

Ageing, Motion sensitivity and Eye movement

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Thesis Summary

This thesis aimed to address two separate issues: 1) the effect of fixation and smooth pursuit eye-movement on motion sensitivity and 2) the effect of age on motion sensitivity. Speed, direction and motion coherence thresholds were measured in older and younger observers during fixation and smooth pursuit.

Observers of all ages found it more difficult to discriminate direction during smooth pursuit compared to fixation. An age-related decline in direction discrimination was evident during fixation and smooth pursuit at slow speeds only (Experiment 1). An age-related decrease in retinal luminance failed to explain the decline in direction sensitivity in older observers (Experiment 2). The effect of relative motion was assessed and was found not to influence the threshold difference between eye-movement conditions (Experiment 3). Similar effects of speed and eye-movement condition were found in the trajectory-matching task (Experiment 4).

Speed discrimination thresholds were also higher during pursuit compared to fixation (Experiment 5). No age effects were found in either eye-movement condition for speed discrimination. Classification analysis demonstrated that in speed and direction discrimination, old and young observers combined retinal and extra-retinal motion cues to make motion judgements regardless of instructed eye-movement. Overall, the discrimination results support the idea that performance in these tasks is limited by internal noise associated with retinal and extra-retinal motion signals that feed into a combination stage responsible for estimating head-centred motion.

Motion coherence thresholds were higher for pursued stimuli compared to fixated stimuli (Experiment 6). In addition, observers of all ages found it more difficult to detect collinear signal motion compared to orthogonal signal motion during pursuit. This pattern was significantly worse in older observers. There was no age-related decline in motion coherence for fixated stimuli. Retinal slip due to inaccurate eye-movements could explain the motion coherence findings.

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1. Introduction

The population is steadily growing older; by 2031, 23% of the UK population will be aged over 65 years (Shaw, 2004). The rapidly ageing population has raised concerns amongst health professionals regarding the inevitable increase in demand for nursing care for those suffering from debilitating conditions. A recent report from the World Health Organisation suggests the best way of tackling this issue is to encourage and help individuals maintain a level of independence and activity as they get older (World Health Organisation [WHO], 2007). Recent studies have shown that by keeping active in older age, the incidence of falling can reduce (Rekeneire et al., 2003), while reports of cardiovascular impairment (Patel et al., 2002) and depression (Biderman, Cwikel, Fried, & Galinsky, 2002) decrease.

Visual perception plays an important role in our level of activity, allowing us to identify obstacles and manoeuvre safely through the environment. A crucial part of this, involves the movement of our eyes, head and body for optimal detection of object speed and direction. Although visual processing involving these type of movements is fundamental for everyday mobility, very little research has addressed how it influences visual perception in older age. This is highlighted in a U.S. survey regarding visual function and driving safety. Keltner & Johnson (1987) found that older observers had a higher incidence of accidents involving failure to yield right of way, turns, stop signs and oncoming traffic. Hakamies-Blomqvist (1993) came to similar conclusions in a Finnish study. A central component in successfully completing these types of driving manoeuvres is the correct estimation of velocity. Underestimation of

vehicle velocity can lead to drivers taking greater risks on the road, which has been particularly evident in older drivers (Faulkner, 1975; Hills & Johnson, cited in (Hills, 1980); Sheppard & Pattinson, 1986).

Prior research has shown that during fixation (eyes stationary), motion sensitivity declines (Ball & Sekuler, 1987; Bennett, Sekuler, & Sekuler, 2007; Norman, Ross, Hawkes, & Long, 2003; Owsley, Sekuler, & Siemsen, 1983; Raghuram, Lakshminarayanan, & Khanna, 2005; Snowden & Kavanagh, 2006). This implies that an age-related decline due to changes in mechanisms sensitive to retinal-image motion. During smooth pursuit however, the simple relationship between motion in the world and motion on the retina is disrupted because additional retinal motion is created by the eye-movement itself. A solution to this problem is to use the extra-retinal motion signals emanating from the oculomotor system to recover object motion with respect to the ego (von Holst, 1954). By comparing age-related effects of motion perception during smooth pursuit and fixation, the aim of this thesis is to investigate the impact of eye-movement on visual perception, specifically the effect of smooth pursuit eye-movement on motion sensitivity in older adults.

This introductory chapter will begin by discussing the current research relating to retinal motion sensitivity in older adults, followed by possible neural explanations why retinal sensitivity is prone to age-related decline. Particular emphasis will be given to the smooth pursuit eye-movement system, the origins of the extra-retinal signal and research relating to the extra-retinal

signal and age. The next section will then discuss factors that, could predict a reduction in motion sensitivity during smooth pursuit, including oculomotor control and sources of internal noise. Finally, I will outline a summary of the experimental chapters.

1.1. Motion Perception and Age

1.1.1. Retinal motion sensitivity

Motion sensitivity has been shown to decline in older adults across a range of psychophysical tasks. For example, Ball & Sekuler (1987) reported that older observers were less sensitive at judging whether the direction of two sequentially presented stimuli were the same or different across a series of trials. In 'same' trials, dots moved in the same direction during both intervals, while in 'different' trials the two directions were separated from one another by either 2°, 4°, 6°, or 8° (from a standard). Both age groups benefited from discrimination training over the course of 7 sessions, although the effect of age remained. Contrast detection also shows evidence of decline. Owsley, Sekuler, & Siemsen (1983) measured contrast detection in young and old observers, using stationary and moving gratings presented at low and high frequencies. Their results suggested specific ageing effects for stationary gratings at high spatial frequencies. For drifting gratings, however, contrast sensitivity increased at low spatial frequencies in younger observers when compared to the static gratings. This enhancement in contrast sensitivity was not evident in the older adult group.

Speed sensitivity has also been shown to decrease in older observers. For example, older adults who were asked to judge the velocity of a moving vehicle, overestimated the speed when compared to younger adults (Scialfa, Kline, Lyman, & Kosnik, 1987). Furthermore, sensitivity to speed differences when observing moving vehicles have also been shown to decrease with age (Scialfa, Guzy, Leibowitz, Garvey, & Tyrrell, 1991). In the psychophysical literature, there have been a number of reports of age-related decline in speed discrimination. Bidwell, Holzman, & Chen (2006) found speed sensitivity decreased in a 2-alternative forced choice task (2-AFC) for aged observers but only at the intermediate speed of $10^\circ/\text{s}$. No effects were found for slow ($3.6^\circ/\text{s}$) and fast ($26.3^\circ/\text{s}$) speeds. Norman, Ross, Hawkes, & Long (2003) measured speed discrimination thresholds for standard speeds $1.22^\circ/\text{s}$, $5.48^\circ/\text{s}$ and $24.34^\circ/\text{s}$. The random dot stimuli used were presented simultaneously 2.86° above and below a central fixation point, with one of the stimuli moved at standard speed and the other moving slightly slower. The observers were given unlimited presentation time to judge which (top or bottom) was moving faster. Norman et al. reported age-related decline in speed discrimination for all speeds tested. They also had older observers with the highest thresholds practice for three additional sessions, yet failed to eliminate any ageing effect. Snowden and Kavanagh (2006) reported similar age-related decline in a speed 2-AFC discrimination task with drifting gratings presented for $\sim 400\text{ms}$ in sequential intervals for speeds $0.125^\circ/\text{s}$, $1^\circ/\text{s}$ and $8^\circ/\text{s}$. Stimulus duration has been shown to interact with speed discrimination thresholds using first-order drifting luminance gratings. Raghuram et al. (2005) investigated two stimulus speeds ($2^\circ/\text{s}$, $8^\circ/\text{s}$) at two durations (500ms

and 1000ms). Raghuram et al. found older observers had higher thresholds for short stimulus durations (500ms) when compared to long durations (1000ms). They suggest that differences may be due to temporal integration of speed with age.

Other studies have shown age-related decline in sensitivity to 'global motion', using stimuli that involve integrating visual motion information over time into coherent moving objects (Atchley & Andersen, 1998; Betts, Sekuler, & Bennett, 2007; Billino, Bremmer, & Gegenfurtner, 2008; Gilmore, Wenk, Naylor, & Stuve, 1992; Kline, Scialfa, Lyman, & Schieber, 1990; Snowden & Kavanagh, 2006; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991; Wojciechowski, Trick, & Steinman, 1995). Motion coherence sensitivity is often measured using a random dot kinematograms (RDK), a technique first introduced by Newsome and Pare (1988). Here, observers are presented with stimuli containing a number of individual dots that can be move independently of each other. Signal dots move in a coherent direction while noise dots move in random directions and sometimes, random speeds. There are a number of ways in which the noise can be presented, for example, the dots can be replotted in random positions in each new frame or random-walk method, where the dots move with a set displacement from frame to frame (Scase, Braddick & Raymond, 1996). The percentage of signal dots is manipulated to determine the coherence threshold of the observers. In some tasks, observers are asked to indicate which direction the signal was going and in others they are asked to differentiate a noise-only pattern from one containing signal and noise dots.

The rate of motion coherence decline in the older adults has been shown to vary, with studies reporting declines of 1% per decade (Trick & Silverman, 1991) to 0.4% per decade (Tran, Silverman, Zimmerman, & Feldon, 1998). Gilmore et al. (1992), in a direct comparison of young (<25years) and old (>60years) adults, found motion coherence thresholds in the older group were double that reported in the younger group. Wojcichowski et al. (1995) measured coherence thresholds at stimulus speed of 28°/s for five locations in the visual field, one in the central fovea, the other four displaced 18° from fovea (nasal, temporal, superior and inferior). Motion sensitivity varied as function of test location, but the largest absolute difference between age groups was reported in the central location. Atchley & Anderson (1998) also investigated motion thresholds at various eccentricities (0°, 10°, 20°, and 40°) using two stimulus speeds (4.8°/s and 22 °/s). In contrast to Wojcichowski et al. (1995), they report ageing effects at all eccentricities at the faster speed of 22°/s, but only in the fovea for speed 4.8°/s. Andersen & Atchley (1995) also reported higher coherence thresholds in older adults at a stimulus speed of 2.8°/s, again presented centrally. These findings imply that for a range of speeds, there is an age-related decline in motion coherence thresholds for centrally displayed stimuli. However, this age-effect reduces for increasingly peripheral stimuli moving at faster speeds.

In a recent study, Bennett et al. (2007) found that by increasing stimulus duration from 75ms to 470ms, all their participants ranging in age from 23 to 81 years, showed improved sensitivity to coherent motion. This is similar to Raghuram et al. (2005) findings in the speed discrimination task, where

observers' motion sensitivity increased with stimulus duration. Bennett et al. also showed that increased stimulus duration correlated with an observed increase in the accuracy of perceived direction. An age-related decrease in coherent motion sensitivity and accuracy at identifying directional movement was particularly significant for observers over the age of 70 years. While these studies have found age-effects across a range of speeds, Snowden & Kavanagh (2006) only reported age-related decline during motion coherence for the slow speeds of 0.5 °/s and 1°/s, but not for faster speeds 2 °/s and 4 °/s. In combining the results across speed, direction, and coherence experiments, there appears to be a relationship between age-effects in motion sensitivity and the duration and speed of stimulus speed presented.

There has also been mixed results with relation to observed gender effects and motion sensitivity. For instance, a number of studies have shown that older women are significantly worse at discriminating speed (Norman et al., 2003; Raghuram et al., 2005) and coherent motion (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Gilmore et al., 1992; Schieber, Hiris, White, Williams, & Brannan, 1990) compared to older men. Conversely, Tran et al. (1998) and Billino et al. (2008) in a motion coherence task could find no difference in psychophysical thresholds between men and women. Equally, for contrast sensitivity, Owsley et al (1983) reported no sex differences for stationary and moving gratings. Tang & Zhou (2009) noted age differences in contrast sensitivity for first and second order stimuli, but gender was not a significant factor.

Not all ageing studies show a decline in motion perception. For example, Brown & Bowman (1987) failed to find a significant difference in speed discrimination thresholds between young and old participants. In this study, observers were asked to judge whether a vertically moving single target moved faster than one standard speed. Meanwhile, Betts, Taylor, Sekuler, & Bennett (2005) in a detection task using large, high contrast patterns found that older observers performed better than younger observers. Normally, it is more difficult for observers to discriminate motion of high contrast patterns, which increase in size. This is referred to as spatial suppression (Tadin et al. 2003). Betts et al. (2005) argued that the improvement in older observers is linked to reduced spatial suppression. In senescent monkeys, a decline in spatial suppression resulted from reduced efficacy of GABA-mediated cortical inhibition (Leventhal, Wang, Pu, Zhou, & Ma, 2003).

Betts et al. (2005) also showed that reduced retinal luminance had no influence on direction discrimination thresholds of older observers. In a different group of younger observers, they repeated the motion sensitivity task using a range of stimuli luminances (5.6cd/m^{-2} , 27.7cd/m^{-2} and 65cd/m^{-2}). Even for the lowest stimuli luminance, the younger observers' were less sensitive to the large, high contrast stimuli than the older adults. Similarly, Wojciechowski et al. (1995) found no effect of stimulus luminance in their motion coherence task.

In summary, the weight of the evidence suggests that there is an age-related decline in retinal motion sensitivity during speed, direction and motion

coherence tasks. The extent of age-related decline appears to be dependent on both stimulus duration and speed, where most ageing effects are found for slower moving stimuli at shorter durations. There is also evidence that stimuli presented centrally show more ageing effects than those in the periphery. Meanwhile, the effect of gender on motion sensitivity remains inconclusive.

