration was 200 ms than when it was 500 or 800 ms, and the duration x mask offset interaction did not vary across age groups ($F(2, 69) = 0.80$, $p = 0.45$) or target directions ($F(2, 69) = 2.39$, $p = 0.10$). Finally, the significant age group x mask offset interaction, which is illustrated in Figure 3.8c, reflects the fact that the difference between thresholds in the 0 and 90 deg mask offset conditions was larger in the JS groups than in the SS groups. Furthermore, the ANOVA found that this age group x mask offset interaction did not vary significantly with the direction of target motion ($F(1, 69) = 1.47$, $p = 0.23$) or with stimulus duration ($F(2, 69) = 0.8$, $p = 0.45$).

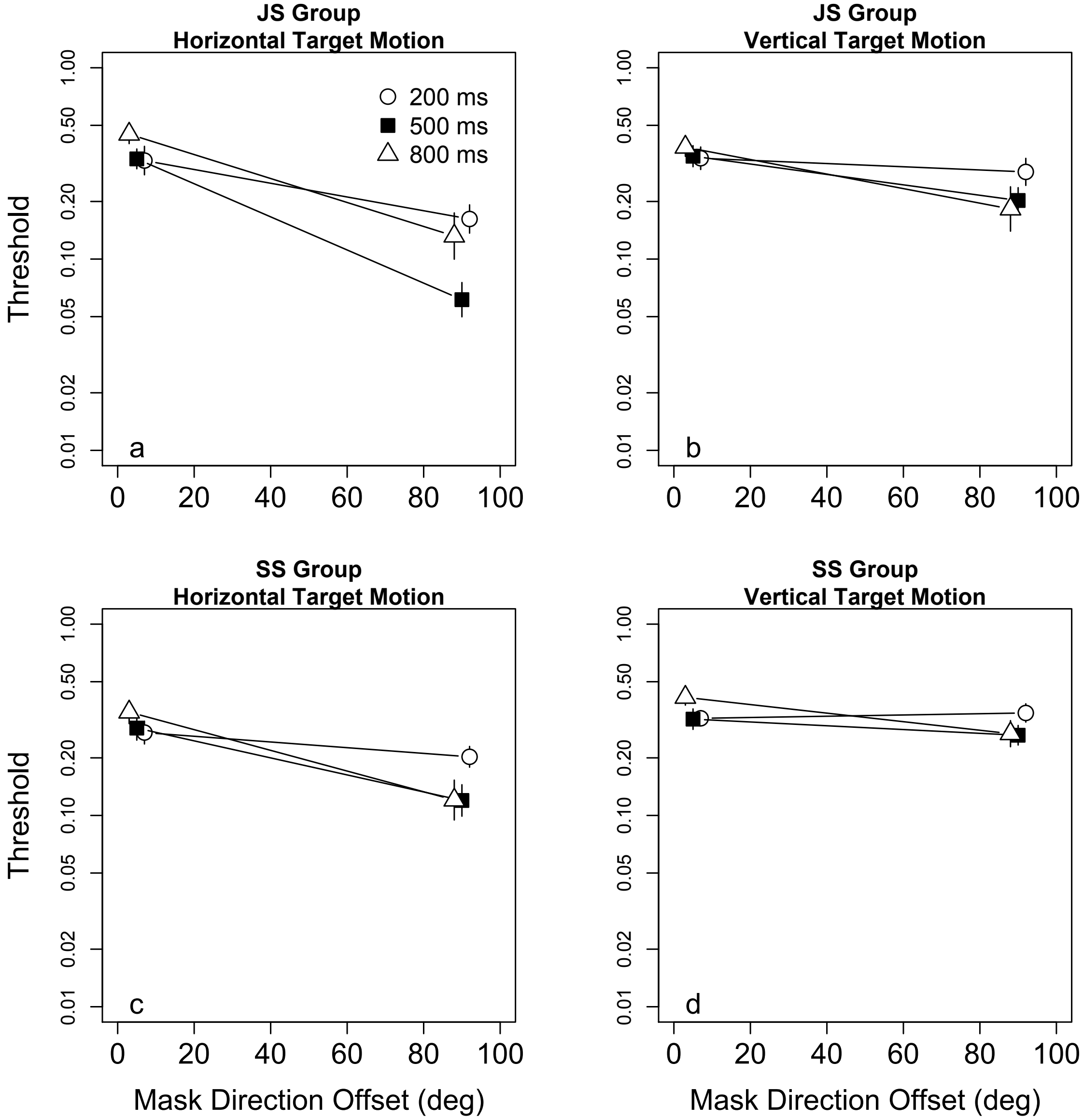
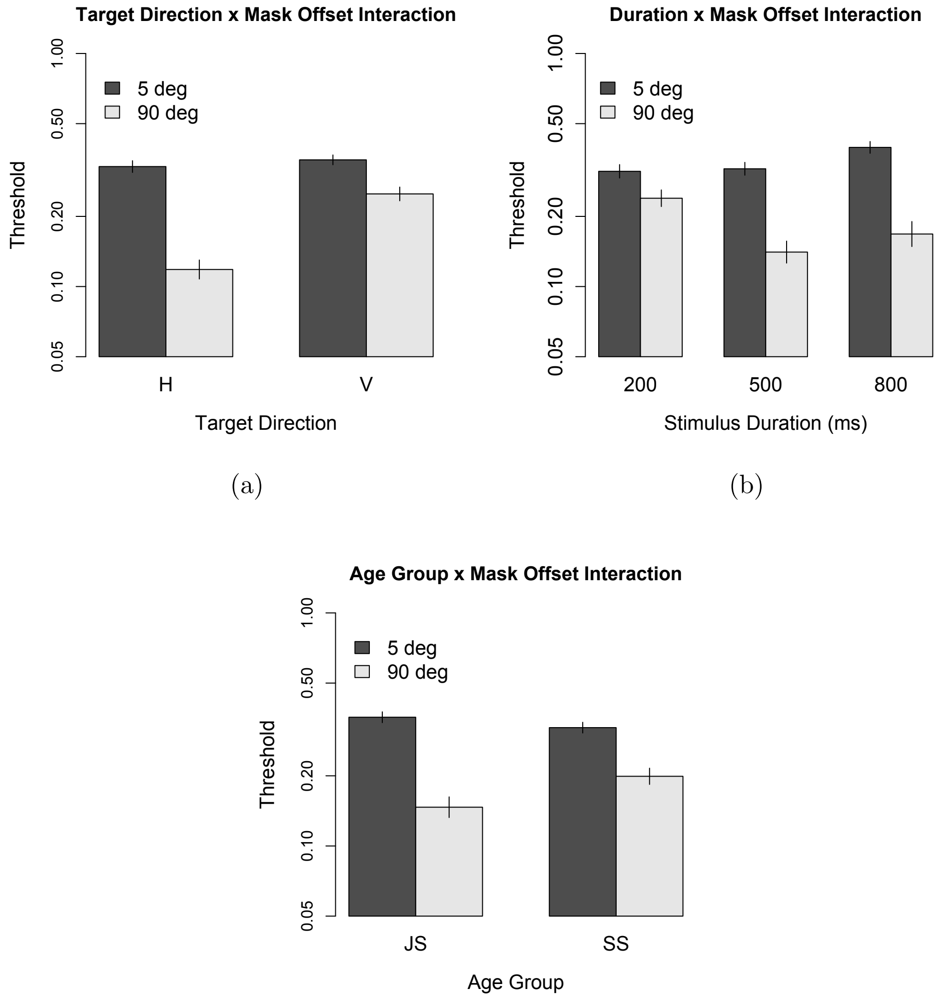


Figure 3.7: Mean thresholds measured in conditions using mask offsets of 5 and 90 deg condition with stimulus durations of 200, 500, and 800 ms. Thresholds in the JS groups with horizontal and vertical motions are shown in panels *a* and *b*, respectively. Thresholds in the SS groups with horizontal and vertical target are shown in *c* and *d*, respectively. Data in the 500 ms condition are from Experiment 3.1. To improve clarity, the data points have been displaced slightly along the horizontal axis. Error bars represent ±1 SEM. Where error bars are not visible, the SEM was smaller than the width of the symbol.



(a) (b)

(c)

Figure 3.8: Illustrations of significant two-way interactions found by an ANOVA performed on the data shown in Figure 3.7. (a) Illustration of the target direction x mask offset interaction. The vertical axis plots mean thresholds averaged across age groups and stimulus durations. (b) Illustration of the stimulus duration x mask offset interaction. The vertical axis plots mean thresholds averaged across age groups and mask direction offsets. (c) Illustration of the age group x mask offset interaction. The vertical axis plots mean thresholds averaged across stimulus durations and target directions. Error bars represent ±1 SEM.

3.4.3 Discussion

We investigated the potential influence of eye movements on performance in Experiment 3.1 by varying stimulus duration. We hypothesized that the results we observed in older adults may have been due to inadvertent eye movements during presentation of the stimulus. In general, we found that neither the interaction between age and mask offset, nor the interaction between target direction and mask offset were dependent on stimulus duration. The primary effect of reducing stimulus duration to from 500 to 200 ms was to increase thresholds in the 90 deg offset condition. The shorter stimulus duration reduced the probability of making eye movements, but did not eliminate the differences in performance between the vertical and horizontal target directions, or affect the differences between the two oldest subjects groups (the JS and SS groups). Increasing stimulus duration (and consequently, increasing the likelihood of eye movements), from 500 to 800 ms also did not affect the difference between vertical and horizontal target directions, or the difference between the JS and SS subject groups. Together, these results suggest that the shallower threshold-vs-mask offset functions that we observed in the SS subjects (and also with vertical target motions) cannot be explained simply as being a by-product of eye movements during stimulus presentation. Future investigations could monitor eye movements to directly confirm or deny this tentative conclusion.

3.5 General Discussion

In this chapter, we further investigated the hypothesis that older human adults have more broadly tuned directionally selective mechanisms. We expanded on the results from the previous chapter by using a slightly different noise mask, as well as a different performance measure (i.e.,coherence thresholds rather than contrast thresholds). In an attempt to generalize our results, we also tested vertical motion perception as well as horizontal. Our results suggest that older human adults do show evidence of more broadly tuned mechanisms, and that this broadening appears to be more evident when making vertical motion judgments. Also, it appears that, in some ways, our JS and SS groups show different patterns of performance (see Figures 3.4 and 3.5), suggesting that there may be task-specific age-related changes even within an older adult population. The overall result from this investigation is consistent with the main result from Chapter 2, and since our approach differed, we were able to show that this result was not specific to the contrast-detection paradigm we used previously. Our eye movement control results seem to indicate that the differences we observed with age, or between vertical and horizontal target motion, were not solely due to eye movements.

