UNDERSTANDING AND IMPROVING DEPTH PERCEPTION FROM MOTION PARALLAX IN OLDER ADULTS

A Dissertation
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

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In Partial Fulfillment of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY

Major Department:
Psychology

March 2016

Fargo, North Dakota

North Dakota State University
Graduate School

Title

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

Successful navigation in the world requires effective visuospatial processing. Unfortunately, older adults have many visuospatial deficits, which can have severe real-world consequences. It is therefore crucial to understand and try to alleviate these deficits whenever possible. One visuospatial process, depth from motion parallax, has been largely unexplored in older adults. Depth from motion parallax requires retinal image motion processing and pursuit eye movements, both of which are affected by age. Given these deficits, it follows logically that sensitivity to motion parallax may be affected in older adults, but no one has yet investigated this possibility. The goals of the current study were to characterize depth from motion parallax in older adults, to explore the mechanisms by which age might affect depth from motion parallax, and to develop training programs that might alleviate the effects of age on motion parallax. In Experiment One, older and younger adults' motion parallax depth thresholds were characterized. Motion thresholds and pursuit accuracies were also measured. The results of Experiment One revealed that older adults had higher MP depth thresholds than younger adults, and that these age changes were primarily driven by age changes in pursuit eye movements. In Experiment Two, older adults were provided with motion and pursuit training programs to use at home, following the logic that training in motion and pursuit would improve older adults' depth thresholds. Improvements of performance at these training tasks were assessed. Depth thresholds, motion thresholds, and pursuit accuracy pre- and post-training were evaluated as well, using the same methods as in Experiment One. The results of Experiment Two revealed that motion and pursuit training did not affect observers' performance throughout the course of training, and there were no effects of training on depth or motion thresholds or pursuit eye movements. The current study is the first to examine age changes in motion parallax depth thresholds, and to investigate the mechanisms of age changes in the perception of depth from motion parallax. Though the training programs in Experiment Two did not produce improvements of perceptual performance, this study was successful in implementing an easy-to-use, at-home training technique.

ACKNOWLEDGEMENTS

There are many people who were instrumental in the successful completion of this dissertation. First, I'd like to thank my two mentors, Dr. Mark Nawrot and Dr. Farley Norman, for teaching me pretty much everything I know about doing good science. I'd also like to thank my committee, Dr. Linda Langley, Dr. Melissa O'Connor, and Dr. Michael Robinson, for their valuable feedback on my dissertation proposal. Special thanks go to Dan Gu of the CVCN—without his formidable programming powers, I might have never succeeded in completing this project.

Along with the people directly involved in the completion of this dissertation, there are also many people who provided me with the moral and social support I needed to succeed. To my father, stepmother, grandmother, and siblings: thank you for believing in me, and supporting my move to Fargo. I especially would like to thank my mother and my best friend Ashley, for their constant love and encouragement, and for showing a curiosity about my research that is rarely found outside of academia.

I believe that, to succeed in graduate school, one needs to find support within the graduate school community. Shanda, Andrew, Andrea, and Christina have provided me with that support. We have commiserated in our downfalls and celebrated our accomplishments together, and provided valuable advice to one another. My graduate school experience would not have been the same without them.

Lastly, I'd like to thank the people who made my transition from Kentucky, where I was born and raised, to Fargo, where I didn't know a soul, more bearable: Deirdre, for being one of my first friends in Fargo; my book club friends, Amanda, Felix, Alyson, Little Amanda, and

Jamie, for giving me an excuse to do two of my favorite things (overeat and talk about books); and Mark and Lisa Nawrot, for welcoming me into their home for Thanksgiving every year.

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MP	Motion parallax
GABA	γ-aminobutyric acid
CNS	Central nervous system
SNR	Signal-to-noise ratio
RPE	Retinal pigment epithelium
RGC	Retinal ganglion cell
LGN	Lateral geniculate nucleus
ERG	Electroretinogram
RNFL	Retinal nerve fiber layer
P	Parvocellular
M	Magnocellular
OB	Orientation bias
DB	Direction bias
fMRI	Functional magnetic resonance imaging
BOLD	Blood oxygenation level dependent
3-D	Three-dimensional
AIT	Anterior inferotemporal area
CIT	Central inferotemporal area
PIT	Posterior inferotemporal area
VIP	Ventral intraparietal area
MST	Medial superior temporal area
LIP	Lateral intraparietal area

MT	Middle temporal area
PET	Positron emission tomography
rCBF	Regional cerebral blood flow
FFA	Fusiform face area
EEG	Electroencephalography
RDC	Random-dot cinematogram
VEP	Visual evoked potentials
OKR	Optokinetic reflex
VOR	Vestibulo-ocular reflex
FEFsem	Smooth eye movement area of the frontal eye fields
PON	Basilar pontine nuclei
PMN	Premotor nuclei
SC	Superior colliculi
MAE	Motion aftereffect
2-D	Two-dimensional
M/PR	Motion/pursuit ratio
PL	Perceptual learning
UFOV	Useful field of view
TDT	Texture discrimination task
SOA	Stimulus onset asynchrony
PTM	Perceptual Template Model
NT	No training group
TG	Training group

INTRODUCTION

Effective navigation for the completion of all daily tasks—from driving a car to making a sandwich—requires accurate visuospatial processing. Even small visuospatial deficits can have large effects on normal functions, and, unfortunately, older adults have a variety of these deficits. In normal (i.e., non-pathological) older adults, deficits include problems with motion processing, eye movements, and extracting important information (signal) from unimportant information (noise) (Owsley, 2011). These deficits can have significant functional consequences: for example, age-related visual deficits are responsible for higher incidences of falls during navigation (Lopez et al., 2011). Decreased driving abilities are also attributable to visuospatial deficits (Conlon & Herkes, 2008). It is therefore vital to understand the causes of age-related visual deficits, and to try to alleviate their effects when possible. Some areas of aging and visual processing and function have been very thoroughly studied (for reviews, see Owsley, 2001; Spear, 1993). However, the impact of age on one important visuospatial process, sensitivity to depth from motion parallax (MP), remains a relatively unexplored area of research.

The unambiguous perception of depth from MP is a result of the combination of relative motion of images on the retina and extraretinal signals (in the form of pursuit eye movements) (Nawrot & Joyce, 2006). Although the research on MP has been fairly prolific in the last 35 years (see Rogers, Braunstein, Harris, Lappin, & Ono, 2009), there have been very few investigations of the effects of age on unambiguous depth perception. The few studies on this topic that exist have focused on the ability of older adults to make depth magnitude judgments for suprathreshold stimuli (Norman, Clayton, Shular, & Thompson, 2004; Norman, Crabtree, Bartholomew, & Ferrell, 2009), rather than on older adults' absolute thresholds, or their sensitivity, to depth from MP.

One of the goals of Experiment One is to characterize depth thresholds in older adults, in order to understand the changes in sensitivity to depth that might occur with age. Another goal of Experiment One is to understand *why* older adults might be different from younger adults. The goal of Experiment Two concerns the possibility of improving sensitivity to depth from MP. To fully understand the mechanisms by which age may affect depth from MP, and how these effects may be alleviated, it is first necessary to have an understanding of the effects of age on basic visual processes that affect the perception of depth from MP, including the effects of age on the visual system in general, as well as on motion processing and pursuit systems in particular.

Aging and the Visual System

Many changes occur in the visual system with age (Owsley, 2011). The eye itself undergoes many structural changes as one ages—for example, the cornea changes in curvature, the pupil size decreases, and the lens loses its power of accommodation and becomes opaque (Schieber, 2006). However, though changes in the optics of the eye certainly contribute, in many cases, to declines in visual abilities that accompany aging, they cannot completely account for these declines (Trick & Silverman, 1991). Many visual deficits, such as the loss of spatial contrast sensitivity, motion sensitivity, and scotopic vision, are thought to be due to changes in the retina or central visual pathways (Spear, 1993). A major contributor to age-related functional degradation of visual cortical areas is changes in the transmission of the neurotransmitter γ-aminobutyric acid (GABA), the main inhibitory transmitter in the central nervous system (CNS) (Hua et al., 2006; Schmolesky, Wang, Pu, & Leventhal, 2000). Degradation of inhibitory intracortical communication is thought to cause decreases in neuronal selectivity by increasing peak activity and responses to non-optimal stimuli, as well as spontaneous firing (activity occurring in the absence of stimuli) (Leventhal, Wang, Pu, Zhou, & Ma, 2003). This combination of increased activity and overall responsiveness (referred to as “signal”) with increased spontaneous firing (referred to as “noise”) results in decreased signal-to-noise ratios (SNRs): a decreased ability to respond to preferred stimuli over background activity (Leventhal et al., 2003, p. 812). The effects of age-related degradation of GABA transmission and decreased SNRs will be returned to in more detail in the subsections on primary visual cortex and extrastriate cortex. This section will describe the anatomical and functional changes in the aging visual system, with subsections devoted to the retina, the lateral geniculate nucleus and magnocellular and parvocellular pathways, primary visual cortex, and association visual cortex.

The Retina

The retina is the only part of the human CNS that is observable through non-invasive techniques. It is made up of photoreceptor cells embedded in the retinal pigment epithelium (RPE) at the back of the retina. Moving inward (from the back of the eye), are layers of horizontal, bipolar, and amacrine cells, which converge on the retinal ganglion cells (RGCs). The layer of RGC axons, along with support tissue, is called the retinal nerve fiber layer (Harwerth, Wheat, & Rangaswamy, 2008). The RGCs bundle together to form the optic nerve, which exits the retina and ascends to the lateral geniculate nucleus (LGN) of the thalamus, a subcortical structure located in the middle of the brain.

The photoreceptors, called rods and cones (due to their respective shapes), are responsible for transducing incoming light in to neural signals (Schieber, 2006). Rods are responsible for vision in dark or dimly-lit settings—called scotopic vision—and cones are responsible for vision in well-lit settings—called photopic vision (Lovasik, Kergoat, Justino, & Kergoat, 2003). Aging affects the number, density, and makeup of rods and cones, but in different ways. Cones are not as affected by aging as rods, but there are some notable age-related changes in these photoreceptors (Curcio, Millican, Allen, & Kalina, 1993).

In the center of the retina, called the fovea, is the highest density of cones. Although investigations of cadaver eyes find considerable variability in cone density in the fovea of older retinas (with the most variability in the eighth decade), there are no significant differences in foveal cone density between younger and older retinas (Curcio et al., 1993; Gao & Hollyfield, 1992). In contrast, there is evidence of age-related loss of cones in the periphery of the retina. Gao and Hollyfield (1992) found a linear loss of cones at a rate of 16 cones/mm^2/year, which translates to an approximate 23% decrease in number of cones by the ninth decade of life. Likewise, Curcio et al. (1993) found an age-related 22% decrease in cone density in the peripheral retina. In addition to the loss of cones in the periphery, the photoreceptors also undergo structural changes, becoming misshapen and accumulating lipofuscin. Lipofuscin is a pigment granule that accumulates as part of the normal aging process, and is found in the cones of older adults (Curcio et al., 1993; Spear, 1993).

Although there is age-related loss of cones, this decrease is small compared to the dramatic loss of rod photoreceptors with age. Studies have found an average rod loss of 570-680 rods/mm^2/year (Curcio et al., 1993; Gao & Hollyfield, 1992). Overall, the number of rods are reduced by 69% from the ages of 39 to 94 (Curcio et al., 1993); this loss is not linear, like that of cones, but is most dramatic between the second and fourth decades of life, accounting for approximately 46% of the total rod loss throughout the lifespan (Gao & Hollyfield, 1992). Rod density also dramatically decreases: the density in eyes ages 61-75 is 81% of those ages 27-37. However, in the far periphery (outside the 28.5 degrees of central vision), rod loss is not affected by age. The reason rods are far more susceptible to death than cones has yet to be determined, but it is likely that accumulated damage from light may be a contributing factor (Curcio et al., 1993).

Age may also affect chemicals within rods that enable vision in scotopic conditions. Rhodopsin, a photo pigment in rods, is photo-bleached when exposed to light and breaks down (Hubbard & Wald, 1951). It takes approximately 45 minutes for the broken down rhodopsin to fully regenerate, and regeneration requires the chemical 11-*cis*-retinal, which is produced in the RPE (Jackson, Owsley, & McGwin, 1999). It has been suggested, based on psychophysical findings, that older adults do not properly produce 11-*cis*-retinal, likely because of age-related changes in the RPE (Jackson et al., 1999; Owsley, 2011).

The loss of, or molecular changes in, photoreceptors are not solely manifested anatomically—these age-related changes also have functional consequences. Electroretinograms (ERG) have been used to assess retinal function in young and old adults (Freund, Watson, Gilmour, Gaillard, & Sauve, 2011). ERG records neural activity of the retina through electrodes placed around the eye. ERG can be used to isolate rod and cone activity from ganglion cell activity by presenting flashing light stimuli in controlled light conditions. By varying the light stimuli in photopic and scotopic conditions (i.e., during and after 20 minutes of dark adaptation), rod, cone, and mixed responses can be isolated and measured. ERG activity has revealed that a-waves associated with photopic processing have longer latencies in older adults than in younger adults (Freund et al.). This finding indicates that cones decrease in efficiency and phototransduction (processing) speed with age. B-waves, associated with scotopic processing, have smaller amplitudes and longer latencies in older compared to younger adults, indicating an age-related deficiency in rod functioning. These changes in photoreceptor function in older adults are likely a consequence of the anatomical changes detailed above.

Similarly, pattern electroretinogram can be used to assess neural function of young and old adults (Lovasik et al., 2003). The pattern ERG measures two components of neural activity in the retina. The first component, the P50, is generated by pre-RGC activity (i.e., activity of photoreceptors and horizontal, bipolar, and amacrine cells). The second component, the N95, is generated by RGC activity. By presenting a checkerboard-patterned stimulus while measuring ERG activity from the retina, one can isolate pre-RGC and RGC responses. The P50 has a smaller amplitude and longer latency in older adults (ages 75-88) than in younger adults (ages 20-31), indicating an age-related decrease in the processing efficiency of photoreceptors and other pre-RGC cells (Lovasik et al.).

In addition to age-related changes in rods and cones, the RPE in which the photoreceptors are embedded undergoes modification with age. The RPE is made up of a layer of hexagonal cells, and these cells provide nutrients for the embedded photoreceptors by transmitting needed blood and oxygen from the underlying layer of blood vessels (Schieber, 2006). There are no significant changes in the number or density of RPE cells in the fovea of older adults (Gao & Hollyfield, 1992). However, in the peripheral area, RPE cells decreases linearly, at approximately 14 cells/mm^2/year. The loss of RPE cells is parallel to that of rods, and the density of rods to RPE cells is approximately equal across the lifespan. RPE cells also accumulate lipofuscin with age, much like cones do, and become misshapen (Polidori, Zeng, Zaccheo, & Amenta, 1993). These changes in RPE cells, along with the decrease in number associated with age, may result in a decrease in production of 11-*cis*-retinal, which is needed for rhodopsin generation and, functionally, scotopic vision (see above; Jackson et al., 1999; Owsley, 2011).

Age affects not only photoreceptors and the RPE, but RGCs as well. In the peripheral retina, the number of RGCs decreases at a rate of 5.6 cells/mm^2/year, but, like the loss of rods, this decrease is not linear (Gao & Hollyfield, 1992). There is a RGC loss of 40% between the second and ninth decades of life, with 46% of this loss occurring between the second and fourth decades. This pattern of RGC loss is very much like the rod loss Gao and Hollyfield documented, and indeed, rod and RGC losses are correlated. RGC loss in the fovea, though not quite as dramatic as in the peripheral retina, is still significant, with reports of loss ranging from 15% to 25% throughout the lifespan (Spear, 1993).

Clinical and ophthalmological measures can be used to estimate age-related changes in the number of RGCs and the thickness of the retinal nerve fiber layer (RNFL) (Harwerth et al., 2008). Standard automated perimetry is a clinical assessment that measures visual sensitivity across the visual field, the results of which are linearly related to RGC count. Investigations using this method show that the number of RGCs decreases from approximately 1,000,000 in younger adults, to 700,000 in older adults. This loss is similar to the 40% loss in peripheral retina reported by Gao and Hollyfield (1992). In contrast, the RNFL is thinner in older adults than in youngers, but the decline in thickness is much smaller, about -0.27% per year. The discrepancy between RGC loss and RNFL thickness may be reconciled by considering the non-neuronal tissue that helps support RGCs in the RNFL (Harwerth et al., 2008). Although the number of RGCs decreases dramatically with age, glial cells (the non-neuronal support tissue) increase, so the decline in RNFL thickness is not as dramatic as would be expected based solely on RGC loss.

These age-related RGC losses and RNFL thinning have functional consequences. As described above, RGC responses to pattern stimuli are reflected in the N95 component of the pattern ERG (Lovasik et al., 2003). In older adults, the amplitude of the N95 is smaller than in younger adults, indicating reduced processing efficiency of RGCs—that is, RGCs in older adults are not as active in response to pattern stimuli, compared to younger adults. There is also an age-related decrease in RNFL thickness, by approximately 22.5%, and RNFL thickness and the N95 component are positively correlated.

The bundle of RGC axons, which forms the optic nerve, travels to the brain and connects to the LGN. RGCs come in several types, the most well understood being parvocellular (P) and magnocellular (M) neurons (McKendrick, Sampson, Walland, & Badcock, 2007). At the LGN, the two types of neurons project to different areas, forming six layers. Layers one and two are made up of M cells, while layers three through six are made up of P cells (Schiller & Malpeli, 1978). The two types of cells are functionally different in several ways, though there is much overlap: in general, M cells are insensitive to color, and respond more strongly to stimuli of higher temporal and lower spatial frequencies and have higher contrast sensitivities than P cells. Many P cells are color-opponent, and have slower conduction velocities than M cells (Merigan & Maunsell, 1993). The laminar segregation in the LGN of the M and P pathways is largely maintained throughout the cortex. The following subsection will review the age-related changes of the M and P pathways and the LGN.

LGN and M and P Pathways

Anatomical studies of the aging LGN have most commonly been conducted with rats and rhesus monkeys. These studies have investigated changes in neuronal size, density, and number, as well as LGN overall volume (Spear, 1993). Other studies have investigated the effects of aging on the function of M and P cells.

Quantitative light microscopy studies of the dorsal LGN of young (3-5.5 months) and old (29-31 months) rats reveal that the diameters of neuronal nuclei and somas are reduced by approximately 10% in old compared to young rats (De la Roza, Cano, Satorre, and Reinoso-

Suarez, 1986). Electron microscopy reveals that the myelin sheaths of many cells degenerate with age. The reduction in size of the neurons in old rats could be due to the age-related loss of RGCs that innervate the LGN. Despite the differences in neuronal size and the degeneration of myelin, there are very few differences between the dorsal LGNs of young and old rats. Using other techniques, such as staining, it has been found that the overall volume of the rat dorsal LGN increases by approximately 33% between the ages of 24 and 28 months (i.e., in old age) (Diaz et al., 1999). Neuronal volume fraction (which measures the volume occupied by neurons per volume of tissue) decreases by approximately 17%, and neuronal density (which measures the number of neurons per surface area) decreases by approximately 24%, in rats between 24 and 28 months. However, the total neuronal count does not differ between young and old rats. The changes in neuronal volume and density can be explained by an increase in dorsal LGN volume, not decreases in the number of neurons.

The results from the Diaz et al. (1999) study mirror earlier findings from studies of the rhesus monkey LGN. In old rhesus monkeys, M cells are 31% larger in the foveal area and 36% larger in the peripheral area, and P cells are 30% larger in the foveal area and 31% larger in the peripheral area, compared to young monkeys (Ahmad & Spear, 1993). As would be expected from an increase in neuronal size, M and P layers are approximately 20% and 27% larger (respectively) in volume in old monkeys than in young monkeys, though this difference is not statistically significant. In rhesus monkeys, as in rats, there is an age-related decrease in neuronal density—29% in M and 41% in P layers—but no significant difference in total neuronal count. It seems that the age-related decrease in neuronal density is caused by non-significant decreases in the number of neurons and non-significant increases in LGN layer volume (Ahmad & Spear, 1993; Diaz et al., 1999). This increase in LGN volume is thought to be due to increases in neuronal size and the volume of glial (support) cells and blood vessels (Spear, 1993).

In addition to studies of age-related anatomical changes to the LGN, functional and psychophysical studies have also been conducted with aging animals and humans. Using single-cell recordings, researchers have plotted the receptive fields of rhesus monkey M and P neurons and categorized them as color-opponent or broadband (Spear, Moore, Kim, Xue, & Tumosa, 1994). There is no difference found between young and old monkeys in the percentage of cells that are color-opponent or broadband. There are, however, differences in the responsiveness of cells in the P layers. Older monkeys' P cells have higher baselines (greater spontaneous activity) than younger P cells. There are also fewer P cells with high contrast gains in old compared to young monkeys, and the optimal temporal frequency for P cells is higher in young than in old monkeys.

There is psychophysical evidence from studies with older humans that indicate age-related changes in the M and P pathways. McKendrick et al. (2007) explored changes in contrast sensitivity of younger and older adults using stimuli that were designed to stimulate either the M or the P pathway exclusively. They presented Gabor patches at different orientations, centered on a square luminance background (pedestal) that was set against another, larger, lighter luminance background; the pedestal and stimulus either pulsed on and off together (to stimulate the P pathway), or the stimulus was pulsed on and off while the pedestal remained in the background (to stimulate the M pathway). The sine wave grating was oriented at 45 or 135 degrees, and the participants' job was to identify the orientation. Four different spatial frequencies were tested, and the participants were tested at the fovea and two peripheral areas. McKendrick and colleagues found that, in the fovea, older adults had higher contrast sensitivities in the steady (M pathway) paradigm than in the pulsed (P pathway) paradigm, at all but the highest spatial frequencies tested. In the peripheral locations, older adults had lower contrast sensitivities than younger adults for both paradigms.

Although the results of McKendrick et al. (2007) and Spear et al. (1994) indicate age-related functional changes in the M and P pathways of the LGN, their findings should not be viewed as conclusive. Spear and colleagues (1994) point out themselves that though they found statistically significant differences in their single-unit recordings between young and old monkeys, the differences were very small, and the effects of aging on the LGN and M and P pathways appear to be very subtle. Likewise, McKendrick and colleagues' (2007) findings, though bearing further investigation, are difficult to interpret clearly. Designing stimuli that stimulate either the M or the P pathway exclusively is very difficult, if not impossible, considering the amount of overlap in responsiveness between the two pathways (Merigan & Maunsell, 1994). More research on the effects of aging on the LGN and M and P pathways should be conducted before making conclusive statements concerning age-related changes in these areas.

Primary Visual Cortex

From the neuronal cell bodies in LGN, axons travel directly to layer four of the primary visual cortex (also called striate cortex, V1, or area 17) in the occipital lobe. Neurons in V1 process simple stimulus characteristics, such as direction of movement and orientation, and project information of stimulus characteristics to association visual cortices (collectively referred to as extrastriate cortices). Studies of age-related changes in V1 may explore cortical anatomy and structure and/or neuronal function. Psychophysical experiments may also be used to assess V1 function in humans.

Anatomical and structural studies indicate little or no age-related neuronal loss in V1. Histological counts in monkey V1 have revealed no significant difference between young and old monkeys in number of neurons (Nielsen and Peters, 2000; Peters, 2002). Evidence of neuronal loss in layers two and three in area 17 of old mice has been found (Polidori et al., 1993), but this evidence conflicts with many studies that found non-significant neuronal loss with age (for review see Spears, 1993), and therefore this result may be attributed to differences in species studied. Similarly, there is evidence of changes in area 17 neurons (i.e., in axon size, dendritic growth and projections, reductions in dendritic spine density) in mice, but there is no substantial evidence of these same or similar changes in primate V1 neurons (Spear, 1993). There is also no documented change in volume of primate primary visual cortex (Nielsen & Peters, 2000).

In contrast to the lack of evidence of age-related neuronal loss and morphological changes, there is some evidence of age-related changes in myelin in V1. In the nerve fibers of layer 4C of monkey V1 there are indications that some myelin sheaths increase in thickness with age, while at the same time other myelin sheaths degenerate altogether (Peters, Sethares, and Killiany, 2001). This result suggests that oligodendrocytes (non-neuronal CNS cells), which produce myelin, do not deteriorate with age, but that myelin degenerates at a rate faster than the rate at which oligodendrocytes can produce new myelin. Loss of myelin may result in slower intracortical communication rates in older animals and adults, which may manifest behaviorally as, for example, increased response times during perceptual tasks (Peters, 2002).

Although changes in the anatomy and morphology of the aging primary visual system are few, there is considerable evidence of age-related functional changes. Several studies, conducted by Leventhal and colleagues, indicate age-related changes in neuronal selectivity, latency, firing rates, and neurotransmitter activity. Evidence from single-cell recordings in monkey V1 suggests that fewer neurons in old monkeys respond selectively to certain stimuli (i.e., are functionally selective), compared to young monkey neurons (Schmolesky et al., 2000). A cell can be categorized as having either a significant or strong bias for orientation or direction, depending on which response threshold criterion is met. Schmolesky and colleagues found that 42% of neurons in old monkeys show a significant orientation bias (OB), compared to 90% in young monkeys. Only 15% of neurons in old monkeys have a strong OB, compared to 73% in young monkeys. Results for direction bias (DB) were similar: 25% of neurons in old monkeys show a significant DB, compared to 70% of neurons in young monkeys, and only 5% of neurons in old monkeys show a strong DB, compared to 31% of neurons in old monkeys. Neurons in old monkeys are more responsive to non-optimal stimuli than neurons in young monkeys, and peak activity in old monkeys is as high as or higher than in young monkeys. Spontaneous firing is also higher in old than young monkeys. An age-related decrease in significant and strong OB and DB, coupled with increased peak activity, responses to non-optimal stimuli, and spontaneous firing rates, indicates that neuronal selectivity is degraded in old monkey V1. The increase in peak activity and responses to all stimuli, as well as the increase in spontaneous firing, also indicates a decreased SNR (peak activity/baseline activity) in old monkey V1 neurons. Similar results have been found in layer four of old macaque monkey V1 (Wang, Zhou, Ma, & Leventhal, 2005).

Hua et al. (2006) found results similar to Schmolesky et al. (2000) in their study of area 17 of young and old cats. In their study, the percentage of cells showing significant OB was 72.5% in old cats, compared to 98.1% in young cats. Likewise, the percentage of cells showing strong OB was smaller in old (30.6%) than in young (84.8%) cats. There were also fewer neurons in old than young cats showing significant DB (61.3% compared to 87.3%); similarly, only 20.6% of neurons in old cats showed strong DB, compared to 51.9% in young cats. Similar to Schmolesky et al.'s (2000) results with monkeys, responsiveness to optimal and non-optimal stimuli (measured as spikes/second) was higher in old than in young cats, and spontaneous firing rates were higher in old cats compared to young cats, resulting in decreased SNRs in old cats.

It is not only V1 cells' SNRs that may be affected by age. In layer four of V1, response latencies of macaque monkey cells do not vary by age (Wang et al., 2005); this is likely due to the fact that layer four is innervated by the LGN, which does not change much with age (Spear, 1993). However, outside of layer four, response latencies are approximately 13 ms longer in old than in young monkeys (Wang et al., 2005). This age-related change in response latency suggests that intracortical processing is degraded in old monkeys, perhaps due to degeneration of myelin in area V1 of old animals. This idea is supported by evidence of myelin degeneration found by Peters et al. (2001).

As mentioned in this subsection's introduction, loss of GABA transmission is believed to be the cause of age-related degradation in functional selectivity, including decreased SNRs. In support of this hypothesis, research shows that manipulating GABA levels systematically changes cell selectivity (Leventhal et al., 2003). Injection of GABA and muscimol (a GABA agonist) narrows the range of preferred orientations and directions in old monkey V1 neurons, meaning that GABA application does not simply lower responsiveness to all stimuli, but actually increases selectivity. GABA and muscimol have little to no effect on young monkeys' strongly selective cells. In contrast, an injection of bicuculline (a GABA antagonist) has little or no effect on old monkeys' responsiveness, but results in decreased selectivity and increased responsiveness in V1 cells of young monkeys. GABA and muscimol decrease peak response and spontaneous activity in old monkey V1, resulting in increased SNRs. In contrast, bicuculline has no effect on SNRs in old monkeys. Taken together, the findings of this study, along with those of Schmolesky et al. (2000) and Hua et al. (2006), suggest that degradation of functional selectivity and decreased SNRs in old animals is due to senescent changes in inhibitory intracortical communication, as detailed in the section introduction. This explanation may also account for some differences between younger and older adults that are evident in psychophysical studies. Findings from a few of these important studies will be discussed later in this subsection.