1.1.2. Age-related decline: Possible Explanations

Both neural and optical factors contribute to the age-related deterioration in many visual capabilities, including differential luminance thresholds, dark adaptation, colour discrimination and spatial resolution (Spear, 1993; Weale, 1963). With increasing age, the optics of the eye undergoes a series of physical change, including presbyopia; a loss in accommodative amplitude, senile miosis; a decrease in pupil size as well as increased lenticular density and lenticular yellowing (Weale, 1963). Reports have also shown increased optical density and light scattering, even in the absence of cataracts. Meanwhile other optical structures avoid the signs of ageing, including the cornea and aqueous humour, which remain clear (Weale, 1992).

Motion sensitivity has been shown to be unaffected by optical degradation (Spear, 1993). Studies have also shown that reduced retinal illuminance in younger observers to match that of older observers, failed to replicate an age-related reduction in speed and coherence thresholds (Betts et al., 2005; Norman et al., 2003; Wojciechowski et al., 1995). If ageing optics play only a minor role in age-related losses in motion sensitivity, then motion perception

deficits of older observers are likely to be the result from degeneration or dysfunction in the central visual areas.

1.1.2.1. Visual pathway

The central visual pathway is composed of neural structures that control our perception of motion, namely the primary visual cortex (V1), the middle temporal visual area (MT), the medial superior temporal visual area (MST) Maunsell & Newsome (1987). Before I discuss age-related neural change that may influence retinal motion perception, I will briefly outline these more important structures.

Striate Cortex / Primary visual Cortex

The striate cortex, also known as the V1 or primary visual cortex, receives projects from both the magnocellular (M) and parvocellular (P) pathways via the lateral geniculate nucleus (LGN). The parvocellular pathway is reportedly involved in high acuity and colour vision. In contrast, the magnocellular (M) pathway is associated with achromatic, low vision, movement and luminance detection. The striate cortex contains 100 million cells arranged in layers whose receptive fields are known to respond to edge orientation and the motion of lines, bars and edges (Hubel & Wiesel, 1968). Each V1 cell maximally responds to a component of motion, which moves in a direction perpendicular to its preferred orientation. Motion parallel to the preferred orientation exhibits little or no response. Therefore, during object motion, the V1 neurons can only respond to the local motion of one-dimensional features in the image. This is often referred to as the 'aperture problem' (Adelson &

Movshon, 1982). The receptive fields of the striate cells are topographically arranged according to the contralateral visual field, with a foveal bias with 80% of the cells represented the central 10° of the visual field (van Essen, Newsome, & Maunsell, 1984).

Extra-striate Cortex (MT/MST)

Projections from V1 continue into the extrastriate cortex, which divide into two important neural areas, Middle temporal area (MT) and Medial Superior Temporal area (MST). Area MT consists of dense myelination, and similar to the striate cortex has the contralateral visual field represented topographically (Zeki, 1974). It receives projections from the striate cortex, prominently by the M pathway (Maunsell, Nealey, & DePriest, 1990). MST lies adjacent to MT in the occipital-temporal-parietal junction (Dukelow et al., 2001).

The receptive field of MT neurons although 10 times larger than those in the striate cortex (Albright & Desimone, 1987), show the same pattern of increased size with eccentricity. Similar results were reported for human striate and extra-striate cortex using fMRI (Smith, Singh, Williams, & Greenlee, 2001). These neurons are particularly sensitive to first order motion, which includes speed and direction of moving stimuli (Albright, 1984; Baker, Petersen, Newsome, & Allman, 1981; Dubner & Zeki, 1971; Maunsell & van Essen, 1983; Snowden, Treue, & Andersen, 1992). By lesioning MT, studies have shown disruption in the detection and discrimination of visual motion (Newsome & Pare, 1988; Siegel & Andersen, 1986). MT contains two types of directional-tuned neurons, namely component and pattern cells. Movshon,

Adelson, Gizzi, & Newsome (1986) introduced plaid stimuli to distinguish component from pattern cells. These plaids form by intersecting two sinusoidal gratings, each moving in different direction. While the component cells respond to one of the individually moving gratings, as seen in V1, pattern cells respond to the combined direction of the two moving plaid patterns (Adelson & Movshon, 1982). Animal studies have shown that while virtually all the neurons in the striate cortex consist of component cells, ~25% of MT neurons are selective to pattern motion (Albright, 1984; Movshon et al. 1986; Rodman & Albright, 1989).

MST neurons differ slightly from those found in MT. Macaque studies have shown that MST neurons are sensitive to stimulus that extends beyond their receptive fields, which can influence how different or conflicting retinal stimuli are processed (Eifuku & Wurtz, 1998). MST neurons are also capable of encoding eye-movement information thus allowing motion to be encoded in head-centred co-ordinates (Duffy & Wurtz, 1995; Ilg, Schumann, & Thier, 2004; Page & Duffy, 2003). In an fMRI study, Smith, Ball, Williams, & Singh (2006) measured sensitivity of human MT and MST to different types of optic flow including translation, rotation, and expansion. Results showed larger activation in MST for motion stimuli containing global expansion and rotation compared to MT. Therefore, MST is largely associated with the perception of motion during smooth pursuit as it combines retinal and extra-retinal signals during head-centred motion (Dursteler & Wurtz, 1988; Newsome et al., 1988; Rudolph & Pasternak, 1999).

1.1.2.2. Age-related decline in the visual pathway

Cell degeneration within the central visual pathway was first proposed to explain age-related decline observed in retinal motion sensitivity (Weale, 1975). Subsequent studies however revealed that neuronal death did not occur in the primary visual cortex, that in fact the number of neurons remained stable throughout the lifespan (Ahmad & Spear, 1993; Morrison & Hof, 1997, 2007; Peters, Morrison, Rosene, & Hyman, 1998). In view of these findings, researchers began to investigate cell dysfunction. Using single-neuron in vivo electrophysiology, Schmolesky, Wang, Pu, & Leventhal (2000) compared the stimulus selectivity of cells V1 in young adult and very old macaque monkeys and found that decreased selectivity and increased excitability of direction-oriented cells of old animals. Similar findings were reported for ageing cats, where V1 neurons showed decreased stimulus selectivity (Hua et al., 2006; Yu, Wang, Li, Zhou, & Leventhal, 2006).

Leventhal et al. (2003) reported that a degradation of GABA-mediated intracortical inhibition specifically could explain these age-related changes in cell activity. By administering of GABA and muscimol (GABA agonist) to ageing monkeys, they showed an improvement in visual function. Here the V1 cells treated with GABA and GABA-agonists exhibited similar response patterns to young cells. Meanwhile, administration of the GABA antagonist bicuculline produced larger inhibition in young cells when compared to the old cells, again indicating a dysfunction in the GABAergic inhibition in older macaques.

Later in visual pathway, MT contains a high proportion of direction-selective cells. Using in-vivo single-cell recording, Liang et al. (2008) showed that the cell direction selectivity reduces in older macaques. Furthermore, loss of direction selectivity in V1 was comparatively less than the reports for MT. Interestingly, this loss was more pronounced for pattern cells in MT in comparison to component cells. As already discussed, pattern cells are located in the human MT (Huk & Heeger, 2002) and are associated with our ability to detect coherent motion as they detect the direction of moving objects independently of their particular spatial pattern (Albright & Stoner, 1995). Liang et al. (2008) proposed that the reduction in GABA inhibition in the ageing brain weakens the pattern cells response to the overall direction of a moving stimulus (Rust, Mante, Simoncelli, & Movshon, 2006; Rust, Schwartz, Movshon, & Simoncelli, 2005). This subsequently reduces the proportion of pattern cells in old MT. Reduced efficacy of cortical GABA inhibition has also been suggested as an explanation to why older observers were better at detecting large high-contrast stimuli compared to younger observers (Betts et al., 2005).

1.1.2.3. Neuronal tuning and the 'Oblique effect'

Another example of how neuronal tuning can influence retinal motion sensitivity is the 'oblique effect'. This generally describes a decrease in orientation sensitivity for oblique directions compared to cardinal directions (Appelle, 1972; Coletta, Segu, & Tiana, 1993; Heeley & Buchanan-Smith, 1990; Matin, Rubsamen, & Vannata, 1987; Orban, Vandebussche, & Vogels, 1984). The oblique effect has also been shown for motion discrimination (Ball

& Sekuler, 1980; Coletta, Segu, & Tiana, 1993; Gros, Blake, & Hiris, 1998; Matthews & Welch, 1997).

To explain the oblique effect in direction discrimination, Gros et al. (1998) suggested that neurons that are maximally responsive to cardinal directions are more narrowly tuned compared to oblique-tuned neurons. However, neurophysiological evidence for orientation stimuli indicates that this anisotropy results from a reduction in cells tuned to oblique representations relative to cardinal representations within the early visual cortex such as V1 (Li, Peterson, & Freeman, 2003; Mansfield, 1974). This has been supported using neuroimaging techniques. Furmanski & Engel (2000) used functional magnetic resonance imaging (fMRI) to measure the responses to oriented stimuli in V1. Results showed that an asymmetry in neural activity, with larger responses for cardinal stimuli compared to oblique, activity, which co-related with behavioural results.

Brain areas MT and MST are also associated with oblique anisotropies. Heeley & Buchanan-Smith (1992) measured retinal orientation discrimination thresholds using 'plaid' stimuli, which consisted of two super-imposed independent drifting sine-wave gratings. Higher orientation thresholds were found for plaids whose global motion drifted in an oblique direction, irrespective of the individual components, which drifted in cardinal directions. This finding suggests that pattern cells, located further along the visual pathway in MT and MST are sensitive to the oblique effect (Movshon et al., 1986). There is evidence to suggest that GABAergic inhibition influences

direction sensitivity by increasing the tuning properties of neurons. In a recent study, Edden et al. (2009) showed that observers' individual anisotropy in an orientation discrimination task correlated with their resting GABA concentration. This supports ageing literature, where a reduction in GABA inhibition is thought to explain the decline in retinal motion sensitivity in older observers (Leventhal et al. 2003).

1.1.3. Ageing and models of motion perception

1.1.3.1. Two-system models of motion perception

A number of models have been proposed to explain motion detection with reference to the response of direction selective neurons in the visual system. One of the earlier examples introduced the concept of a two-system model of motion perception, consisting of short-range and long-range motion (Anstis, 1980, Braddick, 1974, 1980). The short-range motion system referred to motion detected using spatiotemporal variations in luminance over small displacements and small temporal intervals. Alternatively, the long-range system referred to motion detected using higher-order stimulus attributes such as contrast over larger spatio-temporal displacements and longer intervals (Albright & Stoner, 1995). This model based on a stimulus complexity was limited, as subsequent psychophysical experiments failed to find any difference between motion detection for small versus large spatio-temporal displacements (Cavanagh & Mather, 1989). As an alternative to the short/long range distinction, Cavanagh & Mather (1989) proposed a two-system theory based on the type of image contrast that defines a moving feature. They

defined the two motion subsystems as “first-order” and “second-order”. The first-order system was described as sensitive to changes in luminance or colour whereas the second-order system was sensitive to “secondary” dimensions such as texture, binocular disparity, or luminance contrast modulation. There is both psychophysical (Derrington & Badcock, 1985; Edwards & Badcock, 1995; Hammett, Ledgeway, & Smith, 1993; Ledgeway & Smith, 1994; Lu & Sperling, 1995; Mather & West, 1993) and neurophysiological evidence (Zhou & Baker, 1993, 1994, 1996) to suggest that first-order motion is detected independently from motion defined by second-order cues. As the next section describes, the computational models that describe the mechanisms of first and second order motion are also distinct.