The masking functions in Chapter 2 were presented as contrast threshold x notch width plots. Notch width referred to the size of the angular restriction placed on the mask dots, restricting movement in the directions of the target motion. In this chapter, we used coherence thresholds to calculate masking, and this was plotted as a function of mask offset. When one looks at thresholds in the horizontal condition from this chapter (Figure 3.2) and compares it to the threshold diagram from Chapter 2 (Figure 2.4), we see that the Y group shows the steepest functions in both plots, suggesting they have the narrowest directional tuning. Second, we see a progressive change that occurs with age, with the functions becoming shallower. It is worth highlighting these similarities because together they confirm that the effects we saw were not dependent solely on the measures used; they are not 'method-sensitive'. These similarities act in some ways to confirm for us that the evidence for broadened tuning we found was not spurious, but rather a true evaluation of performance in older adults.

A surprising finding from this set of experiments is the difference between horizontal and vertical motion perception, specifically in older adults. Although the difference between vertical and horizontal motion perception is not often directly examined, there have been numerous documented anisotropies in direction perception, including some related to the vertical/horizontal difference. For instance, de Grind et al. (1993) measured signal-to-noise thresholds for coherent motion detection as a function of motion direction. They found that near the vertical axis, thresholds varied by motion direction, with thresholds for vertical motion (up or down) being the highest and thresholds on the oblique axis were lower than those found near the vertical axis. Gros et al. (1998) found that while motion detection was isotropic, motion discrimination varied according to the direction of motion, and was worse at the oblique directions compared to the cardinal ones, although he did not directly compare vertical and horizontal motions. Directional sensitivity also differs within the central, right, left and lower visual field (Ohtani and Ejima, 1997), with downward motion being perceived more frequently than upward motion; this same study found no anisotropy with horizontal motion. These are also asymmetries in the strength of illusory motion perception (Lott and Post, 1993), with upward motion soliciting faster illusory motion than downward motion. In infants, vertical motion tracking is inferior to horizontal tracking (Grönqvist et al., 2006). In adults, when making judgments of displacement (Hubbard, 1990), the magnitude of perceived displacement differs between the horizontal and vertical meridians. Raymond (1994) showed, using coherence thresholds, that foveally presented motion coherence thresholds were higher for vertical motion than they were for horizontal motion. In general, it appears that the oblique directions, and - when tested - vertical direction judgments present a challenge for the visual system and result in impairments in performance.

It is not entirely clear what causes these directional differences. Gros et al. (1998) hypothesized that observed anisotropies could be the result of narrower tuning of directionally selective cells for the cardinal directions compared to the oblique ones. However, one study by Blake and Holopigian (1985) investigated orientation tuning in both cats and humans, using masking to test vertically and obliquely oriented stimuli, and found no differences between the two orientations. This result from Blake and Holopigian (1985) does not completely eliminate the possibility raised by Gros et al. (1998) though, as they measured orientation tuning, not motion. In fact, previous work from our lab has shown that orientation selectivity of masking also does not differ between younger and older humans (Govenlock et al., 2009). The expansion of this current work to include measurements at oblique directions could help paint a broader picture of directional tuning for all age groups (and in some ways, test the hypothesis of Gros et al. (1998)).

While there may be an explanation for the difference between the cardinal directions and the oblique ones, what then, could cause such a difference in the masking functions between the vertical and horizontal directions for older adults? It seems unlikely that the processes that degrade a cell's tuning in general (for instance, changes in inhibition) would selectively target vertically-selective cells. This would imply a pattern to the degradation that is difficult to explain as we are not aware of any physiological marking or identifier that might result in selective degradation of cell populations. A more plausible explanation could be that vertical motion judgments are less needed in older age, and so, the cells responsible for these judgments fall into disuse. They might then be more susceptible to age-related neural changes. Also, as Hubbard (1990) suggests, our own mental representation of the world (and the role of gravity, for instance) could also help explain differences relating to the vertical direction.

In general, the findings from the experiments in this chapter suggest that older adults indeed show perceptual evidence of broader directionally-selective mechanisms that is not due to eye movements, and that the direction of target motion may have subtle effects on performance. These results are similar to those seen in Chapter 2 and continue to paint a picture of how direction discrimination changes with increasing age.

3.6 Acknowledgements

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Chapter 4

The effect of aging on peripheral motion perception

Abstract

Older adults show a variety of impairments when making judgments about motion stimuli presented foveally. The current experiments sought to expand upon this result and evaluate the direction discrimination abilities of older and younger adults in the near peripheral visual field. Three groups of subjects (Young, under 30; Junior-Seniors, 60-70; Senior-Seniors, over 70) were asked to discriminate the direction of a coherently moving field of dots embedded in noise masks of varying contrast levels. The main findings are that both groups of older adults show elevated contrast thresholds at all mask contrast levels compared to the younger adults, but when differences in contrast sensitivity are considered, the form of the masking function is similar across age groups.

4.1 Introduction

Age-related changes in the ocular media and retina result in lower visual acuity, decreased field of view (such as the tunnel vision seen in glaucoma), clouding of the lens, thinning of the retina, poorer contrast sensitivity and a loss of photoreceptors, especially in the periphery (Jackson and Owsley, 2003; Conn, 2006; Polidori et al., 1993; Bonnel et al., 2003). These anatomical changes, which alone cannot fully explain perceptual visual deficits seen with age (Spear, 1993), can combine with other more up-stream changes in the visual pathway and lead to perceptual impairments in older human adults, and also may play a role in falls in the elderly (Dhital et al., 2010).

Aging has significant effects on motion perception. For stimuli presented in the central visual field, older adults show poorer motion detection and direction discrimination abilities as well as impaired speed perception (Bennett et al., 2007; Snowden and Kavanagh, 2006; Tran et al., 1998; Norman et al., 2003). They also show impairments when making judgments about optic flow patterns (Atchley and Andersen, 1998), biological motion patterns with short durations (Norman et al., 2004) and in automobile traffic-related scenarios (Lobjois and Cavallo, 2007). The ability to correctly identify and classify motion presented foveally is important particularly in these latter types of cases because ambulating in society often requires difficult judgments about moving vehicles and pedestrians.

Just as important to ambulation though, is the ability to perceive motion presented in the periphery. Peripheral motion cues can be crucially important for maintaining posture and balance. Simply presenting motion patterns in the periphery, for example, can induce feelings of self motion, both when sitting and lying down (Kano, 1991). While locomoting, peripheral motion can be a rich source of information and aid in accident prevention. For instance, the finding from Tynan and Sekuler (1982) that responses to slowly moving targets changes as the targets move into the periphery has direct consequences for adjusting one's own movement to that of other peripherally approaching or receding objects. Older adults are also less sensitive when forced to detect collisions, especially when they experience simulated motion (Andersen and Enriquez, 2006) or at high speeds (Andersen et al., 2000) and are generally less accurate when judging potential collisions (Delahunt et al., 2008).

The aim of the present experiment is to further explore how peripheral motion perception changes with increasing age, specifically looking at changes in performance related to poorer contrast sensitivity. By using random dot kinematograms whose noise masks are at different contrasts we hope to gain a better understanding of how peripheral motion perception interacts with the loss in contrast sensitivity found with increasing age. By separating our older adults into a younger and older group we can also evaluate differences that occur within the older population as well.

4.2 Methods

4.2.1 Subjects

All subjects were recruited from the McMaster University community and surrounding neighbourhoods. Subjects were split into three age groups: Young (Y; $<$ 30 years old), Junior-Seniors (JS; 60-70 years old) and Senior-Seniors (SS; $>$ 70 years old). Table 4.1 shows the mean age, near and far visual acuity, and Pelli-Robson contrast sensitivity for each group, as well as the Mini-Mental State Exam (MMSE) scores for all older subjects. We administered a questionnaire to ensure that all subjects had good health, visual or otherwise. All procedures were approved by the McMaster Ethics Review Board, and subjects were compensated for their time.

Table 4.1: Number of subjects, age, acuity, contrast sensitivity and Mini-Mental State Exam (MMSE) scores for the young (Y), junior-senior (JS), and senior-senior (SS) groups. The second column shows the total number of subjects and the number of female subjects in parentheses. The remaining columns show the mean and standard deviation (in parentheses) for each measure. The MMSE was not administered to subjects in group Y.

Group	N (# females)	Age (years)	Near acuity	Far acuity	Pelli-Robson	MMSE
Y	18 (9)	22.22 (3.10)	1.38 (0.29)	1.40 (0.26)	1.94 (0.04)	N/A
JS	19 (10)	65.63 (2.63)	1.00 (0.24)	1.20 (0.24)	1.90 (0.09)	28.95 (1.22)
SS	18 (9)	74.44 (2.79)	0.98 (0.18)	1.10 (0.33)	1.86 (0.13)	28.05 (3.28)

4.2.2 Apparatus and Stimuli

The experiment was programmed in MatLab v7.4 (The Mathworks) using the Psychophysics and Video Toolbox (Brainard, 1997; Pelli, 1997) running on an Apple G4 PowerMac computer. The monitor had a resolution of 1280 × 1024 pixels and a refresh rate of 75 Hz. Average luminance was 30 cd/m^2. The room was dark, and the only light came from the display screen, which subtended 17.2 x 13.5 deg of visual angle when subjects were seated 114 cm away. Head position was maintained using a chin/forehead rest. Responses were made by pressing one of two keys on a standard QWERTY Macintosh keyboard.

The stimuli were random dot kinematograms presented within an annulus that had an inner diameter of 11 deg and an outer diameter of 17 deg. The dots were 0.01 deg in diameter, moved at 5 deg/sec and were refreshed on every frame. When a dot reached an inner or outer edge of the annulus, it was extinguished and randomly replaced somewhere within the annulus. On each frame, 5% of the dots were extinguished and repositioned randomly within the annulus. There were 500 total dots presented within the annulus: 25 of them moved coherently to the right or to the left on any given trial (Signal dots, 5% coherence) while the remaining 475 dots independently moved in random directions (Mask dots, 95%).

4.2.3 Procedure

Each trial began with a fixation point in the centre of the screen. Subjects were instructed to keep their gaze on the fixation point for the entire trial, though we did not monitor this with eye-movement measurements. The fixation point briefly flickered between black and white to indicate that the trial was about to start and then the kinematogram was displayed for 500 ms. Once the stimulus was extinguished, subjects indicated the direction of the Signal dots (right or left) by pressing one of two keys on the keyboard. The response was un-speeded, but subjects were encouraged to develop a consistent rhythm.