Studies of age-related functional changes in human striate cortex have used functional magnetic resonance imaging (fMRI) to focus on measuring blood flow to cortical regions in response to stimuli. In response to flickering light (photic stimulation), which stimulates V1 without requiring cognitive effort, older adults have decreased blood oxygenation level dependent (BOLD) signals compared to younger adults (Ross et al., 1997). The smaller BOLD signal may be due to reduced neuronal response, structural changes in striate cortex, or an overall decrease in vascular response. Relatedly, older adults’ degree of activation to pictures of intact or scrambled faces is less than that of younger adults (Brodtmann, Puce, Syngeniotis, Darby, & Donnan, 2003). Specifically, the numbers of voxels in the regions of interest that are active are reduced with each decade.

Psychophysical studies may also reveal age-related changes in perception, which may be attributed to changes in V1 function. For example, visual contour integration and segmentation is thought to rely on striate cortex, because many neurons in this cortical area are responsive to orientation, a critical component of contour perception (Roudaia, Farber, Bennett, & Sekuler, 2011). Visual contour integration and segmentation operates through two mechanisms. The first is facilitatory, and integrates the segments. This mechanism is speculated to be reliant on excitatory V1 connections. The second mechanism is suppressive, reducing the response to noisy backgrounds, and may rely on inhibitory V1 connections (Casco, Robol, Barollo, & Cansino, 2011). Aging may affect contour integration in two ways: orientation-selective neurons become less selective and SNRs decrease with age (see Hua et al., 2003; Schmolesky et al., 2000), making it more difficult for older adults to extract contours from noisy backgrounds (Casco et al., 2011).

Casco et al. (2011) presented older and younger participants with circular contours that were defined by segments of Gabor patterns (i.e., sinusoidal gratings that have been passed through a Gaussian window in order to reduce image noise). The patterns could be oriented in an alternate tangential and orthogonal pattern. The contours could be embedded in varying numbers of Gabor patterns, introducing noise in some conditions. The participants' job was to suppress irrelevant contour information and background noise, in order to select which of two patterns deviated from circularity. The older adults had higher thresholds to detect deviation from circularity, compared to younger adults, meaning that the Gabor patterns had to have larger displacements for older adults to recognize their deviation. The older participants were also more affected by background noise than younger adults. Similarly, older adults need longer stimulus duration to make reliable discriminations about the location of a gap in a 'C' shaped contour made up of Gabors (Roudaia et al., 2011). The inability to suppress irrelevant information may be due to age-related changes in GABAergic systems, a conclusion that is grounded in physiological evidence from studies with monkeys and cats (Hua et al., 2003 Leventhal et al., 2003; Schmolesky et al., 2000).

From V1, the visual system splits in to the ventral (temporal) and dorsal (parietal) streams, which are anatomically and functionally segregated. The ventral and dorsal streams are made up of many different visual areas, which are collectively called extrastriate cortex

(Mishkin, Ungerleider, & Macko, 1983). Given the many changes in the functional integrity of the aging striate cortex, one would expect to find age-related changes in extrastriate cortex as well. The following subsection reviews human and animal studies of the anatomical and functional changes in the aging extrastriate visual areas.

Extrastriate Cortex

Area V2/area 18 is the earliest area of extrastriate cortex, adjacent to V1. From V2, the visual pathways anatomically and functionally split in to two streams: the dorsal stream (parietal cortex) and the ventral stream (temporal cortex). The M and P pathways remain split throughout most of the striate and extrastriate cortices as well, though there is considerable overlap and cross-talk (see Figure 1; Merigan & Maunsell, 1994). The dorsal stream is thought to be responsible for processing spatial information, while the ventral stream is believed to process object information (Mishkin et al., 1983). This subsection will review evidence of age-related changes in areas V2 and in both processing streams, as well as evidence of dedifferentiation, that is, decreases in the functional segregation between the two streams.

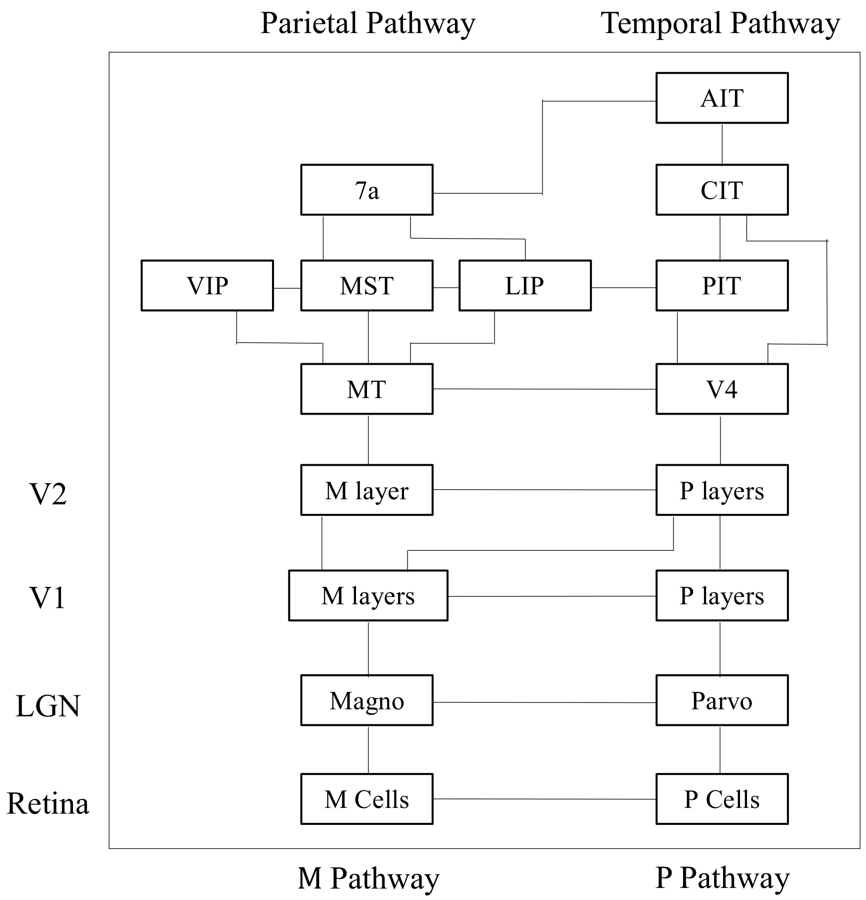

Figure 1. Parallel pathways in the visual system. The schematic should be read from the bottom (retinal ganglion cells) to the top (extrastriate cortex). The regions of the M/parietal pathway are grouped on the left, and the regions of the P/temporal pathway are grouped on the right. The lines represent the connections between and within the pathways. Abbreviations: AIT, anterior inferotemporal area; CIT, central inferotemporal area; PIT, posterior inferotemporal area; VIP, ventral intraparietal area; MST, medial superior temporal area; LIP, lateral intraparietal area; and MT, middle temporal area.

Area V2. Studies of area V2 (or area 18) have been largely concerned with single-cell recordings of neural function. Similar to results of recordings in V1 (see Hua et al., 2006; Schmolesky et al., 2003), old monkey neurons are less biased for orientation and direction than young monkeys (Yu, Wang, Li, Zhou, & Leventhal, 2006). Seventy percent of neurons in young monkeys show significant OB [orientation bias], compared to only 28% in old monkeys. The age disparity is even greater for strong OB—35% of neurons in young monkeys show strong OB, compared to only 1.1% in old monkeys. There are age-related differences in DB [direction bias] as well. Thirty-eight percent of neurons in old monkeys show significant DB, compared to 54% in young monkeys. Similar to results for strong OB, while 21% of neurons in young monkeys show strong DB, only 2.2% of neurons in old monkeys showed strong DB. Overall, young monkeys have more orientation-biased than direction-biased cells, but this is not so for old monkeys. Orientation selectivity is generally more affected by age than direction selectivity. Old monkeys also have more spontaneous activity and higher peak responses, resulting in a lower SNRs than in young monkeys. This finding is similar to results from studies of V1, and is again likely due to loss of inhibitory intracortical communication (GABAergic systems; Leventhal et al., 2003).

Results from single-cell recording studies that examined cell latencies, spontaneous activity, and peak responses to spot or bar stimuli in young and old monkey V2 reveal that response latencies are 32 ms longer in neurons of old monkeys than in young, and neurons in old monkey V2 have lower SNRs (Wang et al., 2005). The longer response latencies in older monkeys are likely due to degradation of intracortical information processing. Comparing these results with results of the same measurements in V1 from the same study (see Primary Visual Cortex subsection), it appears that aging affects V2 more strongly than V1.

V2/area 18 neurons process not only orientation and direction, but also other higher-order stimulus characteristics: border-ownership, relative disparity, speed, and color, to name a few (Yu et al., 2006). Mendelson & Wells (2002) investigated the speed selectivity of simple, complex, and hypercomplex area 18 neurons in young and old rats. Overall, neurons in young rats preferred faster speeds than in old rats. Speed selectivity also varied by cell type (simple, complex, or hypercomplex) for young rats, but old rats' cells showed no difference in mean preferred speed among the different cell types. Interestingly, though there were differences in the selectivity of the cells between young and old rats, the distribution of cell types did not differ by age.

Given the variety of stimulus characteristics to which V2 neurons respond, it is likely that age differences in figure-ground segregation and shape discrimination are due to degradation of GABAergic systems in area V2 (Yu et al., 2006). Habak, Wilkinson, and Wilson (2009) conducted a psychophysical study of shape discrimination with younger and older adults. Participants were required to discriminate between a true circle and a radial frequency (i.e., a circle deformed by the sinusoidal modulation of the circle's radius; see Wilkinson, Wilson, & Habak, 1998, p. 3556). In addition to the variations in texture created by the radial frequency, the stimuli also varied in luminance. Older adults had higher discrimination thresholds than younger adults when the stimuli were defined by texture, but not by luminance. The authors speculate that this age difference may be due to age-related decreases in selectivity of V2 neurons. Older adults have also been found to have longer reaction times in figure-ground segregation (Kandil & Fahle, 2001) and decreased accuracy in three dimensional (3-D) shape discrimination tasks (Norman, Dawson, & Butler, 2000). These perceptual deficits may be attributed to decreased selectivity and/or increased response latencies in aging V2 neurons.

Dorsal Stream. Much of the work on the aging visual system in the dorsal stream has concerned middle temporal area (area MT/V5), which is thought to be important for motion processing. In macaques, MT is located in the superior temporal sulcus. The physiology of area MT in old animals will be reviewed in this subsection, but a more in-depth analysis of motion processing (including psychophysical results) in old animals and humans will be presented in the later section on aging and motion perception.

Using drifting sine-wave gratings set at the optimal speed, direction, spatial and temporal frequency, size, and position for recorded cells, Yang et al. (2008) examined contrast response functions of MT neurons in young and old rhesus monkeys. The researchers chose to study contrast response because stimulus contrast can affect perception of other stimulus parameters such as speed. The percentage of MT cells showing significant contrast sensitivity was lower for old monkeys (40%) compared to young monkeys (99%), and the percentage showing strong contrast sensitivity was only 2% for old monkeys, compared to 34% for young monkeys. MT cells in old monkeys also had lower SNRs than those of young monkeys.

Speed selectivity of MT neurons is also affected by age (Yang et al., 2009). The percentage of cells preferring high speeds (i.e., greater than or equal to 10 deg/sec) is 45% in old monkeys, compared to 82% in young monkeys. The percentage of cells preferring very high speeds (20 deg/sec or higher) is 16% in old monkeys, and 28% in young monkeys. The mean preferred speed of all cells is 14.09 deg/sec in young monkeys, compared to only 9.21 deg/sec in old monkeys. This finding is reminiscent of Mendelson and Wells's (2002) results from their study of old rat area 18. Overall, MT neurons in old monkeys have larger tuning curves and are significantly less selective than neurons in young monkeys. Old monkeys also have decreased SNRs, compared to young monkeys.

In addition to contrast sensitivity and speed selectivity, MT neurons are also selective for direction. The directional selectivity of MT neurons in young and old macaque monkeys can be studied using drifting sinusoidal gratings or drifting plaids, which are created by overlapping two sinusoidal gratings that differ in orientation by 120 deg (Liang et al., 2010). Some MT neurons respond to the direction of one of the gratings that make up the plaid (referred to as component cells), while others respond to the entire plaid as a whole (called pattern cells). Pattern cells respond to the direction of the stimulus, disregarding its spatial characteristics. The percentage of MT cells that are classified as pattern cells is smaller in old monkeys (11.4%) than in young monkeys (28.1%). There are also age differences in the percentage of cells showing directional bias. In old monkeys, 40.8% of MT neurons show strong DB, compared to 90.5% in young monkeys. The pattern is similar for the percentage of neurons showing very strong DB: 50.0% in young monkeys, compared to only 8.2% in old monkeys. Neurons in old monkeys also exhibit lower SNRs than those of young monkeys (Liang et al, 2010).

There are several explanations for the findings of Yang et al. (2008), Yang et al. (2009), and Liang et al. (2010). Area MT receives input from V1, and is largely innervated by neurons in the M pathway. It is likely that there is age-related degradation of M pathway cells (McKendrick et al., 2007), and, as reviewed in the subsection on primary visual cortex, it is well-known that there is degradation in the selectivity and processing speed of V1 neurons (Hua et al., 2006; Schmolesky, 2000; Wang et al., 2005). Another likely explanation for decreased function in aging MT is an age-related change in inhibitory intracortical communication: that is, GABAergic systems. As has been demonstrated by Leventhal and colleagues (2003), application of GABA and a GABA agonist, muscimol, to V1 neurons in old monkeys increases their selectivity for orientation and direction.

Ventral Stream. The ventral stream is responsible for processing both lower-order form elements (e.g., shape, color) and higher-order stimuli, including faces, body parts, houses, and animals, among others (Haxby et al., 2001). Many of the studies examining aging of the ventral stream (i.e., temporal cortex) have focused on responses to form and face stimuli in humans: do the patterns of brain activation and/or intensity of activation differ between young and old adults?

It appears that during form processing (requiring extraction of feature information), older adults do have deficits compared to younger adults. Levine et al. (2000) conducted a passive-viewing positron emission tomography (PET) study, in which participants were presented with a random texture (for baseline measurements) or an organized texture (the experimental stimulus) from which form could be extracted. Regional cerebral blood flow (rCBF) was used as an index to describe activation patterns and amount of activation. In response to the experimental stimulus, younger adults showed bilateral activation in ventral areas, as expected, whereas activation sites in older adults included bilateral anterior (frontal lobe) areas. Overall, older adults had less rCBF increases in the left temporal cortex than younger adults, but more activation in non-visual areas such as frontal cortex. These findings indicate that changes in rCBF with age may be due to a loss of processing efficiency—older adults may recruit cortical areas outside visual association cortex to compensate for losses in visual processing areas. Because Levine and colleagues used a passive-viewing paradigm, it is impossible to tell, in this instance, if age-related changes in cortical activation are associated with behavioral changes as well.

One particular area of ventral extrastriate cortex, the fusiform face area (FFA), has garnered much attention and research concerning its function. The FFA seems to be specialized for processing faces; it is possible that the specialization of this cortical area evolved because of the biological significance of face recognition in primates (Haxby et al., 2001). It appears that the pattern of activation in response to coherent and scrambled faces is the same in older and younger adults: the FFA is activated by coherent faces, striate cortex by scrambled faces (Brodtmann et al., 2003). However, the number of voxels activated in cortical areas decreases with decade, indicating that the ability of older participants to quickly and efficiently process the stimuli is degraded compared to younger adults.

Research that examines not only cortical function, but also associated behaviors, provides richer information about age-related changes in visual processing than imaging studies alone. In a face-matching task, in which the test faces varied in the amount of noise present, older adults were less accurate than younger adults when faces were non-degraded (i.e., contained no noise) (Grady, McIntosh, Horwitz, & Rapoport, 2000). Degradation of the face stimuli had equal effects on both age groups (performance decreased compared to the non-degraded condition). During non-degraded face matching, older adults had less activity in prestriate areas, but more activity in the FFA and prefrontal areas than younger adults. There was no difference between groups in activation during the degraded condition. When brain activity was correlated with behavioral performance in the degraded condition, age differences emerged: for older adults, there was a positive correlation between accuracy and activation of the posterior occipital cortex, thalamus, and hippocampus, whereas for younger adults, there was a positive correlation between accuracy and activation in the FFA. These results are reminiscent to those of Levine et al. (2000), who speculated that older adults might recruit brain areas outside of the FFA during face processing in order to compensate for loss of processing efficiency.

Electroencephalography (EEG) is another method used to explore the functionality of brain regions, and when coupled with behavioral measures, can provide a rich source of information about the association between brain and behavior. The N170, an EEG component, is particularly strong for faces (Itier & Taylor, 2004), and is speculated to originate in multiple ventral extrastriate regions, including the FFA and occipitotemporal areas (Allison, Puce, Spencer, & McCarthy, 1999). The N170 has a longer latency in older than in younger adults, and the N170's amplitude in response to noise is larger in older adults (Rousselet et al., 2009). Older adults also are less accurate than younger adults at matching faces, and require more signal in degraded faces in order to identify a face (Grady et al., 2000; Rousselet et al., 2009). The EEG and behavioral results taken together indicate that the N170 becomes less face-sensitive with age. Rousselet et al. speculate that the age differences in behavioral and EEG measures could be explained by loss of GABAergic systems, which, as seen in studies of V1 and other extrastriate areas (see Leventhal et al., 2003; Yu et al., 2006), may result in loss of neuronal selectivity and decreased SNRs.

Overall, the physiological and behavioral evidence from studies of extrastriate cortex (i.e., V2/area 18, and ventral and dorsal areas), using many different methods, indicates a loss of functional selectivity in old non-primate mammals, non-human primates, and humans. This functional degradation is due to loss of inhibitory intracortical communication, or GABAergic systems. The degradation of GABAergic systems may also contribute to dedifferentiation, which will be reviewed in the next subsection.

Dedifferentiation. Dedifferentiation is defined by a loss of functional specialization at the neural or behavioral levels (Spear, 1993). More precisely, neural dedifferentiation in older adults is a "change in the spatial pattern of brain activation with age as a result of decreased neural specificity" (Voss et al., 2008, p. 122). Neural dedifferentiation may manifest in several ways: diffuse activation; activation in areas that are not related to a particular stimulus or task; and/or activation in the hemisphere not generally associated with the current stimulus or task. One way to examine neural dedifferentiation is by investigating patterns of activation in response to object and spatial visual processing, which have shown to be dissociable, activating temporal (ventral) and parietal (dorsal) cortex, respectively (Haxby et al., 1991). Another method is to restrict studies of neural dedifferentiation to ventral visual cortex, which contains regions that are responsible for processing stimuli of a single category (e.g., faces, houses, body parts).

Using the latter method in an fMRI paradigm, Voss et al. (2008) studied age differences in BOLD activation of localized brain areas during processing of color, word, face, and place stimuli. In this study, dedifferentiation was quantified as an index, subtracting average activation to a non-preferred stimulus from average activation to a preferred stimulus for a given region of interest. The dedifferentiation indices were not significantly different between young and old adults for color and word stimuli. However, dedifferentiation indices for faces and places were significantly different—older adults had lower indices (less differentiation) than young adults, and their dedifferentiation indices were correlated with gray matter volume (which was not the case for young participants). For all participants, regardless of age, color and word activation were lateralized to the left hemisphere, while face and place activation were lateralized to the right hemisphere. Given this finding, and the fact that face and place processing were less differentiated in older adults while color and word differentiation remained intact, the researchers speculated that aging may affect the right hemisphere more so than the left, an idea known as the right hemisphere hypothesis (Dolcos, Rice, & Cabeza, 2002).

Park et al. (2004) also used fMRI to study dedifferentiation of the ventral visual cortex in younger and older adults. The researchers presented participants with stimuli from five different categories (faces, places, chairs, pseudowords, and noise). Faces, places, and pseudowords are, in particular, well-suited to studies of neural dedifferentiation. Faces are known to activate the FFA bilaterally; places, the parahippocampal place area bilaterally; and pseudowords, the left fusiform gyrus and collateral sulcus. As in Voss et al. (2008), younger participants showed more differentiation than older participants. Specifically, in old participants, a region of interest was not only activated by stimuli from the specific category associated with that region, but also by stimuli from other categories. For example, the FFA in older adults was activated by faces, but also by pictures of houses and by pseudowords. Although there was cross-activation in younger adults, it was not significant.

As noted above, dedifferentiation may be seen not only in ventral visual cortex, but also in studies examining object and spatial processing, which activate ventral and dorsal visual cortex, respectively. Older participants show more activation (measured as rCBF) of prefrontal areas in face and spatial matching tasks, and more activation of inferior and medial parietal cortex during location matching than younger adults (Grady et al., 1994). Older adults also have slower reaction times than younger adults for both tasks, but more so for the location task. The recruitment of cortical areas not required for a task, such as activation of prefrontal, prestriate, or parietal areas during face/space matching tasks (see Grady et al., 1994; Grady et al., 2000), is a clear indication of dedifferentiation. The greater age-related changes in rCBF during location matching, coupled with the differences in RT between tasks for older adults, also suggests that spatial processing may be more affected by age than is object processing.

Behavioral studies provide another way to study dedifferentiation in older adults. Chen, Myerson, and Hale (2002) assessed dedifferentiation in older adults using a battery of seven speeded tasks designed to assess ventral (object) or dorsal (spatial) functions. The ventral tasks included comparing/contrasting shapes and integrating object feature information, and the dorsal tasks included tests of locations, spatial attention, and mental object rotation. The authors conducted principal components analysis to determine how many factors could account for the results of the tasks. In young adults, the tasks loaded on to two factors—one was a general factor, and one was bipolar, where ventral tasks loaded positively and dorsal tasks loaded negatively, indicating differentiation of tasks. In older adults, all the tasks loaded strongly on one factor and in the same direction, indicating a general factor but no differentiation. This result provides behavioral evidence for the neural dedifferentiation revealed in imaging studies of older adults.

There are no clearly accepted explanations for age-related dedifferentiation. One account holds that processing efficiency may decline in older adults, making compensatory recruitment of other brain regions necessary (Voss et al., 2008). It certainly may be the case that neural dedifferentiation relies on intact architecture of the human brain, and that this architecture degrades with age. This argument is supported by Voss et al.'s finding that dedifferentiation was correlated with gray matter volume in older adults. An alternative explanation is a loss of inhibition. There is abundant evidence of age-related degradation of GABAergic systems, which is believed to affect functional selectivity in V1/area 17 (Leventhal et al., 2003), V2/area 18 (Yu et al., 2006), and regions in both ventral and dorsal visual cortex (Liang et al., 2010; Rousselet et al., 2009). Although not mentioning GABAergic systems specifically, Grady et al. (1994) allude to the possibility that the inability to inhibit rCBF to cortical regions not associated with the task at hand may contribute to dedifferentiation in older adults—that is, in younger adults, GABA transmission may allow for inhibition of activity in cortical areas not necessary for specific tasks, but the decrease in GABA transmission with age results in a loss of this inhibition. Future research should focus on the cause of age-related neural dedifferentiation, exploring the roles of cortical architecture and inhibitory intracortical communication systems.

This section presented evidence of changes in the aging visual system, including evidence from single-cell recordings in non-human animals, PET and fMRI scans measuring changes in cerebral blood flow, physiological studies utilizing EEG, and psychophysical studies.

This information provides a thorough background from which to consider aging and motion processing, the topic discussed in the following section.

Aging and Motion Processing

The ability to process motion is vital to our everyday lives. Psychophysical investigations of motion processing provide an important avenue for studying the visual system, because motion processing relies not on optical factors, but on neural mechanisms, with the earliest components of motion processing occurring in V1 (Billino, Bremmer, & Gegenfurtner, 2008). Therefore, any age-related changes in motion processing are certain to have neural bases, rather than optical ones. The term "motion processing" is an umbrella term, and can encompass many different types of motion perception. This section will focus on two types of motion that are involved in the perception of depth: translational motion and radial flow. Psychophysical evidence of age-related changes in both types of motion processing will be reviewed, as well as changes in the neural mechanisms underlying the perceptual changes. The effect of speed on motion processing will also be briefly discussed.

Translational Motion

Translational motion is by far the most well-studied type of motion processing in the aging literature. Translational motion sensitivity is conventionally defined as motion thresholds for uniform motion in one direction, be it cardinal or oblique, and is often studied using coherent motion (also called correlated motion) paradigms (Newsome & Paré, 1988). In coherent motion paradigms, participants are presented with a field of moving dots, a certain percentage of which are moving in one uniform direction (signal), while the others are moving in random directions (noise). The percentage of signal that is necessary to make an accurate judgment (usually about the direction of motion) 75% of the time is the threshold. At this threshold, participants perceive global motion. Another way to measure motion sensitivity is direction discrimination (Ball & Sekuler, 1986), in which direction of movement is varied to find the smallest angular difference between two directions for participants to be able to accurately report 75% of the time whether two stimuli are the same or different. Translational motion processing is thought to occur largely in area MT/V5, where neurons integrate speed, direction, and disparity information to produce complex pattern motion perception (Mikami, Newsome, & Wurtz, 1986; Nakayama, 1985; Newsome & Paré, 1988). The cerebellum is also thought to play a role in motion processing (Nawrot & Rizzo, 1995, 1998).

The effects of age on translational motion perception are particularly deleterious. Ball and Sekuler (1986) were among the first to study translational motion sensitivity and aging. In their experiment, old and young participants were asked to discriminate between motion directions in a two-interval forced choice task. In the first interval, participants were shown random-dot cinematograms (RDCs) depicting movement in one of three standard directions (two of the four cardinal directions and one oblique direction), and in the second interval were shown either the same RDC or a different one in which movement was offset from the standard direction by 2, 4, 6, or 8 degrees. The participants had to determine if the two RDCs were the same or different. The hit (replying *different* on a *different* trial) and false alarm (replying *different* on a *same* trial) rates were used to calculate each participant's discrimination performance. The older adults were worse at discriminating motion direction at all direction offsets, but particularly so at 4 and 6 degrees (at 2 and 8 degrees performance was limited by floor and ceiling effects, respectively).

Since Ball and Sekuler (1986), many investigators have found reduced sensitivity to translational motion with age. Using motion coherence paradigms, it has been shown repeatedly that older adults have higher thresholds (i.e., need more signal) than younger adults (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Bennett, Sekuler, & Sekuler, 2007; Billino et al., 2008; Conlon & Herkes, 2008; Gilmore, Wenk, Naylor, & Stuve, 1992; Nawrot & Rizzo, 1995; Snowden & Kavanagh, 2006; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991). Although the effects of aging are considerable, the exact amount of deterioration that occurs is still under debate, with various studies reporting thresholds decreasing anywhere from about 2% to 13.5% with age (see Hutchinson, Arena, Allen, & Ledgeway, 2012, for a review).

The evidence that age affects translational motion processing is well documented; however, the question of whether age-related declines in translational motion sensitivity occur early and accumulate across the lifespan, or if the declines begin abruptly around the seventh decade, is still unresolved. Often in aging studies, participants come from two distinct groups—that is, a group of younger adults (often 18-35 years old) and a group of older adults (often 60 or more years old). Another (lesser-utilized) method is to recruit participants from all decades throughout the lifespan. In one such study, the authors found that motion coherence thresholds increased with each decade, at a rate of about 1.36% (Trick & Silverman, 1991). In other words, the thresholds necessary to correctly indicate which direction of motion was depicted increased linearly with age, doubling from 25 to 80 years of age. Likewise, other investigators have found evidence of gradual age changes (i.e., threshold increase of 0.4-2.7% per decade) using similar coherent motion paradigms and participant pools (Billino et al., 2008; Tran et al., 1998). Although there are differences in the exact increases in thresholds among these studies, they all report linear increases throughout the lifespan.

Other evidence suggests, however, that motion processing is well-preserved until late in life, around the age of 70. Bennett et al. (2007) used a coherent motion paradigm to assess motion detection thresholds in participants ranging in age from 20 to 81 years, split in to groups by decade. The investigators found that adults in the oldest age group (ages 70-81) were less sensitive to motion than participants in any other age group, but that there were no differences among any other groups. In other words, participants in their second decade performed as well (were just as sensitive to motion) as participants in their sixth decade of life.