Co-relation model & Fourier Energy model

The mechanism of first-order motion can be explained in terms of co-relation and Fourier energy models. The co-relation or the ‘Reichardt detector’ model was the first developed by Hassenstein and Reichardt (1959). The model proposes that motion is computed from two inputs that sample the visual stimulus using two spatially separate receptor fields. This is illustrated in figure 1.1, where there are two inputs labeled A and B with corresponding receptive fields or linear spatiotemporal filters (SF_A and SF_B) displaced in space and time. The Reichardt detector model operates on a delay-and-compare mechanism. In the R (right) subunit of the detector, the output of SF_A at A is delayed by a temporal delay filter TF that is then multiplied by the direct

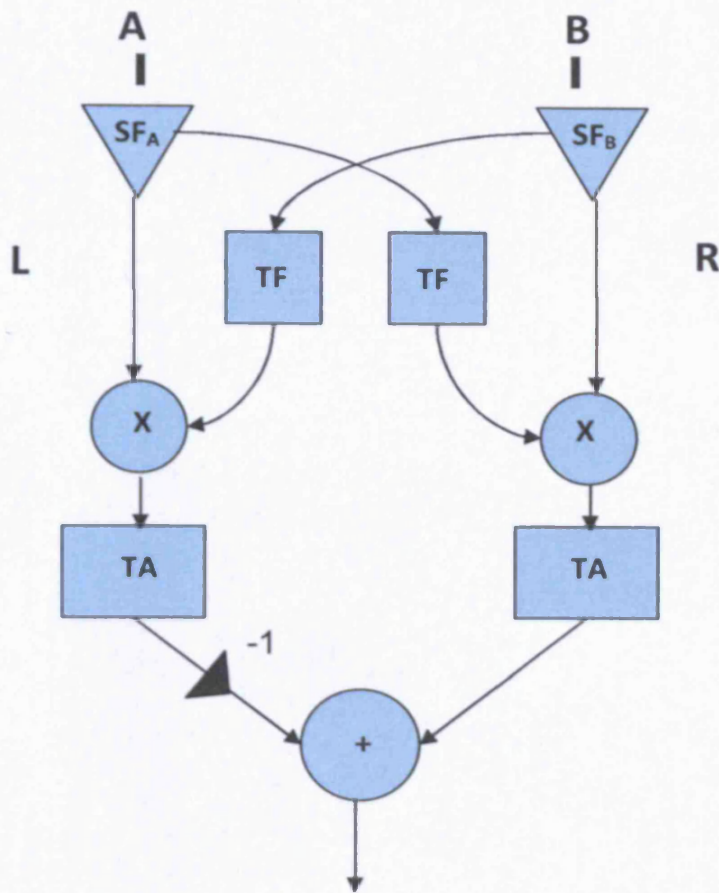


Figure 1.1. Elaborated Reichardt Detector: Two inputs labeled A and B with corresponding linear spatiotemporal filters (SF_A and SF_B) displaced in space and time. In the R (right) subunit of the detector, the output of SF_A at A is delayed by a temporal delay filter TF that is then multiplied (X) by the direct output of SF_B at B. This delays the luminance signal as measured by on photoreceptor temporal filter and compares it by multiplying it with the signal derived from a neighboring receptor. The opposite occurs in the L subunit of the detector. TA (Temporal averaging) represents a low pass temporal filter. Outputs greater than zero indicate stimulus motion from A to B; outputs less than zero indicate stimulus motion from B to A (Lu & Sperling, 2001)

output of SF_B at B. This delays the luminance signal as measured by on photoreceptor temporal filter and compares it by multiplying it with the signal derived from a neighboring receptor. The opposite occurs in the L subunit of the detector. TA (Temporal averaging) represents a low pass temporal filter. By repeating the process in a mirror-symmetrical fashion and subtracting the output signals of both subunits leads to a neuronal response that is directionally selective. Outputs greater than zero indicate stimulus motion from A to B; outputs less than zero indicate stimulus motion from B to A. The Reichardt model was experimentally verified in many species (eg. Barlow & Levick, 1965; Ganz & Felder, 1984) and adapted for human vision (van Santen & Sperling, 1984).

"Motion energy" models consist of spatio-temporal tuned filters oriented in frequency space, which allow the measurement of power in the oriented Fourier transform of the stimulus (Adelson & Bergen, 1985; Watson & Ahmuda, 1985). These oriented filters are produced by linearly combining separate spatial and temporal filters profiles. For each direction, two direction selective spatio-temporal filters are generated, one even and one odd, to produce the even and odd responses. Each of the responses contains phase dependent oscillations, but when combined in a quadrature sum (a pair of filters whose responses are 90 deg out of phase) produces a directional motion energy measure (Adelson & Berger, 1985). Therefore, the sum of the squares of these filters is called the motion energy. The difference in the signal for the two directions is called the opponent energy. It should be noted

that the computations that underlie motion energy and correlation models are formally equivalent to one another (Van Santen & Sperling, 1985),

Slow and Fast Temporal processes

The spatiotemporal filters divide the incoming spatial-temporal signal into a set of energy bands. In human vision, temporal frequency tuning appears to be much broader than is spatial frequency tuning. Psychophysical evidence suggests that the temporal frequency axis is broken up into only two or three bands, while there are seven or more bands of spatial frequency selective channels (Bergen & Wilson, 1985; Thompson, 1984; Watson & Robson, 1981). For example, Hess and Snowden (1992) investigated temporal processing using a masking paradigm. They presented observers with a probe that was set just about detection threshold. The probe consisted of a grating that reversed in contrast at a particular temporal frequency. The contrast of a mask was then set at one of a range of temporal frequencies. They found evidence of three temporal channels, where the mask did not interfere with the detection of the probe, including a low pass channel, a band-pass channel peaking at around 10Hz and another peaking at around 18 Hz. However, there is debate as to the existence of the third temporal channel (Hammett & Smith, 1992).

Whether there are two or three temporal filters, there is a consensus within motion adaptation literature that there are slow and fast temporal processes. For example, van der Smagt, Verstraten, & van de Grind (1999) reported a new transparent motion after effect which revealed simultaneous adaptation in

independent motion channels coded for slow and fast velocities. Typically, when an observer adapts to a moving stimulus followed by a stationary pattern, they perceive motion of the stationary pattern in the opposite direction. This phenomenon is referred to as the motion after effect (MAE). When observers adapt to two superimposed group of dots moving in different directions or speeds, they perceive the adapting stimulus as two segregated transparent surfaces, but the resulting MAE results in a weighted sum of the adaptation vectors. When the transparent adapting stimulus is tested using a static test patterns, the MAE is strongest during slow motion. Alternatively when tested using a dynamic test pattern, the MAE is stronger during fast speeds.

van der Smagt et al. (1999) argue this speed difference between 'static MAE' and dynamic MAE' reveals two separate speed-tuned motion sensor populations which correspond to distinct slow and fast motion channels. They tested this by recording observers reported MAE direction, after adapting to orthogonally directed transparent motion. Adapting stimulus was divided into a) slow speeds only (1.3°/s and 4°/s) where the static MAE is stronger than dynamic MAE, b) fast speeds only (12°/s and 36°/s) where dynamic MAE is stronger than static MAE and c) mixed slow and fast speeds (4°/s and 12°/s). The test frequency pattern varied across trials from 0 to 90 Hz. Results showed for slow and fast conditions that observers reported the MAE as the weighted vector average of the adapting patterns. In the mixed speed condition, the reported MAE corresponded with the direction opposite the fast adapting component for faster test frequencies >20Hz. For lower frequencies,

the reported MAE corresponded with the direction opposite the slow adaptation component. No intermediate directions were reported. van der Smagt et al (1999) conclude that their results provide evidence for independent underlying neural substrates for slow and fast channels of motion perception.

Second and Third Motion Channels

As previously mentioned, second-order motion or non-Fourier motion can be distinguished from first order motion in that it exploits texture information. Second-order motion is thought to be invisible to standard Fourier Energy Models, therefore Chubb & Sperling (1988) proposed a non-fourier model to account for the perception of second-order motion, which involves a form of rectification of first-order input. In addition to the luminance defined Fourier and texture defined non-Fourier motion channels, Lu and Sperling, 1995 suggest a third motion channel. The third-order motion or feature tracking system computes correspondences among features by using top down attention-driven processes as well as bottom-up components and is thought to correspond to the long-range motion system introduced by Braddick (1980).

1.1.3.2. Ageing effects on motion type

As discussed in the previous section there is psychophysical and physiological evidence to suggest that two separate cortical mechanisms underlie the initial processing of first-order and second-order stimuli (eg. Ledgeway & Smith, 1994). It has been shown that first and second order motion mechanisms work in parallel from visual area V1 to area MT (Wilso,

Ferrera & Yo, 1992) while second-order motion requires an additional processing step where rectification occurs (Chubb & Sperling, 1988; Wilson et al., 1992). This is supported by an fMRI study, which reported initial first-order motion activation in the visual cortex in V1 and initial second-order motion activation in V3. Activation in MT was observed for both first and second order motion (Smith, Greenlee, Singh, Kraemer & Hennig, 1998).

Habak & Faubert (2000) argue that an increased number of cortical analysis steps undertaken by second-order mechanisms compared to first-order leads to an age-related decline in the perception of second-order motion sensitivity. They measured motion thresholds with first-order and second-order stimuli in younger and older observers and reported a significant increase in second-order thresholds in older observers. Habak & Faubert (2000) suggest that the age-related decrease in motion sensitivity to second-order stimuli compared to first-order motion sensitivity highlights the difference in their underlying mechanisms. An effect, which may be explained by the age-related physiological changes, discussed in section 1.1.2.2. Age-related changes in the visual pathway potentially increase baseline noise, contributing to a reduction in the sensitivity of the motion perception mechanisms. Habak & Faubert (200) discuss how age-related decreases in functionality may have more of an impact when there is a higher level of cortical integration, for example cortical mechanisms underlying the perception of second-order motion compared to first-order motion.

1.2. Motion perception and eye-movement

The psychophysical and neurophysiological studies outlined in section 1.1.2 provide strong evidence that there is an age-related decline in retinal motion sensitivity. While this might be the case, there is little information regarding how the ageing process might influence motion perception during eye-movements. As mentioned earlier, eye-movements are fundamental for everyday mobility in how we determine object velocity and self-motion as we navigate through the environment. Of particular interest to this thesis, is the role of smooth pursuit eye-movements and extra-retinal signalling in motion perception, which I will now discuss in turn.

1.2.1. Smooth pursuit eye-movements

Smooth pursuit eye-movements exist to track the position of a moving object. They operate to compensate for retinal image displacement caused by head or body rotations by re-centring the image on to the fovea, thus enabling the extraction of good quality spatial information. The central fovea is tightly packed with cones whose spatial and chromatic resolution is much higher than the rods scattered further out in the periphery. The smooth pursuit of a moving stimulus typically has an initiation latency of 100ms following pursuit onset, during which time smooth pursuit is not controlled by internally generated feedback but directly by visual motion information (Rashbass, 1961). This initial period is the open-loop phase (see Figure 1.2). Pursuit maintenance occurs once the speed of smooth pursuit eye-movement matches the speed of the moving target; the observer can then start

observing their eye-movement relative to the target (Barnes & Asselman, 1991; Becker & Fuchs, 1985; Burke & Barnes, 2008). The use of visual feedback to maintain smooth pursuit is the closed-loop phase. Smooth pursuit accuracy is often reported as a pursuit gain, which is defined as the ratio of smooth pursuit velocity over target velocity. High pursuit gains have been reported for target speeds up to 100°/s but optimal performance is for target speeds ranging between 15°/s -30°/s (Ettinger et al., 2003; Meyer, Lasker, & Robinson, 1985). Catch-up saccades often occur to correct position errors due to reduced eye velocity (Van Gelder, Lebedev, & Tsui, 1997).

Smooth pursuit can also occur without any retinal image motion. For instance, observers can make smooth pursuit eye movements to a moving limb in complete darkness, using proprioceptive information about the limb position (Mather & Lackner, 1981; Steinbach, 1968). Moreover, Steinbach (1978) in a study, asked observers to track an ellipsoid as it moved horizontally behind a narrow vertical slit. The eclipse consisted of two spots moving up and down vertically, thus creating vertical retinal motion, but the illusory percept was

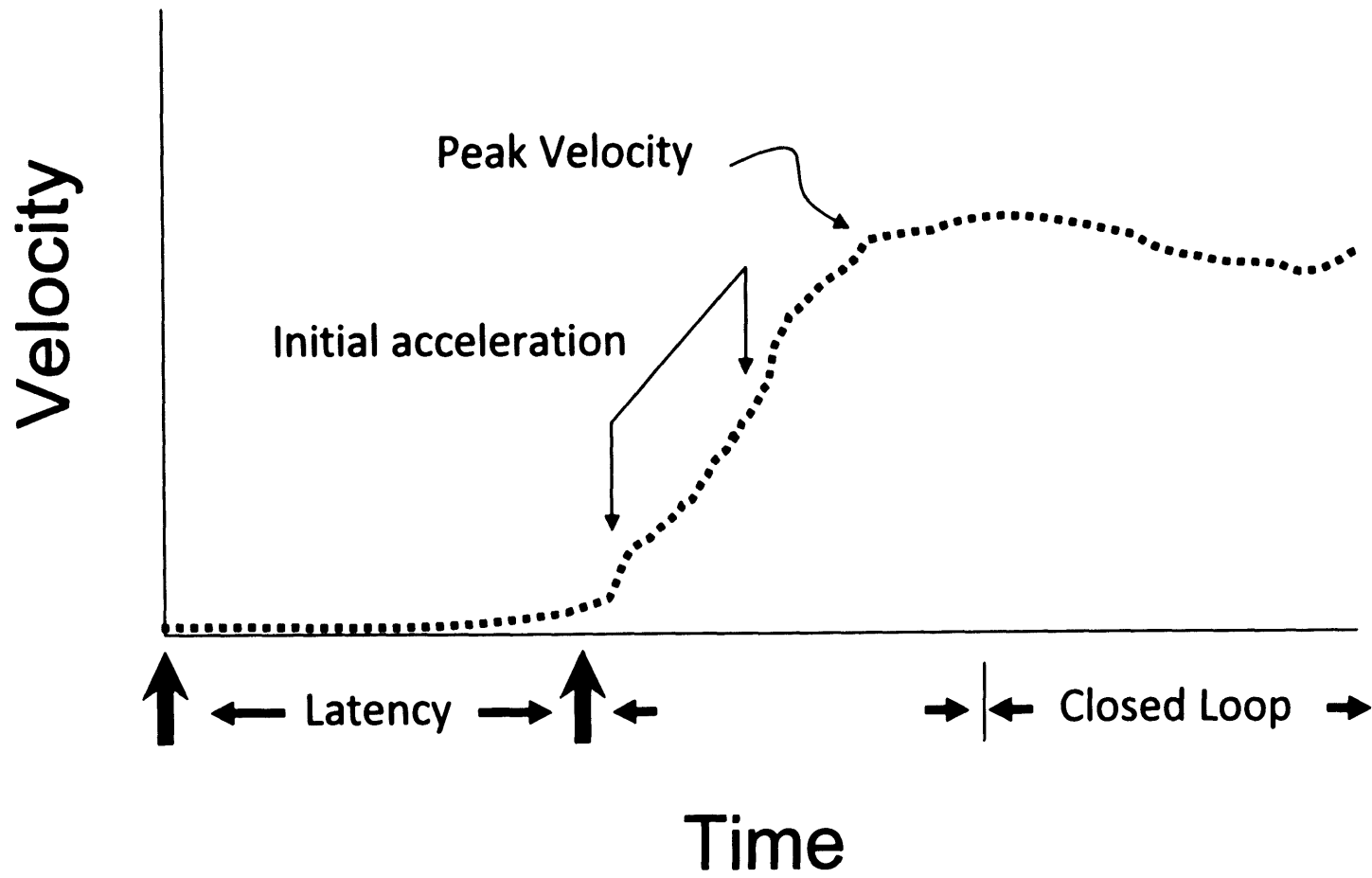


Figure 1.2. Smooth pursuit time-line

that of horizontal motion. Results showed that when the observers perceived the ellipsoid to move behind the slit, horizontal eye-movements were recorded. In contrast, when the observers reported seeing the two spots move up and down, vertical eye-movements were recorded. In the same paper, Steinbach (1978) also reported that observers made horizontal eye-movements when asked to track the centre of a rotating wheel, irrespective of the circular motion created by the retinal stimulus.