The contrast of the Signal dots was adjusted using a Quest staircase procedure (Watson and Pelli, 1983) procedure to estimate the Signal dot contrast that yielded 81% correct responses. The contrast of the Mask dots was held constant at one of four levels (0, 0.1, 0.2 or 0.4) in separate blocks of 50 trials each. Subjects completed all four

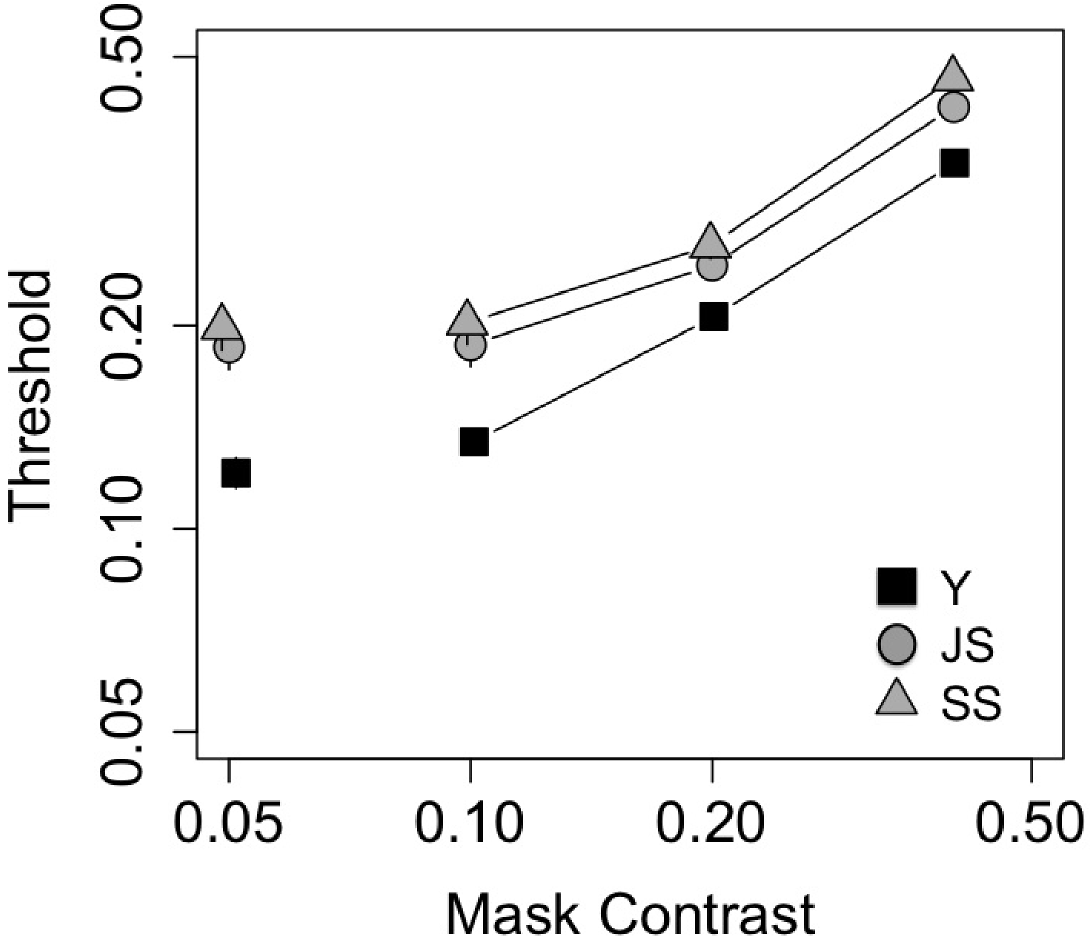

Figure 4.1: Peripheral motion discrimination thresholds plotted as a function of mask dot contrast. Symbols on the left side of the figure represent thresholds obtained with mask contrast set to zero. Error bars represent ±1 SEM. In conditions where the error bars are not visible, the width of the SEM was less than the width of the symbol.

blocks, were given a short break, and then completed all four blocks a second time. The order of blocks was randomized for each subject and session. The entire procedure lasted approximately 45 minutes.

4.3 Results

Thresholds are shown in Figure 4.1. In all three groups, thresholds increased monotonically with increasing mask contrast. Furthermore, in each condition, thresholds in the Y group were lower than thresholds in the JS and SS groups, and thresholds in the latter two groups were very similar. An ANOVA performed on log-transformed thresholds in the zero-contrast mask condition found a significant effect of group ($F(2, 52) = 14.35$, $p < 0.0001$). Planned comparisons revealed that thresholds in the Y group differed significantly from thresholds in the two older groups ($F(1, 52) = 28.23$, $p < 0.0001$), but that thresholds in the JS and SS groups did not differ from each other ($F(1, 52) = 0.48$, $p = 0.49$). An ANOVA on log-transformed thresholds in the masked conditions found significant main effects of age group ($F(2, 52) = 21.74$, $p < 0.0001$) and mask contrast ($F(2, 104) = 395$, $p < 0.0001$); the interaction between age group and mask contrast was not significant ($F(4, 104) = 1.66$, $p = 0.16$).

To see if the effect of age group in the masked conditions remained significant once differences in contrast sensitivity were taken into account, the data were reanalyzed with a linear model that included log-transformed threshold in the unmasked condition as a covariate. This new analysis found a significant association between log-transformed thresholds and the covariate ($F(1, 49) = 34.26$, $p < 0.0001$) and a significant main effect of mask contrast ($F(2, 98) = 44.6$, $p < 0.0001$), but the main effect of age group ($F(2, 49) = 1.24$, $p = 0.30$). and the interaction between age group and mask contrast ($F(4, 98) = 1.48$, $p = 0.21$) were not significant. Hence, age differences in the masked conditions were accounted for by age differences in threshold in the un-masked condition. This point is illustrated in Figure 4.2 which plots masking, defined as the logarithm ratio of masked thresholds divided by unmasked threshold, as a function of normalized mask contrast, defined as the ratio of mask contrast (i.e., 0.1, 0.2, or 0.4) divided by a subject's threshold in the unmasked condition. Similar to what was found in central vision (Experiment 2.3, Figure 2.11), Figure 4.2 shows that peripheral masking values in all age groups were well-fit by a single function in which masking strength is approximately 0 log units when normalized mask contrasts is less than -0.2, and is approximately equal to normalized mask contrast when it is greater than 0.

In summary, our results indicate that peripheral motion discrimination thresholds were significantly greater in older adults than younger adults, but that the form of the masking function was similar across age groups.

4.4 General Discussion

By using a random dot stimulus in the near periphery and varying the contrast of coherently moving target dots we were able to show that older adults have higher thresholds than younger adults in both masked conditions and the no-mask condition. While both groups of older adults showed significantly higher thresholds than then younger group, the JS and SS groups did not differ. The threshold differences in the masked conditions were accounted for by age differences in the unmasked condition, suggesting that while performance is impaired for older adults in the periphery, the form of the masking function is similar to that of younger adults.

Our results differ from those of Wojciechowski et al. (1995) who found that, for older adults, motion sensitivity was essentially equal across a number of areas in the visual field. It was only younger adults in their study who showed reduced performance in the periphery even though they outperformed the older adults in general. In contrast, our younger adults consistently outperformed both groups of older adults. The difference in results could be explained by the task differences; our task varied contrast to determine thresholds whereas Wojciechowski et al. varied stimulus coherence. Additionally, Wojciechowski et al. measured thresholds further in the periphery, and also compared the superior and inferior visual field, whereas we only looked at stimuli centered along the horizontal meridian.

In a related vein, since there are changes in the topography of motion perception with aging it is also reasonable to question whether retinal changes are contributing to this effect. It is known that the peripheral retina responds differently to motion than central retina (Finlay, 1982). There are also many age-related changes in the retina (Bonnel et al., 2003) that include a preferential loss of rods in the peripheral retina (which likely contributes to impaired motion perception). However, since all the subjects in our experiments have good ocular health and were up to date in their eye examinations, it is likely that these sorts of anatomical changes play a minimal role in the results observed

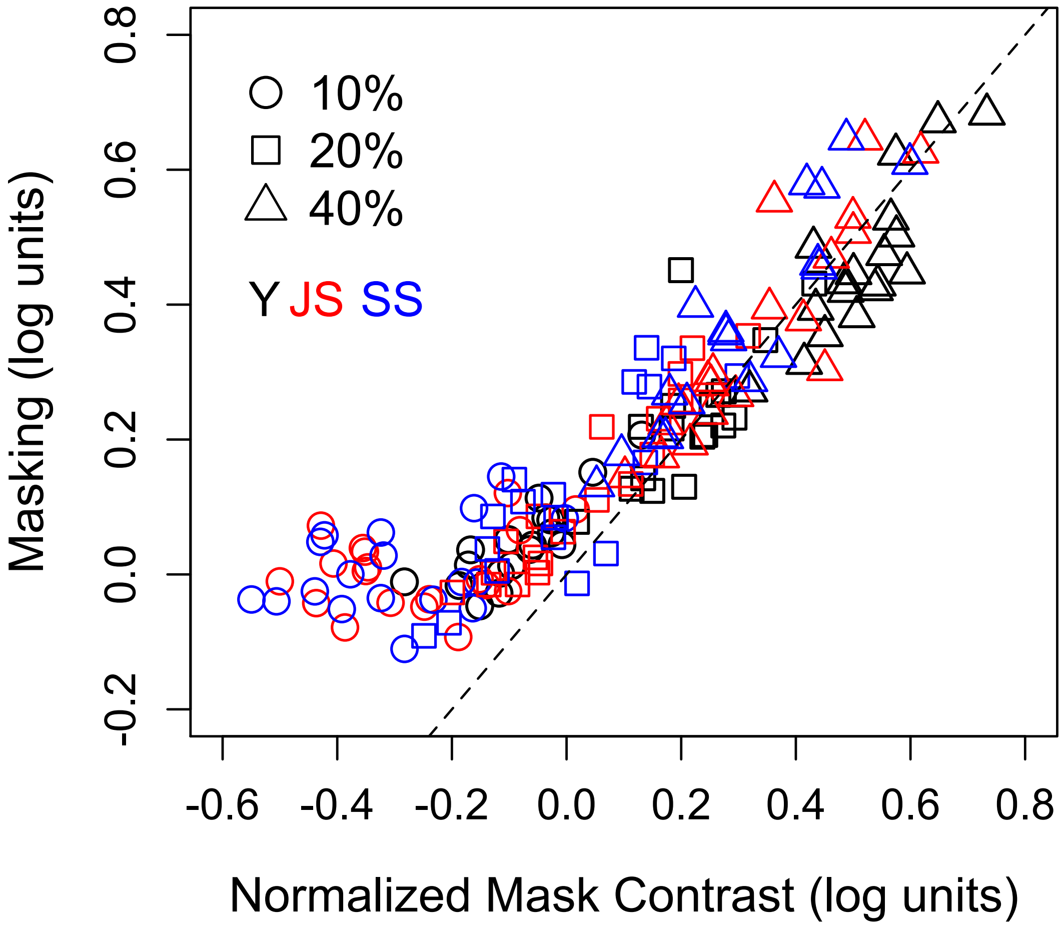

Figure 4.2: Masking plotted as a function of normalized mask contrast. Masking was defined as the $\log_{10}$-difference between thresholds measured with a mask and thresholds measured with mask contrast set to zero. Normalized mask contrast was defined as the $\log_{10}$-difference mask contrast (i.e., 0.1, 0.2, or 0.4) and threshold in the no mask condition. Each point represents the data from a single subject in the Y (black), JS (red), or SS (blue) group in conditions using a mask contrast of 0.1 (circles), 0.2 (squares), or 0.4 (triangles). The dashed line illustrates the line *Masking = Normalized Mask Contrast*.

here.