It is not clear how to resolve the discrepancy in results between Bennett et al.'s (2007) study and those of the studies noted above. Differences in stimulus and display characteristics alone cannot account for the results. Stimulus duration in Bennett et al.'s study ranged from 75-470 ms, and the stimulus duration in Billino et al.'s (2008) study was 400 ms. Similarly, the stimulus speed in Bennett et al.'s study was 6 deg/sec, while stimulus speed was 6.6 deg/sec in Billino et al.'s study, and 5.75 deg/sec in Trick & Silverman's (1991) study. Statistical power may also be ruled out as an unlikely source of discrepancy: in Bennett and colleagues' study, they ran 15,600 trials, four times more than the number run in Tran et al.'s (1998) study. No explanation for the differences in results has been offered in the literature (see Hutchinson et al., 2012, for a discussion). One possible account is that Bennett et al.'s results are due to chance. It is also possible that more studies have found a lack of age effects on motion processing in adults younger than 60 years, but these studies have succumbed to the "file drawer problem" (Rosenthal, 1979, p. 638), wherein studies with non-significant results are never published. There have only been four studies that have recruited participants across a large age range, and their results are not unequivocal. This is an interesting avenue for future research, and investigators should begin to focus not on age differences between groups, but on age changes throughout the lifespan.

Although age deficits are the general rule in motion perception, one interesting and counterintuitive finding is that older adults have better performance than younger adults for large (i.e., => 5.0 deg), high-contrast motion stimuli. Betts, Taylor, Sekuler, and Bennett (2005) found that, in younger adults, increasing the size of a high-contrast pattern increased the duration younger adults required in order to make a motion direction judgment; older adults, in contrast, had improved duration thresholds relative to those for the smaller stimulus size, and their performance became even better than younger adults'. In other words, older adults showed increases in spatial suppression. This surprising result has since been replicated for different spatial frequencies, sizes, and contrasts (Betts, Sekuler, & Bennett, 2009, 2012; Karas & McKendrick, 2012). The mechanism underlying this age difference is thought to be age changes in MT neurons' center-surround antagonism; this issue will be discussed in greater detail below.

The Effect of Speed on Translational Motion Processing

Aging affects the ability of adults to process information about stimulus speed, which undoubtedly influences with the ability of older adults to process motion (Habak & Faubert, 2000; Hutchinson et al., 2012). In studies of speed discrimination, older adults have higher thresholds than younger adults, but the effects of age are not uniform across all speed conditions. Norman, Ross, Hawkes, and Long (2003) studied younger and older adults' thresholds for speed discrimination: participants were presented with two strips of moving dots, and had to indicate which strip was moving faster. One strip was always the standard, which could move at one of three speeds—1.22, 5.48, or 24.34 deg/sec. Older adults had higher thresholds than younger adults at all three standard speeds tested, with the best discrimination (lowest threshold) at the middle speed. Raghuram, Lakshminarayanan, and Khanna (2005) found similar results when they tested speed discrimination using drifting sinusoidal gratings at standard speeds of 2 or 8 deg/sec. Their older participants had higher thresholds than the younger participants, especially at shorter durations and at 8 deg/sec.

Speed and motion processing both occur in area MT (Mikami et al., 1986), and speed and motion selectivity are degraded in old monkeys (Liang et al., 2010; Yang et al., 2009). It follows logically that motion processing is affected by speed, and that age differences in motion processing may depend on stimulus speed. At moderate speeds (i.e., about 5 deg/sec), younger and older adults have similar motion detection thresholds at all eccentricities of the visual field, except at the fovea (zero degrees eccentricity) (Atchley & Andersen, 1998). At fast speeds, older adults are less sensitive to motion in all parts of the visual field, except at the outer 40 degrees of eccentricity. Snowden and Kavanagh (2006) also measured motion coherence thresholds at different speeds, and found that when speed was low (0.5 and 1 deg/sec), older adults were less sensitive to motion than younger adults. At their two faster speeds, 2 and 4 deg/sec, younger and older adults had similar motion coherence thresholds. It appears that, for older adults, motion sensitivity deteriorates at fast and slow speeds but is relatively unaffected at "moderate" speeds (e.g., 2 to 6 deg/sec) (Atchley & Andersen, 1998; Snowden & Kavanagh, 2006). This conclusion is in agreement with results from speed discrimination studies indicating that older adults are less sensitive to speed than younger adults, especially at speeds under 2 deg/sec (Norman et al., 2003) and over 6 deg/sec (Raghuram et al., 2005).

Radial Flow

Radial flow is an expanding or contracting pattern of optic flow (that is, the pattern of images on the retina) that gives one cues to the direction of self-motion, or heading (Warren, Blackwell, & Morris, 1989). Perception of radial flow is believed to arise in dorsal MST, which receives its major inputs from area MT (Saito et al., 1986; Tanaka & Saito, 1989).

Warren and colleagues (1989) studied the effects of age on radial flow using computer displays that simulated traveling forward parallel to the ground, comparable to walking forward down a road. The ground was composed of random dots, and the speed of simulated travel and the ground dot density varied. A vertical target line was placed in the center of the ground display, and heading angle was varied, so that participants appeared to be moving 0.5, 1, 2, 4, or 8 degrees to the left or right of the target line. Participants had to indicate in which direction they thought they were heading, relative to the target line. Thresholds were set at the heading angle at which participants were correct in their direction judgment 75% of the time. The pattern of results was the same for all observers: thresholds decreased (improved) as speed and dot density increased. However, the younger participants, compared to older participants, showed more improvement as speeds increased. Older participants had thresholds approximately 1 degree higher than those of younger adults at all speeds. The similarity in the pattern of results indicates that older adults, though not as efficient in their use of heading information, still use the same radial flow information as younger adults to make perceptual judgments.

Atchley and Andersen (1998) investigated detection of radial flow in younger and older adults at different retinal eccentricities using coherent motion stimuli. Thresholds are obtained by determining what percentage of signal (coherence) participants need to be able to make accurate judgments about motion 75% of the time. In this study, the coherent dots appeared to move toward the participant, simulating forward translation at a rate of .41 m/sec or 1.64 m/sec, while the noise dots moved in random directions. On each trial, the displays started out at 100% or 0% coherence, and the participants were to adjust the displays (increase the percentage of noise) until radial motion was barely detectable. Thresholds measurements were taken at 0, 10, 20, and 40 degrees eccentricity. For all participants, thresholds increased as retinal eccentricity increased, and thresholds were lower for the slow speed than fast speed condition. In contrast to Warren et al. (1989), however, there was no effect of age, indicating that perception of radial flow is well-preserved with age.

Similarly, Billino and colleagues (2008) investigated the effects of age on radial flow perception in a paradigm much like Atchley and Andersen's (1998). Billino et al. also used coherent motion displays to investigate radial flow, but the participants in their study were asked to indicate in which direction they appeared to be heading, relative to the fixation point centered in the display. As in Atchley and Andersen's study, Billino and colleagues found no evidence of age differences in the perception of radial flow.

The results of Warren et al. (1989) may be reconciled with Atchley and Andersen (1998) and Billino et al. (2008) by considering the differences in stimuli used by these researchers. In Atchley and Andersen's and Billino and colleagues' studies, the stimulus displays were centered in the participants' visual fields, and extended in to all quadrants. In Warren et al., however, the elements of the stimulus were on the "ground"—that is, participants were making judgments based on stimuli presented in the inferior hemifields of their visual fields. Wojciechowski et al. (1995) have shown that motion sensitivity (for translating motion, that is) is worse in inferior locations in the visual field in both young and old participants, but even more so in older participants. It is possible that the age differences found by Warren and colleagues are a result of how the stimulus was presented. For now, it seems safe to say that radial flow perception in older adults is well-preserved, though more studies should be conducted, replicating Warren et al.'s

(1989) results and confirming those of Atchley and Andersen (1998) and Billino and colleagues (2008).

Neural Mechanisms Underlying Changes in Motion Processing with Age

As we have seen, aging does not affect the different types of motion processing in a uniform way. The perception of radial flow is relatively unaffected by age (Atchley & Andersen, 1998). In contrast, age has a large effect on translational motion perception, though the approximate amount of deterioration varies from study to study (Hutchinson et al., 2012). The reason for these differential effects of age on different motion processing types is likely due to the fact that distinct neural mechanisms underlie both types of processing, and that effects of aging on the brain are non-uniform (Billino et al., 2008). The following subsections will review the neural correlates of, and explanations for, the effects of age on both types of motion processing.

Mechanisms of translational motion. Intact processing of area MT is necessary and sufficient for translational motion processing (Newsome, Britten, Salzman, & Movshon, 1990; Newsome & Paré, 1988). This area is part of the dorsal stream, innervated largely by the M pathway (Born & Bradley, 2005; Nakyama, 1985). The majority of MT neurons receive their input from layer 4B of area V1, which in turn receives its input almost exclusively from M layers in the LGN. Abolishing M layers in the LGN results in almost complete inactivity of area MT. In addition to MT, the cerebellum is also implicated in translational motion perception (Nawrot & Rizzo, 1995, 1998). The main role of cerebellum in the motion processing system is to disambiguate retinal image motion from self- and object movement (Baumann et al., 2015).

Normal age-related changes in the cerebellum may contribute to deficits in motion processing in older adults. Patients with lesions along the midline of the cerebellum (i.e., the vermis) have higher motion coherence thresholds than normal adults and patients with hemispheric cerebellar lesions (Nawrot & Rizzo, 1995). These deficits are still evident up to two years after initial testing, indicating that the deterioration of motion perception accompanying these lesions is chronic (Nawrot & Rizzo, 1998). Age-related changes in the vermis may explain increases in motion coherence thresholds with age. Imaging studies show that vermal volume decreases with age (Luft et al., 1999; Raz, Dupuis, Briggs, McGavran, & Acker, 1998; Raz, Torres, Spencer, White, & Acker, 1992; Shah et al., 1991; Sullivan, Desmond, Deshmukh, Lim, & Pfefferbaum, 2000), and stereological studies indicate that the number of Purkinje cells in the cerebellar vermis decreases with age (Andersen, Gundersen, & Pakkenberg, 2003; Torvik, Torp, & Lindboe, 1986). Although age changes in the vermis may contribute to deficits in motion processing, the age-related cerebellar changes are not the main source of deficits in motion processing.

As detailed above, the M/dorsal pathway and area MT are heavily implicated in motion processing. It is likely that deterioration of translational motion perception with age is, in part, due to the deterioration of the M/dorsal pathway in general, and of area MT in particular (Conlon & Herkes, 2008; Gilmore et al., 1992). Visual evoked potentials (VEPs) and EEGs are useful in studying the activity of the different visual pathways. The N2 component of these two electrical measures is believed to represent mostly M pathway activity, and is the most reliable motion-onset-specific component (Kuba, Kubová, Kremláček, & Langrová, 2007). N2 (induced through linear motion) has a longer latency in older than in younger adults, in both VEP (Langrová, Kuba, Kremláček, Kubová, & Vít, 2006) and EEG studies (Lorenzo-López, Amenedo, Pazo-Alvarez, & Cadaveira, 2004), indicating that the M pathway matures with age, so that translational motion processing is delayed in older adults.

Stronger evidence concerning the effects of age on the neural substrates of translational motion processing comes from single-unit recording studies of V1 and MT neurons. The percentage of neurons in V1 with significant and strong directional bias is greatly reduced in old monkeys and cats, compared to young (Hua et al., 2006; Schmolesky et al., 2000). Recall that MT receives input from V1 neurons (Merigan & Maunsell, 1994); if V1 neuronal selectivity is decreased, MT neuronal selectivity will be as well. Liang et al. (2010) found decreased directional selectivity in area MT of old monkeys, compared to young monkeys. The decrease in directional selectivity in both of these areas is a result, not of a decrease in response to optimal stimuli, but an increase in responsiveness to all stimuli (i.e., increase in peak responses). This increase in peak response results in larger tuning curves. Deterioration of directional bias can account for psychophysical results, such as those of Ball and Sekuler (1986), in which older adults are not as accurate in discriminating different motion directions as younger adults.

An increase in peak responses contributes not only a larger tuning curve, but also to more noise in V1 and MT neurons (Yang et al., 2008). Recall that, in addition to the increase in peak responses, spontaneous neural activity is increased in older animals, resulting in an overall decrease in SNRs. It is easy to see how this finding can account for results from studies using coherent motion paradigms. In these studies, older adults generally need more signal than younger adults to be able to perceive translational motion (see, e.g., Andersen & Atchley, 1995; Billino et al., 2008; Snowden and Kavanagh, 2006). The degradation of GABAergic systems in the aging cortex is thought to be a major contributor to decreased SNRs in neurons. Leventhal et al. (2003) found that applying GABA and a GABA agonist narrowed the range of preferred directions in old monkeys, increasing their SNRs.

Recall that older adults perform similarly to, or better than, younger adults when stimuli are large and high-contrast (Betts et al., 2005). This finding, though counterintuitive, is likely caused by the same mechanisms that underlie decreased SNRs (both behavioral and neural). Cells throughout the cortex, including area MT, have receptive fields characterized by center-surround antagonism—certain stimuli in the center will cause an increase in the cell's firing rate, and stimuli in the surround will inhibit it (Allman, Miezin, & McGuinness, 1985a). As described above, older adults show an improvement in performance for large (i.e., => 5 deg) motion stimuli. This decrease in spatial suppression is thought to be the result of age changes in center-surround antagonism of MT cells. Older adults experience degradation of GABAergic systems, and concomitant decreases in behavioral and physiological inhibition (Schmolesky et al., 2000). This loss of inhibition can lead to degradation of the antagonistic mechanisms in area MT, so that increasing stimulus size (which overlap both the excitatory center and inhibitory surround of a cell's receptive field) no longer results in spatial suppression, as it does with younger adults (McCourt, Leone, & Blakeslee, 2015; Tadin, Lappin, Gilroy, & Blake, 2003).

Future research should examine the possibility that applying GABA or GABA agonists to V1 neurons also increases functional selectivity of MT neurons (due to the direction of their connectivity), or if selectivity may be increased in MT by applying GABA directly to the cells in that area. If increasing inhibitory intracortical communication can increase directional selectivity in old monkeys, it follows that increasing neuronal inhibition in older adults may also improve translation motion perception. Increasing GABA may also affect the center-surround mechanisms of old MT cells, resulting in changes in older adults' motion processing for large stimuli.

Mechanisms of radial flow. Several visual and non-visual cortical areas are implicated in the perception of radial flow. Parietal and frontal lobe regions are involved in radial flow perception (Billino et al., 2008), as well as areas V1, V2, V3, and VA (Koyama et al., 2005). It is thought, however, that dorsal MST is the cortical region largely responsible for perception of radial flow (Saito et al., 1986; Tanaka & Saito, 1989). Dorsal MST neurons are very large, often covering almost all of the contralateral visual field and part of the ipsilateral visual field, and they respond to large-field visual motion (Duffy & Wurtz, 1991). These characteristics of dorsal MST cells make them good candidates for the processing sites of optic flow stimuli, and indeed, neuroimaging studies indicate that neurons in dorsal MST are responsive to patterns of expansion and contraction (Culham, He, Dukelow, & Verstraten, 2001). Dorsal MST is innervated largely by neurons from MT (Celebrini & Newsome, 1994), and both of these regions are part of the dorsal stream, which is chiefly made up of M cells (Merigan & Maunsell, 1993). M cells are responsive to stimuli of higher temporal frequencies, and are therefore implicated in motion processing.

Although (conscious) perception of radial flow is largely unaffected by age, it may be the case that there are age differences in the (unconscious) objective sensation of expansion/contraction. Langrová et al. (2006) measured younger and older participants' VEPs to expanding and contracting concentric rings. The authors found that, compared to activity evoked by a checkerboard pattern-reversal stimulus (designed to stimulate the P/ventral pathway), N2 activity evoked by the radial stimulus was affected by age—older adults' N2 component had longer latencies, indicating age-related changes in the M pathway.

If the sensation of radial flow is affected by age, as Langrová et al. (2006) speculate, why is perception relatively unaffected? It is possible that the neural areas implicated in perception of radial flow are not as affected by age as other regions. There is strong evidence that areas V1 (Schmolesky et al., 2000), V2 (Yu et al., 2006), and MT (Yang et al., 2008) undergo age-related functional changes, including a decrease in directional selectivity and decreased signal-to-noise ratios of neurons. In contrast, the frontal lobe, though it undergoes many age-related changes, seems to preserve some functionality, particularly for spatial memory (Parkin, Walker, & Hunkin, 1995). Dorsal MST may be less affected by aging as well (Billino et al., 2008). However, research concerning the effects of age on dorsal MST anatomy and functionality is scarce; any conclusions drawn about the senescent dorsal MST are purely speculative, and more work should be conducted before definitive statements are made about aging and this cortical region.

This section has introduced psychophysical evidence of age-related changes in motion processing, with a focus on translational motion and radial flow perception. Age differences in translational motion processing are likely due to age changes in MT and the cerebellum; the effects of aging on radial flow perception are less clear. The next section turns to aging and eye movements, an area of study interwoven with motion processing, and critical for a full understanding of motion parallax.

Aging and Pursuit Eye Movements

Eye movements serve a very important function in visual processing—they hold images steady on the retina, allowing us to move rapidly through the world. Due to object and observer movement through space, visual images move across the retina, and even slow movement can cause degradations in visual acuity (Leigh & Zee, 1983). In order to maintain good visual acuity, eye movements work to minimize retinal “slip,” and even the very smallest object or observer movements are compensated for by changing the velocity of eye movements. There are several classes of eye movements, each with different characteristics and neural substrates, and each serving a different function (Leigh & Zee, 1983). Briefly, optokinetic reflex (OKR) and vestibulo-ocular reflex (VOR) eye movements work together to maintain images on the retina during head/body movements. Vergence eye movements, which move the eyes in opposite directions, are necessary for accommodation and stereopsis, making it possible for both foveas to acquire the same image regardless of the distance between the object and the observer. Saccades are rapid eye movements that help to bring an object falling on the peripheral retina into the area with the highest acuity, the fovea. Saccades may be voluntary or reflexive. Smooth pursuit eye movements are slow eye movements that allow primates to track small, moving targets. The smooth pursuit system is the most relevant to motion processing in general and motion parallax particularly (Nawrot & Joyce, 2006; Newsome, Wurtz, Dürsteler, & Mikami, 1985). The neural substrates and effects of age on pursuit will be reviewed in depth, but first, I will provide a brief overview of senescent VOR, OKR, vergence, and saccadic eye movements.

The rotational VOR is initiated by vestibular signals that arise in response to head rotation. The VOR is mediated by the semicircular canals of the ear, which are sensitive to head movement and help to maintain balance (Tian, Crane, Wiest, & Demer, 2002). As the head rotates, the eyes rotate in the opposite direction, at an angle (ideally) almost equal to that of head rotation (Leigh & Zee, 1983). Therefore, VOR function can be measured by its gain, the ratio of change in eye angle to change in head angle. In healthy young adults, gain is usually right around 1.0. In older adults, however, gain is decreased—their change in eye angle is less than their change in head angle (Wall, Hunt, & Black, 1984). Older adults also have longer VOR latencies than younger adults, that is, the onset of eye movements lag longer behind head movements in older adults (Tian et al., 2002). These age-related deficits are likely due, in part, to degradations in the vestibular signals projecting from the semicircular canals, which send head velocity and acceleration signals to the brain (Tian et al., 2002). The vestibular nuclei, which are particularly implicated in eye velocity information storage during VOR (Raphan, Matsuo, & Cohen, 1979), may be affected by age (Johnson & Miquel, 1974), which might also affect VOR gain in older adults.

While VOR results in eye movements in the direction opposite of head movements, OKR evokes eye movements in the direction of visual motion (Leigh & Zee, 1983). In the real world, OKR is elicited by the movement of a large expanse of the visual field (Donaghy, 1980; Dürsteler & Wurtz, 1988). In the lab, OKR may be stimulated by seating the participant inside a rotating drum painted with vertical black and white stripes. Although the participant is stationary, the rotation of the drum causes a feeling of self-rotation called circularvection. Older adults have longer circularvection latencies (Matheson, Darlington, & Smith, 1998) and lower OKR gains (eye velocity/motion velocity) than younger adults (Baloh, Jacobson, & Socotch, 1993). Evidence from lesion studies suggests that the accessory optic system contributes to optokinetic eye movements (Dürsteler & Wurtz, 1988; Leigh & Zee, 1983). Although there have been no direct studies of the effects of age on the neural substrates of OKR, there is research indicating that GABAergic neurons are one of the dominant cell types in the accessory optic system (Giolli et al., 1985), and as I have reviewed in the sections on the visual system and motion processing, GABA transmission is degraded in older adults (Leventhal et al., 2003). It is possible, then, that loss of intracortical inhibitory communication contributes to deficits in OKR of older adults.

Vergence, or disjunctive, eye movements rotate both eyes in opposite directions in order to bring a single image on to both foveas, allowing for fusion and accommodation (Leigh & Zee, 1983). Accommodative vergence eye movements are accompanied by lens accommodation, in which the lens of the eye contracts and reduces tension in the eye muscles in order to focus the lens on the object of interest. Vergence can be tested using step stimuli (evoking a transient response), or ramp stimuli (evoking a sustained response) (Rambold, Neumann, Sander, & Helmchen, 2006). Although the lens of the eye does lose accommodative power with age (for review see Schieber, 2006), there do not appear to be age differences in accommodative vergence movements in response to transient stimuli (Rambold et al., 2006). Older adults do, however, have longer latencies and smaller velocities than younger adults when completing accommodative vergence movements to sustained stimuli. The same pattern holds for age effects in fusion conditions—there are no age differences for transient stimuli, but there are effects of age on latency, velocity, and peak acceleration for sustained stimuli. As with other age-related deficits in eye movements, it seems unlikely that brain stem changes contribute to deficits in vergence movements (Henson et al., 2003). Rather, it is likely that age-related changes of the cerebellum, which receives connections from the motor nuclei of the brain region, may, at least in part, cause decreases in the latency, velocity, and acceleration of fusion and accommodation (Gamlin, Yoon, & Zhang, 1996).

Like VOR, OKR, and vergence eye movements, saccadic eye movements are also affected by age. The majority of studies investigating the effects of age on saccade velocity report that older adults have lower peak velocities than younger adults (see, e.g., Fahle & Wegner, 2000; Spooner, Sakala, & Baloh, 1980; Warabi, Kase, & Kato, 1984). Older adults also have longer saccadic latencies than younger adults (Abel, Troost, & Dell'Osso, 1983; Sharpe & Zackon, 1987), and their saccades are of longer durations than younger adults' (Munoz, Broughton, Goldring, & Armstrong, 1998; Warabi et al., 1984), perhaps due to the age-related loss of velocity. These age differences have a neural basis: fMRI studies have investigated age differences in cortical blood flow during saccadic tasks and found that activity is shifted from the posterior to anterior regions in older adults; older adults also have less cortical activity in general during saccadic tasks, compared to younger adults (Nelles, de Greiff, Pscherer, & Esser, 2009; Raemaekers, Vink, van den Heuvel, Kahn, & Ramsey, 2006). However, no studies have investigated the effects of aging on saccadic eye movements at a more precise level. Age-related deficits in saccadic function could be due to atrophy of the cerebellum (Raz et al., 2005), but more research is necessary to make definitive statements about the senescent saccadic system.

Smooth pursuit eye movements are continuous eye movements that are evoked by the movement of images over the retina (Rashbass, 1961). Pursuit enables tracking of visual targets, maintaining the image on the fovea (Gottlieb, MacAvoy, & Bruce, 1994). This particular type of eye movement is unique to primates; non-primate animals can make slow eye movements in response to movement of an entire visual scene, but have weak or non-existent pursuit systems (Lisberger, Morris, & Tyschen, 1987). Before reviewing the neural mechanisms underlying the pursuit system, it is important to understand the characteristics and components of pursuit.

Overview of Smooth Pursuit Eye Movements

The latency of pursuit eye movements is approximately 100-130 ms (Leigh & Zee, 1983). The eye movement itself is comprised of two components. The first component is an initiation ("open-loop") phase, which is driven solely by visual motion inputs and lasts approximately 100 ms after onset of eye movements (Leigh & Zee, 1983; Lisberger et al., 1987). The second component, the closed-loop (or maintenance) phase of pursuit eye movements, is dependent on a "negative feedback loop" (Leigh & Zee, 1983; Morris & Lisberger, 1987). The retinal error (i.e., the difference between eye velocity and target velocity) is combined with an efference copy of the eye velocity signal to serve as an input to the pursuit maintenance system. Eye velocity is corrected (and pursuit maintained) by the negative feedback during this phase. Ideally, eye and target velocity are very nearly the same, but not perfectly accurate, as this would stabilize the image on the fovea and cause it to disappear (Leigh & Zee, 1983). The ratio of eye velocity/target velocity can be quantified as gain. If the velocity of target motion is high and the velocity of eye movement is low (i.e., low gain), observers may have to use "catch-up" saccades in order to maintain the image on the fovea (Lisberger et al., 1987).

Neural Circuitry of Smooth Pursuit

Until fairly recently, the pursuit system was thought to be relatively simple (see Figure 2). In this old model (see Gottlieb et al., 1994; Leigh & Zee, 1983), visual motion information from areas MT and MST project in parallel pathways to the smooth eye movement area of the frontal eye fields (FEFsem, located in the posterior bank of the arcuate sulcus of the frontal eye fields) and to the basilar pontine nuclei (PON). In addition to feed-forward projections from visual motion areas to FEFsem, FEFsem also feeds back in to MT and MST, and projects to PON. PON innervates the cerebellum, specifically the flocculus, paraflocculus, and dorsal vermis. These areas project to the vestibular nuclei of the brain stem (and the vestibular nuclei feed back in to the cerebellum), and from the vestibular nuclei, the pursuit signal is sent to the ocular motor nuclei to generate an eye movement. In this old model, areas MT and MST were thought to have the strongest control over pursuit (Krauzlis, 2004).

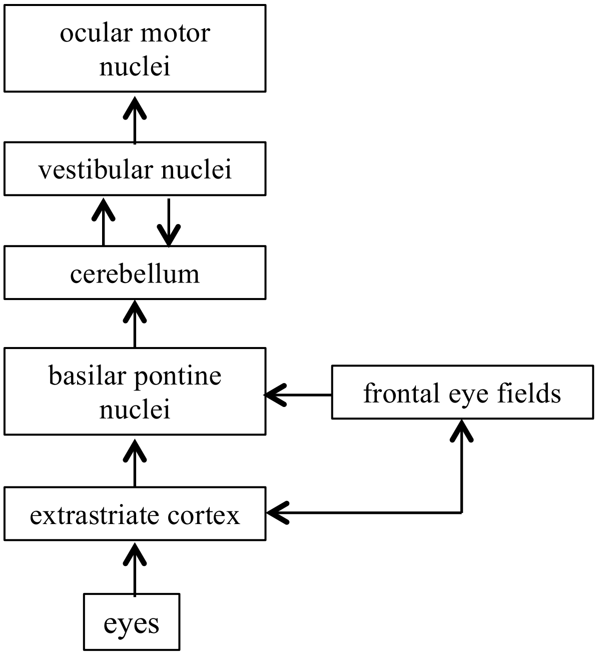

Figure 2. Old neural model of the smooth pursuit eye movement system. The diagram should be read from the bottom (extrastriate cortex) to the top. Adapted from Gottlieb et al. (1994).

Recent studies have suggested that the pathways for pursuit are actually much more complex, and involve several more brain regions than previously thought (Krauzlis, 2004). The brain regions implicated in the initiation and maintenance of pursuit can be roughly divided in to four categories, each playing a different role: cerebral cortex and basal ganglia; premotor nuclei (PMN) of the brainstem; superior colliculi (SC); and cerebellum (Krauzlis, 2005; see Figure 3 for a graphical depiction).