The predictability of motion has an important impact on smooth pursuit behaviour. An expectation of target movement can elicit low velocity anticipatory drifts (Kowler & Steinman 1979). For targets whose motion onset and direction is unknown, these anticipatory drifts tend to remain slow at speeds less than $1^\circ/\text{s}$, however this is proportional to target velocity. For example, Kowler & Steinman (1979) observed anticipatory velocities of approximately 25% of a slow expected target velocity ($0.68^\circ/\text{s}$) compared to Becker & Fuch (1985) who observed anticipatory velocities of 10% for faster target motion of $10^\circ/\text{s}$. Once the target starts to move, a predictive acceleration of the eye occurs. Becker & Fuch (1985) measured smooth pursuit behaviour over a series of predictable and unpredictable motion trials. In some trials where target motion was unknown, the target disappeared when observers expected it to move. Irrespective of the lack of target, predictive acceleration of the eye occurred reaching $5^\circ/\text{s}$ within 300ms. This acceleration rate was found to be independent of target velocities. Moreover, the predictive acceleration of the eye can exceed target velocity if there is an unexpected reduction in target motion (Kao & Morrow, 1994).

It has also been suggested that anticipatory drifts and accelerations of the eye are more reliant on perceived motion rather than retinal image displacement alone (Boman and Hotson, 1988; Boman and Hotson, 1989). Using an apparent motion stimulus, Boman and Hotson (1988) detected anticipatory eye-movements for visually guided saccades when the eye-movement and perceived motion were in the same direction. No anticipatory eye-movements were detected when the saccades and perceived motion were orthogonal.

Physiological evidence suggests that smooth pursuit and the motion perception share a common motion processing stage. Studies using micro stimulation and lesions have highlighted MT and MST as key neural areas involved in motion perception and smooth pursuit perception (Britten & van Wezel, 1998; Celebrini & Newsome, 1995; Dursteler, Wurtz, & Newsome, 1987; Dürsteler & Wurtz, 1988; Komatsu & Wurtz, 1989; Newsome, Wurtz, Dursteler, & Mikami, 1985; Newsome & Pare, 1988; Pasternak & Merigan 1994; Rudolph & Pasternak, 1999; Salzman, Britten, & Newsome, 1990; Salzman, Murasugi, Britten, & Newsome, 1992). For example, Newsome et al. (1985a) chemically lesioned MT using ibotenic acid and studied how this affected eye-movements made in response to moving as opposed to stationary targets. They found that the monkey's eye-movement accuracy decreased as it failed to match the speed of its eye to the speed of the moving target. Equally, the monkey's ability to adjust the amplitude of a saccadic eye-movement to compensate for target motion was impaired. This is in contrast to stationary targets which were unaffected by MT lesions. In a subsequent

study, the same investigators results showed that saccade deficits following the injections of ibotenic acid were similar to saccadic deficits following surgical ablation of striate cortex (Mohler & Wurtz, 1977), however the time course of recovery was much quicker for the injections (Newsome et al., 1985b). Furthermore, MST lesions cause a disruption in steady-state pursuit towards the side of the lesion (Dursteler et al., 1987).

1.2.1. Eye-movement compensation

During a smooth pursuit eye-movement, retinal image motion of stationary objects sweeps across the retina, yet we do not normally perceive those objects as moving. In contrast, a pursued object if accurately followed will remain relatively fixed stationary on the retina, yet we perceive this object to move. How the visual system extracts real world motion as well as maintain visual stability in the face of eye rotations has been of interest for many years.

A general solution to this problem is to use object and self-movement (or eye-movement) information in order to factor out retinal motion related to self-movement. This can be achieved in a number ways. For example, Brenner & van den Berg (1996) suggest we compensate for the effect of eye-movement by using patterns of image motion (retinal flow) to judge object movement with respect to the scene. In this study, observers were asked to judge the velocity of a target before and during simulated ego-motion. During stimulated motion, target velocity was largely determined by the retinal motion relative to the most distant background object. These results show that retinal motion can help compensate for self-motion by providing an estimate of the objects

movement relative to the observer. Another method of distinguishing self-motion from object motion is flow-parsing. As we travel through the environment, optic flow provides the observer with a three-dimensional layout of the environment and a direction of heading. Rushton & Warren (2005) ‘flow-parsing hypothesis’ argues that optic flow detectors can act as filters which parse retinal motion created during optic flow into motions related to self-motion and object motion. In order to achieve a correct estimate of object motion, self-motion is subtracted from the overall retinal flow.

Along with estimates of retinal motion, extra-retinal signals can also be used to judge the motion of the pursued target. These are non-visual eye velocity estimates emanating from the motor system. Studying how extra-retinal motion signals change as a function of age is central to the current thesis will discuss them in detail in the following section.

1.2.2. Extra-retinal motion signals

Helmholtz (1867) was first to propose that motor signals sent to the eye-muscles provided an observer with eye-movement information. He concluded that this extra-retinal information was able to cancel out retinal image motion created from eye-movements themselves, allowing the observer to perceive a stable visual world. This is illustrated in figure 1.3; the head is shown to be stationary, therefore when the eye pursues the target at a certain velocity, the retinal image of the earth-stationary background moves in equal and opposite velocity. By adding the extra-retinal estimate (E) to the retinal image motion (R), the background motion equates to zero (given that extra-retinal and

retinal estimates have the same accuracy). By combining estimates of retinal motion with eye-velocity signals, this yields object motion with respect to the head (Freeman & Banks, 1998; Freeman, 2001; Souman & Freeman, 2008; Wertheim, 1987; 1994).

The existence of an extra-retinal signal proposed by Helmholtz has been supported by a number of behavioural studies. For example, in a classic experiment, Von Holst & Mittelstadt (1950; also see Von Holst, 1954), surgically rotated the head of a fly by 180°, so that the position of its right and left eyes were interchanged. When the fly attempted to move on its own, it would start to circle continuously. Normally when a fly moves to the right, there is retinal displacement to the left, and *visa versa*. Von Holst & Mittelstadt (1950) argued, due to spatial rearrangement of the eyes, the expected retinal displacement from the eye-movement signal, and the obtained retinal displacement did not match. The eye-movement signal in this case was referred to as *efference copy*. Subsequently, the fly compensated by moving its own body in the wrong direction to counteract the reversed retinal motion.

Sperry (1950) reported similar findings when he surgically inverted the eye of a fish. He observed that the fish swam in circles indefinitely in one direction, a

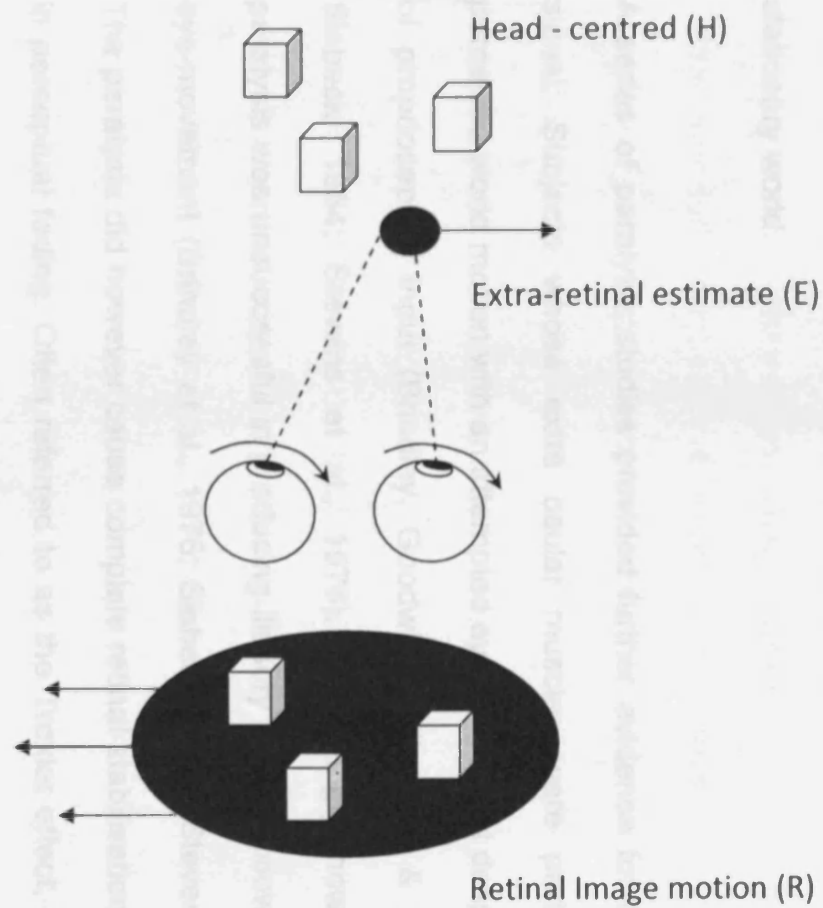


Figure 1.3. Image motion during eye-movement, where Head-centred motion (H)= Extra-retinal estimate (E) + Retinal Image motion (R). Eye-movement compensation allows background objects to remain stationary.

behaviour that was only recorded when the lights were on. In the dark, the fish returned to its normal swimming pattern. From this, Sperry concluded that the effects he observed were not due to brain damage but resulted from a problem in the internal monitoring of eye-movement, for which he coined the term '*corollary discharge*'. As described by Von Holst & Mittelstadt (1950), due to the inverted eye, the expected retinal displacement from the fish's eye-movement did not match the obtained retinal displacement, causing compensatory moving behaviour in the fish. Both these studies demonstrate the role of eye-movement or extra-retinal signals in the perception of a stationary world.

A series of paralysis studies provided further evidence for the 'extra-retinal signal. Subjects whose extra ocular muscles were partially paralysed, perceived world motion with an attempted eye-movement despite the absence of proprioceptive input (Brindley, Goodwin, Kulikowski, & Leighton, 1976; Siebeck, 1954; Stevens et al., 1976). Interestingly however, complete paralysis was unsuccessful in producing illusory motion following an intended eye-movement (Brindley et al., 1976; Siebeck, 1954; Stevens et al., 1976). The paralysis did however cause complete retinal stabilisation, which resulted in perceptual fading. Often referred to as the Troxler effect, it highlights that image motion is never completely stabilised on the retina because even during fixation our gaze is still disrupted by small involuntary movements which are necessary for visual perception (Ditchburn & Ginsborg, 1952; Martinez-conde, Macknik, & Hubel, 2004).

Bridgeman & Shark (1991) demonstrated the role of efference copy in visual guided behaviour using an eye-press method. Their subjects were asked to report the motion of a stationary target viewed by an unoccluded eye and pressed causing the eye to rotate when the other eye was occluded. By pressing on the fixated eye, the oculomotor system adds compensatory innervation to maintain the position of the target on the retina, and in turn causes the perception of motion. Bridgeman & Shark (1991) hypothesised that if the efference copy determined perceived motion, the amount of perceptual deviation reported by the observers should match position deviation of the occluded eye. This condition was compared to perceived motion reported when observers were asked to press the occluded eye which by changing ocular posture, altered proprioceptive inflow without changing efference copy. Results showed that changes in the efference copy dominate the perception of pointing and judging tasks.

As noted, visual stability can be achieved by adding eye-movement velocity and overall retinal stimulus velocity vector. The resulting vector sum is equal to 'real world' motion. A mismatch between an eye-velocity estimate and retinal image motion caused by the eye-movement can sometimes cause illusionary motion in the stationary world. An example of this is the Filehne illusion (Filehne, 1922). The Filehne illusion results from a pursuit eye-movement made over a stationary object, where the object is perceived to move in the opposite direction of the eye-movement. Haarmeier, Their, Repnow, & Petersen (1997) described a patient with bilateral extra striate cortex lesions who was unable to compensate for his eye-movements during

a Filehne illusion task. In the task, the observer was asked to pursue a target over a stationary background where the amount of background motion was manipulated until the observer perceived a stationary background. This is called the point of subjective stationarity (PSS) and refers to the amount of background motion that is equal and opposite to the direction of the Filehne illusion. Haarmeier et al. (1997) compared the patient with the lesion against normal observers in the Filehne illusion task. The lesion patient R.W. showed a large increase in PSS that co-related with eye-velocity speed. In other words, the patient perceived the stationary background to move at the same velocity of his own eye-movement because retinal slip created by pursuing the target was not compensated. This provides evidence that the extra-retinal signal plays a pivotal role in disentangling self-motion from real world motion.