Absolute contrast sensitivity undoubtedly plays a role in explaining our results, particularly since the unmasked condition essentially was a measure of the contrast threshold for our stimulus. Previous work has shown that older adults are simply less sensitive to contrast than younger adults using various types of stimuli (Tang and Zhou, 2009; Habak and Faubert, 2000). Allen et al. (2010) found a similar result. When comparing older and younger adults on a global motion coherence task they found a lateral shift in the threshold vs contrast sensitivity function, indicating the role of contrast deficits in the older adults. The same result has even been found in senescent primates (Yang et al., 2008), where neurons in V1 and MT are less sensitive to contrast than neurons in younger monkeys. Even though the results presented here show that the masking function does not differ across age, performance still does, highlighting the importance of considering the effects of changes in contrast sensitivity when evaluating perceptual abilities in older adults.

In a practical sense, impairments in peripheral vision, be it specifically motion perception or not, can have profound effect on one's life. In patients with retinitis pigmentosa, peripheral visual field loss was highly correlated with a measure of quality of life (Sugawara et al., 2009). Poor vision in aging (including, for instance, poorer contrast sensitivity) can contribute to balance issues and falls (Sturnieks et al., 2008) and blur can also affect stepping and also lead to increased risk of falls (Heasley et al., 2005). When age-related visual changes combine with pathologies or perceptual deficits, the resulting impairments could significantly affect an older adult's ability to interact with society. Further investigation into the age-related changes in peripheral motion perception in particular may provide useful ways to increase safety and prevent accidents as the population of the world ages.

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Social Interaction in Healthy Aging.

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Chapter 5

Aging, peripheral motion perception and attention

Abstract

Older adults show impairments in motion perception, both foveally and in peripheral vision, but in the real world, judgments about moving objects are rarely performed in isolation. These experiments explored the effect of dividing attention on peripheral motion perception in a group of younger (under 30) and two groups of older adults (Junior-Senior, 60-70 and Senior-Senior, over 70). Subjects were asked to judge the direction of coherently moving fields of dots embedded in noise and positioned at a variety of locations along the horizontal meridian. This was done under two conditions: focused conditions, where they only made judgments about the motion stimulus, and divided conditions, where they made judgments about both the motion stimulus and a central letter stimulus. The principal finding is that older adults were impaired when making motion judgments in the periphery, but they were not differentially affected when required to divide their attention across tasks.

5.1 Introduction

The rapid aging of the global population (StatisticsCanada, 2010) is outpacing our knowledge and understanding of perceptual changes associated with healthy aging. Known changes in the perceptual abilities of older adults can have consequences for normal living in society. For instance, impaired direction and speed discrimination abilities (Bennett et al., 2007; Norman et al., 2003) combined with poor judgments about street-crossings (Lobjois and Cavallo, 2007) can result in dangerous drivers out on the road. This current chapter, exploring the interaction between motion perception in the near periphery and attention, can contribute to our understanding of how older drivers may change with age.

Motion perception in and of itself can change dramatically with age. In addition to poorer direction and speed perception, previous research has reported changes in biological motion perception (Pilz et al., 2010) and the ability to extract information from optic flow (Atchley and Andersen, 1998). Changing responses to objects moving in the peripheral visual field (Tynan and Sekuler, 1982) also speak to impairments outside of foveal vision. Our own work from Chapter 4 found that older adults were outperformed by young adults when asked to judge the direction of coherent dots embedded in noise when the stimuli were placed in the near periphery.

In addition to showing deficits with individual tasks, older adults also show impairments when asked to divide their attention between two tasks. For instance, Sekuler et al. (2000) tested older and younger adults on a paradigm that required responses on both a central identification and a peripheral localization task. The older adults showed a pattern of impairment that suggested a decrease in the efficiency with which they can extract information from a cluttered scene. Older adults have also been found to be slower and less accurate when searching for traffic signs under dual-task attentional conditions (McPhee et al., 2005). These observed impairments are meaningful because standardized tests that rely heavily on measures of dual-task performance have been highly correlated with automobile crash risk, especially in the elderly (Ball and Owsley, 1993). In this vein, we wondered if an additional central task would cause greater impairments when tested with a motion task for older adults. With the experiments presented in this chapter, we investigated the way that peripheral motion discrimination performance would change with the addition of the central task (intended to distract attention) for both younger and older adults .

5.2 Methods

5.2.1 Subjects

All of our subjects were recruited from the McMaster University population or from our lab's subject pool, which is made up of younger and older adults from the communities surrounding the university. Subjects were split into three age groups: Young (Y; under 30 years old), Junior-Senior (JS; 60-70 years old) and Senior-Senior (SS; over 70 years old). All subjects completed a health questionnaire to ensure they had no health issues, visual or otherwise, that would affect the experiment. We also measured near acuity, far acuity and contrast sensitivity (using the Pelli-Robson sensitivity chart), and subjects in the JS and SS groups were tested in the Mini-Mental State Exam (MMSE). Group results for all of these tests, as well the number of subjects in each group for our two conditions are shown below in Table 5.1. All procedures were approved by the McMaster Ethics Review Board, and subjects were compensated for their time.

Table 5.1: Number of subjects, age, acuity, contrast sensitivity and Mini-Mental State Exam (MMSE) scores for the Young (Y), Junior-Senior (JS), and Senior-Senior (SS) groups in each condition (Focused or Divided attention). The second column shows the total number of subjects per age group and the number of female subjects in parentheses. The remaining columns show the mean and standard deviation (in parentheses) for each measure. The MMSE was not administered to subjects in group Y.

Condition	N (# females)	Age (years)	Near acuity	Far acuity	Pelli-Robson	MMSE
Focused	20 Y (11)	23.4 (3.9)	1.35 (0.22)	1.35 (0.22)	1.94(0.07)	N/A
Attention	19 JS (10)	65.8 (2.4)	1.05 (0.22)	1.13 (0.20)	1.90 (0.10)	28.9 (1.2)
	17 SS (9)	74.1 (2.9)	1.00 (0.19)	1.00 (0.24)	1.93 (0.05)	28.8 (1.5)
Divided	20 Y (10)	23.6 (3.4)	1.38 (0.18)	1.37 (0.19)	1.96 (0.59)	N/A
Attention	21 JS (10)	65.0 (2.4)	1.02 (0.24)	1.12 (0.21)	1.89 (0.10)	28.9 (1.3)
	20 SS (10)	75.2 (3.2)	1.00 (0.20)	0.96 (0.25)	1.87 (0.10)	29.1 (1.3)

5.2.2 Apparatus & Stimuli

For both the Focused and Divided attention conditions, subjects viewed the stimulus display binocularly from a viewing distance of 57 cm. Viewing position was stabilized with a forehead/chin rest. The stimulus display was the only source of illumination in the testing room. The monitor had a spatial resolution of 1280 × 1024 pixels (subtending approximately 18.4 x 14.7°) and a refresh rate of 75 Hz (non-interlaced). Responses were collected using a standard Macintosh keyboard.

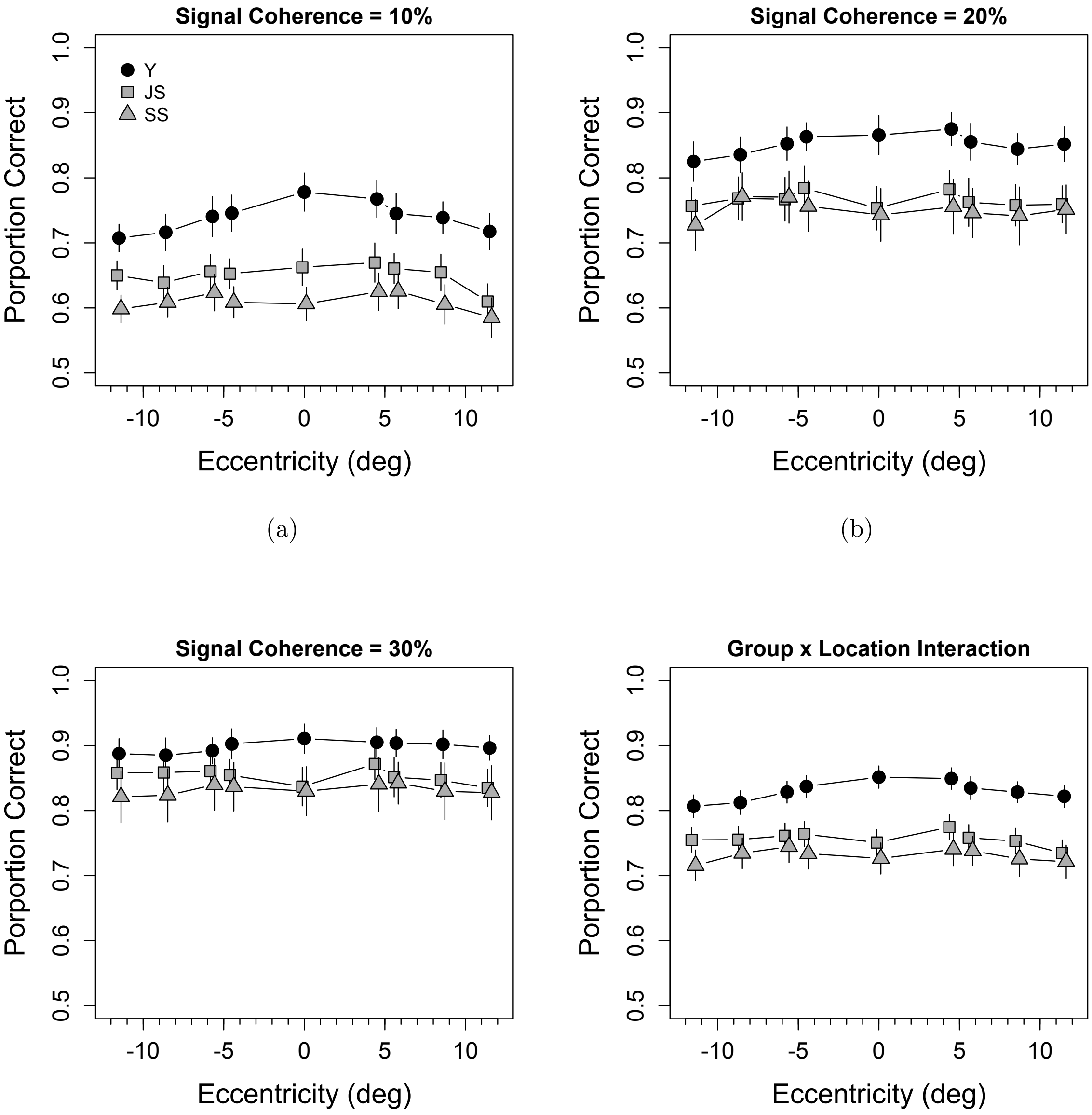
The stimuli were random dot kinematograms consisting of 100 square dots subtending 0.08°. Each stimulus consisted of Signal and Mask dots. All Signal dots moved coherently, in the same direction, up or down. Each Mask dot, on the other hand, moved in a direction that was selected randomly from a uniform distribution spanning all possible directions. There could be 10, 20 or 30 Signal dots (depending on the condition), resulting in 90, 80 or 70 Mask dots, respectively. Thus, the Signal coherence could be either 10, 20 or 30%. The dots were presented in small circular patches, 7.65° in diameter, centered at various eccentricities along the horizontal meridian. The contrast of both the Signal and Mask dots was kept consistently high (at a value of 0.8) over the course of the experiment.