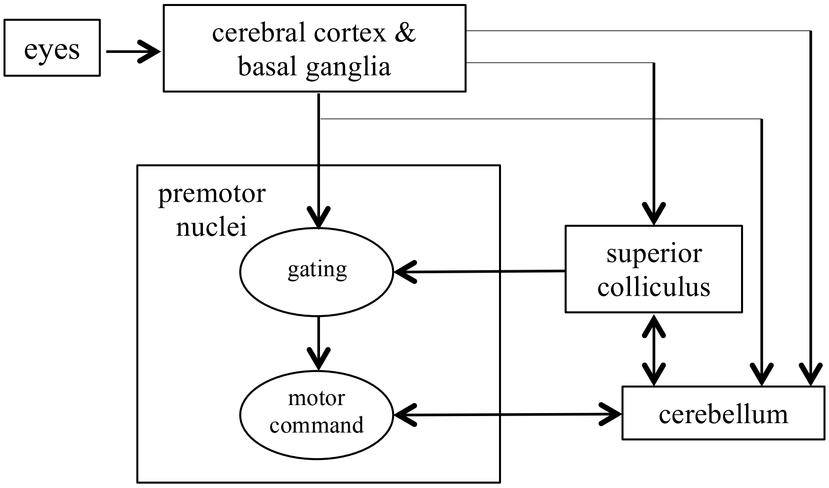

Figure 3. New neural model of the smooth pursuit eye movement system. Adapted from Krauzlis (2004). The diagram should be read from the top to the bottom.

The cerebral cortex includes FEFsem, supplementary eye fields, lateral intraparietal area (LIP), and MT and MST. The basal ganglia include the caudate nucleus and substantia nigra pars reticulate. Together, these areas send target location information to the SC and cerebellum, and image motion information to the cerebellum and PMN (Krauzlis, 2004). The PMN select ("gate") the sensory information, along with help from the SC. The PMN generate the motor command for the eye movements and project this information to the cerebellum, which also receives contributing gating information from the SC. The SC is involved in generating an eye movement goal during saccades by indicating discrepancies between eye and target position (Krauzlis, Basso, & Wurtz, 2000), and it is therefore not surprising that it plays a role in gating in the pursuit system. The cerebellum (specifically, the vermis, flocculus, and ventral paraflocculus) receives both integrated sensory-motor information and motor commands. Its role is to adjust the final motor program for the eye movements (Moschner et al., 1999), which are sent back to the PMN for execution.

The role of the cerebellum in pursuit was less clear in the old model (Leigh & Zee, 1983), and it was thought to be involved more heavily in saccadic motor commands than in pursuit

(Büttner, Straube, & Spuler, 1994; Suzuki, Noda, & Kase, 1981). Now, however, we know that the cerebellum is implicated in both the open- and closed-loop phases of pursuit: the vermis is thought to initiate pursuit movements based on the integrated sensory-motor information sent from the cortex, and the ventral paraflocculus is thought to be critical in generating and modifying the ongoing pursuit command necessary for pursuit maintenance (Krauzlis, 2004, 2005; Rambold, Churchland, Selig, Jasmin, & Lisberger, 2002; Suzuki & Keller, 1988a, 1988b; Suzuki et al., 1981). The vermis is sensitive to image motion (Nawrot & Rizzo, 1995; 1998) and important in pursuit initiation (Moschner et al., 1999). Many vermal Purkinje cells (i.e., cerebellar output neurons) are responsive to both eye and target stimulation, and it is thought that the target velocity signal necessary to initiate pursuit eye movements is formed in the vermis (Suzuki & Keller, 1988a, 1988b). In contrast, Purkinje cells in the ventral paraflocculus are sensitive to eye position and velocity information, not image motion (Krauzlis, 2004; Rambold et al., 2002).

As previously stated, it was long thought that MT and MST were the areas most crucial for pursuit (see, e.g., Lisberger et al., 1987). However, lesions of these areas do not permanently abolish pursuit eye movements; only pursuit of targets that are in the receptive fields of the damaged cells are affected, and only during the open-loop phase (Newsome et al., 1985). It is now thought that these areas are the sites of visual motion information and eye movement integration, creating a unified signal that is sent downstream (Dicke & Their, 1999; Komatsu & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988). Although this is an important step in creating a smooth pursuit signal, it is not the most crucial: it is now thought that the FEFsem is the region most integral for pursuit (Krauzlis, 2004). Stimulation of neurons in this area initiates pursuit, and lesions of the FEFsem reduce pursuit gain and anticipatory tracking.

The SC was absent from the previous model of the pursuit pathways (see Gottleib et al., 1994; Leigh & Zee, 1983), but this area does play a role in pursuit. As noted above, neurons in rostral SC seem to be involved in identifying the eye movement “goal” (Krauzlis, 2005), rather than planning or generating a motor command. So-called fixation neurons in rostral SC are active in the presence of retinal error (discrepancy between eye and target position), regardless of the type of eye movement that is being required, supporting the idea that these neurons are involved in communicating target location and not motor commands (Krauzlis et al., 2000).

The Effects of Aging on Smooth Pursuit Eye Movements

There are several characteristics of pursuit that may be assessed in order to investigate the integrity of pursuit movements. These include pursuit latency, overall velocity, gain, the number of catch-up saccades and saccadic errors, and prediction and anticipation (Rashbass, 1961; Sharpe & Sylvester, 1978; Sprenger et al., 2011). Many studies of pursuit use center-ramp paradigms, in which a centered, stationary target makes a smooth movement (ramp) to the left or right; studies using these paradigms report an initial saccade preceding the smooth pursuit movement (Rashbass, 1961). An alternative technique, the step-ramp paradigm, allows for an immediate initiation of smooth eye movements, bypassing the initial saccade. In this paradigm, the target is presented in the center, and after a certain time interval, makes a jump (a step) of varying amplitude to the left or right. Once this step is made, the target immediately begins moving (ramping) toward the center. Rashbass (1961) showed, using a step-ramp paradigm, that pursuit is immediately initiated, without a saccade, in the same direction as that of the ramp, indicating that the initiation of pursuit relies on visual motion information, not target location. The step-ramp paradigm can be used to measure pursuit initiation (quantified as latency or initial acceleration) (Morrow & Sharpe, 1993). While center-ramp studies are very informative, step-ramp studies are especially useful in aging research, as it is possible to separate changes in pursuit initiation that are due to a lag in the initial saccade from delays due to a lag in the actual pursuit eye movement.

The effects of age on the open-loop (pursuit initiation) component of pursuit have been studied using center- and step-ramp paradigms, measuring latency and initial velocity and acceleration. Saccadic latency, considered part of pursuit initiation and measured in center-ramp paradigms, is prolonged in older adults, compared to younger adults (Morrow & Sharpe, 1993; Sharpe & Sylvester, 1978). Studies employing step-ramp paradigms similarly show increased latencies in older adults, though in these studies the latency being measured is time to onset of the actual pursuit movement (Handke & Büttner, 1999; Knox, Davidson, & Anderson, 2005).

Morrow & Sharpe (1993) used both center- and step-ramp paradigms in their study to investigate the effects of age on initial eye movement acceleration and velocity. In the center-ramp condition, initial pursuit velocity was 26% lower in older than in younger adults. In the step-ramp condition, initial pursuit acceleration was 29% lower in older than in younger adults, with no difference in acceleration between the two ramps tested (20 and 40 deg/sec). Similarly, initial pursuit velocities are decreased in older adults compared to younger adults for step-ramp paradigms with 10, 30, and 50 deg/sec ramps (Straube, Scheuerer, & Eggert, 1997). In this study, the differences between younger and older adults in initial velocity increased with increasing ramp velocity, indicating that initial eye acceleration decreases with age.

Measurements of overall velocity, gain, catch-up saccades, and saccadic errors can be used to assess the integrity of the closed-loop component (pursuit maintenance) in older adults. Numerous studies show that overall velocity is decreased in younger adults, at target speeds as low as 10 deg/sec (Hutton, Nagel, & Loewenson, 1983; Morrow & Sharpe, 1993; Spooner et al., 1980; Sprenger et al., 2011; Straube et al., 1997). Gain is also affected by age: Sharpe and Sylvester (1978) found that younger adults have gains of 0.96 or better for target velocities up to 30 deg/sec. In contrast, older adults only have gains close to 1.0 when target velocity is 5 deg/sec; their gains start dropping dramatically even at the next slowest velocity tested, 10 deg/sec. The age-related decrease in gain is not only evident in center-ramp studies; older adults have decreased gains, compared to younger adults, in studies that use step-ramps as well, and this decrease is present whether the direction of the step and the ramp are predictable or not (Handke & Büttner, 1999). This decrease in gain appears to be greater in old than middle age. When pursuit gains of older and middle-aged adults were tested using targets moving in a triangular or sinusoidal waveform, the older adults had lower gains than the middle-aged adults at even the slowest (10 deg/sec) velocity (Zackon & Sharpe, 1987).

Age differences in the frequency and accuracy of catch-up saccades are another indicator of the integrity of the closed-loop system, and can be used to evaluate how well eye velocity is being maintained. Catch-up saccades enable the target to be brought back on to the fovea when the target is moving too quickly for the pursuit system to be able to keep pace (Lisberger et al., 1987). Even at a target velocity of 5 deg/sec, when older adults' gains are close to 1.0, they still have higher frequencies of catch-up saccades than younger adults (Sharpe & Sylvester, 1978). Similarly, using a step-ramp paradigm, Morrow and Sharpe (1993) found that older adults made more saccadic errors than younger adults. A saccadic error means that the target was over- or undershot when trying to bring it on to the fovea; this "miss" of the fovea results in the necessity of more saccades to foveate the target.

The increased use of catch-up saccades in older adults may be a result, not just of a loss of pursuit velocity, but also of a more general degradation of the pursuit system as a whole.

Karlsen, Hassanein, and Goetzinger (1981) described four types of smooth tracking curves: 1) normal; 2) normal with a few interruptions (i.e., saccades); 3) sinusoid with saccadic/nystagmic eye movements super imposed; and 4) eye movement ataxia (a non-specific disorder that may be characterized as a loss of ability to pursue). The first two types of eye movements are considered normal, while the last two are not. Only 4% of younger adults make a type 3 response, and no younger adults make a type 4 response. In contrast, 33% of older adults make type 3 responses and 25% make type 4 responses. This finding translates to 71% of older adults using a great many saccades in their pursuit eye movements, or generally having trouble maintaining pursuit.

Surprisingly, pursuit prediction and anticipation are intact in older adults. When participants are tracking a target, blanking the target at the beginning of the ramp necessitates predictive pursuit, while blanking a target at the end of the ramp necessitates anticipatory pursuit (Sprenger et al., 2011). In the predictive condition, older and younger adults' initial accelerations are the same, though in regular pursuit conditions (no blanking), younger adults have higher initial accelerations. In the anticipatory condition, there is no age difference in pursuit deceleration in response to the blanking. These results indicate that older adults retain their predictive and anticipatory pursuit mechanisms, and in fact, the increased frequency of catch-up saccades may contribute to predictive pursuit and help to compensate for losses in pursuit velocity.

To summarize, older adults show deficits in both the open- and closed-loop components of pursuit. Longer latencies and slower initial accelerations and velocities provide evidence of deficits in the open-loop phase. In the closed-loop phase, slower overall velocities, lower gains, and higher frequencies of catch-up saccades and saccadic errors are evidence of deficits. In contrast, pursuit prediction and anticipation are intact in older adults. What changes in neural mechanisms can account for these different results? There have been no studies directly investigating age-related changes in the neural circuitry of pursuit. It is possible, however, to draw some conclusions about age-related pursuit degradation based on the deficits associated with the different pursuit components. We may think of these components as visual motion input, sensory-motor integration, motor command generation, and motor command execution, and explore the effects of age on each.

Motion input. Pursuit initiation is driven by information of target motion, and the deficits in the open-loop (initiation) phase experienced by older adults may be due to deficits in motion processing (Morrow & Sharpe, 1993). Areas LIP, MT, and MST are responsible for motion processing, and project to the FEFsem, the area most crucial for pursuit. It is well documented that older adults have deficits in motion sensitivity. Age-related degradation of motion sensitivity is likely due to decreases in functional selectivity in motion processing areas. Neurons in MT are less selective for direction and speed, and have decreased SNRs (Liang et al., 2010; Yang et al., 2009). Because older adults' sensitivity to motion is reduced, it follows that pursuit initiation (latency and initial acceleration and velocity) should also be reduced in older adults, as motion input drives pursuit initiation. Noise in MT neurons may also contribute to the higher variability in pursuit initiation latency in older adults (Niu & Lisberger, 2011).

Sensory-motor integration. Recall that the integration of sensory and eye speed signals likely occurs at the cortical level (Newsome et al., 1988) and then this integrated signal is sent further downstream in the pursuit system (Krauzlis, 2004). A likely site of integration is area MST, which contains neurons responsive to image location and eye movements, and codes for retinal error (Dicke & Their, 1999; Komatsu & Wurtz, 1988). It is possible that sensory-motor integration is disturbed with age, which would explain many age effects found in pursuit studies.

However, unlike investigations into area MT, no research has looked at the effects of aging on area MST, and it is impossible to make conclusive statements regarding the integrity of this area in older adults. It is probable, however, that area MST is affected by age. The major source of input to MST is area MT (Celebrini & Newsome, 1994), an area that experiences age-related changes in functional selectivity (Liang et al., 2010; Yang et al., 2009), which may result in age-related decreases in the selectivity of area MST neurons as well.

Motor command generation. The vermis, flocculus, and paraflocculus of the cerebellum are responsible for generation and modification of the motor program for pursuit (Krazulis, 2005), and it is likely that age-related changes in the cerebellum (especially the vermis) contribute to older adults' deficits in initiating and maintaining pursuit eye movements. Stereological studies of the cerebellar hemispheres in both cats (Zhang, Hua, Zhu, & Luo, 2006) and humans (Zhang, Zhu, & Hua, 2010) indicate that overall gray matter volume decreases with age. This gray matter decrease is probably due to normal Purkinje cell loss (Woodruf-Pak et al., 2010). Similarly, *in vivo* magnetic resonance image studies find that hemispheric cerebellar volume decreases with age (Raz et al., 2005). Additionally, the number of Purkinje cells in the vermis (Andersen et al., 2003; Torvik et al., 1986) and flocculus (Hall, Miller, & Corsellis, 1975), decrease with age, resulting in decreases in vermal volume (Luft et al., 1999; Raz, et al., 1998; Raz et al., 1992; Shah et al., 1991; Sullivan et al., 2000).

Motor command execution. In contrast to the age-related deficits in visual motion inputs, sensory-motor integration, and motor program generation/modification, there do not seem to be age-related deficits in the oculomotor command execution. Although there are no studies on the effects of age on the execution and speed of the pursuit eye movement motor component in isolation, we may take what information is available about the motor component of other classes of eye movements, and about the functional and anatomical integrity of PMN, associated with executing the pursuit eye movement. Fixation stability in older adults is comparable to that of younger adults, indicating preserved motor control of the extraoculomotor muscles (Kosnik, Kline, Fikre, & Sekuler, 1987). Likewise, reflexive (as opposed to voluntary) saccadic latencies are well-preserved in older adults, implying that the extraoculomotor muscles associated with these eye movements are intact (Pratt, Dodd, & Welsh, 2006). Additionally, the brain region associated with executing the motor command itself, the PMN, does not seem to be affected by age (Henson et al., 2003; Munoz et al., 1998; Vijayashankar & Brody, 1977). These results, taken together, suggest that the effects of age on the smooth pursuit system are due to senescent changes in the visual or sensory-motor pathways in the system, and not to changes in the ability to execute the motor command (Moschner & Baloh, 1994).

EXPERIMENT ONE

We have seen that aging affects visual processing in general and motion processing in particular, and causes deficits in both the initiation and maintenance phases of smooth pursuit. It is important to understand how age affects motion and pursuit, because both of these processes are necessary for the unambiguous perception of depth from MP. In Experiment One, the effects of age on sensitivity to depth from MP are investigated, as well as what mechanisms underlie age changes in depth perception. To fully appreciate how Experiment One extends our knowledge of age effects on MP, it is necessary to be familiar with the mechanisms of MP in general, as well as the research on MP depth thresholds, the neural mechanisms of MP, and what we have learned about age effects on MP to date.

Aging and Motion Parallax

Overview of Motion Parallax

The perception of depth from MP arises from the relative retinal image motion of different objects in the optic array as an observer translates through space. MP provides information about the relative depth between objects, rather than estimates of absolute depth. von Helmholtz (1867/1962) pointed out the importance of motion parallax as a cue for depth, comparing it to depth perception from stereopsis (binocular disparity). von Helmholtz was not the first scientist to acknowledge the value of motion parallax, however; as early as the seventeenth century, philosophers were describing how changes in motion direction of both the eye and the objects relative to fixation give rise to depth perception (see Ono & Wade, 2005, for an historical background of motion parallax). Researchers in the mid-1900s studied the characteristics of depth perception from MP and the factors that influence percepts, including stimulus size (Graham, Baker, Hecht, & Lloyd, 1948), absolute distance (Ferris, 1972; Gibson,

Gibson, Smith, & Flock, 1959), and the effects of presenting only two velocities versus a flow field of velocity gradients on the perception of depth and the magnitude of that perceived depth (Gibson & Carel, 1952; Gibson et al., 1959). This research was crucial to furthering our understanding of depth perception from MP, but the stimuli used in these investigations were limited, in that there was no way to isolate the motion parallax depth cue from other cues that might contribute to depth perception (such as stereopsis and relative size). In 1960, however, Julesz developed random dot stimuli that isolated depth cues for binocular disparity (BD), and adapting these stimuli to study MP was a logical next step.

Rogers and Graham (1979) were the first to use random-dot stimuli to study MP. In their study, participants viewed random-dot patterns that were the same as those developed by Julesz (1960). In this study, the generation of stimulus movement allowing for MP was dependent on observer head movement (observer-produced parallax), or movement of the oscilloscope upon which the stimuli were displayed (object-produced parallax). When the observer translated from side to side, alternate bands in the stimulus moved relative to the surrounding bands, in the direction opposite of head movement. When the display translated from side to side, alternate bands in the stimulus moved in the same direction as display movement. This combination of relative stimulus movement and observer or object movement produced a vivid depth percept, with the bands moving in the opposite direction of head movement or same direction as display movement perceived as nearer than the surround. Although there was a clear and unambiguous perception of depth (in this case, unambiguous meaning that depth-sign, or direction of depth, is consistent), there was no perception of motion during observer or display movements—participants reported a rigid 3-D stimulus.

Rogers and Graham (1979), by using a stimulus that did not provide any other depth cues except those of relative stimulus motion, showed unequivocally that motion parallax is an important cue to depth. Their study sparked interest in a line of research that until the late 1970's had been little explored, and researchers began investigating the characteristics of depth perception from MP, new methods in which depth from MP may be stimulated in the lab, how MP interacts with other depth cues, and other topics (Rogers et al., 2009). Some notable findings since the 1979 study include the fact that adaptation to MP stimuli results in an afterimage, so that when viewing a flat test stimulus, the participant perceives a stimulus that is corrugated in depth, but with an opposite depth-sign from the adaptation stimulus (Graham & Rogers, 1982). It has also been found that observer and/or display screen motion are not the only means to produce depth from MP—by translating a stimulus window (and the dots within it) on a stationary display screen, observers report a vivid depth percept, though the display screen itself remains stationary (Braunstein & Tittle, 1988). Another interesting finding is that accuracy in reporting depth-sign is highest when the ratio between fastest- and slowest-velocity dots are small, while the magnitude of perceived depth is largest when this same ratio is high (Braunstein & Tittle). In addition to these studies, researchers have investigated the interaction of MP and binocular disparity depth cues, as both are often present at the same time in real-world situations (Bradshaw & Rogers, 1996; Rogers & Collett, 1989).

For many years the study of unambiguous depth perception from MP was assumed to be solely a product of relative motion between objects in the visual field (i.e., parallax): objects moving in opposite directions are perceived as having opposite depth signs, and objects moving more quickly are perceived as nearer than objects moving more slowly (Braunstein, 1976; Braunstein & Tittle, 1988; Rogers & Graham, 1979; Rogers & Rogers, 1992). Relatively recently, however, more attention has been paid to the role of extraretinal (i.e., non-visual) signals in the perception of depth from MP.

Rogers and Rogers (1992), in investigating the different roles of non-visual and visual signals in unambiguous depth perception, manipulated head movements, real and simulated vertical perspective, and optic flow information arising from the visual field surrounding the MP stimulus. They found that perceived depth-sign was stable (i.e., the depth-sign did not reverse) and consistent with their predictions in all but the control and simulated vertical perspective conditions. Rogers and Rogers concluded that both visual (optic flow and real perspective transformations) and non-visual information (in this case, vestibular information arising from head movements) are, by themselves, sufficient to produce unambiguous, consistent depth percepts. Moreover, because each is sufficient alone, neither is necessary to create a strong perception of depth from MP.

However, the Rogers and Rogers (1992) study, and other early studies of MP, did not control for extraretinal signals that may contribute to disambiguating depth-sign, beyond manipulating head movement (see, e.g., Braunstein, 1968; Gibson et al., 1959; Rogers & Graham, 1979). It is important to note that vestibular information from head movements is not the only available source of extraretinal signals. Extraretinal signals are generated in all conditions that generate unambiguous depth from MP, whether the head is moving or not. Specifically, to generate a strong unambiguous depth percept from an MP stimulus, the observer, display monitor, or stimulus window on the monitor face must translate (Braunstein & Tittle, 1988), generating extraretinal signals. During head movements, smooth eye movements are generated in order to maintain fixation (Miles & Busettini, 1992). These eye movements are in the direction opposite head movements. Eye movements are also generated in conditions in which head movements are not required: when the display or stimulus translates. Braunstein and Tittle (1988) suggest that eye movements may play a role in depth perception from MP, but quickly dismiss this idea as unimportant, maintaining that the velocity field/relative motion of the stimulus provides the vital information about depth from MP. Similarly, Rogers and Rogers (1992) suggest that extraretinal information is not necessary to disambiguate depth-sign from MP, though their suggestion relies on evidence from studies in which each of the conditions that produce an unambiguous depth-sign also generate eye movements (due to display/stimulus movement).

Despite the claims of earlier work, more recent research has revealed the necessity of an extraretinal signal in the unambiguous perception of depth from MP (Naji & Freeman, 2004; Nawrot, 2003a, 2003b). One interesting paradigm used to study depth from MP involves the use of motion aftereffects (MAEs). The advantage of MAEs is that their use abolishes all retinal motion input—the perception of stimulus motion arises strictly from neural signals (Barlow & Brindley, 1963). As noted above (and see Graham & Rogers, 1982), after adapting to a motion parallax stimulus, viewing a stationary test stimulus during observer head translation generates a depth percept in the direction opposite the original MP depth-sign. When translation stops, the depth percept disappears, but the stimulus appears to be moving. An explanation of unambiguous depth perception from MP that relies solely on relative motion information cannot account for results from studies using MAEs (Nawrot, 2003a); therefore, extraretinal signals must play a necessary role in depth from MP.

The source of the necessary extraretinal signals has been a point of some contention. Vestibular signals, which were posited to be a possible source of disambiguating extraretinal signals (Rogers & Rogers, 1992), were ruled out by studies showing that eye movements disambiguate depth from MP in the absence of head translations (vestibular signals), and that vestibular signals alone, without eye movements, are not enough to disambiguate depth (Nawrot, 2003a). The next most logical candidate for the role of disambiguation of depth from MP is smooth pursuit eye movements (Nawrot & Joyce, 2006).

To understand the role of pursuit in MP, it may be helpful to consider depth percepts arising from the kinetic depth effect: when a solid or wire figure is projected on a screen, it creates a shadow that is perceived as a flat, two-dimensional (2-D) projection; however, once the figure is rotated, it is perceived as 3-D (Wallach & O'Connell, 1953). The direction of rotation (i.e., the depth-sign) is ambiguous in that participants may experience a perceived reversal in depth-sign during a trial. Like depth perception in MP, the direction of retinal motion that is nearer or farther than fixation is inherently ambiguous, causing the depth-sign reversal in the kinetic depth effect (Nawrot & Joyce, 2006). In MP, depth-sign is ambiguous without information from the pursuit signal.

The necessary role of the pursuit signal in disambiguating depth-sign is demonstrated in several studies that use different paradigms and that all control for pursuit eye movements. For example, when an MP stimulus is presented without translation (shear only), participants report seeing depth, but their perception of depth-sign is ambiguous (Naji & Freeman, 2004). In contrast, when translation is added, necessitating a pursuit eye movement, participants are consistently able to report depth-sign. More evidence comes from studies manipulating pursuit gain: when pursuit gain is varied, the magnitude of perceived depth scales with the gain, so that smaller gains result in smaller-magnitude depth percepts (Nawrot, 2003b). In another study, head and stimulus translation were yoked together, abolishing the need for eye movements; however, pursuit movements were still generated, in the direction opposite head movement, to suppress translational VOR eye movements driven by the head movement. In this case, depth-sign was unambiguous, because though the eyes were stationary, a pursuit signal was still generated (Nawrot & Joyce, 2006). These pieces of evidence, together, provide support for the pursuit theory of motion parallax. Although a depth percept from MP may be generated by relative motion alone, the disambiguation of depth-sign requires smooth pursuit eye movements.

Knowing the characteristics (e.g., direction, magnitude) of the pursuit movement produced in any given task can provide valuable information about the depth percept generated from MP. During head movements, dots translating in the direction opposite the head movements appear closer; conversely, during display movements, dots translating in the same direction as the display appear closer (Rogers & Graham, 1979). This seemingly confusing finding can be explained by accounting for pursuit movements: motion in the direction of pursuit movements is perceived as nearer, while motion in the direction opposite pursuit movements is perceived as farther (Nawrot & Joyce, 2006). Not only does information about pursuit disambiguate depth-sign, but it also provides information about the magnitude of perceived depth in an MP stimulus. The motion/pursuit ratio (M/PR) provides a simple approximation of the estimation of the magnitude of relative depth from MP based on the geometry of MP (Nawrot & Stroyan, 2009; Stroyan & Nawrot, 2011). The M/PR is

$$d \approx (\mathrm{d}\theta/\mathrm{d}\alpha)/f \tag{1}$$

where d is estimated depth, $\mathrm{d}\theta$ is the angular change in retinal image motion, $\mathrm{d}\alpha$ is the angular change in gaze angle (pursuit), and f is the viewing distance (to fixation) (Figure 4).

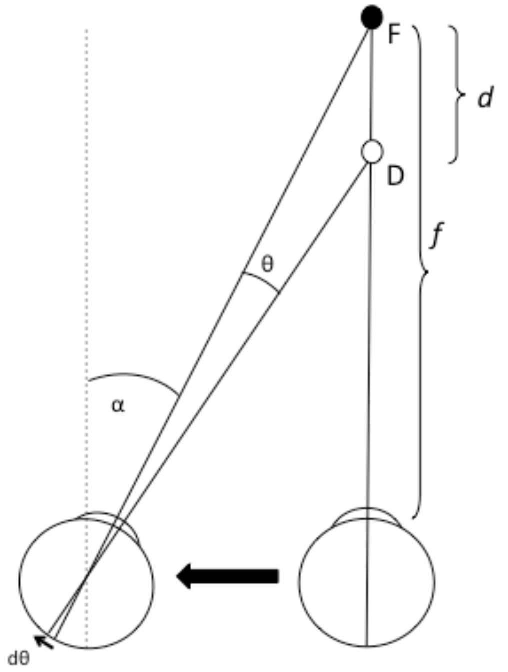

Figure 4. MP diagram. On the right side of the diagram, an observer is looking straight ahead, at the fixation point (F). A distractor (D) is in the observer's line of sight. *d* represents the distance from D to F, and *f* indicates fixation distance. The arrow represents the observer's movement to the left. As the observer translates, maintaining fixation, there is a change in dθ and dα. See text for a detailed explanation of the relationship among dθ, dα, and *f*.

In summary, the perception of unambiguous depth from motion parallax relies not just on retinal image motion, but on the pursuit eye movement signal (Nawrot & Joyce, 2006). In the next subsection I will review the neural mechanisms of MP; in the subsection following I will review the studies concerning aging and depth perception from MP.