1.2.3. Extra-retinal motion sensitivity and age

Very little research has addressed how extra-retinal motion signals change as a function of age. The current understanding of extra-retinal signals and age is limited to studies investigating perceptual bias. For example, Wertheim & Bekkering (1992) discuss extra-retinal motion signals and age with reference to the Filehne illusion. The illusion is thought to occur when the extra-retinal signal created by the pursuit eye-movement underestimates the speed of the eye when compared to the corresponding retinal signal (Mack & Herman, 1973; Wertheim, 1994). Wertheim & Bekkering (1992), using large low frequency gratings, measured the Filehne null velocities for short (<300ms) and long (>600ms) durations in old and young observers. For short durations, they found that the Filehne illusion inverted for older observers. This inverted

Filehne illusion suggests a reversal of the relationship between retinal and extra-retinal estimates, with the retinal signal now underestimated with respect to the extra-retinal eye-velocity signal.

The Aubert-Fleischl illusion occurs when moving objects appears to move slower when pursued (Aubert, 1886; Fleischl, 1882). An explanation for the Aubert-Fleischl illusion follows the same lines as the Filehne illusion. The perception of slower moving objects during pursuit reportedly results from an underestimate of the extra-retinal signal (Wertheim, 1994). Given the similar explanations for the two illusions, it is conceivable that older observers could perceive an identical inverted Aubert-Fleischl illusion for short durations. Freeman, Naji, & Margrain (2002) investigated this by comparing both illusions in an old and young group. Surprisingly, while Freeman et al. (2002) reported a similar age-related trend for the Filehne illusion, no effect of age was present during the Aubert-Fleischl illusion. This suggests that relative signal size cannot solely explain illusions perceived during smooth pursuit.

Both the Filehne and Aubert-Fleischl illusion estimate change in perceptual bias. In these cases, perceptual bias is thought to result from accuracy differences between extra-retinal signals that encode pursued target motion and retinal signals related to image motion. An alternative explanation suggests retinal and extra-retinal motion signals remain accurate, but are instead susceptible to variability during uncertainty. In a recent study, Freeman, Champion & Warren (2010) showed that perceptual bias in Aubert-Fleischl illusion resulted in differences between extra-retinal and retinal signal

uncertainty. Their Bayesian model suggests that the underlying signals measuring the motion of pursued targets are corrupted by greater levels of internal noise, with the noisier signal then being more greatly influenced by a zero-motion prior. In support of the model, Freeman et al. (2010) measured speed discrimination thresholds for standard speeds ($4^\circ/\text{s}$, $8^\circ/\text{s}$, and $12^\circ/\text{s}$) during fixation and pursuit. Results showed higher speed thresholds when observers were pursuing the stimulus compared to fixation.

Perceptual bias studies represent the current knowledge of how extra-retinal signals change as a function of age. Research has yet to address whether extra-retinal sensitivity is susceptible to age-related decline, which is surprising, given the ubiquitous role of smooth pursuit eye-movements in a host of everyday perceptual tasks. Understanding how younger and older observers discriminate speed and direction provides useful information on the precision of low-level motion mechanisms and possible ageing effects associated with them. Furthermore, it also investigates whether the precision of retinal and extra-retinal motion signals differentially affects motion perception. Thus, the aim of this thesis is to address the gap in the literature by comparing motion sensitivity during fixation and smooth pursuit in old and young observers in a series of psychophysical tasks.

1.3. Factors to affect Extra-retinal sensitivity

To understand how age might influence extra-retinal sensitivity, I will first consider two factors, oculomotor control and internal noise, and how these might influence motion sensitivity with and without pursuit. For all the

experiments outlined in the thesis, the observers viewed the stimuli in complete darkness. The velocity of the stimuli was ramped over the early portion of the presentation duration. This was to minimize motion on retina in the pursuit trials, so in this case extra-retinal signals should dominate the observers' judgements. Assuming that retinal and extra-retinal signals limit motion discrimination performance respectively in the fixation and pursuit conditions, then any differences in threshold will depend on the levels of internal noise associated with each signal and oculomotor precision. These are now discussed in turn.

1.3.1. Oculomotor control

Precision describes how well a response can be reproduced from trial to trial (Bevington, 1969). Assuming that the magnitude of the extra-retinal signal is directly proportionally with the velocity of the eye, oculomotor precision or *variability* may be an influential factor in how sensitive observers are to motion, with and without pursuit. Increased eye-movement variability could potentially increase motion sensitivity thresholds by making extra-retinal signals noisier.

Previous studies have demonstrated a close link between pursuit variability and motion discrimination. Eye-movement precision variability was first quantified by Kowler & McKee (1987) using an 'oculometric difference threshold' that corresponded to perceptual measures of variability. This allowed for a direct comparison between the precision of smooth pursuit and precision of sensory coding. They measured perceptual and oculomotor

velocity discrimination thresholds for a range of stimulus speeds. By converting the eye-movement responses into velocity judgements, the oculometric analysis generated an oculometric function that was comparable to the psychophysical function. Results showed that oculomotor difference thresholds were higher than perception thresholds during the initial 200ms open-loop period of target motion. However, approximately 600ms after target onset, in the closed-loop period, the oculomotor and psychophysical thresholds were comparable. Kowler & McKee (1987) argued that this similarity in oculomotor and perception thresholds was due to an equally precise sensory presentation of target velocity in both conditions. Gegenfurtner, Xing, Scott, & Hawken (2003), who reported similar speed discrimination thresholds during smooth pursuit and perception, confirmed their findings. Unlike Kowler & McKee (1987), however, they measured the oculomotor difference thresholds and perception thresholds on a trial-to-trial basis. In a subsequent study, Rashe & Gegenfurtner (2009) compared speed thresholds with pursuit variability in the initiation period of smooth pursuit and a longer period during the steady-state pursuit. As with Kowler & McKee (1987), pursuit variability was shown to be higher in the initiation phase, but match perceptual variability during steady-state pursuit in the closed loop period.

Oculomotor and psychophysical thresholds have also been shown to be proportional in direction judgement tasks. For example, Beutter & Stone (1998) presented observers with a plaid stimulus that generated perceptual errors by changing the shape of surrounding aperture (Beutter, Mulligan, &

Stone, 1996). The observers' task was to track the moving plaid and identify its direction as leftward, rightward, or straight down. In this case, perceived motion was biased towards the longer axis of the aperture. Beutter & Stone (1998) reported similar perceptual and psychophysical biases, although it was noted that the oculometric functions were generally shallower than the corresponding psychometric functions. This difference in slope was also present in a subsequent study. Beutter & Stone (2000) compared the perceived direction of motion and pursuit direction for a parallelogram moving behind vertical apertures. In this stimulus, the retinal motion from the visible individual lines remained vertical; however, Beutter & Stone (2000) reported that both perception and pursuit were biased towards global motion. Using random dot kinematograms, Watamaniuk & Heinen (1999) also showed that smooth pursuit direction precision and direction discrimination thresholds were similar across a range of direction noise.

The studies outlined above provide evidence for a link between pursuit variability and perception; however, the research tends to concentrate on the initial eye-velocity and its relationship to early retinal motion signals. Both of these occur in the open-loop phase of the eye movement. This differs from the experiments described in the thesis, which were designed to target the later 'closed-loop' portion of the eye movement.

With reference to ageing and oculomotor control, a recent study, Kolarik, Margrain & Freeman (2010) addressed eye-movement accuracy and precision in older and younger observers. For this, they identified two forms of

precision; namely 'shake' and 'drift'. Shake referred to short-term variability, and was calculated by taking the standard deviation of eye-velocities within psychophysical trials. Drift, on the other hand, measured long-term variability, and was computed as the standard deviation of pursuit gains across psychophysical trials. Kolarik et al. (2010) compared accuracy and precision for each age group while making deliberate or reflexive ocular-following eye-movements. They found that older observers were less precise at higher eye speeds in all measures of precision except for shake during the reflexive condition. In a follow-up experiment, they asked observers to pursue a moving target over a stationary background comprising of either dots or gratings. Again, older adults were less precise at faster pursuit eye-speeds. This precision decrease for pursuit eye-movements and corresponding extra-retinal signals suggests motion discrimination during pursuit may be compromised with older age.

Age also affects accuracy (Moschner & Baloh, 1994; Paige, 1994; Ross et al., 1999; Spooner, Sakala, & Baloh, 1960; Valmaggia et al., 2004; Zachon & Sharpe, 1987). For example, Sharpe and Sylvester (1978) calculated the pursuit gain for a group of old and young observers across a range of target velocities (0° - 100°). Results showed that younger observers accurately tracked targets moving at speeds $30^{\circ}/s$ or less, at higher speeds pursuit gain steadily declined. In contrast, the older observers could only accurately pursue targets moving at $10^{\circ}/s$ or less. Speeds higher than $10^{\circ}/s$, showed a steady drop in pursuit gains for the older observers. This impairment was present whether the head remained stationary or not (Leigh, 1982). The

difference in pursuit gain between the two age groups reportedly increases with faster velocities (Moschner & Baloh, 1994; Sharpe & Sylvester, 1978; Spooner, Sakala, & Baloh, 1960) while others report a consistent difference between age groups for pursuit gains regardless of target velocity (Kolarik et al. 2010; Paige, 1994; Zackon & Sharpe, 1987). It is possible that pursuit accuracy could influence motion discrimination during smooth pursuit if internal noise varies with the magnitude of extra-retinal signals.

1.3.3. Internal Noise

Differences in the levels of internal noise associated with retinal and extra-retinal signals suggests another way in which motion sensitivity may differ between pursuit and fixation. Any neural signal such as those encoding retinal motion of eye velocity will fluctuate from trial to trial and consequently will have a certain amount of variability associated to them. This variability has been shown to correlate with perceptual thresholds of older observers. For example, Bennett et al. (2007) successfully modelled retinal age-related decline in a direction identification and judgement task. In the model, trials were simulated to generate motion detection thresholds and absolute direction errors for young and old observers. Age-related decline in direction sensitivity was accounted for by increasing the internal noise by a fixed amount in the model. Whether similar age-related differences in internal noise are associated with extra-retinal motion signals is unknown.

The arguments above assume that retinal motion signals limit discrimination performance during fixation, and extra-retinal signals limit performance during

pursuit. However, it has also been suggested that motion discrimination during fixation and pursuit could be limited at a combined processing stage, where both motion signals are integrated. For example, studies have shown no difference in retinal and extra-retinal estimate variability in velocity (Stevenson et al., 1998) and direction discrimination (Krukowski et al., 2003). Stevenson et al. (1998) measured velocity discrimination thresholds for pedestal speeds 0.2°/s, 0.8°/s, 3.2°/s and 6.4°/s during smooth pursuit and fixational. Eye-tracking methods were used to ensure fixation and smooth pursuit accuracy, so the conditions were limited to retinal and extra-retinal estimates respectively. Similar velocity thresholds were reported for the eye-movement conditions, which suggested that the precision of the velocity estimate was equally high for the eye velocity as for retinal image motion. Similarly, in a direction discrimination task, Krukowski et al. (2003) compared direction sensitivity thresholds during fixation and smooth pursuit. Using a single-dot stimulus, observers were presented with two sequential intervals of directional motion; the task was to indicate which of the two intervals contained clockwise motion. Two experiments were run. In the first experiment, both long (800ms) and short (200ms) durations were tested, No difference was found between the conditions; however, there was a slight improvement in thresholds for both conditions at the longer duration. A possible explanation for the similar thresholds was the initial retinal motion in the pursuit condition was used to make their direction judgements. To make retinal motion in the initial pursuit phase less informative, Krukowski et al. ran a second experiment where the trajectory of the dot stimulus travelled along a bent line. Initially the dot travelled in a straight path, but then extinguished for

30ms and once it reappeared, continued on a slightly different path. The second experiment was carried out only on the long duration. Again, no difference was found between pursuit and fixation in the direction discrimination thresholds.

In a subsequent analysis, Krukowski et al. showed these direction thresholds did not depend on the proportion of eye velocity to retinal slip. Pursuit trials were divided into those with low pursuit gain averaged at 78% and high pursuit gain averaged at 101%, however, no difference between the direction thresholds for the two subsets of trials. Krukowski et al. argued that pursuit and fixation direction thresholds were therefore robust to changes in the proportion of retinal and extra-retinal input. They concluded that a common noise source limits thresholds in the two eye-movement conditions. It was proposed that this noise source was located in MST, due to the area's involvement in smooth pursuit and ability to combine retinal and extra-retinal signals during head-centred motion (Dursteler & Wurtz, 1988; Newsome et al., 1988; Rudolph & Pasternak, 1999). In support of this idea, Welchman et al. (2009) recently reported that motion-in-depth direction discrimination thresholds were best predicted using combined head-centred motion rather than eye movement or retinal slip alone. Using what is termed later in the thesis as 'classification analysis', Welchman et al. (2009) calculated the amount of retinal and eye-velocity information available on a trial-to-trial basis by subtracting the eye vergence velocity from the on-screen motion. Psychometric functions were then re-fitted by plotting the direction judgements against retinal motion, eye-velocity estimates and head-centred

motion separately. The steepest psychometric function was observed when observers were using head-centred motion in their direction judgements.