On each trial in the Focused condition, a single patch appeared at one of nine eccentricities: -11.5, -8.6, -5.7, -4.5, 0, 4.5, 5.7, 8.6 or 11.5°, with positive values being to the right of a central fixation point and negative values being to the left. Each dot moved in a constant direction at a speed of 5°/sec, with the direction determined by what kind of dot it was (Signal, moving up or down, or Mask, moving in a random direction). If a dot reached the edge of the patch, it was extinguished and randomly replaced somewhere within the patch. On each frame, a random selection of 5% of the dots were extinguished and repositioned randomly within the patch.

On each trial in the Divided condition, again a single patch appeared, but it appeared at one of only four eccentricities (-11.5, -4.5, 4.5, and 11.5°). The difference from the Focused condition was in the addition of a central letter target (either an E or an H, Courier font, size 32, subtending approximately 0.8 x 1.1°) in the centre of the screen during each trial.

5.2.3 Procedure

Each trial in the Focused condition began with the presentation of a fixation point in the centre of the screen. Subjects were instructed to always keep their gaze on the fixation point (though we did not monitor this with eye-movement measurements). The fixation point briefly flashed to indicate that the trial was about to start, and then a single patch was displayed for 150 ms at a randomly-selected eccentricity. At the end of each trial,



(a) (b)

(c) (d)

Figure 5.1: Panels a-c: Results of the focused attention condition in Experiment 5.1. Data points for the JS and SS groups have been displaced horizontally by a small amount to improve clarity. Panel d: Illustration of the age group x location interaction: proportion correct for each group, averaged across the three levels of stimulus coherence, is plotted as a function of stimulus eccentricity. Error bars represent ±1 SEM.

subjects indicated whether the Signal dots were going up or down by pressing a button on a computer keyboard (2-AFC). Subjects were told that the Signal dots moved up or down with equal probability on each trial. Signal coherence varied across blocks, and subjects completed 360 trials of each block per session (i.e., 40 trials at each of the nine eccentricities, presented in random order). The order of blocks was randomized across subjects, and each subject completed two sessions on separate days (each session lasting approximately an hour).

With the addition of the central letter in the Divided condition, subjects were now required to make two responses on each trial. Both the letter and the motion stimulus onset and offset at the same time (that is, they appeared together on the screen for 150 ms). The first response was always the letter choice while the second was the direction of motion. Responses in this experiment were made using the mouse. Both options (E vs H; up vs down) were presented on the screen and subjects used the mouse to click on the answer they wished to submit. Our criteria for click accuracy were very lenient so as to eliminate any issues that might arise from an inability to control the mouse appropriately, especially in the older adults. The screen for both responses was divided in half (right-left halves for the letter response, up-down halves for the direction response). Subjects were told to click on the word to respond, but in reality, as long as they clicked somewhere within the half the response was counted. In this way, subjects did not have to be extremely precise in their mouse movements (even though they were encouraged to be). Subjects again completed 40 trials at each eccentricity in a random order, presented within randomly ordered coherence blocks.

	SS	df	Error SS	Error df	F	p
Group	4.202	2	29.49	52	3.70	0.031
Coherence	16.97	2	4.14	104	213.3	< 0.0001
Location	0.23	8	2.17	416	5.50	< 0.0001
Group × Coherence	0.22	4	4.14	104	1.39	0.239
Group × Location	0.17	16	2.17	416	1.98	0.013
Coherence × Location	0.07	16	3.17	832	1.08	0.373
Group × Coherence × Location	0.07	32	3.17	832	0.54	0.983

Table 5.2: Results of ANOVA performed on data from focused attention condition.

5.3 Results

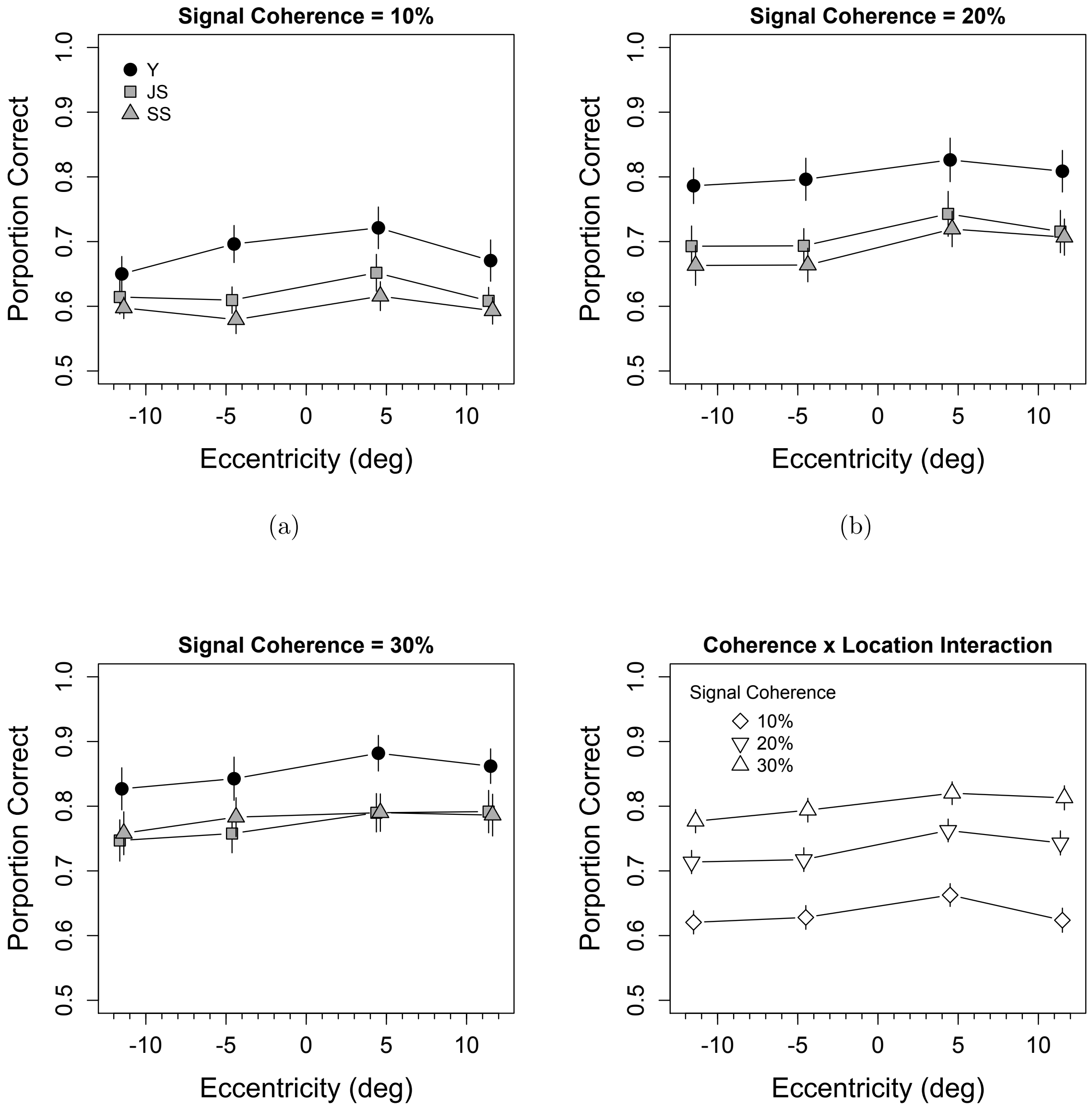
5.3.1 Focused Attention

The results from the focused attention condition are shown in Figure 5.1. Response accuracy was relatively constant across stimulus eccentricity and, in all three age groups, increased with increasing signal coherence. In every condition, average response accuracy was higher in younger adults than in older adults.

The arcsin-transformed proportions of correct responses were analyzed with a 3 (age group) x 3 (stimulus coherence) x 9 (stimulus location) ANOVA. The main effects of age group, coherence and location were significant, as was the age group x location interaction (see Table 5.2). The interaction between age group and location was analyzed by evaluating the effect of location for separate for each group after averaging proportion correct across the levels of stimulus coherence (Figure 5.1d). The effect of stimulus location was significant for the Y ($F(8, 152) = 8.18$, $p < 0.0001$) and JS ($F(8, 144) = 2.48$, $p = 0.015$) groups, but not the SS group ($F(8, 120) = 1.11$, $p = 0.36$). Inspection of Figure 5.1d suggests that performance in the JS group was slightly worse in the 0 deg condition than in the peripheral conditions, but the effect of stimulus location was still significant after removing the central condition from the analysis ($F(7, 126) = 3.21$, $p = 0.004$).