Neural Mechanisms of Motion Parallax

Although the neural substrates underlying depth perception from motion parallax are not well understood, there is evidence to suggest that neurons in area MT integrate motion and pursuit signals to provide an unambiguous perception of depth (Nadler, Angelaki, & DeAngelis, 2008; Nadler, Nawrot, Angelaki, & DeAngelis, 2009; Nawrot & Joyce, 2006). Lesions of area MT disrupt both the open- and closed-loop phases of pursuit (Dürsteler, Wurtz, & Newsome, 1987). MT neurons are selective for motion direction (Newsome & Paré, 1988) and speed (Mikami et al., 1986); the processing of both these stimulus characteristics are crucial for depth perception from MP. MT neurons have also been shown to process stereoscopic depth cues (Bradley, Qian, & Andersen, 1995; Maunsell & Van Essen, 1983): neuronal activity in response to motion signals in different directions is often suppressed (Mikami et al., 1986), unless the motion signals are of different disparities (depths), allowing for the disambiguation of motion signals (DeAngelis, Cumming, & Newsome, 1998; Roy & Wurtz, 1990). Therefore, it is not surprising that MT neurons might signal depth from MP, as it has already been shown that MT neurons are sensitive to depth information from stereopsis.

Single-unit recordings in macaque MT show that neurons in this area are selective for depth similarly to the way they are selective for direction: some MT neurons respond to depths that are “near,” suppressing responses to “far” depths, while other MT neurons show the opposite pattern (Nadler et al., 2008). In Nadler and colleagues’ study, macaques were presented with stimuli that were defined by retinal image motion alone or defined by retinal image motion and extraretinal signals (MP condition). In the MP condition, the extraretinal signal was produced by translating the monkeys, generating both vestibular and pursuit signals. In both conditions, retinal image motion was identical, so any differences in neural activity between the two groups is attributable to extraretinal signals.

In the retinal motion condition, neurons showed directional selectivity, as expected, but the magnitude of their activity did not differ by depth (i.e., near or far; Nadler et al., 2008). In contrast, depth-sign selectivity was apparent in MP conditions, so that the magnitude of a neuron’s response to the direction of motion was dependent on whether the stimulus was near or far. This finding indicates that depth-sign is signaled only when extraretinal signals are present—

extraretinal signals modulated the responses of MT neurons to signal depth-sign. Although this study provides strong evidence that the disambiguation of depth-sign in motion parallax occurs in MT, and relies on extraretinal signals, the source of the extraretinal signal is not clear. Because the animals moved their heads, the signal could be vestibular (from the head movement), or could be from the pursuit system (because head movement generates pursuit in the opposite direction).

The role of extraretinal signals in depth-sign disambiguation from MP was clarified by Nadler et al. (2009). In their study, macaques that made head movements without eye movements in response to MP stimuli did not show depth-sign selectivity in area MT neurons. In contrast, MT neurons were depth-sign selective in conditions in which pursuit eye movements were necessary, but the head was stationary. These results mirror those from psychophysical studies by Naji and Freeman (2004), Nawrot (2003a, 2003b), and Nawrot and Joyce (2006), and provide further support for the pursuit theory of MP. It is important to note that the pursuit signal that MT neurons use to modulate depth perception from MP does not arise in area MT itself (as MT neurons are not active for pursuit in isolation; Newsome et al., 1988); rather, it is likely that area MT receives a copy of the pursuit motor command (called an efference copy), from either the cerebellum or brainstem. However, it is not known how the efference copy is relayed to area MT, as there are no inputs from the brainstem and cerebellum to MT (Nadler et al., 2009). Future research should investigate the source and pathway of the pursuit signal efference copy used by MT neurons.

Integrating information from studies of the properties of MT neurons, Nawrot and Joyce (2006) proposed a neural network model (based on Bradley, Chang, & Andersen, 1998, and Nawrot & Blake, 1991) that provides a simple mechanism for how MT neurons use pursuit signals to disambiguate depth. In this model, each neuron has a preference for direction (e.g., left-right) and for depth (near-far). During head translation, for example, to the right, objects in front of fixation will generate rightward retinal image motion, while those behind fixation will generate leftward retinal image motion. This pattern of retinal image motion will activate both leftward and rightward direction-selective neurons. The retinal motion itself is ambiguous in regards to depth-sign, so neurons responsive to both near and far depths will be active. Depth-sign may be disambiguated by facilitatory pursuit signal inputs (in this example, leftward pursuit signals), which innervate neurons active for rightward-far depths and leftward-near depths.

Although evidence is strong that pursuit and retinal motion signals are integrated in area MT, providing a mechanism for depth-sign disambiguation in MP, more research is needed in this area. There are only three studies (Moeeny & Cumming, 2011; Nadler et al., 2008, 2009) that directly investigate the neural substrates of depth perception from MP, and the neural model proposed by Nawrot & Joyce (2006), though supported by the studies by Moeeny and Cumming and Nadler et al., should be explored in more detail. The source of the efference copy that provides the pursuit input to MT is as yet unknown; future research should focus on isolating the source for this pursuit signal and its pathway to area MT. The next subsection will review the effects of aging on depth perception from MP, a topic that is relatively unexplored in research on aging and the perceptual system.

The Effects of Age on Depth Perception from Motion Parallax

Recent research (Holmin & Nawrot, 2015) has characterized the roles of motion ($d\theta$) and pursuit ($d\alpha$) signals in limiting depth thresholds in younger adults. However, research on the perception of depth from MP in older adults is scarce. As reviewed in Chapter One, older adults have a well-documented deficit in motion perception and pursuit eye movements. Given these deficits in motion and pursuit (dθ and dα signals; see Figure 4), it follows that older adults might have deficits in the perception of depth from MP as well. Surprisingly, only three studies have compared younger and older adults' perceptions of MP: one concerned with the detection of 3-D surfaces, and two concerned with the magnitude of depth perceived in MP stimuli.

Older adults are less sensitive than younger adults to 3-D surfaces defined by MP. Andersen and Atchley (1995) presented participants with random dot stimuli that lie either within a 3-D rectangular volume, or on a corrugated surface. The corrugated surface was defined by the velocity gradient of the points; the points that had faster velocities appeared closer on the corrugated surface, while points with slower velocities appeared farther away. Participants indicated when they detected the corrugated 3-D surface. Stimuli were varied by dot density. The older participants did not detect the 3-D surface as reliably as younger adults, indicating that aging reduces sensitivity to MP-defined 3-D stimuli.

Two studies have explored the way that aging affects the perception of depth magnitude from MP. Norman and colleagues (2004) presented younger and older adults with random-dot sinusoid waves, the relative motion of which was yoked to head movement. After translating their heads to perceive the MP stimulus, participants indicated the amount of perceived depth in the stimulus by adjusting the length of a response bar to be equal to the magnitude of depth. The actual depths presented in the sinusoid stimulus were 2, 4, or 6 cm. The perceived depth magnitude was overestimated for each condition, for both younger and older adults: in this study, there were no age differences. Younger and older adults perceived the same amount of depth from MP.

In another study, MP was simulated by random dots that defined a frontoparallel plane slanting away in depth at 20, 35, 50, or 65 degrees (Norman et al., 2009). All the dots on the stimulus moved at 15 cm/sec (12 deg/sec), but the slant of the stimulus created a velocity gradient, so the stimulus was actually defined by relative motion: faster dots appeared nearer and slower dots appeared farther in depth. Participants indicated the degree of slant by adjusting the angle of a palm board. The same pattern emerged for both groups of participants: slant was overestimated at the smaller angles and underestimated at the largest angle. Once again, younger and older adults perceived the same amount of slant from the MP-defined stimulus.

There are several possible reasons why no age differences were found in either of these studies (Norman et al., 2004; Norman et al., 2009). One possibility, of course, is that there are simply no effects of age on depth perception from motion parallax. Although older adults show deficits in the two components of depth perception from MP (i.e., motion processing and pursuit), it could be that these deficits are compensated for by the visual system when generating a depth percept, or perhaps that the deficits are too small to have an effect on depth from MP. Another possibility is that the magnitudes of stimulus depth presented to observers by Norman and colleagues were suprathreshold, and that there are no effects of age on suprathreshold MP magnitude estimates; however, it is important to note that a lack of suprathreshold age effects would not preclude an effect of age on threshold MP depth perception. To illustrate this concept, consider an observer with a deficit in motion processing. This observer might be able to perform a suprathreshold task, such as discriminating 5 deg/sec from 2 deg/sec motion, but show a deficit in motion detection at 1 deg/sec. Similarly, an observer might have no difficulty distinguishing two MP stimuli with different depth magnitudes, as long as the magnitudes of both stimuli are above threshold. If older observers have higher MP depth thresholds than younger adults, we might say that age affects absolute *sensitivity* to depth from MP.

The Current Study

In the current study, I sought to characterize depth from MP in younger and older adults across a range of stimulus conditions by measuring depth thresholds at slow, medium, and fast pursuit velocities, as well as measure motion thresholds and pursuit accuracy. I quantified depth thresholds using the simple M/PR ($d\theta/d\alpha$). I also examined how changes (or lack thereof) in older adults' depth thresholds might be explained using the M/PR model, by asking if age changes in motion ($d\theta$) and pursuit ($d\alpha$) could explain older adults' performance in our depth threshold task.

Method

Observers

Thirty-two younger (*M* = 25.3 years, *SD* = 3.8) and 32 older adults (*M* = 66.3 years, *SD* = 4.7) participated in the experiment. In the older age group, 26 observers were female and six were male. In the younger age group, 17 observers were female and 15 were male. The younger observers were student volunteers from North Dakota State University, who were either paid or given course credit for their participation. Older observers were recruited from the surrounding community, and were paid for their participation. All observers gave informed consent to participate.

Prior to beginning the study, observers underwent screening for a variety of exclusionary criteria. Visual acuity was assessed using a Snellen visual acuity chart (Graham-Field, Atlanta, GA). Contrast sensitivity was assessed using a Pelli-Robson Contrast Acuity chart (Haag-Streit, Essex, UK). Observers' neurological health status was assessed using a revised form of Christensen, Armson, Moye, and Kern's (1992) health questionnaire (Appendix A). Observers who scored a 20/40 or worse on the (best corrected) acuity test or scored 1.65 or worse on contrast sensitivity test, or indicated any neurological problems on the questionnaire, were not included in the study. During the study, observers adjusted their corrective lenses for viewing distance if necessary. The procedures were overseen by North Dakota State University's Institutional Review Board.

Apparatus

For depth and motion tasks, stimuli were generated using MATLAB PsychToolbox (Brainard, 1997; Kleiner, 2007; Pelli, 1997) and presented on an Apple 5K iMac computer with a 27" retina display and a resolution of 5120 x 2880 pixels x 60 Hz. At 200 cm viewing distance, the monitor subtended 15.4 degrees of visual angle and each pixel subtended 10.8 arcsec. For eye tracking, stimuli were generated on a Macintosh computer and presented on a 20" flat screen NEC CRT monitor with a resolution of 1600 x 1200 pixels x 85 Hz. At 57 cm viewing distance, the monitor subtended 34.8 degrees of visual angle and each pixel subtended 90 arcsec. An ASL Eye-trac 6000 (Applied Science Laboratory, Bedford, MA) with D6 remote optics and a sampling rate of 120 Hz was used to measure eye position. The eye tracking system has a precision of 0.25 deg and accuracy of 0.5 deg. The system communicated eye position information to the stimulus computer through a 16-bit analog connection with a National Instruments multifunction I/O board.

The experiment was conducted in a dimly-lit (~ 1 lux) room. During all three tasks, observer movement was restricted by a chinrest and an eye patch occluded the observers' left eyes for monocular viewing.

Stimuli

These stimuli and methods were modeled after Holmin and Nawrot (2015). Depth stimuli were composed of 6,400 43 x 43 arcsec black dots positioned randomly on a white background, contained within a 6.3 x 6.3 deg stimulus window. A small black square (6 arc min) in the center of the stimulus window served as a fixation point. In separate conditions, the stimulus window translated leftward or rightward at one of three velocities (2.3, 10.1, and 25 deg/sec) to generate pursuit eye movements (dα) as the observer maintained fixation on the center point of the translating stimulus. Stimulus window translations began with a positional offset opposite the direction of translation so that the fixation point at the center of the stimulus window would traverse the vertical midline midway through the window's translation. To generate smooth stimulus window translation, an updated window position was calculated and redrawn every 16.7 ms.

Stimulus parallax was achieved through relative motion of the dots, translating in opposite directions, within two different regions of the stimulus window during translation of the entire stimulus window (see Figure 5). Dots within the bounds of one region of the stimulus moved in the same direction as the stimulus window, thereby generating dθ in the same direction as dα. This region should appear nearer than the fixation point. Dots within the bounds of the other region moved in the direction opposite the direction of stimulus window movement, and should appear farther than the fixation point. The two regions corresponded to the upper and lower halves of the stimulus window, and the direction of dot movement within the two regions varied randomly between trials. The speed of dot movement relative to the window movement (0.013-0.92 deg/sec) was the same for both directions of dot motion, and was determined for each trial using a staircase procedure (see below); retinal image motion was created by translating stimulus dots laterally every 100 ms. That is, the stimulus window was translated every 16.7 ms, and the dots within the stimulus were translated seven times throughout the 800 ms stimulus presentation; the dots within the depth stimulus appeared to move smoothly. The overall perception of the motion parallax stimulus was approximately that of a square-wave grating.

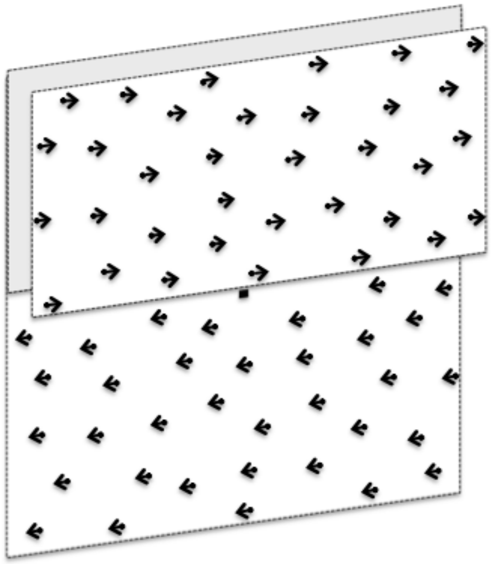

Figure 5. Schematic of the stimulus used in the depth threshold task. In this example, background motion is leftward. A rectangle, positioned flush with the horizontal meridian, contains dot motion in the rightward direction. This rectangle appears to be nearer in depth to the observer. Note that in the stimulus, there is no shadow visible behind the rectangle in depth; the shadow in the schematic is meant to represent the fact that this rectangle is nearer in depth compared to the background.

Our motion threshold stimulus and method were modeled after Snowden's (1992) experiment measuring minimum displacements (d_{min}), or the smallest magnitude of displacement observers could reliably detect. The stimulus was identical to the depth threshold stimulus, except that the stimulus window did not translate and remained stationary at the center of the display. Similar to the depth threshold stimulus, the dots in the region above fixation moved to the left or right, and the dots in the region below fixation moved in the direction opposite that of the dots in the upper half of the stimulus. The dots moved once during the stimulus presentation, at 100 ms, as in the depth task; the minimum magnitude of displacement that could be presented on a given trial was 10.8 arcsec. It is important to note that although the motion threshold and depth stimuli were as similar as possible, except for the presence of pursuit and stimulus duration, in no case did observers report a depth percept in viewing the motion stimulus. The motion stimulus contained only shearing motion, with the dots in the lower and upper regions of the stimulus moving at the same speed; this lack of a relative velocity gradient coupled with the absence of a pursuit signal diminished any cues to depth.

In the pursuit condition, the pursuit target was a single white dot presented on a black background. At 57 cm viewing distance the target subtended 0.23 x 0.23 deg. The target was translated leftward or rightward every 11.76 ms (85 Hz) at one of three velocities (2.1, 10.6, and 25.5 deg/sec).

Procedure

Depth thresholds. A trial began when the fixation spot was presented in the center of the screen. Following a button press by the experimenter to initiate a trial, the fixation spot jumped to the left or to the right to indicate the starting position of the stimulus translation. The magnitude of the fixation point jump was calculated from the pending stimulus velocity such that the stimulus, when it appeared, would cross the vertical midline halfway through its translation. Following a variable interval from 0.5-3.5 sec, the stimulus window appeared and began to move. Observers maintained fixation in the center of the translating stimulus window throughout the 800 ms duration trial. Note that observers remained stationary, and MP was generated with stimulus dot movement tied to stimulus window translation, rather than stimulus dot movement yoked to observer head movement. The same pursuit mechanisms are operating under both head-stationary and head-translating conditions; however, by keeping the head stationary, the translational VOR eye movements that are generated during head translation are eliminated, removing this confounding variable (Nawrot & Joyce, 2006; Nawrot, Ratzlaff, Leonard, &

Stroyan, 2014). The direction of movement (left or right) was randomly determined on each trial. The order of condition presentation was determined using a Latin Square.

Observers performed a depth-phase judgment task in which they were asked to indicate verbally the location of the half-cycle of stimulus depth (above or below fixation; see Figure 1) that was closer in depth, relative to the other half-cycle. The observers' responses were recorded on the computer by the experimenter. No feedback was given. The threshold M/PR ($d\theta/d\alpha$) for unambiguous depth perception was found for each direction of stimulus translation (leftward and rightward) at each of the stimulus speed conditions using a staircase procedure with a three-down, one-up decision rule (Wetherill and Levitt, 1965). The initial dot motion ($d\theta$) was set to 0.24 deg/sec, and each step in the staircase increased or decreased dot motion by 0.026 deg/sec. Each staircase ended either when the observer had had six reversals, which would track to the 79% threshold, or when the ceiling (0.92 deg/sec) had been reached. For the block to end at ceiling, the participant had to reach the ceiling, and have no reversals for the following five trials. If a block ended at ceiling, and the observer had made fewer than six reversals, the data from that block were not included in the data analysis. Observers completed two blocks of trials for each pursuit direction, for each pursuit speed. Each block typically contained 20-40 trials. At the slow and moderate pursuit speeds, all observers were able to generate six reversals in at least one of the two blocks for each pursuit direction. Two older observers were not able to perform the task at 25.0 deg/sec, and were not included in the data analysis.

Motion thresholds. To begin each trial a fixation spot was presented in the middle of the screen. Following a button press by the experimenter to initiate a trial, the stimulus window was presented, centered on the fixation spot. Observers were to maintain fixation throughout the duration of the stimulus presentation (200 ms). The observers reported which direction (left or right) the dots in the *top* region (i.e., the region of the stimulus above the fixation point) were moving. The experimenter recorded observer responses on the computer. No feedback was given. As in the depth threshold task, a three-down, one-up procedure (Wetherill & Levitt, 1965) was used to determine d_{min}, or the minimum amount of displacement observers needed to reliably discriminate motion direction. Staircases started with a dot displacement of 97.2 arcsec, moved in steps of 10.8 arcsec, and ended with nine reversals. Observers completed two blocks of trials in the motion threshold task.

Pursuit gains. The eye tracker was calibrated for each observer using a 9-point calibration of the ASL system, followed by a 2-point calibration of the experimental computer's recording of the eye position signal, and a final 5-point calibration along the horizontal axis of the pursuit target's movement. On each trial, the target was presented in the middle of the screen, and a button press by the experimenter initiated target movement. The experimenter did not initiate a trial until the observer was fixating on the centered target. Once the trial was initiated, the target "stepped" either to the left or to the right (Rashbass, 1961), before translating in the direction opposite that of the step. The magnitude of the step varied depending on the pending stimulus velocity, such that for each trial the target would pass through the vertical midline of the screen 100 ms after onset of translation. The target was erased from the display at 870 ms, and eye position was recorded for an additional 306 ms, giving a trial duration of 1176 ms. The observer's task was to maintain fixation on the target as it translated. The target translated twice leftward and twice rightward at one of three different speeds (2.1, 10.6, and 25.5 deg/sec), for a total of 12 trials per block. The order of pursuit speed presentation was randomly determined at the beginning of each block for each observer. Observers completed three blocks of trials, for a total of 36 trials per observer.

Results

Analyses were conducted in Microsoft Excel, MATLAB 2014B (The MathWorks, Natick, MA), and SPSS 21 (SPSS II, New York, NY). Depth thresholds were quantified using the M/PR ($d\theta/d\alpha$; Nawrot & Stroyan, 2009). For each of the two blocks, in each of the three conditions, the threshold $d\theta$ (measured in deg/sec) for each direction of stimulus translation (left and right) was determined from the last four reversals. For each observer, threshold $d\theta$ for each stimulus direction was averaged across the two blocks to give two mean threshold $d\theta$s (one for each stimulus direction). A 3 (pursuit speed ($d\alpha$): 2.3, 10.1, and 25.0 deg/sec) x 2 (age group: young and old) x 2 (stimulus translation direction: left and right) ANOVA revealed that there was no significant main effect of direction of stimulus movement, and no interaction with any other variables, in the depth task (all Fs < 1). Directional differences were therefore dropped from all further analyses. Results from the depth task are shown in Figures 6 and 7. In Figure 6, threshold $d\theta$s found in the depth task are plotted for older and younger observers. Threshold $d\theta$s were converted to depth measures using the M/PR: in each condition, the ratio of threshold $d\theta$s to pursuit speed ($d\alpha$) that defined that particular condition was calculated (Figure 7). These M/PR values can be converted to expected relative depth magnitudes (d_{MP}) using Equation 1 and an expected viewing distance. Similar to binocular disparity, a particular M/PR corresponds to different physical depth magnitudes depending upon viewing distance. For example, a threshold M/PR of 0.1 would correspond to a $d_{\mathrm{MP}} = 20$ cm at a viewing distance of 200 cm, but a $d_{\mathrm{MP}} = 5$ cm at a distance of 50 cm.

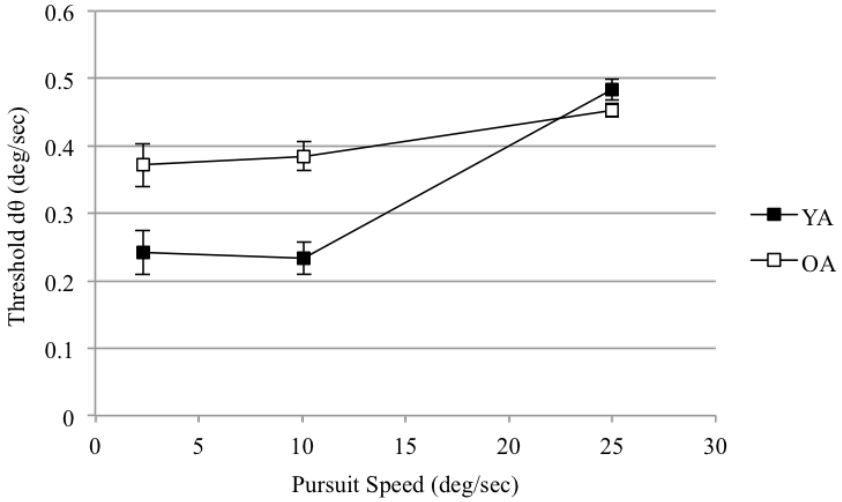

Figure 6. Threshold dθs for younger and older observers. The minimum within-stimulus motion (dθ) in deg/sec that observers required to perceive depth is plotted against pursuit speed condition (2.3, 10.1, and 25.0 deg/sec) on the x-axis. Black squares represent younger adults (YA), and white squares represent older adults (OA).

A 2 x 3 mixed factorial ANOVA was conducted on depth thresholds, with age group (young and old) as the between-subjects factor, and pursuit speed (2.3, 10.1, and 25.5 deg/sec) as the within-subjects factor. Older adults had significantly higher thresholds than younger adults overall ($F(1, 59) = 10.58$, $p < 0.01$, $\eta^2 = 0.03$; all η^2 are complete η^2). There was also a significant main effect of speed: as pursuit speed increased, depth thresholds decreased ($F(1.04, 61.42) = 121.63$, $p < 0.01$, $\eta^2 = 0.66$). There was also an interaction between age and speed ($F(1.04, 61.42) = 7.21$, $p < 0.01$, $\eta^2 = 0.04$). At the slowest speed, older adults had significantly higher thresholds than younger adults ($t(62) = 3.04$, $p < 0.01$). Older adults also had higher thresholds than younger adults at 10.1 deg/sec ($t(61) = 4.54$, $p < 0.01$). There was no difference in thresholds between younger and older adults at the fastest speed ($t(60) = -1.58$, $p = 0.12$).

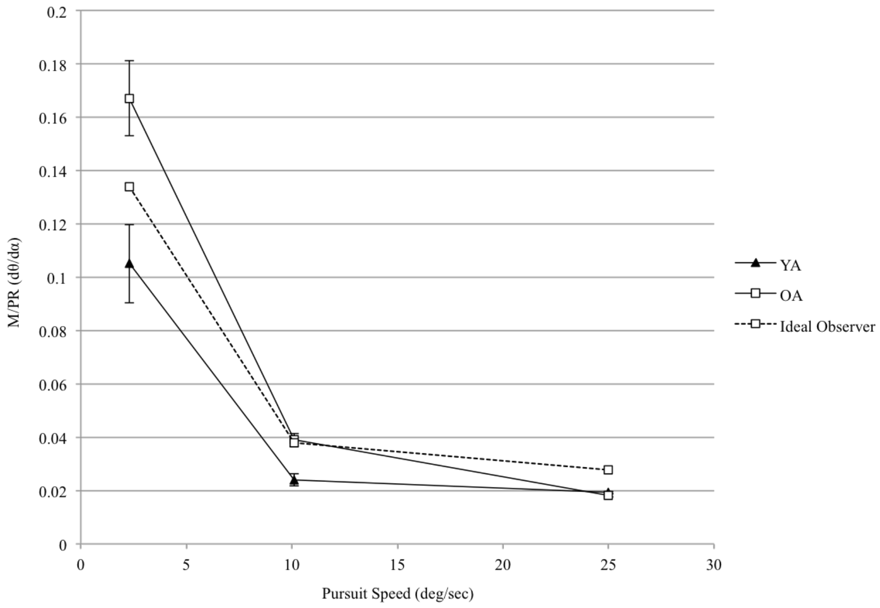

Figure 7. Depth thresholds (dθ/dα) for younger and older observers. Depth thresholds are plotted against pursuit speed (dα: 2.3, 10.1, and 25 deg/sec) on the x-axis. The data plotted on solid lines represent obtained thresholds for younger (YA) and older adults (OA). The data plotted on the dashed line represent the depth threshold values predicted for older adults (see text).

Motion thresholds (or d_{min}) were found for each observer using the last six reversals in each of the two blocks, and then averaging across the blocks. Older adults' motion thresholds were more than six times higher than younger adults' motion thresholds ($t(59) = 8.72$, $p < 0.01$), as seen in Figure 8. In a simple ideal observer analysis, it is possible to use these older observers' motion threshold values ($M = 144.70$ arcsec, $SE = 13.41$), found during a 1 step/200 ms stimulus duration, to extrapolate the minimum dθ that older adults would need during a 7 step/800 ms stimulus duration (as in the depth threshold task). This extrapolated dθ value is 0.35 deg/sec, and represents the "best" dθ we might expect older observers to achieve during the depth threshold task, in order to reliably report depth-sign. We can also estimate the magnitude of the pursuit signal (dα) generated by each observer in response to the stimulus translation in the depth task. Actual dα was estimated for each observer by multiplying the obtained gains in each pursuit task condition (i.e., gains for 2.1, 10.6, and 25.5 deg/sec) by the stimulus speed in each depth task condition, for each observer. This extrapolated dθ value and actual dα can be used to generate an ideal observer model for older adults—that is, the results we would expect if observers were performing using all of the information available in the motion and pursuit signals, and combining these two signals optimally. Ideal M/PRs are plotted on the dashed lines in Figure 7.

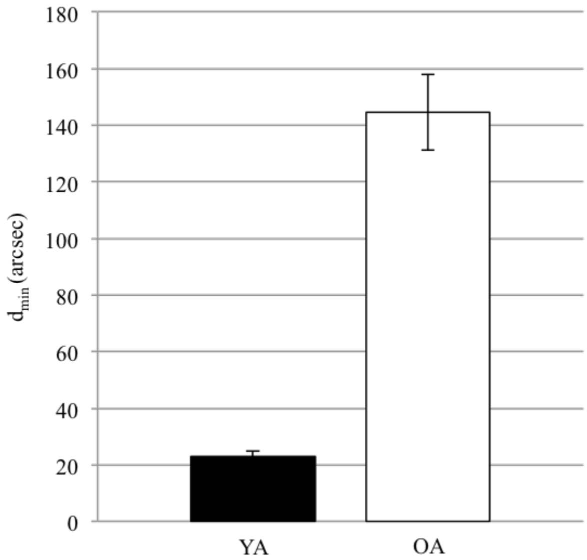

Figure 8. Motion thresholds (d_{min}) for younger and older observers. Thresholds are plotted as magnitudes of displacement, in arcsecs. YA = younger adults; OA = older adults.