A difficulty with these types of experiments is isolating the noise that limits performance. Is it a question of noise at the combination stage, noise at the input stage or both? Krukowski et al. (2003) conclude from their results that in order for thresholds to be the same during fixation and pursuit, both eye-movement conditions must be limited from a combined source of noise. Alternatively, Welchman et al. (2009) showed higher direction discrimination thresholds during smooth pursuit compared to fixation in motion-in depth task during vergence eye-movement. This suggests that extra-retinal vergence signals were noisier than retinal signals. Similarly, Freeman et al. (2010) found higher speed discrimination thresholds during pursuit, again implying noisier extra-retinal signals. Another issue with drawing conclusions from these experiments is that each study used different types of motion judgements (direction, speed and motion-in-depth), as well as different stimuli sizes. For example, the use of large stimuli, like that presented in Freeman et al. (2010), could reduce retinal noise dominating fixation conditions, because more motion mechanisms are recruited. On the other hand, Krukowski et al. (2003) presented a single dot to their observers during fixation. The small target in this case may have increased judgement uncertainty.

1.4. Summary and structure of experiments

This introductory chapter provided background literature relevant to further discussions related to the effects of eye-movement and age across a series of motion discrimination tasks. In order to investigate the precision of pursued and fixated stimuli as a function of age, Chapter 2 investigates variation in direction sensitivity between old and young observers across two oculomotor conditions (smooth pursuit and fixation). Using similar methods to Welchman et al. 2009, classification analysis was also carried out to determine what motion signals were being used by observers during fixation and smooth pursuit conditions. Furthermore, potential confounds of luminance and relative motion were addressed. Chapter 3 continues to investigate direction sensitivity in younger and older adults, with the aim to uncover whether the direction discrimination results from Chapter 2, generalize to a trajectory-matching task. Previous literature has shown that retinal speed sensitivity decreases as a function of age. In order to determine whether similar effects occur for extra-retinal sensitivity, Chapter 4 examines speed discrimination as a function of age during fixation and smooth pursuit eye-movement. Further investigation is given to the effects of retinal slip during smooth pursuit condition on speed sensitivity. Finally, chapter 5 will examine motion coherence comparatively across two age groups and two eye-movement conditions.

2. Direction Sensitivity

To date, our knowledge of direction sensitivity is largely limited to studies using foveally presented stimuli where the eyes are kept fixated (Ball & Sekuler, 1987; De Bryun & Orban, 1988; Levi, Klein, & Aitsebaoma, 1984; Pasternak & Merigan, 1984; Raymond, 1994). While these studies provide valuable information about retinal direction sensitivity, very little research has addressed sensitivity during smooth pursuit. In particular, the effect of age on direction sensitivity is relatively unexplored as most ageing studies on motion perception have concentrated on speed discrimination (Bidwell et al., 2006; Norman et al., 2003; Raghuram et al. 2005; Snowden & Kavanah, 2006). Research has therefore overlooked how age influences both extra-retinal and retinal signal precision. The aim of this chapter was to compare direction discrimination thresholds between young and old observers during smooth pursuit and fixation. Two separate questions were addressed. Firstly, is there a difference in direction sensitivity between fixation and pursuit eye-movements? Secondly, are older observers less sensitive to direction in both fixation and smooth pursuit discrimination tasks?

As discussed in detail in the introductory chapter, oculomotor control is a possible reason why pursuit direction sensitivity might differ from fixation sensitivity, across age group. If the magnitude of extra-retinal signals and eye-speed are proportional, then eye-movement variability could be a factor in increasing direction sensitivity thresholds during pursuit. In addition, any neural estimate such as retinal and extra-retinal motion signals will have a

certain amount of variability (or noise) associated with it. The variability of retinal and extra-retinal signals might influence how sensitive fixation and smooth pursuit eye-movements are to motion. Krukowski et al. (2003) found no difference in direction thresholds between fixation and smooth pursuit, which led them to conclude that motion sensitivity during both eye-movement conditions are limited by a common noise source. As mentioned in the introduction, their results could also be explained by separate noise sources with similar variance.

In terms of ageing, Bennett et al. (2007) showed that retinal age-related decline in a direction identification and judgement task could be modeled by increasing levels of internal noise. They also modelled ageing effects by increasing the bandwidth of the direction tuning curves, in combination with a smaller amount of additional noise. It is well supported by neurophysiological evidence that neuronal tuning and internal noise of older cells affects retinal motion sensitivity (Leventhal et al., 2003; Schmolesky, Wang, Pu, & Leventhal, 2000). Psychophysical studies also imply a reduction in GABA inhibition in older adults that can lead to changes in retinal neuronal tuning (Betts et al., 2005; Butler & Zacks, 2006). Thus, the question remains whether a similar age-related increase in neuronal noise or changes to neuronal tuning during smooth pursuit?

By comparing direction discrimination in older and younger subjects across two eye-movement conditions, the aim of this chapter was to investigate whether oculomotor control or internal noise had an effect on direction

sensitivity and if the ageing effects described in retinal motion sensitivity extended to motion sensitivity during smooth pursuit eye-movement.

2.1. Experiment 1: Direction Discrimination

2.1.1. Methods

2.1.1.1. Stimuli

Stimuli were created in OpenGL and rendered by a Radeon 9800 Pro graphics card. All stimuli were rear projected through a Sony Multiscan projector (VPH 1272QM) onto a large screen (209cm X 158cm) at a refresh rate of 72Hz. The screen had an embedded Fresnel lens, which collimated light evenly throughout the display. Gamma correction was achieved using standard techniques. For all the experiments described in the thesis, participants viewed the screen binocularly at a distance of 2m in a completely darkened lab, with no visible background objects. Head position was also stabilised using a chin-and-forehead rest.

Stimuli consisted of dots (0.1° radius, density of 1.5 dot/deg^2) randomly positioned within a circular aperture (5° radius). A fixation point (0.2° radius) was centred within the random dot pattern. In the 'fixation' condition, the participants were instructed to fixate their eyes on a central stationary point whilst judging the direction of the surrounding random dot pattern, which moved behind a stationary window (see Fig 2.1a). In the 'pursuit' condition, the participants pursued the dot pattern whilst judging its direction. Here the dot pattern, fixation point and window all moved in unison (see Fig 2.1b). It

should be noted that relative motion was present in the fixation condition when the dot pattern moves behind the stationary fixation point and static window. This issue will be discussed in more detail later in the chapter. In all conditions, the stimulus direction was ramped over the first 0.3s. The ramp started at the standard direction (defined below) and changed linearly over time until it reached the target direction for that particular interval. The stimulus continued to move in this target direction for 0.5s. To prevent observers from utilising the initial retinal motion available in the pursuit condition, the ramp duration was randomised by ± 0.05 s, so that the shortest and longest ramp lasted 0.25s and 0.35s respectively (see inset to Fig.2.1). A similar 0.1s jitter was added to the total stimulus duration. Therefore, the longest possible display lasted 0.9s in total: a maximum of 0.35s ramp and maximum of 0.55s movement in the final direction.

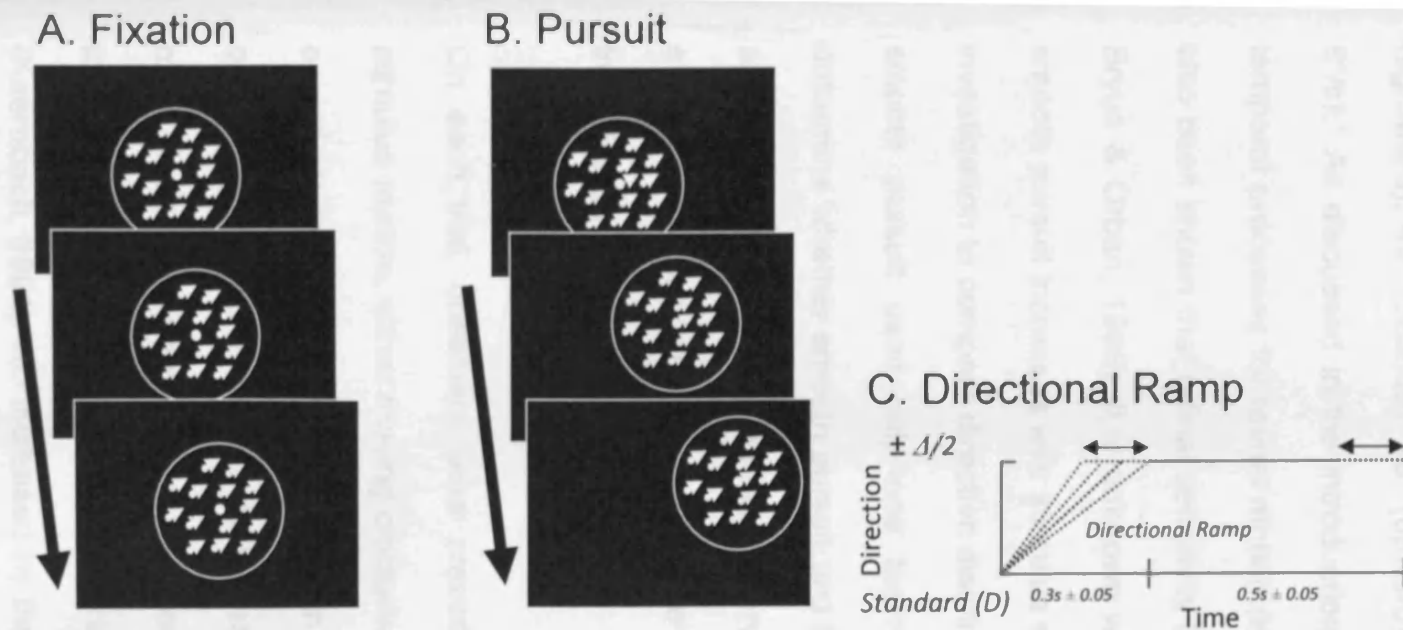


Figure 2.1. Schematic diagrams of the sequence of the visual stimuli for direction discrimination task . A. *Fixation*: participants fixated their eyes on the stationary point in the centre and judged the direction of the surrounding random dot pattern for $0.8s \pm 0.1$. B. *Pursuit*: participants judged the direction of the random dot pattern whilst pursuing the centre fixation point for $0.8s \pm 0.1$. The random dot pattern was present throughout the entire trial. C. *Time course of directional ramp*: the direction of the stimulus was linearly ramped before it reached target direction ($D \pm \Delta D/2$) in order to reduce the amount of retinal motion available to the observer during the pursuit condition. The duration of the linear ramp was then randomised from trial to trial ($0.3s \pm 0.05$)

2.1.1.2. Procedure

Direction discrimination thresholds were determined using a 2-alternative-forced-choice paradigm for three different standard directions ($D = 0^\circ$ (rightward), 45° (oblique), 90° (upward)) and two different speeds ($2^\circ/\text{s}$ and $8^\circ/\text{s}$). As discussed in the introduction, there is evidence for slow and fast temporal processes for retinal motion (e.g. van der Smagt et al, 1999). It has also been shown that retinal sensitivity increases a function of speed (e.g. De Bryun & Orban, 1988). It is unknown whether direction discrimination during smooth pursuit increases with stimulus speed. Krukowski et al. (2003), in their investigation to compare direction discrimination thresholds during fixation and smooth pursuit used only one fast moving stimuli ($10^\circ/\text{s}$). In order to determine whether smooth pursuit and fixation discrimination thresholds differ as a function of stimulus speed, observers were presented with both a slow and fast stimulus speed. Due to time constrictions, only two speeds were investigated.

On each trial, observers were presented with two sequential intervals of stimulus motion, either moving clockwise from a standard direction ($D - \Delta D/2$) or anti-clockwise ($D + \Delta D/2$). The mean direction D was held constant in any one session. The observer's task was to choose which interval appeared more clockwise. The difference between the two intervals (ΔD) was adjusted logarithmically using two randomly interleaved 1-up 1 down staircases (Kaernbach, 1991). ΔD increased by three step sizes following each incorrect response and decreased by one step size following each correct response.

Each staircase was designed to converge on the 75% correct responses and terminate after eight reversals. Pursuit and fixation conditions were run in separate sessions, yielding a total of six types of trials per speed condition (2 conditions X 3 standard directions). The order of the six conditions was randomised, with a break in between to explain the type of eye-movement to use in the subsequent session. Each observer carried out each condition just once, with each testing session lasting about an hour. The fast and slow speed conditions were run on separate sets of observers

2.1.1.3. Psychophysical analysis

Psychometric curves were fitted to the experimental data using Probit analysis (Finney, 1971). First, the frequency of choosing interval 2 was plotted as a function of the signed difference ΔD between the two intervals. Percentage correct therefore ranged from 0% to 100%. A cumulative Gaussian was then fit to the data using maximum likelihood estimation and the just noticeable difference (JND) or threshold was calculated by subtracting ΔD at 75% from ΔD at 50%. This indicates the amount of direction needed to increase a participant's discrimination rate from 50% to 75% on the fitted psychometric function: the steeper the function, the smaller the JND. Outliers were defined as psychometric thresholds that were more than three standard deviations away from the mean. Observers with two or more outliers across conditions were excluded from subsequent analysis. For the direction discrimination experiment, this amounted to 4 young observers and 3 old observers.