5.3.2 Divided Attention

The proportions of correct responses in the central letter identification task, averaged across stimulus coherence, are shown in Table 5.3. Accuracy in the central task was high in all three groups and did not vary significantly across conditions. The results from the peripheral task are shown in Figure 5.2. The arcsin-transformed data were analyzed with a 3 (age group) x 3 (stimulus coherence) x 4 (stimulus location) ANOVA. The main effects of age group, stimulus coherence and stimulus location were significant, as was the coherence x location interaction (see Table 5.4). The interaction is illustrated in Figure 5.2d, which plots response accuracy for each level of signal coherence, averaged across age groups, as a function of stimulus eccentricity. It appears that the effect of signal coherence was slightly greater when the stimulus was located at 11.5° to the right of the fixation point. Consistent with this view, when this condition was removed from



(a) (b)

(c) (d)

Figure 5.2: Panels a-c: Results of the divided attention condition in Experiment 5.1. Data points for the JS and SS groups have been displaced horizontally by a small amount to improve clarity. Panel d: Illustration of the coherence x location interaction: response accuracy for each level of coherence, averaged across age groups, is plotted as a function of stimulus eccentricity. Error bars represent ±1 SEM.

the ANOVA, the coherence x location interaction was not significant ($F(4, 232) = 1.23$, $p = 0.30$).

	-11.5	-4.5	4.5	11.5
Y	0.98	0.99	0.98	0.98
JS	0.98	0.98	0.98	0.97
SS	0.97	0.96	0.97	0.97

Table 5.3: Average proportion of correct responses in the central letter identification task in the divided attention experiment.

Close inspection of Figure 5.2 suggests that accuracy was greater for stimuli presented in the right visual field. We evaluated this idea by computing the difference between accuracy measured with stimuli presented in the right and left visual field at each eccentricity, and then evaluated the difference scores with a 2 (stimulus location) x 3 (coherence) x 3(age group) ANOVA. The average difference score ($M = 0.029$) was significantly different from zero ($F(1, 58) = 22.4$, $p < 0.0001$), and interaction between coherence and stimulus location was significant ($F(2, 116) = 3.33$, $p = 0.039$). The interaction was analyzed by evaluating the effect of stimulus coherence separately at each eccentricity. At an eccentricity of ±4.5°, the average right-left difference ($M = 0.035$) was significantly different from zero ($F1, 60) = 25.8$, $p < 0.0001$), and the difference score did not vary significantly across stimulus coherence levels ($F(2, 120) = 1.08$, $p = 0.34$). At an eccentricity of ±11.5°, the average right-left difference ($M = 0.023$) also was significantly different from zero ($F1, 60) = 9.18$, $p < 0.004$), but the difference score did vary significantly across stimulus coherence levels ($F(2, 120) = 4.45$, $p = 0.014$). Follow-up t tests indicated that the right-left difference was smaller when the coherence level was 10% ($M = 0.003$) than when it was 20% ($M = 0.030$) or 30% ($M = 0.036$). In summary, it appears that accuracy in all age groups was slightly but significantly greater for stimuli presented in the right visual field.

5.3.3 Comparison of Focused and Divided Attention

In this section we evaluate the effect of dividing attention in 42 subjects – 12 Y (mean age 24.4, 7 females), 16 JS (mean age 65.5, 8 females) and 14 SS (mean age 74.7, 8 females) – who completed both the focused and divided attention experiments. For

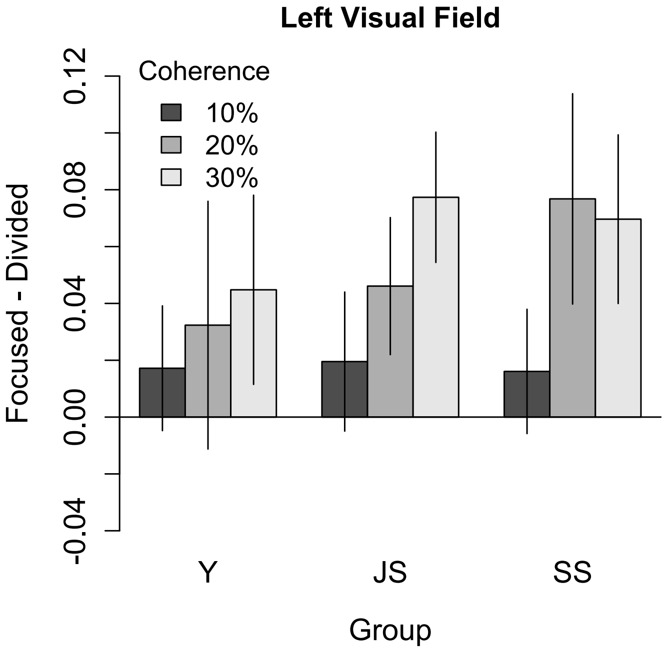
	SS	df	Error SS	Error df	F	p
Group	2.33	2	15.61	58	4.32	0.018
Coherence	5.65	2	1.90	116	172.5	< 0.0001
Location	0.39	3	1.44	174	15.56	< 0.0001
Group × Coherence	0.11	4	1.90	116	1.69	0.156
Group × Location	0.05	6	1.44	174	0.91	0.492
Coherence × Location	0.05	6	1.20	348	2.61	0.017
Group × Coherence × Location	0.04	12	1.20	348	0.88	0.565

Table 5.4: Results of ANOVA performed on data from divided attention condition.

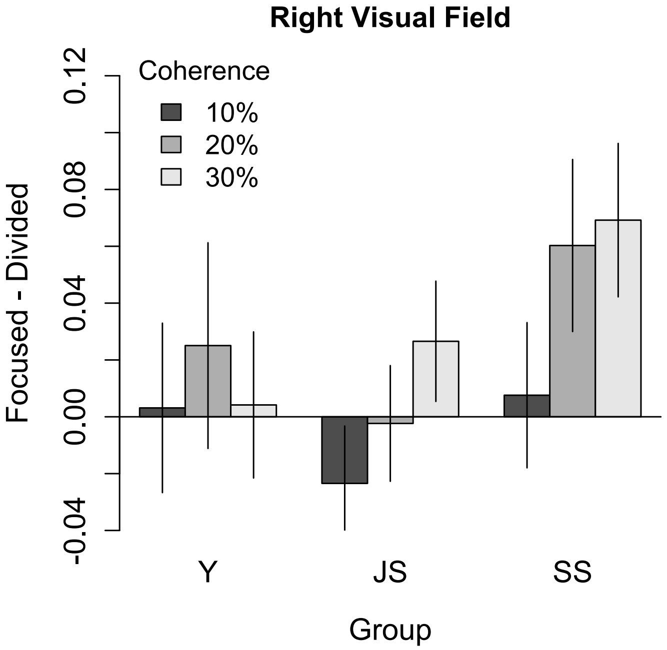
each subject, response accuracies in the $-11.5°$ and $-4.5°$ conditions were averaged, as were accuracies in the $+11.5°$ and $+4.5°$ conditions, to yield one accuracy score each for the left and right visual fields. Accuracies in the divided attention conditions were then subtracted from accuracies in the focused attention conditions, yielding one difference score for the left visual field and one for the right visual field. The focused-divided difference scores, shown in Figure 5.3, represent the cost of dividing attention, with a positive score indicating that accuracy was lower in the divided attention condition.

The difference scores were submitted to a 2 (visual field) x 3 (coherence) x 3 (age group) ANOVA. The grand mean differed significantly from zero ($M = 0.032$, $F(1, 39) = 5.79$, $p = 0.021$), indicating that on average response accuracy was higher in the focused attention condition. The main effects of visual field ($F(1, 39) = 13.1$, $p < 0.001$) and coherence ($F(2, 78) = 7.60$, $p < 0.001$) were significant. The main effect of age group was not significant ($F(2, 39) = 0.47$, $p = 0.62$). The significant effect of visual field reflects the fact that the cost of dividing attention was greater for stimuli presented in the left visual field than stimuli in the right visual field. The effect of coherence indicates that the cost of dividing attention was greater, on average, in the 30% coherence condition than in the 10% coherence condition. Inspection of Figure 5.3 suggests that the effect of visual field was much smaller for subjects in the SS group than subjects in the Y and JS groups, but the group x visual field interaction was not significant ($F(2, 39) = 2.59$, $p = 0.09$).

In summary, there was a cost associated with dividing attention that was larger for high-coherence stimuli and for stimuli presented in the left visual field. This cost did not, however, differ across age groups.



(a)



(b)

Figure 5.3: Error bars represent ±1 SEM.

5.4 General Discussion

We had younger adults and two groups of older adults complete a peripheral motion perception task, both with and without the addition of a concurrent central letter task. We also manipulated the signal coherence of the motion task to vary difficulty. In general, older adults performed worse than younger adults, and for all groups, increasing coherence improved performance and accuracy was slightly higher for stimuli in the right visual field. When asked to divide attention, performance decreased, as one might expect, and the data suggest that the cost of dividing attention was greater in the high-coherence condition and for stimuli in the left visual field (which corresponds to the higher levels of performance seen in the right visual field). Interestingly, the effect of dividing attention did not differ across age groups, suggesting that older adults were not differentially impaired by the addition of the central letter task.

One could discuss the level of difficulty inherent in our tasks. As mentioned above, all subjects did extremely well on the central letter task, reaching what were essentially ceiling effects. If this central task, which was intended to increase difficulty and distract from the motion task, was too easy, it could explain why we did not find age effects when looking at the difference scores. This relates in some ways to previous work done in our lab. Richards et al. (2006) found that both older and younger adults were able to reduce and eliminate the cost associated with dividing attention following extended training on a useful field of view task. One key manipulation in this training though was that stimulus duration for the older adults was lengthened so as to equate the level of difficulty between the age groups. Somberg and Salthouse (1982) also found that when single-task differences across age were controlled for there was no effect of dividing attention. Perhaps we inadvertently equated attentional cost or single-task difficulty by having our tasks be too simple to begin with. To combat this, follow up work could conduct a pilot study to see how we could adapt our stimulus parameters to make the task harder, or, we could use coherence thresholds rather than accuracy as our measure of interest. This might allow for greater age differences to emerge.

It is also possible though, that the question is not really about dividing attention. McDowd and Craik (1988) suggest that dividing attention per se may not necessarily present special difficulty for older adults, but rather it simply increases task complexity to a point that they cannot deal with. This thought is similar to that of Sekuler et al. (2000) who conceptualized age-related deteriorations as decreases in the efficiency with which observers could extract information from a scene, which was exacerbated when these adults were forced to divide their attention. This idea has implications for driver relicensing. How would one measure any impairments in observer efficiency during the short driver evaluation protocol? Since vehicular crash rate in older adults is highly correlated to visual attention measures taken as part of a useful field of view task (Owsley et al., 1998), which is a measure of the information one can extract from the visual scene in a single glance (Ball and Owsley, 1993), then perhaps these measures need to be added to the standard protocol. Some sort of remedial training could also be put into place (for all drivers, not only older adults). It also could be the case that performance on attentionally difficult tasks is being limited by either one's skill for each component of the task, and/or an inability to develop an appropriate strategy for completing the task. With sufficient time to practice, apparent limits to attentional capacity could be overcome (Spelke et al., 1976). This could be time consuming, but may be cost effective if the improvements show lasting effects (Richards et al., 2006).