For eye tracking analysis, eye velocity was derived from eye position using a two-point central difference algorithm. Data were then low-pass filtered at 40 hz using a 3-term moving average filter. Saccades were identified as velocities greater than 40 deg/sec (Burke & Barnes, 2006) and those sections were removed from further analysis. The first 223 ms and the last 306 ms were discarded, to exclude open-loop pursuit and pursuit after the target had disappeared from the screen. Gains were then analyzed by averaging velocity over the remaining data points (647 ms) and computing the average eye velocity/target velocity. A 2 x 2 x 3 mixed factorial ANOVA, with age group (young and old) as a between-subjects factor, pursuit direction (left and right) as a within-subjects factor, and pursuit speed (2.1, 10.6, and 25.5 deg/sec) as a within-subjects factor, revealed a significant interaction between pursuit speed and age ($F(1.31, 83.13) = 24.45$, $p < 0.01$, $\eta^2 = 0.09$) in the pursuit task. At a pursuit speed of 2.1 deg/sec, older adults had higher gains than younger adults; at 10.6 and 25.5 deg/sec, older adults had lower gains than younger adults (Figure 9). There was no effect of pursuit direction or, and pursuit direction did not interact with any other variables (all *F*'s < 1).

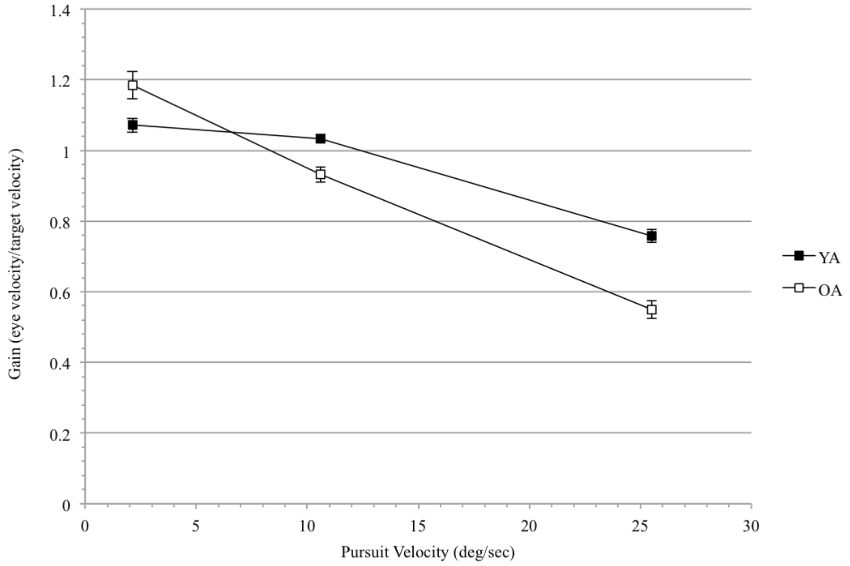

Figure 9. Pursuit gains for younger and older observers. Gains (eye velocity/target velocity) are plotted against the target speed (2.1, 10.6, and 25.5 deg/sec) on the x-axis. Black squares represent younger adults (YA), and white squares represent older adults (OA). Note that a gain of 1.0 represents perfect performance (i.e., eye velocity = target velocity).

While the ideal observer model (Figure 7) predicts observers' results if they are combining the two independent sources of information (motion and pursuit) optimally as described by the M/PR, a regression analysis provides another way to assess how changes in motion, pursuit, and the mechanism that combines them are affected by normal aging. To investigate the effects of age changes in dθ and dα on thresholds, difference scores for each older observer were generated for each of the three tasks. Difference scores were calculated by subtracting the mean of the younger adults' scores from each individual older adult's score. For example, in the depth task, for each older adult, the younger adults' mean M/PR in the 2.3

deg/sec condition was subtracted from that older adult's M/PR, giving a difference score for each older adult in that condition. The process was repeated for each of the other two conditions in the depth task (10.1 and 25 deg/sec), for the actual dα values estimated for each observer (as detailed above), and for the motion task. The absolute values of the difference scores were found, and these values underwent a natural log transformation, generating $\log\Delta_{mpr}$, $\log\Delta_{d\theta}$, and $\log\Delta_{d\alpha}$ scores for each older observer (the relationship of dθ, dα, and depth thresholds is not linear in the M/PR model; transforming these difference scores enabled us to treat this relationship as linear and perform a regression analysis; Nawrot et al., 2014). A regression analysis was used to assess how well age related changes in motion perception ($\log\Delta_{d\theta}$) and pursuit ($\log\Delta_{d\alpha}$) accounted for changes in depth perception from MP ($\log\Delta_{mpr}$). The full model was significant ($R^2 = 0.22$; $F(2, 86) = 11.52$, $p < 0.00$):

$$\log\Delta_{mpr} = -3.87 + \log\Delta_{d\theta}(0.10) + \log\Delta_{d\alpha}(-0.23) \tag{2}$$

Change in pursuit ($\log\Delta_{d\alpha}$) was a significant independent predictor of change in depth perception ($\log\Delta_{mpr}$) ($p < 0.01$), but change in motion perception ($\log\Delta_{d\theta}$) was not ($p > 0.05$). A comparison of the age related changes in pursuit (Figure 9) and depth thresholds (Figure 7) illustrate that both varied together with pursuit speed ($r = -0.45$, $p < 0.01$) thereby resulting in the predictive power of $\log\Delta_{d\alpha}$. In contrast, while there was a large age-related change in motion perception (Figure 8), there was no correlation with change in depth perception ($r = 0.006$) meaning that some older adults who had larger changes in motion thresholds had smaller changes in depth thresholds, and vice-versa. This finding is not unprecedented—Andersen and Atchley (1995) similarly found that older adults' performance on a 2-dimensional motion task was not related to their performance on a 3-dimensional motion task.

Discussion

Older adults had higher depth thresholds than younger adults in the slow (2.3 deg/sec) and moderate (10.1 deg/sec) MP pursuit speed conditions. When the stimulus was moving at a fast speed (25.0 deg/sec), older and younger adults had similar depth thresholds. Age had an effect on pursuit and motion processing, as expected. At the three speeds tested in the pursuit task (2.1, 10.6, and 25.5 deg/sec), older adults had less accurate pursuit than younger adults. Older adults also had higher motion thresholds than younger adults, by a factor of six.

It is interesting to note that, despite age changes in $d\theta$ and $d\alpha$, the older observers' obtained thresholds were very similar to the depth thresholds generated by the ideal observer model (see dashed line, Figure 7). Indeed, although their motion thresholds were higher than younger adults', and their pursuit eye movements were considerably less accurate, older adults were apparently using the available motion and pursuit signals in an optimal way. The threshold $d\theta$s obtained in the slow and moderate conditions of the depth task (and used along with pursuit speed to find the M/PR) were 0.37 and 0.39 deg/sec, respectively (see Figure 6). These obtained threshold $d\theta$s are very similar to the optimal motion threshold, 0.35 deg/sec, which was extrapolated from d_{min} and added as a constraint to the ideal observer model. Older observers' threshold $d\theta$s were higher in the fast depth condition than in the slow and moderate depth conditions (Figure 6), perhaps because older adults' eye velocities were too slow to be able to accurately track the stimulus when it moved at 25.0 deg/sec. Gain at 25.5 deg/sec was 0.55 for older adults, meaning that older adults' average eye velocity was only 55% of the target velocity. It is not surprising that older adults could not optimally use motion signals at the fast stimulus velocity; they could not move their eyes quickly enough to "keep up" with the stimulus, making motion processing in this stimulus condition difficult (Stone & Krauzlis, 2003). However, although older observers needed stronger motion signals for depth perception at 25.0 deg/sec, they still had relatively low depth thresholds at this speed.

The similarity in depth thresholds between younger and older adults at 25.0 deg/sec is due to the fact that younger adults' depth thresholds did not continue to decrease with increasing stimulus velocity, as older observers' did (Figure 7). At 25.0 deg/sec, older and younger adults had similar threshold dθs, although the increase in threshold dθ from 10.1 to 25.0 deg/sec is markedly larger in younger adults than it is in older adults (Figure 6). If younger adults' threshold dθs had stayed stable when MP pursuit velocities increased from 10.1 to 25.0 deg/sec, younger adults would have lower M/PRs at 25.0 deg/sec than older adults. This increase in threshold dθ in younger adults is not entirely unexpected, however; recent research has shown that younger adults require higher dθs for depth perception at fast velocities compared to moderate velocities (Holmin & Nawrot, 2015), and that younger observers' depth thresholds are stable at moderate and fast pursuit velocities.

At all velocities tested, older adults had less accurate pursuit eye movements than younger adults (Figure 9). An inaccurate dα signal will contribute to higher thresholds, as may be seen in the difference between age groups at 2.3 and 10.1 deg/sec. The similarity between younger and older adults' thresholds at 25.0 deg/sec is likely due, not to an increase in pursuit accuracy in older observers, but rather to the non-optimal use of motion signals in younger adults, as described in the paragraph above.

Recall that and Norman and colleagues (2004; 2009) found no effect of age on MP depth magnitude judgments, whereas the current study finds an effect of age on MP depth thresholds. This seeming difference is not unusual as these studies measured different aspects of the same perceptual process: the current study determined factors affecting the minimum detectable depth (thresholds) whereas Norman and colleagues studied the perceptual magnitude of suprathreshold stimuli. That is, it would be unusual to study perceived depth magnitudes for stimuli that older observers could not even detect. Unfortunately, a quantitative comparison of the parameters in these studies is difficult due to: the unknown stimulus velocities of Norman and colleagues; the differences between head-moving and head-stationary viewing conditions (Nawrot et al., 2014); and the effect of viewing distance changes on perceived depth (Nawrot et al., 2014).

EXPERIMENT TWO

In Experiment One, I found that older adults have higher thresholds for perceiving depth from motion parallax. Older adults optimally combine the motion and pursuit signals ($d\theta$ and $d\alpha$) available to them, and perform as predicted by an ideal observer model. However, despite their optimal combination of available signals, older adults still have significant deficits in detecting depth at slow and moderate speeds. Although older adults have higher thresholds for perceiving motion, motion perception performance was not a predictor of depth thresholds; rather, increases in depth thresholds (or lessened *sensitivity*) is driven more by inaccuracies in older adults' pursuit eye movements. These findings are a novel and important addition to our understanding of how aging affects visuospatial processes.

Given the serious real-world consequences of visuospatial deficits (Conlon & Herkes, 2008; Lopez et al., 2011), understanding the manifestations and mechanisms of visuospatial deficits in older adults is only the first (albeit important) step in trying to alleviate these deficits. Perceptual learning (PL) provides one avenue by which we may ameliorate the effects of age on visuospatial processes. PL is a long-lasting improvement in the perception of a stimulus that is a result of practice or training with that stimulus. The effects of PL in younger adults have been well documented (for reviews see Sasaki, Náñez Sr., & Watanabe, 2010; 2012). Following training, younger adults show improvement in performance in many different types of tasks, including texture discrimination (Karni & Sagi, 1991), orientation discrimination (Jeter, Dosher, Petrov, & Lu, 2009), useful field of view (UFOV) (Sekuler & Ball, 1986), contour integration (McKendrick & Battista, 2013), and motion detection (Huang, Lu, Tjan, Zhou, & Liu, 2007) and discrimination (Ball & Sekuler, 1986). The improved perceptual performance found in these tasks is often specific for stimulus features, retinal locations, trained eye, etc. For example, improvement following motion direction discrimination training for one direction (i.e., the trained direction) does not transfer to an untrained motion stimulus that is rotated away from the trained stimulus by 45 deg (Ball & Sekuler, 1986). The mechanisms underlying PL are still under debate, though recently progress has been made in proposing a unifying theory that accounts for PL in younger adults under most training conditions (Watanabe & Sasaki, 2015).

Eye movement training provides another avenue by which certain characteristics (e.g., accuracy, acceleration, prediction) of voluntary eye movements may be improved through learning (Kahlon & Lisberger, 1996). Eye movement training does not qualify as PL—rather, it is considered motor, rather than perceptual, learning (Madelain, Paeye, & Darcheville, 2011). Studies of eye movement training are scarce, but the available evidence seems to suggest that the generation and maintenance of voluntary eye movements (including smooth pursuit) are amenable to training, at least in younger adults and non-human primates.

Given the evidence that (in younger adults) PL results in perceptual improvement, and that eye movement training can improve characteristics of smooth pursuit, it is a logical next step that similar principles be applied to research with older adults. If learning, both perceptual and motor, can be induced in older adults, then researchers can focus on improving visuospatial deficits in older adults in a way that may benefit their daily lives. In Experiment Two, older adults took part in two training tasks, one perceptual and one motor, with the goal of improving the perception of depth from motion parallax. Before describing the methods and results of Experiment Two, I will review the evidence of the effects of perceptual learning on older adults and the neural mechanisms underlying these effects, as well as the research on eye movement training.

Aging and Perceptual Learning

Interpretations of the effects of PL are predicated on the idea of cortical plasticity. Until relatively recently, general consensus held that the adult sensory cortices were fixed, or non-plastic (Lowel & Singer, 2002). This assumption was called into question by seminal work concerning the somatosensory cortex of monkeys (Merzenich et al., 1984) that showed that young adult sensory cortex is plastic and malleable through experience. It is not necessarily the case, however, that older adults show the same amount of plasticity as younger adults, or that the manifestations of plasticity be the same in younger and older adults. Older brains undergo considerable atrophy of gray and white matter (Raz et al., 2005; Raz & Rodrigue, 2006; Reuter-Lorenz & Lustig, 2005), which could perhaps influence the plasticity of older brains, making them less amenable to perceptual learning. Despite these concerns, there is considerable evidence that older adults show improvement in performance following PL, though the mechanisms of PL in younger and older adults may not be the same.

Behavioral Evidence for Perceptual Learning in Older Adults

One of the most common vision complaints in older adults is that of acuity loss (Gittings & Fozard, 1986). Presbyopia, the loss of accommodative power of the lens, is ubiquitous in older adults, and results in decreases of near acuity (Schieber, 2006). Although PL cannot improve the function of the eye, there is evidence that near acuity can be improved in older adults as a result of contrast sensitivity training (DeLoss, Watanabe, & Andersen, 2015; Polat et al., 2012). Polat et al. (2012) varied the target duration, inter-stimulus interval (ISI), and masking and crowding in a forced-choice task in which observers were required to indicate which of two intervals contained the target, a Gabor patch that varied in spatial frequency. Compared to baseline, the observers' near acuity and reading performance improved following training, indicating an effect of contrast training. Similarly, contrast discrimination training on Gabor patches in varying amounts of added noise improves near acuity in older adults (DeLoss et al., 2015). It is important to note again that though optical factors are a major contribution to age-related acuity loss, PL does not improve optical functioning; rather, it is thought that PL improves the “quality” of the neural signals that reach the brain by reducing blur (through contrast sensitivity training) (Polat et al., 2012).

Other low-level visual processes also seem to be improved through PL. Orientation discrimination thresholds decrease following training (DeLoss, Watanabe, & Andersen, 2014). DeLoss and colleagues trained older adults in different tasks: two “easy” tasks, in which observers made orientation discriminations for orientations that differed by 15 deg, and two “difficult” tasks, in which the offset of the two orientations were decreased by 5% each day of training. In both the easy and hard tasks, one task had added noise and one did not, resulting in four different conditions. Orientation thresholds across five different noise levels were assessed post-training. In the easy/noise condition and the two difficult conditions, the observers had lower orientation thresholds at the higher noise levels.

Older adults also show improvement in texture discrimination tasks (TDT), in which participants perform a task at central fixation while identifying the orientation of patterns presented in the periphery. Stimulus-to-mask stimulus onset asynchrony (SOA) is a common measurement in TDT tasks, and indicates the time between stimulus onset and onset of a mask. Following TDT training with near-threshold SOAs, older adults had lower threshold SOAs compared to baseline (Andersen, Ni, Bower, & Watanabe, 2010).

It is not only low-level visual processes that can be improved through PL. Form processing occurs higher up in the visual system than orientation, contrast, and TDT processing.

In Chapter One, I reviewed the deficits older adults have in form processing, which are associated with functional changes in area V2 and the ventral stream. Form processing can be studied at the local or global level—it requires integration of the individual contours/elements that make up the form (i.e., spatial integration), and detecting or discriminating a global percept. Several studies have shown that both integration and global form perception can be improved in older adults using PL. Global form discrimination (e.g., discriminating between a circle and ellipse) improves as a result of training, as does spatial integration (Kuai & Kourtzi, 2013; Mayhew & Kourtzi, 2013; McKendrick & Battista, 2013), though the learning gains for spatial integration are not as large as those for global form.

Other higher-level visual processes may be assessed and trained using the UFOV task (Sekuler & Ball, 1986). UFOV is defined as the area in visual field in which observers can acquire information without making a saccade (Ball, Beard, Roenker, Miller, & Griggs, 1988, p. 2210). The UFOV task measures processing speed, divided attention, and visual crowding (Ball et al., 1998). In a typical UFOV task, observers are required to localize a stimulus that is presented at a variable degree of eccentricity, in a variable position in the visual field. Distractors may also be present, and observers may be required to complete a concurrent task that requires attention at the central fixation point. Generally, older adults have smaller UFOVs—that is, the area of central vision in which observers may acquire information is smaller in older than in younger adults (Ball et al., 1998). Performance on the UFOV task is correlated with driving competency (Ball & Owsley, 1991; Ball, Owsley, Sloane, Roenker, & Bruni, 1993; Ball et al., 1998; Goode et al., 1998; Owsley, Ball, Sloane, Roenker, & Bruni, 1991) and mobility issues such as gait and balance, as well as performance of some instrumental activities of daily living (Ball, Edwards, & Ross, 2007). Expanding the UFOV, then, can have a meaningful impact on older adults' daily lives, and several researchers have employed training tasks aimed at improving UFOV task performance.

Sekuler and Ball (1986) asked observers to localize a face that was presented 5, 10, or 15 deg in the periphery at one of 24 locations. In the distractor conditions, 47 outlines boxes were added to the display. In the central task conditions, observers were required not only to localize the target, but also to identify the expression on a face presented at the center of the display. At baseline, older adults and younger adults had similar error rates for all eccentricities, in the absence of distractors and the central task. However, adding the distractors and the central task had a deleterious effect on older adults, compared to younger adults: adding a central task had the least effect on performance, while adding both distractors and a central task had the most effect on performance. To improve UFOVs, older adults were trained in all conditions over the course of four days. Observers improved (i.e., made fewer errors) at all eccentricities in all conditions, with the most improvement found in the conditions that had been more difficult pre-training. Several other researchers have investigated training techniques to expand the UFOV in older adults, with similar results (Ball et al., 1988; Richards, Bennett, & Sekuler, 2006). Ball and colleagues (2007) investigated the impact of UFOV training in 2,000+ older adults across six studies, and found that training significantly reduced the time observers needed to process information presented at varying levels of display complexity. Improvements in UFOV were correlated with speed of processing and psychomotor speed, as measured by several well-known visuocognitive tasks.

Perceptual learning in motion tasks. Three studies that I am aware of have investigated motion PL and aging, and the results of all three indicate that it is possible to improve older adults' performance for motion tasks following training. PL for motion in older adults is of particular relevance for Experiment Two, and the three studies will be reviewed in depth below.

In Chapter One, I reviewed the work of Ball and Sekuler (1986), who were among the first researchers to study the effects of age on motion processing. Interestingly, they were also among the first who sought to *improve* motion perception in older adults. Older and younger observers' baseline motion discrimination performance was first assessed: on each trial, a standard and a test stimulus were presented, each containing translational motion in one direction. On a given trial, the translating dots in the standard stimulus could move along two of the four cardinal directions (constrained to be separated by 90 degrees) or one oblique direction—each observer was randomly assigned a pair of cardinal directions and an oblique direction. The direction of motion in the test stimulus was offset from the standard stimulus by 2, 4, 6, or 8 degrees. Observers were asked to make same/different judgments, and received feedback and monetary compensation for each correct judgment. Results indicated that older adults were significantly worse than younger adults at discriminating between motion stimuli separated by 4 and 6 degrees; at 2 and 8 degrees there was a trend towards an age difference, though this difference was not significant (likely due to floor and ceiling effects, respectively).

A subset of the original young and old observers agreed to undergo additional discrimination training (Ball & Sekuler, 1986). These observers completed four sessions of 500 discrimination trials each, in which 2- and 4-degree trials were equally represented. Observers were trained with one cardinal direction as the standard direction, and did not receive feedback for their responses. Discrimination performance was measured twice, once after the first training session and once after the last training session; performance at these training sessions was compared to baseline. Although observers were trained only with 2 and 4 degrees offset and one standard direction, they were tested at all degree offsets and all three baseline directions. Both younger and older adults' discrimination performance was improved at each testing session, with the rate of improvement for younger and older adults approximately the same. Observers improved at all degrees of offset, despite only being trained at the two smallest degrees; conversely, discrimination performance did not improve for untrained directions, showing specificity in performance for trained directions only. Subsequent research has supported the lack of transfer found by Ball and Sekuler—improvements of performance in PL tasks are often specific to the trained stimulus, showing little or no transfer to untrained stimuli (Sasaki et al., 2010).

Two more recent studies have expanded on Ball and Sekuler's (1986) findings by investigating older adults' PL for motion stimuli embedded in noise (Bower & Andersen, 2012) and for high- and low-contrast stimuli (Bower, Watanabe, & Andersen, 2013). Bower and Andersen measured the effects of training on motion perception for sine wave gratings embedded in noise. Observers were to indicate the direction of motion presented in the grating; contrast was varied using an adaptive procedure to find contrast thresholds for each of six noise levels. There were six blocks of 140 trials each (one for each noise level), and six days of training, resulting in 5040 total trials over the course of the experiment. Contrast thresholds improved over the course of training for all but the lowest noise level, and thresholds improved the most at the three highest noise levels. Younger and older adults performed similarly, both on day 1 (when training had just begun) and throughout the course of training.

The fact that older and younger adults had similar contrast thresholds at all noise levels and at all training days is surprising, given that older adults have a well-known deficit in motion processing (Ball & Sekuler, 1986; Bennett et al., 2007). A possible explanation for this result is that Bower and Andersen (2012) failed to find an age difference due to the nature of the stimuli—that is, different stimuli may tap different aspects of motion perception. In their second experiment, Bower and Andersen trained observers in a paradigm similar to that of their first experiment, but used RDCs (see Chapter One) rather than sine wave gratings. There was a main effect of training, such that contrast thresholds improved from day 1 to day 6. There was also a main effect of noise level: generally, contrast thresholds increased as noise level increased (except for at the two lowest noise levels, in which thresholds were the same). In this second experiment, age did affect contrast thresholds, at all noise levels. The higher contrast thresholds for RDCs in older adults is in agreement with Ball and Sekuler (1986), who found that older adults had higher discrimination thresholds than younger adults when tested and trained with RDCs. In both of Bower and Andersen's (2012) experiments, and in Ball and Sekuler's (1986), the rate of learning was similar for older and younger adults, demonstrating that the effects of PL do not change much with age, at least in motion perception learning.

A counterintuitive finding in research on the effects of age on motion perception is that, for large stimuli (i.e., => 5 deg), older adults' motion perception performance is similar to or better than younger adults'. This effect is due to decreasing spatial suppression in older adults, which in turn is caused by age changes in center-surround antagonism of MT cells (Betts et al., 2005; see Chapter One for details and an explanation of underlying mechanisms). Bower and colleagues (2013) trained younger and older observers in a motion direction discrimination task, in an effort to increase older adults' spatial suppression. Observers' threshold stimulus durations were measured moving Gabors that subtended 0.7 or 5 deg diameter and varied over three contrast levels. At baseline, younger adults had lower thresholds than older adults for the small stimulus, at all contrast levels. Conversely, there was no age difference in thresholds for the large stimulus at any of the contrast levels. Older adults had higher thresholds at baseline for the small stimulus than the large stimulus, but only at the lowest contrast level. Following six days of training, all observer thresholds improved for all combinations of stimulus size and contrast; however, there was no change in spatial suppression in either age group. Surprisingly, older adults showed a greater overall effect of training than younger adults, perhaps because older adults had initially higher thresholds than younger adults, and therefore had more room for improvement.

Taken together, the results of these three studies (Ball & Sekuler, 1986; Bower & Andersen, 2012; Bower et al., 2013) indicate that some aspects of motion perception may be improved as a result of PL. Bower and Andersen did not find training effects for noisy sine-wave gratings, but found improvements in performance for noisy RDCs. In a similar vein, training in Bower et al.'s study did not result in lower spatial suppression, but was associated with changes in duration thresholds. In Ball and Sekuler's and Bower and Andersen's studies, the effect of training was similar in younger and older adults (i.e., both age groups learned at the same rate), whereas in Bower et al.'s study, training effects were greater in older than in younger adults. It is clear from PL studies in general, and PL motion studies in particular, that training in any one domain (e.g., motion) does not affect all aspects of that domain in the same way, and that training in younger and older adults may not recruit the same mechanisms. In the following section, I will review theories of the neural underpinnings of PL, and in particular, how the mechanisms of training in younger and older adults may differ.

Models of Perceptual Learning

One comprehensive theory of PL is the dual plasticity model (Watanabe & Sasaki, 2015). The dual plasticity model, rather than modeling the neural mechanisms of PL, provides a general theoretical framework for explaining the results of PL studies. The greatest advantage of this model is that it accounts for both task-relevant and task-irrelevant stimulus learning. In task-relevant PL paradigms, learning for an attended stimulus is measured; in task-irrelevant paradigms, researchers measure learning for stimuli that are not relevant to the task, and therefore not attended to (Watanabe et al., 2002). In the dual plasticity model, learning occurs in two stages. First, the visual system's representations of stimulus features are changed through the course of learning via feature-based plasticity (the first of the "dual" components). Feature-based plasticity can explain learning for both task-relevant and task-irrelevant stimuli. The second component is task-based plasticity, and describes changes in responses or decision criteria as a result of learning. Task-based plasticity is specific for the responses required by a particular task, and therefore can only describe task-relevant learning.

The dual plasticity model provides no explanation of the neural mechanisms of PL, but any postulated mechanism of PL can be described as occurring at the feature-based or task-based level. PL may occur through: 1) narrowed neuronal tuning curves for trained stimuli, making stimulus judgments more precise; 2) reweighting of neurons so that units tuned to the stimulus are given more weight in decision-making and "noise" units are given less weight; 3) improvements through Hebbian learning, in which the connections between sensory neurons and "correct response" neurons are strengthened; or 4), some combination of all of these mechanisms (Fine & Jacobs, 2002; Sagi & Tanne, 1994).

The Perceptual Template Model (PTM; Dosher & Lu, 1998; Lu & Dosher, 1998) proposes that learning occurs through the reweighting of neuronal channels so that stimulus-tuned neuronal units are given more weight in decision-making. The PTM models the effects of training as a product of three mechanisms: changes in tolerance to external noise, changes to additive internal noise, and changes to multiplicative internal noise. Multiplicative internal noise is directly related to the strength of the stimulus, while additive internal noise is random and not associated with stimulus strength. In the PTM, the stimulus is represented by our visual system as a template, containing both signal and noise properties. The perceptual decision is the final output. The reweighting of neuronal channels occurs between the template and the perceptual decision, making the PTM a mid-level model compatible with the task-based plasticity component of the dual plasticity model (Watanabe & Sasaki, 2015). PL-induced changes in external noise tolerance are associated with increased exclusion of noise in the template, and improvements of behavioral performance for stimuli embedded in high amounts of external noise. PL-induced changes in additive internal noise are associated with performance improvements for stimuli embedded in low external noise. Changes in additive noise are not discernable from stimulus enhancement (i.e., lowering the threshold for signal detection at the template level). PL-induced changes in multiplicative internal noise are associated with changes at all levels of external noise, as a result of decreasing internal noise between the template and output stages (Dosher & Lu, 1999). In younger adults, improvement in performance following PL is attributed to changes in external noise exclusion and decreases in additive internal noise (Dosher & Lu, 1999). Changes in additive internal noise and increased exclusion of external noise are thought to be due to the reweighting of channels selective for the signal and for the noise in the perceptual template—channels selective for the stimulus are weighted more heavily during and following training, while the weights of channels that are irrelevant for learning (such as noise channels) are reduced (Dosher & Lu, 1998).