Typically, response curves are fitted by plotting the unsigned difference against percent correct. In this chapter however, the signed difference was plotted against percent correct. This gives probabilities that range from 0 to 1 (Kontsevich, Chen, & Tyler, 2002). By plotting both limbs of the psychometric function, response curves could be compared based on increments

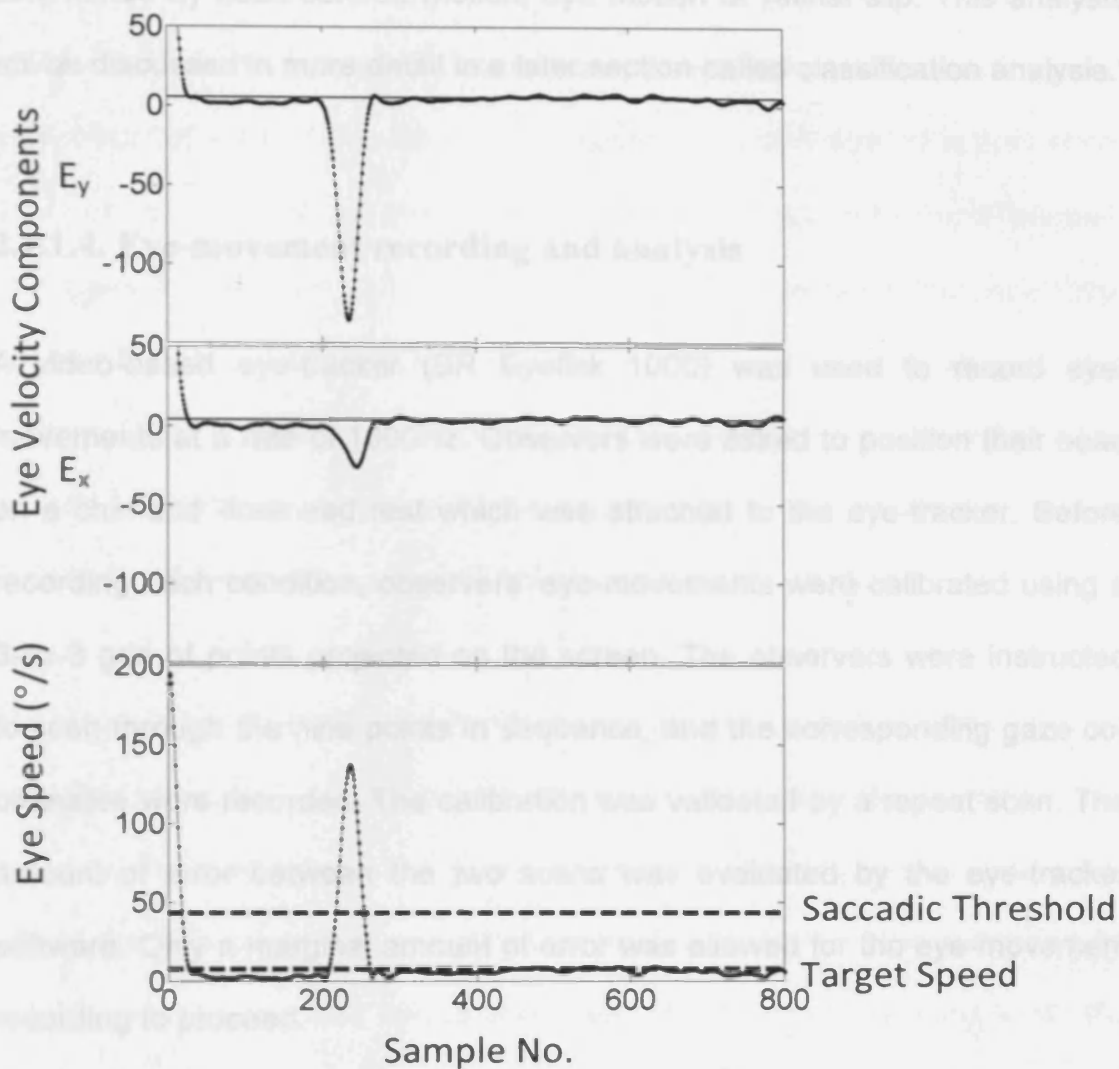


Figure 2.2. Sample Eye-movement trace. Top two panels show the Cartesian components of eye velocity (E_x , E_y). Bottom panel: Saccades were detected by locating peaks in eye speed (equation 1) that corresponded to zero-crossings in the acceleration profile and exceeded a threshold of $40^\circ/\text{s}$ above the target stimulus speed. Samples which corresponded to the linear ramp were not analysed.

determined by head-centred motion, eye motion or retinal slip. This analysis will be discussed in more detail in a later section called classification analysis.

2.1.1.4. Eye-movement recording and analysis

A video-based eye-tracker (SR Eyelink 1000) was used to record eye-movements at a rate of 1000Hz. Observers were asked to position their head on a chin-and -forehead rest which was attached to the eye-tracker. Before recording each condition, observers' eye-movements were calibrated using a 3-by-3 grid of points projected on the screen. The observers were instructed to scan through the nine points in sequence, and the corresponding gaze coordinates were recorded. The calibration was validated by a repeat scan. The amount of error between the two scans was evaluated by the eye-tracker software. Only a marginal amount of error was allowed for the eye-movement recording to proceed.

The Cartesian components of eye velocity (E_x , E_y) (B. R. Beutter & Stone, 1998) were determined offline for both X and Y channels by first passing the position recordings through a Gaussian filter (SD = 16 Hz) and then taking time derivatives. An example of an individual eye-movement trace can be seen in figure 2.2, where the top two panels plot respectively E_x , E_y against sample number. Saccades were detected by locating peaks in eye speed (equation 1):

$$|E| = \left(\sqrt{E_x^2 + E_y^2} \right) \quad (1)$$

that corresponded to zero-crossings in the acceleration profile and exceeded a threshold of $40^\circ/\text{s}$ above the stimulus speed. This is illustrated in the bottom panel of figure 2.2 where eye-speed ($^\circ/\text{s}$) is plotted against sample number. The peak of the eye-speed which exceeds the saccadic threshold (see dashed line labelled saccadic threshold) is located at approximately sample number 235. Samples $\pm 35\text{ms}$ either side of the peak were excluded. This insures the complete removal of the saccade from start (\sim sample number 200) to finish (\sim sample number 275) from subsequent analysis.

There are a number of ways in which fixation and pursuit accuracy can be calculated from E_x , E_y . For example, one could use a polar representation and compute the speed (equation 1 below) and direction (equation 5 (see page 49) of the eye-movement separately. Speed accuracy is then computed by dividing the target speed by the eye speed (often called the gain), while the angular difference between the target direction and the eye direction would give a measure of direction accuracy. By calculating speed and direction accuracy separately, this method does not provide information about how speed and direction relate to each other in any given trial, and therefore, fails to provide a coherent estimate of eye-velocity.

An alternative method is to use a Cartesian representation and subtract the components of the stimulus velocity (S_x , S_y) from E_x and E_y , where a deviation of zero in both the x and y channel would indicate perfect pursuit. For perfect fixation, however, the deviation calculated for the x and y channel would be

equal to the stimulus velocity. In this case, measures of accuracy in fixation and pursuit conditions would differ. Similarly, measures of accuracy would differ depending on the direction as (S_x, S_y) changes as a function of direction. Therefore, this method cannot compute a standardised metric across eye-movement condition, as well as across a set of stimuli moving in different directions.

One way to overcome these problems is to work out the components of eye velocity parallel and orthogonal (E_p, E_o) to the stimulus velocity. Figure 2.3 illustrates the geometry. E_p and E_o can be calculated on the basis of the eye tracker measurements (E_x, E_y) and the stimulus velocity (S_x, S_y) . To normalise with respect to stimulus speed, E_p and E_o were divided by stimulus speed (S).

$$e_o = \frac{|E|}{|S|} \sin \mu \quad (2)$$

$$e_p = \frac{|E|}{|S|} \cos \mu \quad (3)$$

Where:

$$\mu = \theta_E - \theta_S \quad (4)$$

$$\theta_E = \arctan \frac{E_y}{E_x} \quad (5)$$

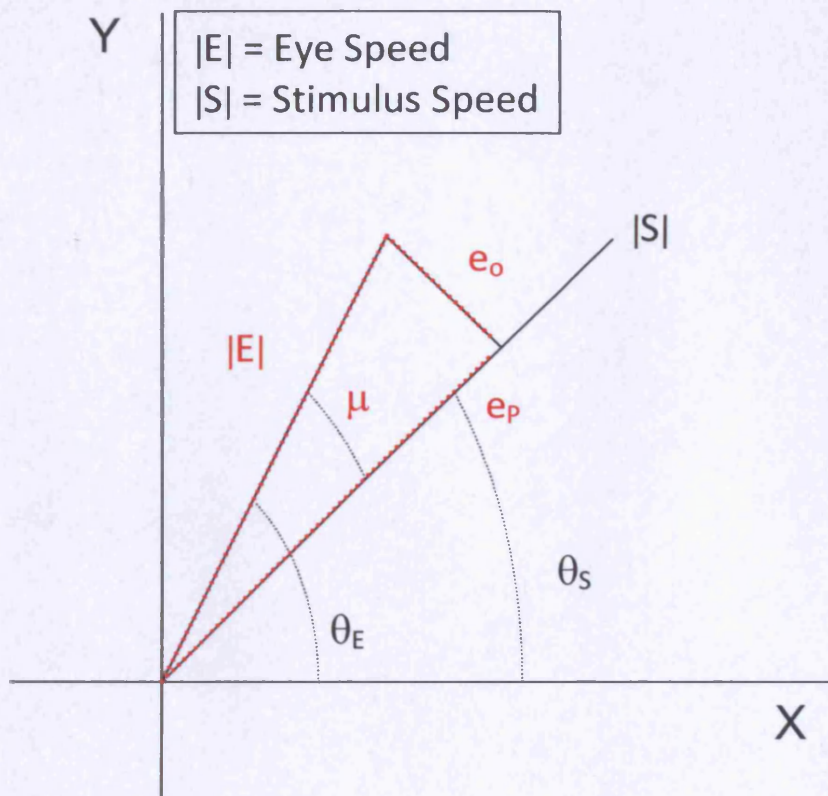


Figure 2.3. Geometry illustrating how the components of eye velocity parallel and orthogonal (e_p , e_o) to stimulus velocity are calculated from pre-determined eye-movement (E_x , E_y) and stimulus velocity (S_x , S_y) co-ordinates. e_p and e_o are normalised by dividing both components by the stimulus speed.

θ_s is the stimulus direction and $|E|$ is the eye speed (equation 1). Perfect fixation corresponds to $(e_p, e_o) = (0, 0)$ and accurate pursuit corresponds to $(e_p, e_o) = (1, 0)$.

2.1.1.5. Participants

The two speed conditions (2°/s and 8°/s) were run on separate groups of young and old observers. For stimuli moving at the slower speed of 2°/s, twenty-four observers participated in the experiment, 12 older than 60 years (mean age = 67.1), and 12 aged 25 years or less (mean age = 23.2). For stimuli moving at the faster speed of 8°/s, twenty-three observers participated, 12 older than 60 years (mean age = 68.8), and 11 aged 23 years or less (mean age = 20.5). For all the experiments in the thesis, older observers were recruited following attendance at the School of Optometry's eye clinic, where they received a full eye examination to rule out any ocular pathology including macular degeneration, glaucoma, cataracts, or other retinal or eye problems. Young observers were recruited through the School of Psychology's participant panel. Young observers were either paid or completed the study for course credit. Older observers were paid for their participation in the experiments.

2.1.1.6. Optical Screening

All observers wore their optical correction if necessary and had their visual acuity and contrast sensitivity measured prior to the main data collection,

using the Bailey-Lovie Log MAR chart (at 2m) and Pelli-Robson CS chart (1m). The Bailey-Lovie acuity chart comprises of 14 rows of 5 letters ranging in logarithmic size in multiple increments of 0.1 log units from bottom to top. Visual acuity is measured as the logarithm of the minimum angle of resolution (log MAR). For reference a Log MAR score of 0.0 is equivalent to 20/20 vision (Snellen). Contrast sensitivity was measured using the Pelli-Robson chart. This chart consists of eight lines of letters, sized equally. Each line contains two groups of three different letters; the letters in each group have equal contrasts. Contrast varies across each group ranging from 100% to 0.6% in 16 steps. Observers were asked to start reading the letters with the highest contrast and continue until two or three of the letters in one group are incorrectly identified. The contrast sensitivity threshold of the individual is measured as the log value associated with the previous group of letters.

The acuity and contrast measurements for experiments 1 are shown in Table 2.1. For this experiment and the remaining experiments throughout the thesis, all subjects had normal to corrected-to-normal acuity. The LogMAR Acuity scores for both age groups fell within the range (0.00 – 0.07) which corresponds with previous studies on visual acuity across age (Elliot, Yang, & Whitaker, 1995). Further, contrast sensitivity scores recorded fell in the range of normal Pelli-Robson test values for each subject's specific age group. (Mantyjarvi & Laitinen, 2001) measured contrast sensitivity scores across ages ranging from 6-75 years. For group aged (20-29), they defined normal values between 1.91 -2.01. This would represent the younger observers tested in experiments 1-6, whose contrast sensitivity scores averaged at 1.92.

Mäntyjärvi & Laitinen (2001) older group ranged in age from 60-75 and reported contrast sensitivity values 1.79-2.01; older participants in experiment 1-6 averaged at 1.85.