In summary, older adults performed worse than younger adults in a motion discrimination task where the stimuli were positioned at different locations along the horizontal meridian. They were not, however, differentially impaired when forced to divide their attention across two concurrent tasks. The results of this work could be expanded to further explore the nature of task difficulty, and how it affects older adults and their perceptual abilities under both focused and divided attention conditions.

5.5 Acknowledgements

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Chapter 6

General Discussion

6.1 Overall Summary

This dissertation has explored the effects of age on motion perception in human adults. By using motion discrimination tasks, presented both foveally and peripherally, as well as under focused or divided attention conditions, we have begun to paint a picture of the aging visual system in a healthy older adult population. By testing older adults who are free from common age-related pathologies, we were able to examine changes that occur in the 'normal' aging process. This allowed us to further characterize the nature and extent of age-related changes in motion perception. In general, we found that older adults are less sensitive to the direction of motion when asked to make judgments about moving dot stimuli compared to their younger counterparts, especially for vertically moving motion stimuli. This deficit is often different even when comparing groups of older adults; sixty year old subjects had, in many of our experiments, different patterns of performance compared to our seventy year old subjects. Older adults in general also showed evidence of broader directional tuning as inferred through notched masking techniques. Taken together, our results fit well in the context of neurophysiological work finding broadly tuned neurons in the visual cortices of older cats and primates, as well as in the context of other psychophysical work finding general age-related deficits in visual perception, though the extent of the role of contrast sensitivity remains to be explored. In addition to broader directional tuning, older adults are also worse at making directional judgments in the near periphery, though these deficits are not as large as those seen foveally. The addition of a central letter component to a peripheral motion discrimination task evaluated the effect of dividing of attention across the visual field, but we found that older adults were not differentially more impaired when forced to do two tasks concurrently.

6.2 Impact of the Thesis

In a broader, societal sense, the findings described in this thesis are meaningful for governments and agencies looking to prepare themselves for an increase in the percentage of older adults making up the population. As the Canadian population ages, especially with the 'boomer' generation reaching their 60's, investigations such as those described here are critical since they impact the quality of life of this aging population. This section outlines some of these impacts.

6.2.1 Driving

Our results clearly show that older adults are less able to accurately perceive motion and this has obvious ramifications for driver license regulation. Simple visual acuity or detection tests currently used to evaluate older driver fitness may overestimate an older adult's abilities and should therefore be used and interpreted with caution. Ideally, a more comprehensive battery of perceptual tests could be developed to determine if an older adult is perceptually fit to drive. For example, one useful test could be a motion coherence threshold task. This would measure the amount of coherent motion required to make an accurate direction discrimination, and relates to the skill of identifying a specific car's trajectory within a congested traffic scene. This battery evaluation should also include a test of motor control. It is known that reaction times to motion onset increase with age, and these are due to both sensory and motor factors (Porciatti et al., 1999). Reaction to motion is required of a driver both while moving (i.e. adjusting trajectory) and while at rest (i.e. initiating motion). Finally, the fact that we see differences between our JS and SS groups in many of our experiments is also very interesting. It highlights the broad spectrum of age-related changes that can be observed and the dangers of making judgments based solely on one' s age. Just as it would be inappropriate to discriminate unfairly against an 85 year old because of their age, similarly one cannot assume that a 60 year old will perform better perceptually.

The issue of driver fitness relates very much to the work on the useful field of view

(UFOV). The UFOV is often defined as the region of the visual field from which information can be extracted in a single glance, without moving the head or eyes (Ball and Owsley, 1993). The extent of the UFOV can be measured under a variety of conditions that modify the difficulty of extracting information. The amount of information that can be successfully processed within the UFOV has been manipulated by having attention be either divided or focused on a single task, having subjects detect, identify, localize, or track stimuli concurrently, or by placing the relevant stimuli within a simple or cluttered scene. Performance on standardized UFOV tasks is highly correlated with automobile crash risk, especially in the elderly (Ball et al., 1993), and the effect sizes are often larger than those obtained with more standard visual or cognitive assessments (Clay et al., 2005). In general, it seems that one of the major deficits associated with aging relates to older adults' ability to divide attention across tasks; they show decreased performance and greater attentional costs when forced to perform a central and a peripheral task concurrently (Sekuler et al., 2000).

With training though, older adults can reach the same level of attentional performance as younger ones. Richards et al. (2006) showed that 9 days of training on a UFOV task can essentially eliminate the attentional cost of dividing attention in both younger and older subjects. With repeated training, performance under divided attention conditions was the same as under focused attention conditions. This type of cognitive training can also translate to improved performance on road tests. Roenker et al. (2003) trained at-risk older adults in either speed of processing tasks (similar to the UFOV tasks) or on a driving simulator. In this study, they defined 'at-risk' as showing a 30% reduction on the UFOV measure at baseline. They found that the speed of processing training resulted in a significant decrease in the number of dangerous maneuvers performed by these older adults, and this improvement was maintained for 18 months post-training. The importance of this finding is that very basic computer tasks performed on a regular basis can result in meaningful improvements in real-world situations.

In preliminary work of ours (Tsotsos et al., 2010), we tried to use UFOV training to improve performance on a driving simulator. While we were able to show trained improvements in the UFOV task itself, these benefits did not transfer to the driving simulator. One of the main reasons we believe this occurred was because the driving task was too simple; the routes presented were simply not challenging enough to really test the limits of the subjects' performance. If we had pushed the subjects to their limits (similar to the way Chapters 2 and 3 used threshold measures), we expect that we would have seen a break-down in their performance, and then, following training, a corresponding improvement. Also, Roenker et al. (2003) tested the aforementioned ‘at-risk’ older adults, whereas our adults were likely not similarly impaired.

Our work with the UFOV relates back to the current thesis because when driving in the real world, the concurrent tasks required of a driver invariably involve motion perception. As mentioned above, driver training protocols could include motion perception tasks, and these would ensure greater safety on the roads, adding an extra dimension of evaluation to ensure that drivers are indeed capable of safe reactions to changes in their driving environment. Future experimental work could more closely examine the responses of older adults when making judgments about complex, changing motion patterns so as to help educate older drivers about the changes they can expect as they age.

6.2.2 Walking

Drivers are not the only ones who have to make complex motion judgments; we know that older pedestrians experience similar impairments in judgment (Lobjois and Cavallo, 2007; Neider et al., 2011). Older adults have also been found to be slower and less accurate when searching for traffic signs under dual-task attentional conditions (McPhee et al., 2005). When navigating a complex pedestrian situation one also has to track the trajectory of multiple moving objects (i.e. other people or other cars), and this ability is also reduced in older adults (Trick et al., 2005). When these perceptual impairments are combined with balance or locomotion issues that are common in aging (Heasley et al., 2005), a serious safety concern emerges. For instance, an older adult with a mobility issue who cannot accurately judge the time they have to cross the street may put themselves at risk of injury or accident. A more thorough understanding of age-related motion perception changes could assist in designing better intersections and crosswalks. Investigating the interaction between perceptual, cognitive and motor tasks (similar to work by Fraser et al. (2007)) could also reveal interesting ways to better equip older adults to stay active in their communities.

6.2.3 Health Care

Since the Canadian population will be aging in the coming decades, it would be worthwhile to consider how science could help prevent or reverse age-related perceptual declines. The experiments in this dissertation were heavily motivated by neurophysiological work suggesting that the broader directional tuning found in older animals is the result of a decrease in the fidelity of the inhibitory neurotransmitter system. This inhibitory system, specifically changes in GABA levels, was further examined by Leventhal et al. (2003) in their investigation of age-related changes in GABA-ergic mechanisms in senescent primates. They administered GABA and muscimol (a GABA agonist) onto the early cortical areas of older primates and found that this resulted in the narrowing of the directionally-selective mechanisms of these animals, making them more like their younger counterparts. Li et al. (2008) found similar changes in older cats after administering GABA. What if something like this could be done with humans? There are a number of pharmaceutical products on the market that purportedly increase GABA levels in humans (Kuzniecky et al., 2002; Martin et al., 2001). Some of these have been used previously for seizures, though not without risk of some side effects (Morris, 1995). If one of these products could be safely and regularly used in humans though, it may provide meaningful benefits for daily motion perception, in the same way that eye glasses correct lens-related visual problems. We would expect that with use of these pharmaceutical products we would see a narrowing of perceptual tuning functions in human adults in tasks similar to those described in Chapters 2 and 3.

Can the implications of this work on inhibitory changes be applied to other areas of health research? As mentioned above, one of the possible explanations for the impairments in direction discrimination comes from work suggesting that changes in GABA-ergic functioning leads to broader directional tuning in older animals. Behaviourally, these proposed neurotransmitter-based changes can also reveal themselves as changes in performance when performing tasks that depend on inhibitory mechanisms, such as surround suppression tasks (Betts et al., 2005; Tadin et al., 2003). It is not only older adults that demonstrate these behavioural changes. Patients with schizophrenia also show these sorts of surround suppression deficits (Rokem et al., 2011; Yoon et al., 2010), in addition to general motion perception problems. This raises an interesting question - how might aging and schizophrenia be related? It is conceivable that the pathophysiology of schizophrenia somehow results in the same kinds of changes that are seen with aging. The individuals with schizophrenia could be considered to exhibit certain 'early aging' characteristics. This was measured directly by Bidwell et al. (2006). They measured speed of motion discrimination ability in patients with schizophrenia and normal adults across four decades of life (ages 18-55). In general, the patients performed worse than the controls, but unlike the controls, patients showed no age-related interaction with performance. Across the lifespan, the patients performed at a level matched by the oldest controls tested. Bidwell et al. (2006) proposed that perhaps schizophrenia affects the inhibitory system in the brain to such a extent that the changes associated with age are not large enough to have any further effect. As their study did not measure any adults (patient or control) over the age of 60, it would be worthwhile to continue to explore these changes as age increases past 55.

At the other end of the lifespan, one can investigate the development of motion discrimination abilities in young children or infants. As with many other bodily functions, motion sensitivities develop at different rates in growing infants (Banton and Bertenthal, 1997), and these changes seem to coincide with neurological changes, such as development of the striate cortex. Other evidence suggests that the inhibitory mechanisms that are involved in direction discrimination judgments may develop after 7 years of age (Betts et al., 2011). It would be interesting to directly and purposefully compare the abilities of infants, developing children and older adults. That kind of investigation would reveal which developmental trajectories are mirrored near the beginning and the end of life - it would reveal, essentially, if motion discrimination abilities change in a 'last in, first out' manner.