The dual plasticity model (Watanabe & Sasaki, 2015) and the PTM (Dosher & Lu, 1998; Lu & Dosher, 1998) were constructed based on data from younger adults, and tested with younger participants. It is not immediately clear whether these models hold for older as well as younger adults. In the following subsection, I will review the research on the mechanisms of perceptual learning in older adults, identify how these mechanisms are the same as, or different from, those of younger adults, and, where appropriate, apply the PTM or dual plasticity models.

Neural substrates and mechanisms of perceptual learning in older adults. Though studies of the neural substrates of PL in older adults are scarce, evidence seems to indicate that learning in older and younger adults requires different brain areas. In TDT [texture discrimination] studies, for example, PL-associated brain changes (measured by fMRI and diffusion tensor imaging) are different in younger and older adults (Chang et al., 2015; Yotsumoto et al., 2014). The size of V3 is associated with the magnitude of improvement following PL for older, but not for younger, adults (Chang et al., 2015). This finding may reflect compensatory recruitment of brain regions in older adults—that is, it is possible that older adults may compensate for functional loss of area V1 by recruiting V3, and that this region is crucial for learning in TDT in older adults. Similarly, PL is associated with changes in white matter beneath area V3 in older adults, but not in younger adults (Yotsumoto et al., 2014). Conversely, TDT is associated with increases in BOLD signals in younger adults' V1, but not with changes in BOLD activity in older adults in any other early visual region. In a study on shape learning, Mayhew and Kourtzi (2013) found that learning in older adults was associated with activity in parietal areas, while learning in younger adults was associated with activity in areas involved in perceptual decision-making (i.e., occipital, temporal, and frontal areas). Taken together, the results of these studies seem to indicate that while older adults are capable of learning, the neural substrates of PL change with age, with different regions being recruited to compensate for age-related changes in earlier visual areas.

Although the neural *substrates* of PL appear to change with age, it is not necessarily the case that the neural *mechanisms* of PL undergo similar age-related changes. The same neural mechanisms (e.g., neuronal/channel reweighting following training; Dosher & Lu, 1998; Lu & Dosher, 1998) may be at work in both younger and older adults; however, this channel reweighting that occurs as a result of PL may be occurring in different cortical areas in younger and older adults. Noise, both internal and external, has a profound impact on older adults' perceptual performance, compared to younger adults. For example, it is well known that older adults are less tolerant than younger adults to external noise in the environment (Andersen & Atchley, 1995; Bennett et al., 2007; Gilmore et al., 1992). It is also well established that GABA-ergic systems are degraded with increasing age (Hua et al., 2006; Schmolesky et al., 2000), resulting in increased noise at the neuronal level due to loss of inhibition (though differentiating between additive and multiplicative noise is difficult). Increased internal noise can explain older adults' learning for task-irrelevant stimuli (Chang et al., 2015), and the results of Betts and colleagues (2005; 2009; 2012), who found evidence of decreased center-surround antagonism in older adults. Recall that the PTM (Dosher & Lu, 1998; Lu & Dosher, 1998) postulates that PL may occur as a result of training-related increased tolerance to external noise and decreases in additive internal noise (Dosher & Lu, 1999). These changes in tolerance to noise are thought to be due (in younger adults) to training-related changes in the weights of the neuronal channels selective for the signal (stimulus) and the noise. Some evidence suggests that similar mechanisms for learning are occurring in older as well as younger adults.

Older adults may become more tolerant of external noise following training. DeLoss and colleagues (2014) found that older adults showed higher rates of improvement in an orientation discrimination task when stimuli were embedded in high amounts of external noise, compared to when stimuli were embedded in low external noise. In another study, older adults' contrast thresholds were assessed using an orientation discrimination task, in which observers were required to indicate whether a test Gabor patch was the same or different orientation as a standard Gabor patch (DeLoss et al., 2015). The contrast of the patches was varied, along with the external noise levels. Older observers showed the most learning for stimuli that were embedded in high amounts of external noise, for both trained and untrained conditions. These results are consistent with the predictions of the PTM, which posits that reweighting of external noise channels through learning results in improvements of performance for stimuli embedded in high amounts of external noise (Dosher & Lu, 1999; Lu & Dosher).

Although the results of the studies discussed above (DeLoss et al., 2014; DeLoss et al., 2015) may be characterized within the PTM, they were not conducted to directly test the PTM, or apply the PTM to learning in older adults. Only one study has directly used the PTM to assess PL in older adults. Bower and Andersen (2012) trained older adults in a motion direction discrimination task to improve contrast sensitivity (this study is described in detail in the "Perceptual learning in motion tasks" subsection). Using the PTM, the authors modeled PL as a function of tolerance to external noise and additive and multiplicative internal noise. Following training, older and younger adults both showed increased tolerance to external noise and decreased additive internal noise. These results are consistent with previous findings in younger adults (Dosher & Lu, 1999), and seem to indicate that, at least in terms of noise reduction and channel reweighting, the mechanisms of PL in younger and older adults are similar.

To summarize, it seems that the mechanisms (i.e., channel reweighting) of PL do not change with increasing age (Bower & Andersen, 2012); however, it also seems that these mechanisms that are posited to arise as a result of PL (Dosher & Lu, 1998; Lu & Dosher, 1998) have different neural substrates in younger and older adults (Chang et al., 2015; Yotsumoto et al., 2015). For example, learning in TDT tasks may occur through channel reweighting in area V1 in younger adults, while the same process may be occurring in area V3 in older adults.

The dual plasticity model (Watanabe & Sasaki, 2015) provides a coherent theoretical framework from which to view the mechanisms of PL in older, as well as younger, adults. Recall that the first component of the dual plasticity model is feature-based plasticity. Feature-based plasticity is a change in the neural representation of trained (relevant or irrelevant) features. The neural correlates of feature-based plasticity are likely to be found at lower visual levels, in the regions in which the stimulus is processed. Like in younger adults, PL in older adults is associated with brain changes in the neural areas involved in perceptual processing of the training stimulus. For example, training with motion stimuli resulted in changes in N1, an EEG signal which is associated with early visual processing, including activity in area MT (Berry et al., 2010). We have seen that area MT is heavily implicated in the perception of motion (Newsome & Paré, 1988; Yang et al., 2008); therefore, motion PL-related changes in EEG signals that arise from MT indicate that the activity of area MT is somehow being modulated by training, in keeping with the feature-based plasticity component of the dual plasticity model.

In a similar vein, the magnitude of PL in TDT tasks is correlated with the size (Chang et al., 2015) and white matter function (Yotsumoto et al., 2014) of functionally-defined area V3 in older adults. In younger adults, learning in TDT is associated with activity in area V1 (Pourtois, Rauss, Vuilleumier, & Schwartz, 2008; Schwartz, Maquet, & Frith, 2002). Recall, however, that older adults may recruit area V3 in PL tasks in order to compensate for any possible functional loss of area V1 (Chang et al., 2015). In the case of older adults, it is in likely that TDT stimuli are being processed in area V3, and—consistent with the feature-based plasticity component of the dual plasticity model (Watanabe & Sasaki, 2015)—the neural representation of trained stimuli are being altered as a result of learning.

The task-based plasticity component of the dual plasticity model (Watanabe & Sasaki, 2015) accounts for improvements in performance in a PL task that are due to task-related learning. Mid-level PL mechanisms, such as those described by the PTM (Dosher & Lu, 1998; Lu & Dosher, 1998) can be characterized as task-based, as they describe learning as a mechanism of reweighting of channels between the input (template) and the output (perceptual decision). The PTM can be applied to PL in older adults, and therefore, learning in older adults can be explained with the second component of the dual plasticity model. The neural substrates of task-based plasticity in younger adults and older adults may differ, however; as we have seen above, during shape learning, older adults show activity in parietal regions (Mayhew & Kourtzi, 2013), which are related to task-based plasticity mechanisms, such as attention (in the case of older adults, suppression of irrelevant information), while younger adults show activity in the fronto-temporo-occipital network associated with decision making. Although the neural substrates are different, task-based plasticity is occurring in both age groups.

Eye Movement Training

Considering the recent surge of studies on perceptual learning (Watanabe & Sasaki, 2015), it is perhaps surprising that research on eye movement training, a type of motor learning, is not becoming increasingly popular as well. Studies of eye movement training are scarce, however, especially when compared to the relative wealth of research on sensory (i.e., perceptual) learning. Smooth pursuit and saccades are voluntary eye movements, under conscious control and therefore plastic and amenable to training (Madelain & Krauzlis, 2003; Madelain et al., 2011). Pursuit is by definition an operant behavior: at any given time, executing the next eye movement in a pursuit sequence is reinforced by the consequences of that eye movement (Darcheville, Madelain, Buquet, Charlier, & Miossec, 1999; Madelain et al., 2011). In other words, successful pursuit is reinforced by successful tracking of a target. Given that pursuit is an operant behavior, some characteristics of pursuit can be modulated using external reinforcement. The few studies of pursuit eye movement training that exist have focused on acceleration and deceleration (Fukushima, Tanaka, Suzuki, Fukushima, & Yoshida, 1996; Kahlon & Lisberger, 1996) and predictive pursuit (Madelain & Krauzlis, 2003).

Because pursuit is an operant behavior (Madelain et al., 2011), studies of acceleration/deceleration training (Fukushima et al., 1996; Kahlon & Lisberger, 1996, 2000) qualify as operant learning paradigms, though these studies did not explicitly use operant conditioning. Fukushima and colleagues (1996) trained participants to accelerate or decelerate their eye movements in response to target perturbation. In the training stage, in which participants were trained in one direction only, the target translated at 5 deg/sec for 1-3 sec (the duration varied randomly), then accelerated to 10 deg/sec and translated an additional 150 or 200 msec. Following this acceleration, the target was perturbed once more—it accelerated to 20 deg/sec, or decelerated to 5 deg/sec. To assess training, participants followed a target that translated (in either direction) at 5 deg/sec for 1-3 sec, then accelerated to 10 deg/sec for the rest of the trial. Compared to baseline performance, which was assessed using the same task as in post-training, participants in the acceleration condition had decreased latencies (i.e., they took less time for eye velocity to reach 10 deg/sec after the target perturbation), and participants in the deceleration condition had increased latencies; however learning was only evident for the trained direction. Pursuit learning for acceleration and deceleration has also been found in monkeys (Kahlon & Lisberger, 1996, 2000), using a similar paradigm as Fukushima et al. (1996). In

Kahlon & Lisberger's studies, learning in monkeys transferred to targets that were different sizes and colors from the trained target, and moved at different ranges of velocity; again, however, learning did not transfer to an untrained direction.

There are two studies that have used operant conditioning paradigms to modify pursuit characteristics. In one study, auditory reinforcement was used to elicit pursuit eye movements in infants as young as 1 day old (Darcheville et al., 1999). A second study investigated learning for predictive pursuit in younger adults (Madelain & Krauzlis, 2003). During a pursuit eye movement, the pursuit target can be "blanked," that is, disappear at some point along its trajectory and then reappear after several hundred milliseconds (Sprenger et al., 2011). When the target reappears, it is in the position in which it would be had it continued translating at the same pre-blanking velocity. Predictive pursuit requires maintaining eye velocity that is close to the target velocity during target blanking (when there is no visual feedback); when predictive pursuit is perfect, the eye is in the same location as the target when the target reappears.

Madelain and Krauzlis (2003) investigated the effects of reinforcement on predictive pursuit learning. Participants were split into three groups: a reinforcement group and two control groups. All three groups took part in the learning sessions, in which a translating target disappeared at a variable time point, and the blanking interval was slowly increased throughout the sessions. In the reinforcement group, participants were given auditory reinforcement if they maintained eye velocity close to the target velocity (i.e., maintained a gain of 0.9-1.1) and did not make a saccade; when the reinforcement criteria were met for 80% of a given trial, participants received monetary compensation. In the yoked-control group, participants received an auditory stimulus that was identical to that of the reinforcement stimulus presented in the reinforcement group, but the delivery of the auditory stimulus was not contingent upon the characteristics of the participants' predictive pursuit. In the control group, participants practiced the task independent of any auditory stimulus. Following training, participants in the reinforcement group had higher eye velocities (maintained gains close to one), compared to their baseline velocities; there was no change in either control group. There was also a decrease in the variability of gains in the reinforcement group, relative to baseline, and learning in the reinforcement group generalized to untrained velocities.

Although there has been no research on pursuit eye movement training in older adults, previous studies indicate that older adults are capable of motor learning across a variety of tasks, including those that incorporate feedback (Voelcker-Rehage, 2008). A pursuit eye movement is a low-complexity, high-familiarity motor skill that is both fine (requiring little body movement to carry out) and "open," that is, adjusted by the performer in response to the target (Voelcker-Rehage, 2008). Studies of the effects of age on learning fine visuomotor tasks, such as mirror tracing (Rodrigue, Kennedy, & Raz, 2005) and tasks that require a fixed number of submovements (Seidler, 2006; Smith et al., 2005), show that younger adults learn these tasks at a faster rate than older adults. However, older adults *do* show effects of learning—they improve at these tasks over time. It follows that pursuit, as a fine motor task, might also show improvement as a result of training in older adults.

The Current Study

The goal of Experiment Two was to improve depth perception from MP in older adults using perceptual and motor learning strategies. The two necessary components of depth from MP, motion (dθ) and pursuit (dα) signals (Nawrot & Joyce, 2006), were trained separately, with the logic that improvement in one or both signals should improve the perception of depth from MP—specifically, decrease depth thresholds.

Method

Observers

The observers were the same 32 older adults from Experiment One (*M* = 66.3 years, *SD* = 4.7; 26 females). After completing Experiment One (during which informed consent was obtained and observers were screened for a variety of exclusionary criteria; see Experiment One), each older observer was asked if he or she would like to take part in a training experiment. Eighteen older observers agreed to undergo training, and the other 14 observers (two males) comprised the non-training (control) group. Of the 18 observers who originally agreed to participate in training, four (two males) were non-compliant with training and were not included in the analyses, leaving 14 older observers (two males) in the training group. There was no significant difference in the two groups in age or years of education (see Table One). All observers were paid to participate in pre- and post-training phases, and those who took part in training were paid a flat rate.

Table 1

Demographic Characteristics of Experimental Groups

Group (n = 14)	Age (SD)	Years of Education (SD)
Training	68.00 (1.51)	14.86 (2.69)
Control	65.64 (3.92)	17.36 (4.88)

Stimuli & Apparatus

Pre-and post-training stimuli and apparatus were identical to those in Experiment One. Briefly, in the depth task, a stimulus window containing within-stimulus dot motion ($d\theta$) translated at 2.3, 10.1, or 25.0 deg/sec ($d\alpha$). The combination of stimulus translation and within-stimulus dot movement generated a depth percept; one region of the stimulus, above or below fixation, appeared closer to the observer in depth than the other region of the stimulus. In the motion task, the stimulus was identical to the depth threshold stimulus, except the stimulus window did not translate; observers perceived two-dimensional shearing motion. In the pursuit task, the target was a white square translating at 2.1, 10.6, or 25.5 deg/sec.

Observers who agreed to undergo training were provided with an iPad “care package,” which included the iPad in a case, a stylus, a cleaning cloth, an eye patch to be used to occlude the left eye during training, a small notebook for jotting down notes, an instruction sheet for running both programs, and an iPad charger. The cases in which the iPads came enabled observers to prop up the iPad at eye level, and by propping the case open, it was also ensured that the iPad would not be turned upside down.

Training stimuli were generated and presented on a 4th generation 16 GB iPad (Apple Inc., Cupertino, CA) with a resolution of 2048 pixels x 1053 pixels x 60 hz. Training sessions took place in the observers’ homes. Observers were instructed to complete training sessions in a dimly-lit room, placing the iPad at eye level, an arm’s length away (approximately 50-60 cm). At 57 cm viewing distance, one pixel subtended 35 arcsec. Hereafter, all reported measurements will be based on 57 cm viewing distance, but measurements are approximate, as viewing distance will have varied from observer to observer.

The motion training stimulus was similar in specification to the motion threshold stimulus in Experiment One. Stimuli were composed of 580 105 x 105 arcsec black dots positioned randomly on a white background, contained within a stationary 6 x 6 deg stimulus window. A small black square (6 arcmin) in the center of the stimulus window served as a fixation point. As in the motion threshold stimulus in Experiment One, dots were contained within two different regions, corresponding to the upper and lower halves of the stimulus window. Halfway through the stimulus presentation (100 ms), dots within these regions were displaced in opposite directions. The magnitude of displacement used for training was the smallest possible, ~35 arcsec.

The pursuit training stimulus was a small white square subtending 1 x 1 deg, on a black background. The stimulus translated leftward and rightward at each of the three different velocities used in the MP depth threshold pre- and post-training tasks. During translation, a black dot subtending 70 x 70 arcsec appeared on the target and translated at the same velocity, maintaining its location at the top, bottom, left, or right edges of the target (Figure 10). In order to judge the location of the black target dot, an observer must be able to maintain accurate pursuit on the translating white square.

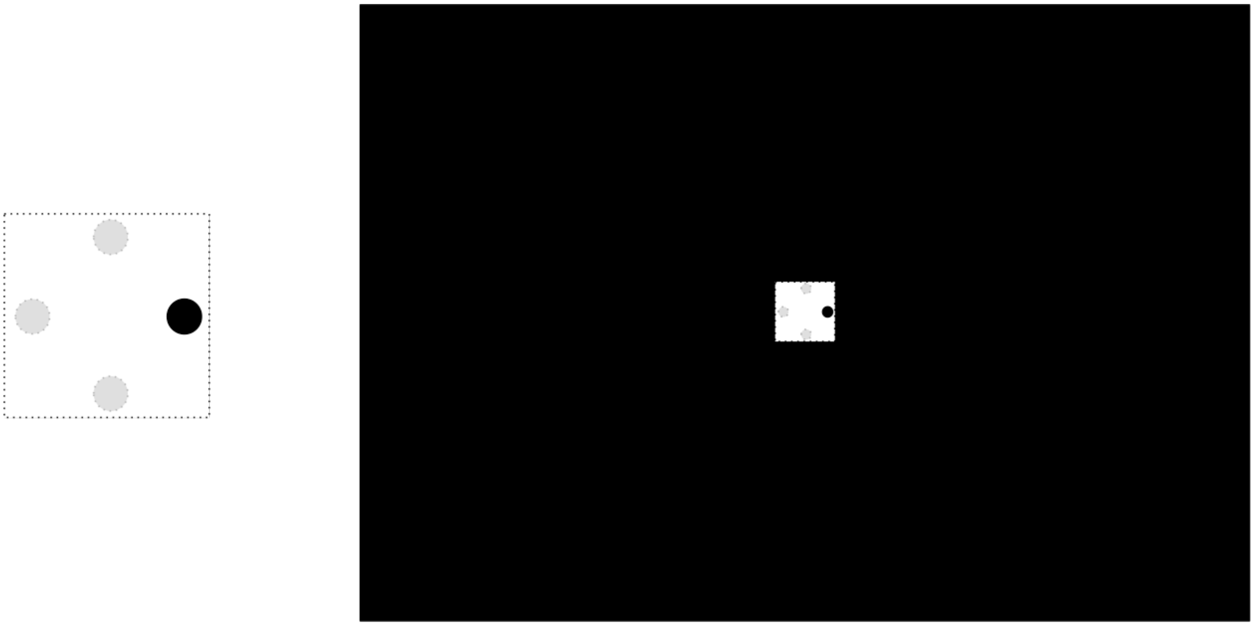

Figure 10. Example of the pursuit stimulus used in the pursuit training task. The left panel shows a close-up of the pursuit target. The right panel shows an approximation of the size of the target on the iPad screen. The target translated across the background. At some time during the target's translation, a black dot appeared at one of four locations (top, bottom, left, right). In this example, the dot appears on the right. The three gray dots represent the other possible locations the dot may appear on a given trial.

Procedure

This experiment comprised three different phases: pre-training, training, and post-training. When observers completed Experiment One (i.e., the pre-training phase), they were asked if they would like to participate in a training program. For observers who did not choose to undergo training (the No Training Group, NT), a post-training return to the lab, 2-3 weeks from the current date, was scheduled. Observers who agreed to participate in training (Training Group, TG) were given a tutorial on general operations of the iPad, and for using the training applications in particular (Appendix B). TG observers were provided with the "care package" described above, and with the experimenter's phone number in the care package notebook, in a note application on the iPad, and on the typed instruction sheet. The experimenter informed the observers that she would call and check in with their progress 2-3 times a week, and the observers were encouraged to call the experimenter with any questions or concerns. TG observers were then scheduled for a post-training return to the lab, 2-3 weeks from the current date, and before they left the lab, signed a form agreeing to return the iPad on the scheduled post-training date (Appendix C).

TG observers opened the training application by tapping the icon with their finger or the stylus. Upon entering the application, the observers had the option to open the Motion Task or Pursuit Task. (The procedure for each task is detailed below). Observers were asked to complete seven sessions of each task over the course of 2-3 weeks. Each session took approximately 30 minutes to complete. To prevent fatigue, observers were instructed to complete no more than one motion session or one pursuit session in one day (though they could complete one session of each task in one day), and they were encouraged to take breaks during and between the sessions. However, it was also required that observers complete each session in one sitting; therefore, if participants took more than a five-minute break (during which they did not touch the screen, start a trial, or make any decision about the stimulus), the session would restart and all their data up to that point would be lost. Observers were informed of this stipulation in person and on their instruction sheets.

Motion task. The motion task opened with an instruction screen, the text of which was identical to the instruction sheet provided to observers in the care package (see Appendix A). On this screen, observers were given the option to “go back” or to “start.” Pressing the “start” button began a session. Before beginning the task, observers were prompted to enter their initials, after which the task opened on a white background with the fixation square in the center of the screen. To begin a trial, the observer pressed anywhere on the screen. On each trial, the stimulus was presented, centered on the fixation point. Observers maintained fixation on the square during stimulus presentation. Following the 200 ms stimulus presentation, the stimulus and fixation point were erased from the screen and replaced by two arrow buttons, left (←) and right (→), which were located on the left and right sides of the screen. Observers indicated the direction in which the dots in the *top* region of the stimulus shifted by touching the corresponding arrow. When the observer entered an incorrect response, a 500 Hz tone of 200 ms duration was played. For each trial the presentation of left or right top motion was determined randomly with an equal probability of either direction of motion. Observers completed 500 trials in a session, and seven sessions, for a total of 3500 trials.

Pursuit training. The pursuit task opened with an instruction screen, the text of which was identical to the instruction sheet provided to observers in the care package (see Appendix A). On this screen, observers were given the option to “go back” or to “start.” Pressing the “start” text opened the task. Before beginning the task, observers were prompted to enter their initials, after which the task opened on a black background with the white pursuit stimulus in the center of the screen. To begin a trial, the observer pressed anywhere on the screen. Initiating a trial caused the pursuit stimulus to "step" either to the left or to the right (Rashbass, 1961), and then begin translating across the screen in the opposite direction. The amplitude of the step varied across pursuit velocity conditions, such that for each trial the translating pursuit target passed through the original fixation spot 400 ms after onset of translation. The pursuit target translated to the left or right at one of three different speeds (2.3, 10.1, and 25.0 deg/sec). The pursuit direction and speed was randomly determined on each trial, with the constraint that each direction and speed had an equal probability of being presented. At some time between 100 and 600 ms after stimulus onset, a black dot appeared at one of four locations on the target, for a duration of 200 ms. The dot translated at the same velocity as the target, maintaining its position at the top, bottom, left, or right edges of the target (see Figure 10). The time point at which the dot appeared in a given trial was determined randomly, as was the location of the dot on the target, with the constraint that the dot had an equal probability of appearing in each position for each velocity and direction. The target was erased from the display at 800 ms, regardless of the distance of translation. After the target disappeared, four white squares (3 x 3 deg) were presented on the top, bottom, left, and right edges of the screen. Observers indicated the location at which the dot appeared on the target by touching the corresponding white square. The purpose of this training task was to encourage accurate pursuit of the target—in order to locate the black dot on the white target, it was necessary to foveate the target, which requires generating a pursuit eye movement with a velocity close to the target velocity.

As in the motion training task, when an observer entered an incorrect response, a 500 Hz tone of 200 ms duration was played. In each session, the target translated 80 times in each direction (rightward and leftward), at each velocity, for a total of 480 trials. Observers completed all 480 trials in a session, and seven sessions, for a total of 3500 trials.

Post-training. On each observer's pre-scheduled date, they returned to the lab. They each signed a form acknowledging the return of their issued iPad, and iPads were inspected for damage at this time. Observers then underwent post-training measurement, the tasks for which were all identical to the pre-training (Experiment One) tasks.

Results

Analyses were conducted in Microsoft Excel, MATLAB 2014B, and SPSS 21. Post-training data screening and analyses were conducted as in Experiment One. Briefly, depth thresholds for the three pursuit velocities (2.3, 10.1, and 25.0 deg/sec) were quantified using the M/PR ($d\theta/d\alpha$; Nawrot & Stroyan, 2009), calculated from the last four reversals from two blocks of trials. Motion thresholds (d_{min}) were found from the last six reversals from two blocks of trials. Pursuit accuracy was be analyzed by finding the mean gain (eye velocity/target velocity) for each observer at each pursuit velocity. For details on all these analyses, see the Results section of Experiment One.

Independent samples t-tests were conducted to assess the possibility that TG and NT observers had baseline differences in motion or depth thresholds, or pursuit gain, that might have influenced their training or post-training performance. The two groups showed no differences in depth thresholds at any of the pursuit velocities (all p's > 0.05). Likewise, there was no difference between the groups in pre-training motion thresholds ($t(26)$, $p > 0.05$) or pre-training gains (all p's > 0.05).

The effectiveness of the training programs was evaluated by monitoring performance in the training tasks. The percent correct for each motion and pursuit training session was recorded in a text file on the iPad. For both training programs, MATLAB Palamedes toolbox (Prins & Kingdom, 2009) was used to convert the percent correct for each session to *d'* ("d-prime"), a measure of observer sensitivity. For the motion task and all three velocity conditions of the pursuit task, the mean *d'* for each session was calculated, and the within-task *d'*s across all seven sessions were compared. As can be seen in Figure 11, the mean change in sensitivity (*d'*) across the motion training task was negligible. This finding was confirmed by a one-way repeated-measures ANOVA. For the motion task, there was no significant main effect of session ($F(2,25) = 2.4$, $p = 0.11$, Greenhouse-Geisser corrected), and none of the pairwise comparisons were significant (all *p*'s > 0.05, Bonferroni corrected).

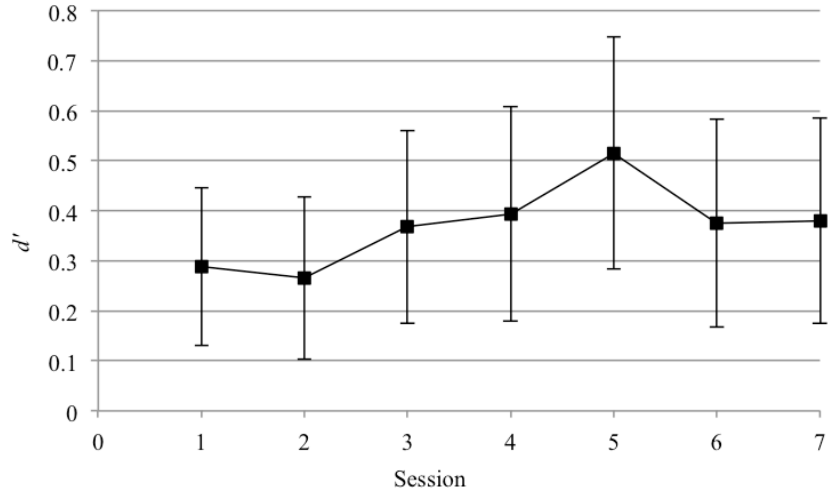

Figure 11. *d'* in the motion task, across sessions. When the number of response choices = 2, *d'* of 0.3 is equal to 58% correct; *d'* of 0.4 is equal to 61% correct; and *d'* of 0.5 is equal to 64% correct. Bars denote standard error.

Likewise, Figure 12 shows that there was negligible change in sensitivity (*d'*) across the pursuit training task, in all three of the velocity conditions. This finding was confirmed by one-way repeated-measures ANOVAs. The main effect of session was not significant for any of the three velocities (2.3 deg/sec: $F(6,78) = 1.41$; 10.1 deg/sec: $F(3,32) = 1.04$, Greenhouse-Geisser corrected; 25 deg/sec: $F(2,26) = 1.12$, Greenhouse-Geisser corrected; all *p*'s > 0.05). (Note that the degrees of freedom for the *F* values are generated from the Greenhouse-Geisser correction, and have been rounded to the nearest whole number.) None of the pairwise comparisons were significant (all *p*'s > 0.05, Bonferroni corrected).

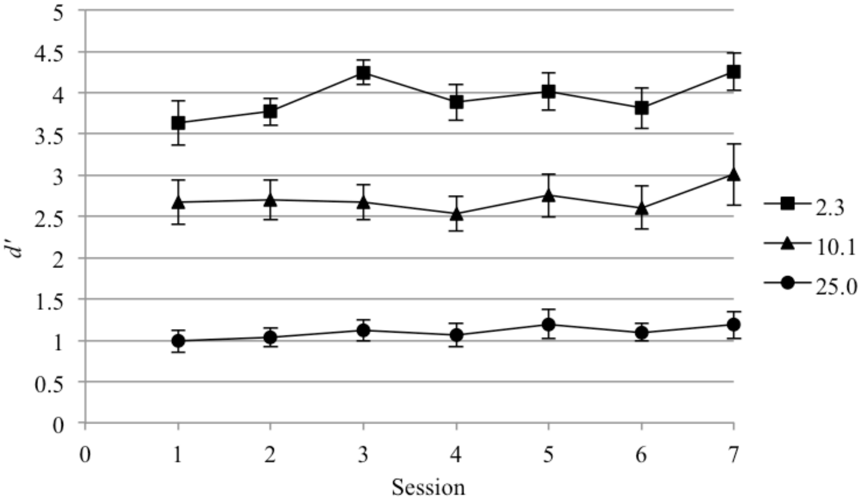

Figure 12. d' in each condition of the pursuit task, across sessions. When the number of response choices = 4, *d'* of 1 is equal to 55% correct; *d'* of 3 is equal to 96% correct; and *d'* of 4 is equal to 99% correct. Bars denote standard error.

Figures 13, 14, and 15 show the pre- and post-training results for both groups in the depth, motion, and pursuit tasks, respectively.

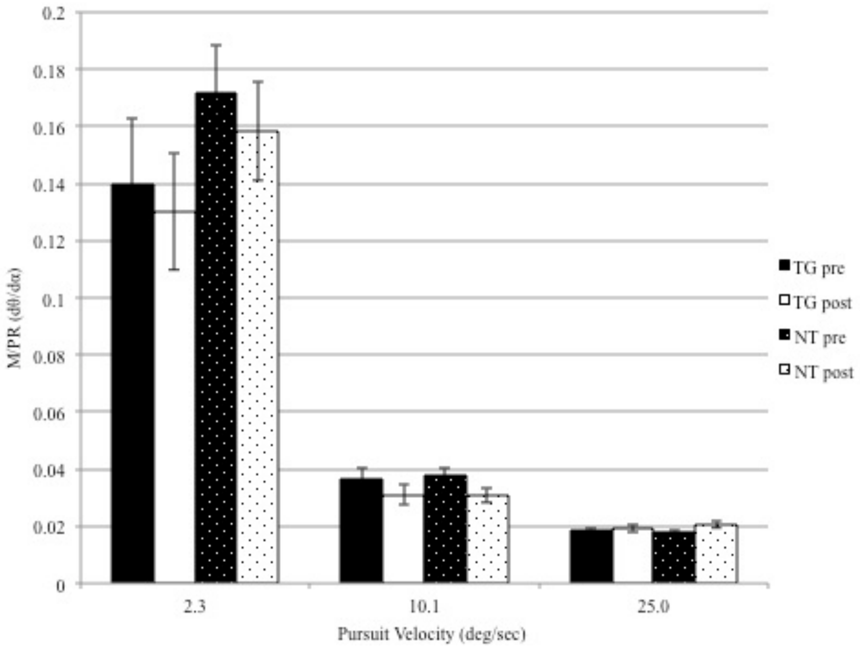

Figure 13. Pre- and post-training depth thresholds across all three pursuit velocity conditions. Bars denote standard error.

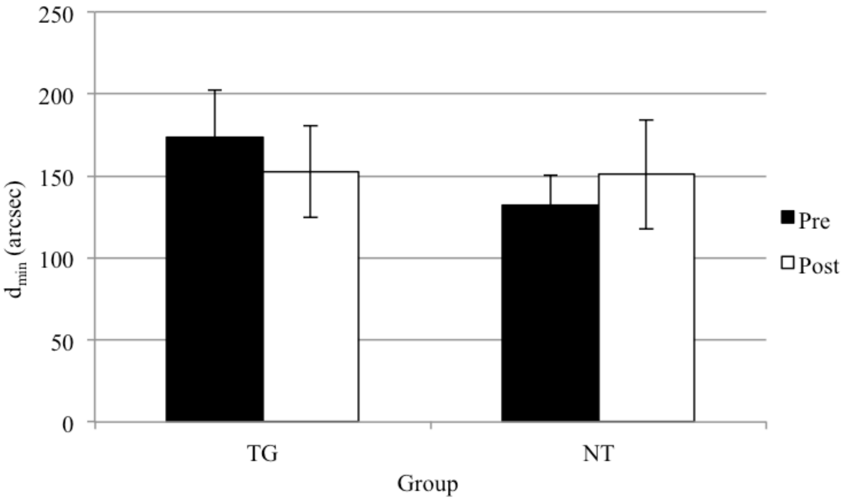

Figure 14. Pre- and post-training motion thresholds for each group. Bars denote standard error.

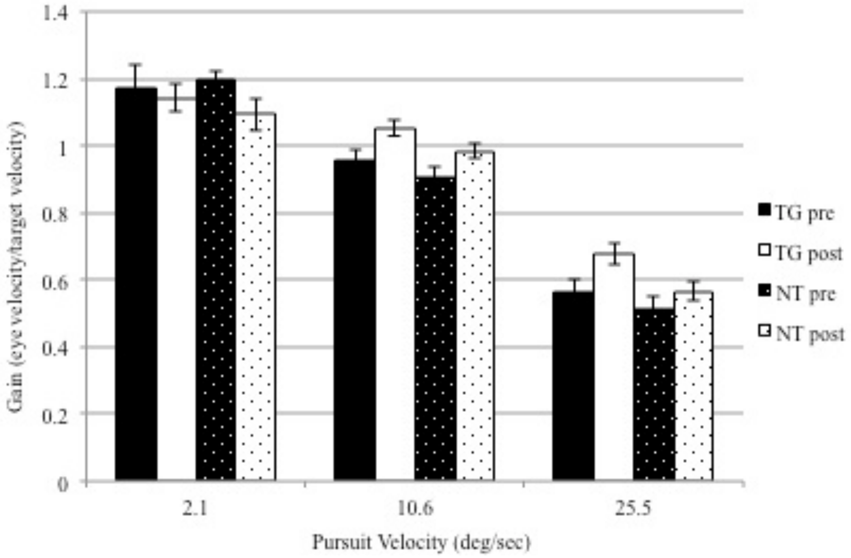

Figure 15. Pre- and post-training pursuit gains across all three pursuit velocity conditions. When gain = 1, pursuit tracking is perfectly accurate; the more gain deviates from one in either positive or negative direction, the less accurate the pursuit eye movement. Bars denote standard error.

The main analysis addressed the effects of training on depth thresholds, motion thresholds, and pursuit gains. For each observer, the post-training M/PR, motion threshold, or pursuit gain was subtracted from the corresponding pre-training datum, generating a difference score. The mean difference score for each group was calculated for each depth threshold and pursuit gain condition, as well as for the motion threshold task. A difference score significantly different from zero indicated an effect of training.

Figure 16 shows the difference scores for the depth task, for both TG and NT groups, across all three pursuit velocity conditions. Independent sample t-tests revealed that, in the TG, there was no significant difference between pre- and post-training performance for any of the three pursuit conditions (all p's > 0.05). In the NT group, there was no significant difference between pre- and post-training performance for the 2.3 and 25.0 deg/sec pursuit velocity conditions (both p's > 0.05). In the 10.1 deg/sec condition, post-training depth thresholds were lower than pre-training depth thresholds ($t(13) = 2.73$, $p = 0.02$, 95% CI [0.002, 0.02]).

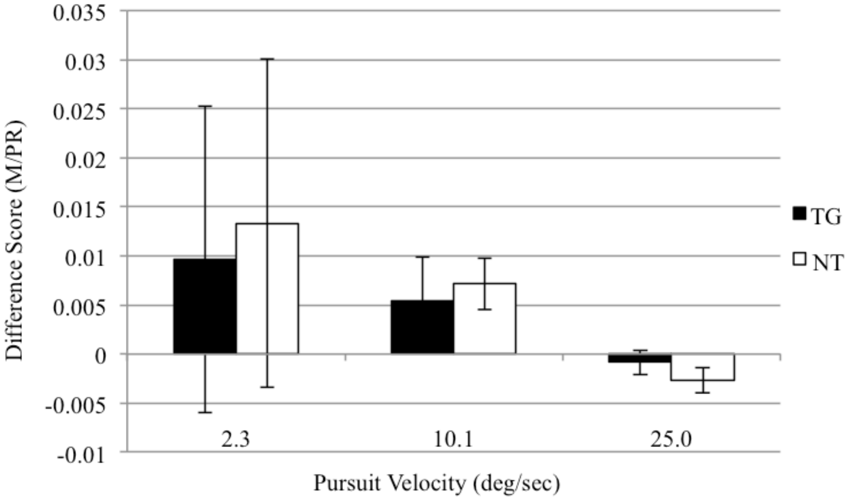

Figure 16. Difference scores for the depth threshold task, across all three pursuit velocity conditions. A positive difference score indicates post-training thresholds lower than pre-training thresholds, and a negative difference score indicates post-training thresholds higher than pre-training thresholds. Bars denote standard error.

Figure 17 shows the difference scores for TG and NT groups in the motion threshold task. Independent sample t-tests confirmed that there was no significant difference between pre- and post-training thresholds in either group (both *p*'s > 0.05).

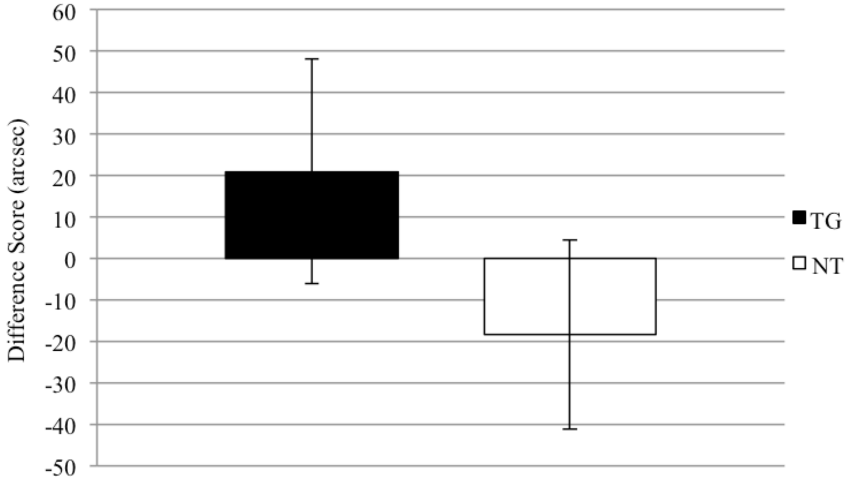

Figure 17. Difference scores for the motion threshold task. A positive difference score indicates post-training thresholds lower than pre-training thresholds, and a negative difference score indicates post-training thresholds higher than pre-training thresholds. Bars denote standard error.

Figure 18 shows the difference scores for the pursuit task, for both TG and NT groups, across all three pursuit velocity conditions. When referring to the figure, note that at 2.1 deg/sec, a positive difference score indicates that post-training gains were *lower* than pre-training gains, moving closer to 1.0 (perfect pursuit accuracy). At 10.6 and 25.5 deg/sec, a negative difference score indicates that post-training gains *increased* compared to pre-training gains, moving closer to 1.0. In the TG, there was no significant difference between pre- and post-training performance in the 2.1 deg/sec condition ($t(13) = 0.65$, $p > 0.05$). In the 10.6 deg/sec condition, post-training gains were significantly higher than pre-training gains ($t(13) = -3.32$, $p < 0.01$, 95% CI [-.16, -.03]). Similarly, post-training gains were significantly higher than pre-training gains in the 25.5 deg/sec condition ($t(13) = -7.41$, $p < 0.001$, 95% CI [-.15, -.08]). In the NT group, post-training gains were marginally lower than pre-training gains in the 2.1 deg/sec condition ($t(13) = 2.21$, $p = 0.05$, 95% CI [.002, .21]). In the 10.6 deg/sec condition, post-training gains were significantly higher than pre-training gains ($t(13) = -2.99$, $p = 0.01$, 95% CI [-.14, -.02]). There was no significant difference in pre- and post-training gains in the 25.5 deg/sec condition ($t(13) = -1.89$, $p = 0.08$).

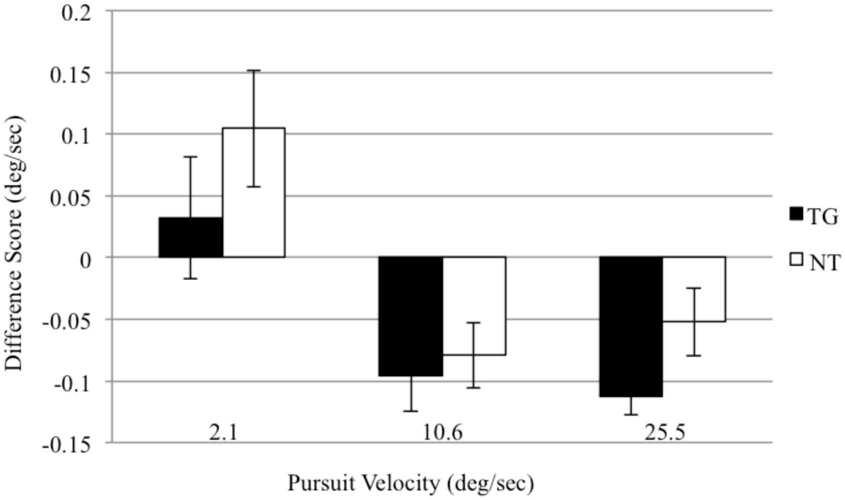

Figure 18. Difference scores for the pursuit accuracy task, across all three pursuit velocity conditions. Bars denote standard error.

Discussion

Participation in the motion and pursuit training programs did not improve sensitivity to motion or pursuit stimuli. In the motion training task, *d'* increased over the course of the seven sessions—the percent correct was approximately 58% in session 1, and had increased to approximately 61% correct in session 7 (see Figure 11). However, there was also a large amount of variability in observers' sensitivity, which obscured any significant differences across sessions overall or among individual sessions. Similarly, in the slow and moderate velocity conditions of the pursuit task, *d'* increased slightly from session 1 to session 7, but variability was too high to allow for a significant difference in sensitivity (see Figure 12).

Training had no impact on post-training performance in the depth, motion, and pursuit tasks: in the TG, observers performed essentially the same in post-training as they did in pre-training. The exception is the significant increase in pursuit gain accuracy between pre- and post-training measures, at 10.6 and 25.5 deg/sec target velocities. However, NT observers also had significantly more accurate post-training pursuit gains, at 2.1 and 10.6 deg/sec target velocities.

The magnitude of post-training improvements (estimated from the size of the confidence intervals) were stronger in the TG compared to the NT group, indicating a larger post-training improvement for observers who underwent training compared to those who did not. Even so, the significant change in pursuit gains from pre- to post-training in the TG cannot be explained by training effects. Rather, the most straightforward explanation of both groups' changes in pursuit gains post-training is that observers from both groups were more accurate in pursuing the target in the post-training phase due to familiarity with the task from the pre-training phase.

Given that sensitivity (*d'*) throughout the motion and pursuit training tasks did not change, it is unsurprising that there was no significant difference in TG observers' pre- and post-training motion threshold and pursuit accuracy performance. It also follows logically that, given the lack of change in motion and pursuit processing, depth thresholds likewise should not improve. Future research in this area should address the possible reasons that the motion and pursuit training techniques of the current study were ineffective.

The motion training stimulus and task in the current study were similar in concept to Ball and Sekuler's (1986) training study, and to PL studies of motion learning in younger adults (Huang et al., 2007). Therefore, it is unlikely that the stimulus or task is inherently inadequate for motion training. Ball and Sekuler (1986) trained older adults to discriminate motion stimuli that were separated in direction by only 2 deg; before training, older observers' discriminability at this angle of separation was very low, with a *d'* of approximately 0.2. However, even with this low baseline sensitivity, older observers' discriminability significantly improved throughout the course of training. As in the current study, in Ball and Sekuler's study, observers' performance in session 1 was low overall (58-61% correct), but above chance levels (50%, or *d'* = 0). Still, sensitivity did not significantly improve over the sessions. The reason that Ball and Sekuler's observers' performance improved throughout training, while the observers' performance in the current study did not, is not immediately clear. It is possible that this discrepancy may be due to the difference in tasks—Ball and Sekuler's task required that observers make same/different judgments about the directional difference between two stimuli, while in the current study observers made judgments about the direction of shearing motion in one stimulus. An alternative for future research would be to make the motion training task adaptive, so that the task starts at an easy level, and becomes more difficult as observers' performance improves. This method has been successfully employed by Bower and Andersen (2012) to improve motion discrimination.

Successful completion of a trial in the pursuit training task required that observers correctly identify the location of the appearance of a black dot on top of a moving target. The goal of the pursuit task was not to improve spatial location, but rather to improve pursuit accuracy (gain). Gain was not directly measured in the training task; however, successfully identifying the black dot's location requires accurate following (matching the eye velocity to the target velocity). Therefore, *d'* in this task reflects how well observers were able to track the moving target. It is possible that observers' sensitivity did not improve throughout the task because they were performing at ceiling. That is, it may have been difficult or impossible for observers to increase their eye velocity (and thereby improve their visual acuity for the dot location task) above a certain speed.

Evidence for this supposition is found in the comparison of training task performance at different velocities (see Figure 12). Performance for the 2.1 deg/sec condition was very high (percent correct ranging from ~98-99%) throughout the task, indicating that observers had no trouble following the target at this slow velocity. At 10.6 deg/sec, percent correct ranged from ~90-96% across all seven sessions. TG observers' pre-training gain at 10.1 deg/sec was 0.96 (see

Figure 15), which, although not "perfect" (i.e., 1.0), seems sufficiently accurate to enable the observers to perform the training task at the percentage correct observers reached; therefore, observers were already performing at ceiling. At 25 deg/sec, TG observers' percent correct in the training task ranged from ~55-60% (note that in this task, chance performance would be 25% correct). Though this is a relatively low accuracy rate, it may be the case that observers were already performing at ceiling, as alluded to above. Specifically, observers' eye velocity may "top out" at a particular velocity, and training may not be able to increase this velocity (at least, in older adults). Recall that there has been very little research on pursuit eye movement training. The handful of studies that have investigated pursuit eye movements have focused only on pursuit acceleration/deceleration and pursuit maintenance during target blanking (Fukushima et al., 1996; Kahlon & Lisberger, 1996; Madelain & Krauzlis, 2003). These studies were conducted with younger adults, using target velocities that younger adults can easily follow. No other study has investigated whether pursuit training can result in faster eye velocities sustained over the course of a target's translation. The results of the pursuit training study indicate that, at least in older adults, pursuit velocity cannot be increased, suggesting that eye velocity is limited by a physiological mechanism, and that this mechanism cannot be altered through training.

GENERAL DISCUSSION

The goals of Experiment One were to characterize MP depth thresholds in older adults, as well as understand the mechanisms underlying the changes in depth perception that might occur with age. The results of Experiment One showed that at slow and moderate pursuit velocities, older adults have higher MP depth thresholds than younger adults. This age difference is primarily driven by age changes in pursuit eye movements. At the highest pursuit velocity, older and younger adults have similar depth thresholds. The ability to recover depth from MP relies on the neural combination of motion ($d\theta$) and pursuit ($d\alpha$) signals (Nawrot & Stroyan, 2009). Older adults had deficits in processing motion and pursuit information, indicating that the $d\theta$ and $d\alpha$ signals available to them were different than the signals available to younger adults; however, older adults appeared to use the available signals more optimally than younger adults. This study is the first to characterize MP depth thresholds in older adults, an important contribution to our understanding of how age affects depth perception. This study also examines the mechanisms underlying age changes in perception, an aspect of aging research that is too often ignored. In any perceptual domain, understanding the mechanisms underlying age changes is a crucial first step to implementing strategies to improve perception, the goal of Experiment Two.

In Experiment Two, older observers were given the opportunity to take part in a training experiment aimed to improve motion and pursuit processing (the logic being that improving motion ($d\theta$) and/or pursuit ($d\alpha$) signals should result in improved MP depth thresholds). However, training did not improve sensitivity to motion or pursuit training stimuli, or improve motion thresholds, pursuit gains, or depth thresholds. Improvement of performance in the motion training task was possibly limited by some aspect of the judgment that observers were required to make (e.g., making a directional judgment about motion in one stimulus versus making a same/different judgment, such as in Ball and Sekuler's [1986] study). Improvement of performance in the pursuit task was likely limited by a physiological mechanism that constrains the relationship of eye velocity and target velocity. That is, slower-velocity targets induce slower-velocity eye movements, and faster-velocity targets induce faster-velocity eye movements, but the peak eye velocity attained in a given target velocity condition cannot be altered through training. Although older adults did not improve following training in Experiment Two, this study provides an important first step in improving PL techniques. Studies of PL usually require that participants return to the lab multiple times over the course of one or more weeks, often working in the lab for two hours or more. Such a training approach is not ideal in terms of practicality, especially with older participants. Developing easy-to-use training programs that run on apparatus that participants can use at home would greatly improve the practicability of these training strategies. Future research should focus on addressing the issues in the current study that limit performance in the training tasks, and on improving the practicality of PL techniques by making them more accessible and user-friendly.

Visuospatial deficits in older adults have many adverse effects on health and on social and physical functioning (Crews & Campbell, 2004). Self-reported visual impairment contributes to the incidence of falls in older adults (Lopez et al., 2011) and is a significant predictor of mortality, especially in women (Lee, Gomez-Marin, Lam, & Zhang, 2002). Beyond visual impairment at the ocular level, research on sensory processing in older adults has revealed that perceptual deficits are associated with many negative outcomes, including difficulties with balance (Choy, Brauer, & Nitz, 2008), reading speed (Yu, Cheung, Legge, & Chung, 2010), and driving abilities (Owsley et al., 1998). Given that the population of older adults in the US is projected to nearly double by 2050 (Ortman, Velkoff, & Hogan, 2014), research on understanding age-related visuospatial deficits, such as deficits in the perception of depth from MP, is especially timely and important.

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APPENDIX A. HEALTH QUESTIONNAIRE

Health Questionnaire

Participant#: _________ Date: ________ Study: ___________ Examiner: _________________

YES NO

___ ___ 1. Have you ever had a stroke or a T.I.A. (transient ischemic attack)?

___ ___ 2. Have you ever been seen by a neurologist or neurosurgeon?

___ ___ (if yes) Was this for a back or neck problem?

___ ___ (if yes) Was this for a tension headache?

___ ___ 3. Do you have trouble with your vision that prevents you from reading ordinary print even when you have glasses on?

___ ___ 4. Do you have glaucoma?

___ ___ 5. Do you have diabetes that requires insulin to control?

___ ___ 6. Have you ever had a head injury with loss of consciousness greater than five minutes?

___ ___ 7. Have you ever been unconscious for more than one hour other than during surgery?

___ ___ 8. Have you ever required overnight hospitalization because of a head injury?

___ ___ 9. Have you ever had brain surgery?

___ ___ 10. Have you ever undergone surgery to clear arteries to the brain?

___ ___ 11. Have you ever had any illness that caused a permanent decreases in memory or other mental functions?

___ ___ 12. Do you have Parkinson’s disease?

___ ___ 13. Do you have multiple sclerosis, cerebral palsy, or Huntington’s disease?

Adapted from Christensen et al. (1992)
Revised 11/10/14

APPENDIX B. TRAINING INSTRUCTIONS

Motion Training Task:

When you open the DotsTask application, you will choose the MotionTask. You can view the instructions, or begin the task.

When you choose to begin the task, a small black square will appear in the center of the screen. Press anywhere on the screen to start the trial.

A second after starting the trial, a square made up of moving black dots will appear. *Please keep your eye on the center square at all times*. When the square appears, it will only remain on the screen for a very short amount of time. The dots in the top and bottom halves will move in opposite directions.

When the square disappears, two arrows will appear, on either side of the screen. If the dots in the *top half* of the stimulus moved to the right, select →. If the dots in the *top half* of the stimulus moved left, select ←.

When you make a selection, the arrows will disappear. If your answer was incorrect, you will hear a beep. If you were correct, you won't hear anything. You can hit anywhere on the screen to start over again.

There are 500 trials in one session. When you have completed all trials, the application will stop automatically. You are encouraged to take a break whenever you wish. Please take a break if you begin to feel fatigued or bored.

If you do not make a response in five minutes, the program will automatically close, and you will have to restart the program from the beginning.

Please do not complete more than one motion training session in one day.

Pursuit Training Task:

When you open the DotsTask application, you will choose the PursuitTask. You can view the instructions, or begin the task.

When you choose to begin the task, a white square will appear in the center of the screen. Press anywhere on the screen to start the trial.

A second after starting the trial, the white square will start to move across the screen, to the left or to the right. *Please keep your eyes on this square at all times*.

Sometime during the movement of this square, a small black dot will appear inside of it. The dot will appear at one of four locations: top, bottom, left, or right. The white square will continue moving for the entire trial, but this dot will only be on the square for a short amount of time.

After the square has reached the edge of the screen, it will disappear, and four buttons will appear. The buttons will be at the edges of the screen, at the top, bottom, left, or right. Your task is to indicate the location in which the black dot appeared by selecting one of these four buttons.

When you make a selection, the buttons will disappear. If your answer was incorrect, you will hear a beep. If you were correct, you won't hear anything. You can hit anywhere on the screen to start over again.

There are 480 trials in one session. When you have completed all trials, the application will stop automatically. You are encouraged to take a break whenever you wish. Please take a break if you begin to feel fatigued or bored.

If you do not make a response in five minutes, the program will automatically close, and you will have to restart the program from the beginning.

Please do not complete more than one pursuit training session in one day.

APPENDIX C. EQUIPMENT AGREEMENT FORM

Off-Campus Use of University Equipment Agreement

NDSU
Accounting

Questions about this form? Please call 701-231-7432

Equipment Description: ____________________

University Inventory #: ____________________ Serial #: ____________________

Equipment Description: ____________________

University Inventory #: ____________________ Serial #: ____________________

Equipment Description: ____________________

University Inventory #: ____________________ Serial #: ____________________

Equipment will be located at:

The equipment will be returned: ____________________

I accept full responsibility for any loss or damage for the following equipment items that I will be taking off-campus.

I understand that the department has the right to request that I return the equipment to the University at any time.

I understand that because the equipment is the property of the University, it may be necessary for auditors to come to the location (mentioned above) to visually verify that the equipment is at that location and is being used as intended.

I understand that personal use of University property is a violation of Section 12.1-23-07 of the North Dakota Century Code.

I understand that if I fail to return the equipment to the University, appropriate sanctions may be taken against me, including withholding of moneys due me by the University until such equipment is returned.

Employee Name: ____________________ EMPL ID: ____________________

Signature ____________________ Date ____________________

Supervisor Name: ____________________ Dept #: ____________________

Signature ____________________ Date ____________________

Equipment Returned

Equipment Description: ____________________

University Inventory #: ____________________ Serial #: ____________________ Date: ____________________

Equipment Description: ____________________

University Inventory #: ____________________ Serial #: ____________________ Date: ____________________

Equipment Description: ____________________

University Inventory #: ____________________ Serial #: ____________________ Date: ____________________

Signature ____________________ Date ____________________

Verified ____________________ Date ____________________

This document is to be printed and retained in your office.

ACCT-OFF_CAMP_USE- **REV 02/2011** **Page 1 of 1**