As outlined above, it will become increasingly necessary to discover the ways in which aging interacts with other health and disease states. All of the older adults in our studies were extremely healthy and active, with no visual health problems. We also screened out any adults who were taking medication that has known effects on visual function. In this way, our sample was an extremely high functioning one, both cognitively and bodily. In order to fully gauge the impact of age-related motion perception changes though, health care practitioners will have to take into account other chronic health conditions that may interact with aging and researchers will have to find ways to accommodate for the diversity of the aging population.

6.3 Other Brain Functions

Our masking work already suggests that the tuning of directionally-selective neurons broadens with age, and this is similar to the results found in older cats and monkeys. These results, when combined with accounts of more neural noise and greater rates of spontaneous firing in older cats (Hua et al., 2006), paint a picture of a much more confused response to a visual stimulus. How might the brain compensate for this more varied neural response?

The aging brain could implement a number of strategies to deal with less sensitive neurons. One option could be to use only the remaining 'good' neurons to make perceptual judgments. Information about direction of motion can be selectively pooled from a subset of neurons, and this subset can change depending on the nature of the task and stimulus (Bosking and Maunsell, 2011). That is, a different group of neurons would be used depending on the kind of decision that is required. Shadlen et al. (1996) attempted to simulate the neurophysiological response that would result in psychophysical threshold decisions. They found that the most accurate simulations included neurons that were in weakly correlated pools, or were not most specifically tuned for the direction of motion in the current stimulus. This suggests that the perceptual decision may be able to take advantage of more sensitive neurons, even if they are not necessarily the neurons that are most tuned to the current stimulus. This pattern of pooling may lead to underestimations of ability - recording action potentials from single neurons could fail to take into account this overall 'network' activity.

Alternatively, in an effort to compensate for a failing system, frontal areas of the brain could be used to add a greater top-down influence to what would normally be a more bottom-up decision. The increase of higher cortical area activity could be used to increase the focus of the system, so to speak, or to compensate for failing sensory mechanisms and a noisier system overall. There is increasing evidence that older adults recruit different brain areas than their younger counterparts to accomplish certain tasks. For instance, in a PET study, when asked to look at textures, older and younger adults activated a different network, suggesting reorganization of early visual processes with aging (Levine et al., 2000), and older adults have been shown to achieve the same performance level as younger adults in a visual memory task by using a novel neural network (McIntosh et al., 1999). These new 'neural networks' are thought to be a strategic compensatory mechanism; if one brain area is no longer able to perform at the same level, using a different area to supplement it can result in the same level of performance. In particular, it appears that more frontal areas are commonly recruited to compensate for more primary sensory areas. This pattern leads to the PASA hypothesis (posterior-anterior shift in aging, (Davis et al., 2008)). This idea suggests that basic perceptual functions (which are typically accomplished by upstream brain areas) are increasingly being carried out by areas that are further downstream from the primary sensory cortices. It would be logical to suppose that the more difficult the perceptual task, the more likely it is to require the recruitment of frontal areas.

Related to this, recent work from Forstmann et al. (2011) has modeled the speed-accuracy trade-off in older adults in order to investigate age-related structural changes. They used a perceptual decision making task and either instructed older and younger participants to respond quickly or accurately. By examining behavioral as well as neuroimaging data the authors concluded that older adults use more conservative decision thresholds and that these are related to weaker white matter connections between the cortex and the striatum. Aine et al. (2006) also found differences in white matter integrity in older adults, and Langrová et al. (2006) measured VEPs and found increased cortical response latencies. Taken together, these could suggest that older adults have overall slower neural communication abilities, which could also lead to impaired perceptual decision making. These impaired decisions, when combined with age-related motor issues could have significant ramifications for ambulation and locomotion.

Our work relates to these changing overall brain functions by providing interesting future avenues of study. Our tasks were cognitively simple - we could attempt to increase the difficulty of our tasks to necessitate the recruitment of additional cortical areas. This could be evaluated by using an imaging technique, such as EEG. Also, we could use such a technique to see if a more challenging motion perception task resulted in changes in neural response latencies, which could speak to the notion of either changes in overall neural processing, or the emergence of these new functional networks.

6.4 Data Modeling

Often it is valuable to take experimental data and try to match it directly to known physiological observations using some sort of model. In an attempt to model their data, Bennett et al. (2007) modified an existing motion perception model to better characterize their observations. Their experiment was very similar to the ones reported in this thesis; the observer was either asked to detect motion or discriminate its direction. The motion (when present) was embedded in noise. By separating their observers by decade of age, they were able to demonstrate that age-related changes do not emerge gradually, but rather, appear only after the age of 70. (This finding is what prompted us to divide our older subjects into two groups, the JS group (60-70) and the SS group (over 70)).

Their model uses 12 directionally selective mechanisms. Each mechanism is defined by a function taking into account channel bandwidth, the direction of motion and the peak of the tuning. The response of the mechanism was determined by combining the direction of motion with Gaussian distributed variables. In the detection trials, overall response strength was used to differentiate between signal and noise; in the discrimination trials, the sum of responses was used to determine which direction the motion was moving. The standard model parameters were used to fit most of the data from these experiments, but they needed to be adjusted to accurately fit the data from the 70 year old subjects. For those cases, the model needed not only to assume a larger bandwidth for each directionally selective mechanism, but also to increase the amount of internal noise.

In the original Williams et al. (1991) model they also had 12 directional mechanisms, each having a half-bandwidth of 30 degrees. For our own data, we used our exponential equation (Equation 2.1) to estimate the tuning bandwidth for each of our age groups in Chapter 2. For the Y group, we estimated an average half bandwidth of about 52 degrees, for the JS group a bandwidth of around 70 degrees and for the SS group one close to 84. It appears that, with age, the bandwidth of the directionally-selective mechanisms tapped in this task increases by about 65%. This would result in an increase on either side of the preferred direction of just over 30%. This increase is meaningful in terms of directional judgments and could result in an erroneous decision.

Our bandwidth estimations are slightly higher and differ more across age groups than previous results, even ones from our own lab (Govenlock et al., 2009) but most previous studies measured orientation tuning, not motion tuning. Perhaps this is what accounts for the increase in estimated half-bandwidths that we see. Since motion tasks tap into different mechanisms (for instance, the inclusion of MT processing compared to an orientation discrimination task), these may be the ones that show greater age-related declines, and these are reflected in the bandwidth estimations. It would be interesting to test the same group of older adults on a variety of static and dynamic discrimination tasks. One could then compare the bandwidths that are calculated in the same adult for different tasks to see how they differ. This would also help to reconcile the fact that static and dynamic displays require different brain areas. Comparing the same adult on both those types of tasks could help pinpoint at which point exactly in the motion processing system the critical break-down in perception occurs. That would then help inform future perception models, perhaps by incorporating both a variable that reflects age and a variable that reflects the nature of the task.

6.5 Limitations

As with any endeavour, it is important to appropriately evaluate the impact that one can realistically expect to have. A brief discussion on the limitations in the experimentation and interpretation of this thesis research follows. Firstly, we did no testing or experimentation on animals other than humans. Therefore, we cannot make direct comparisons between our work on humans and any work done on other animals. All our comparisons are indirect or inferential. Additionally, we did not use any neuroimaging techniques on our human subjects, requiring us to resort to indirect comparisons about what it happening in the brains of our subjects.

It has been mentioned in each chapter that all of our older subjects were thoroughly screened so as to eliminate anyone with a visual health issue or cognitive impairment. This can be seen as both a limitation and a strength. This decision limited our ability to generalize broadly to the aging population, since our sample was so healthy, but it also allowed us to only draw conclusions about what *healthy* aging really means. In child development research there are milestones and expected growth patterns that are used to evaluate the health of a child. In some ways, work with healthy older adults can create the same developmental trajectory for beyond the age of 60, allowing older adults and their families to have clear expectations of what is likely to occur and when.

6.6 Contributions

Having admitted to, and acknowledged, the limitations of this dissertation, let us now outline the unique contributions of this work to the greater scientific community. (Note, these contributions go beyond the actual experimental findings themselves, which all contribute to the body of literature in this area.) There are two specific aspects of this work that could influence the design of future research projects. The first is an issue of methodology. We, in all of our experiments, split our older adults into two age groups; a group of younger seniors and a group of older seniors. We were not the first to do this, but it is not common practice. We have, however, demonstrated in a series of related experiments that it is a valuable methodological modification that can yield interesting and valuable results, and should be pursued. This could be done by either including separate older age groups in the experimental design, or by re-evaluating past results with an eye to differences within old age.

The second contribution is in the form of a question - why are vertical direction judgments more difficult than horizontal direction judgments? As we saw in Chapter 3, there was a marked difference between vertical and horizontal performance, but no clear explanation as to why. We have, in a sense, discovered a unique perceptual pattern of results that may help guide future psychophysical, imaging or neurophysiological work.

6.7 Future Directions

Throughout this thesis we have occasionally referred to many potential future avenues of research that can follow the described results. They will be briefly summarized in this section. One future direction of work that supersedes any methodological avenues is that of further characterizing the trajectory of age-related perceptual changes. We separated our older subjects into two groups, one being 60-70 year olds, and the other being over the age of 70. This was done somewhat arbitrarily, and a different categorization could have yielded slightly different results. It would be valuable to test different ways of grouping the older adult population to evaluate the impact of the ages that we typically use to define old age. For instance, is 65 really the age that corresponds with becoming a 'senior', perceptually? Is 80 years old too late to be starting driver recertification? One could also conduct a longitudinal study and follow adults as they age, helping to pinpoint the beginning of perceptual declines. Exploring the development of these perceptual declines would help bolster our understanding of the aging process and could perhaps lead to the development of a new screening test that would group subjects depending on their visual health, independent of their age. We could then test groups of subjects with similar visual health. Related to this is the issue briefly mentioned in Chapter 2, namely that of gender difference in performance. It may be the case that there is something in the brains of older women that affects their performance on these tasks. The observed differences could also be the result of some kind of cohort effect, caused by the traditional gender roles that existed when the older adults currently being tested were growing up. Either way, this question fits into the broader scope of understanding the aging process better.

Other, more specific future directions include the difference between vertical and horizontal motion perception. What is it about perceiving vertical motion that has such an effect, especially on older adults? While we attempted to control for them, do the different eye movement behaviours of older adults play a role in their perceptual impairments? Adding eye-tracking to our protocols could help answer this question.

How does motion perception change as you go out into the peripheral visual field, not just horizontally, but in all directions? How can we best interpret and compare human and animal results? How does statically-measured contrast sensitivity relate to the task-based effects of contrast sensitivity that we observed? Finally, what is the interaction between age and disease states, and how does this affect motion perception? By starting with the work presented in this thesis one can launch new work in a number of different directions. Since increasing age is a constant in human life and the population of the world is aging overall, any and all of these avenues are valuable and interesting. While we have helped fill in some pieces of the puzzle, there is still much work ahead of us if we are to truly understand the complexities of the effect of age on motion perception.

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