Table 2.1. Participant characteristics for younger and older observers in experiment 1. Age (in years) is reported as a mean followed by the standard deviation and range in parentheses. LogMAR visual acuity and Pelli-Robson contrast sensitivity scores are given as means followed by the standard deviation in parentheses. LogMAR and Pelli-Robson scores are given for binocular viewing.

Experiment 1		Younger	Older
2°/s	N	12	12
	Sex	4 males, 8 females	8 males, 4 females
	Age	23.2(1.74, 21-25)	67.1(5.38, 61-80)
	LogMAR	0.01(0.01)	0.03(0.05)
	Pelli-Robson	1.95(0)	1.89(0.10)
		Younger	Older
8°/s	N	11	12
	Sex	5 males, 6 females	10 males, 2 females
	Age	20.5(1.57, 19-23)	68.8(6.13, 64-85)
	LogMAR	0.00(0.0)	0.07(0.08)
	Pelli-Robson	1.93(0)	1.78(0.15)

2.1.2. Results

2.1.2.1. Psychophysics

Direction thresholds for discriminating clockwise motion during fixation and pursuit in old and young observers are summarized in figure 2.4. The two eye-movement conditions are plotted individually for speed with 2°/s (top row) and 8°/s (bottom row). The results suggest that direction discrimination

improved with stimulus speed, especially for older observers. Direction discrimination was worse during pursuit, but only at the slower speed. Moreover, direction thresholds were lower along the cardinal directions, compared to the oblique direction, especially at slow speeds.

Statistical analysis was carried out to confirm these observations¹. A 2X2X2X3 mixed ANOVA, was performed on the psychophysical data, with age and speed as between-subjects variables and eye-movement condition and direction as within-subject variables. As with later experiments a repeated-measure ANOVA was used, where repeat measurements were taken from each observer. In cases where there is a great deal of variation between observers, error variance estimates from standard ANOVAs are large, thus repeated measures of observer provides a way of accounting for this variance, thus reducing error variance. In addition, suitable observers are difficult to recruit in ageing research; therefore, repeated measures designs are economical because an observer is measured under all conditions.

For all the experiments in the thesis, the ANOVA assumptions of homogeneity (Levene's Test) and Sphericity (Mauchly's Test) were met. For the direction discrimination experiment, a square root transformation of data was carried out to comply with these ANOVA assumptions. A significant main effect was shown for direction [$F_{2, 86} = 10.057, p=0.000$], confirming that observers had higher thresholds for the oblique direction (45°) compared to the cardinal directions (0° and 90°). This finding replicates the 'oblique effect' reported by

¹ Throughout the thesis, only significant and relevant non-significant statistical results are reported in the main text. For a full breakdown of all statistical results and effect size, please refer to the appendices.

Gros et al. (1998), where observers were more sensitive to the direction of motion that moved around the horizontal and vertical axes compared to diagonal axes. A main effect of speed was showed to be significant [$F_{1, 43} = 24.033$, $p=0.000$]. In addition, the ANOVA revealed a significant eye-movement and speed interaction [$F_{1, 43} = 5.794$, $p=0.020$]

The interaction was investigated further by carrying out separate 2X2X3 mixed ANOVAs on the two speed conditions. This confirmed in the slow speed condition (See Fig 2.4a, b), the observed age effect [$F_{1,22} = 4.614$, $p=0.043$], and a statistically significant difference between pursuit and fixation eye-movement conditions [$F_{1, 22} = 5.654$, $p=0.027$]. The effect of direction was close to significant [$F_{1, 22} = 3.265$, $p=0.048$], suggesting a weak oblique effect for direction discrimination at slow speeds. For the fast speed condition (figure 2.4c, d), there was no significant difference in direction thresholds between the age groups [$F_{1, 21} = .014$, $p=0.906$]. However a large effect of direction was found due to the oblique effect [$F_{2, 42} = 9.234$, $p=0.000$].

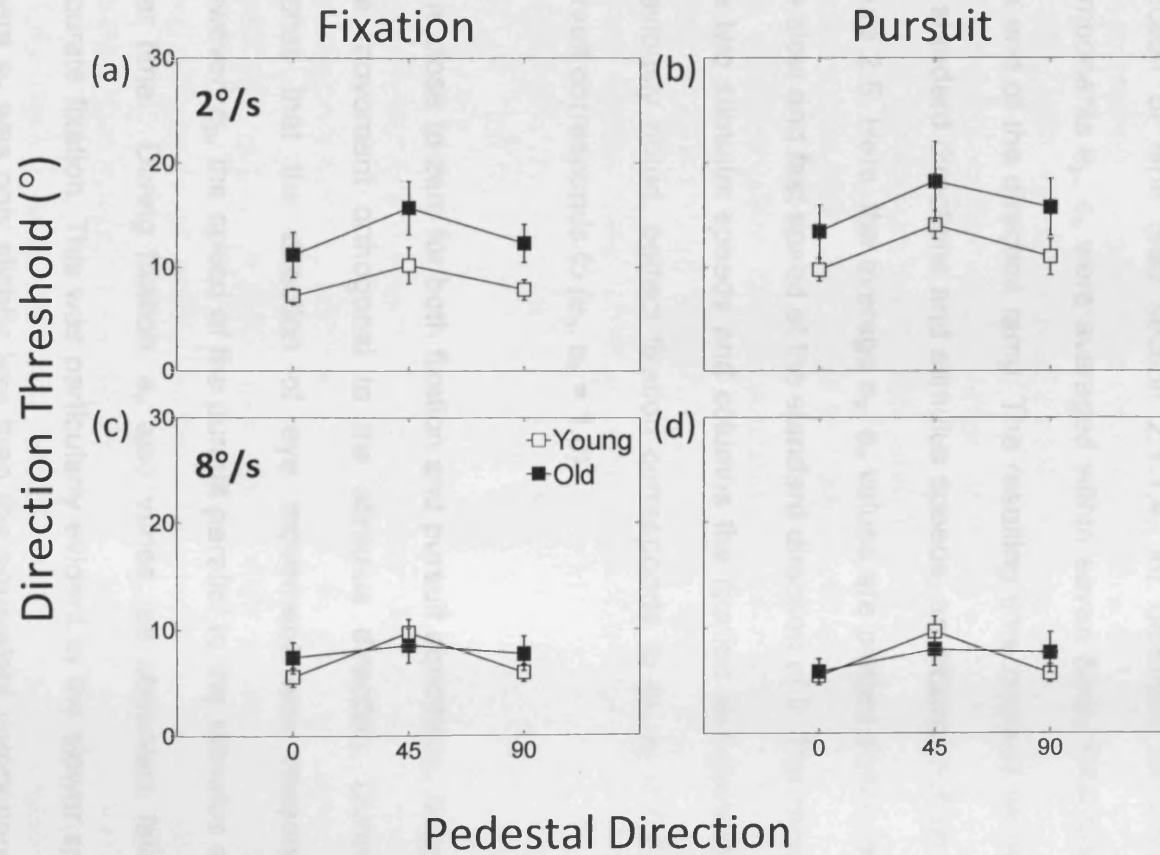


Figure 2.4. Mean direction discrimination thresholds for stimulus speeds 2°/s and 8°/s during fixation and smooth pursuit. Squares (unfilled) correspond to the younger group and squares (filled) correspond to the older group. Error bars are ± 1 SE.

2.1.2.2. Eye-movements

Eye-movement accuracy was investigated by examining the normalised components of eye-velocity parallel and orthogonal to the stimuli (e_p , e_o) as a function of time (see section 2.1.1.4. for definition of components). The components e_p , e_o were averaged within seven 50ms time bins starting from the end of the direction ramp. The resulting time courses were similar across all standard directions and stimulus speeds, an example of which is shown in figure 2.5. Here, the average e_p , e_o values are plotted across all observers for the slow and fast speed at the standard direction of 0. The rows correspond to the two stimulus speeds and columns the fixation and pursuit conditions. As previously noted, perfect fixation corresponds to ($e_p, e_o = 0,0$) and accurate pursuit corresponds to ($e_p, e_o = 1.0$).

e_o is close to zero for both fixation and pursuit conditions, suggesting minimal eye movement orthogonal to the stimulus direction. During pursuit, this implies that the direction of eye movement was reasonably accurate. However, e_p , the speed of the pursuit parallel to the stimulus appears to vary over time. During fixation, e_p also varies, as observers failed to maintain accurate fixation. This was particularly evident in the slower speed condition, where e_p was only slightly less than the equivalent component in the pursuit condition. During the faster speed condition, there is a larger difference in e_p between fixation and pursuit, though perfect fixation was still not maintained. Figure 2.5 highlights that both eye-movement and retinal motion information were available to observers regardless of eye-movement condition, albeit in

different amounts and at different times. This issue will be discussed in more detail below.

Figure 2.6 summarises the parallel component (e_p) averaged over time from the end of the direction ramp across all observers. A 2X2X2X3 (age, speed, eye-movement condition and direction) mixed ANOVA, was carried out on the e_p data, with age and speed as the between-subject variables and the eye-movement condition and direction as within-subject variables. Age was not found to be a significant factor and neither was direction. Figure 2.6 also confirms that observers failed to maintain accurate fixation in both slow and fast conditions. Despite this, a significant main effect of eye-movement was found [$F_{1, 43} = 133.358, p=0.000$]. From the figure, eye-movements recorded during fixation were therefore slower than those recorded in the pursuit conditions.

The non-significant effects of direction and age in the e_p data, contrast with the psychophysical findings. Direction thresholds were shown to be significantly higher in older observers at slow speeds, while direction effects were evident in all cases bar older observers at the higher speed. These results argue against any straightforward relationship between the accuracy of eye-movement and direction discrimination, as eye-movements do not sufficiently explain the psychophysical findings.

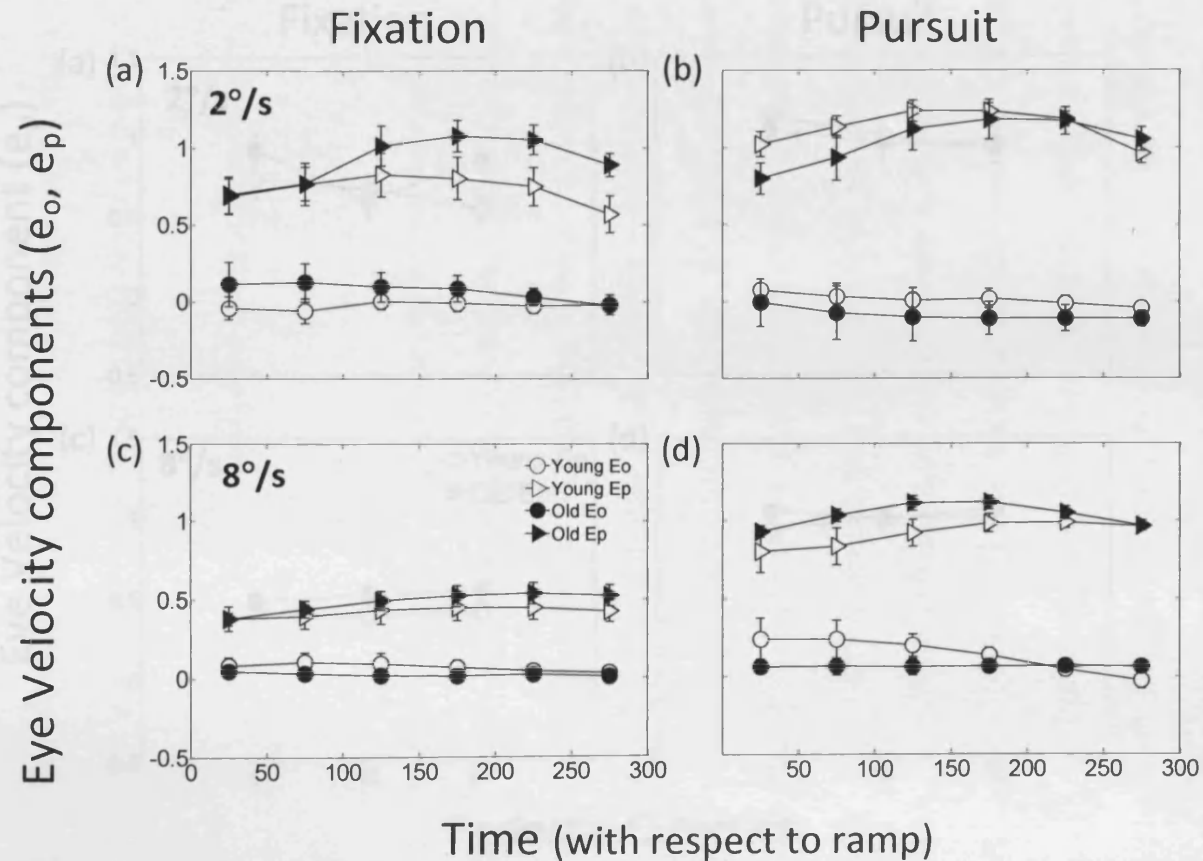


Figure 2.5. Normalised components of eye velocity (e_p, e_o) parallel and orthogonal to the direction of stimulus motion as a function of time (50ms bins) for pedestal direction (0°). Eye-movement accuracy is shown for stimulus speeds $2^\circ/s$ and $8^\circ/s$ during fixation and smooth pursuit. Circles (unfilled) and triangles (unfilled) correspond to e_o and e_p respectively for the younger group. Circles (filled) and triangles (filled) correspond to e_o and e_p respectively for the older group. Error bars are ± 1 SE.

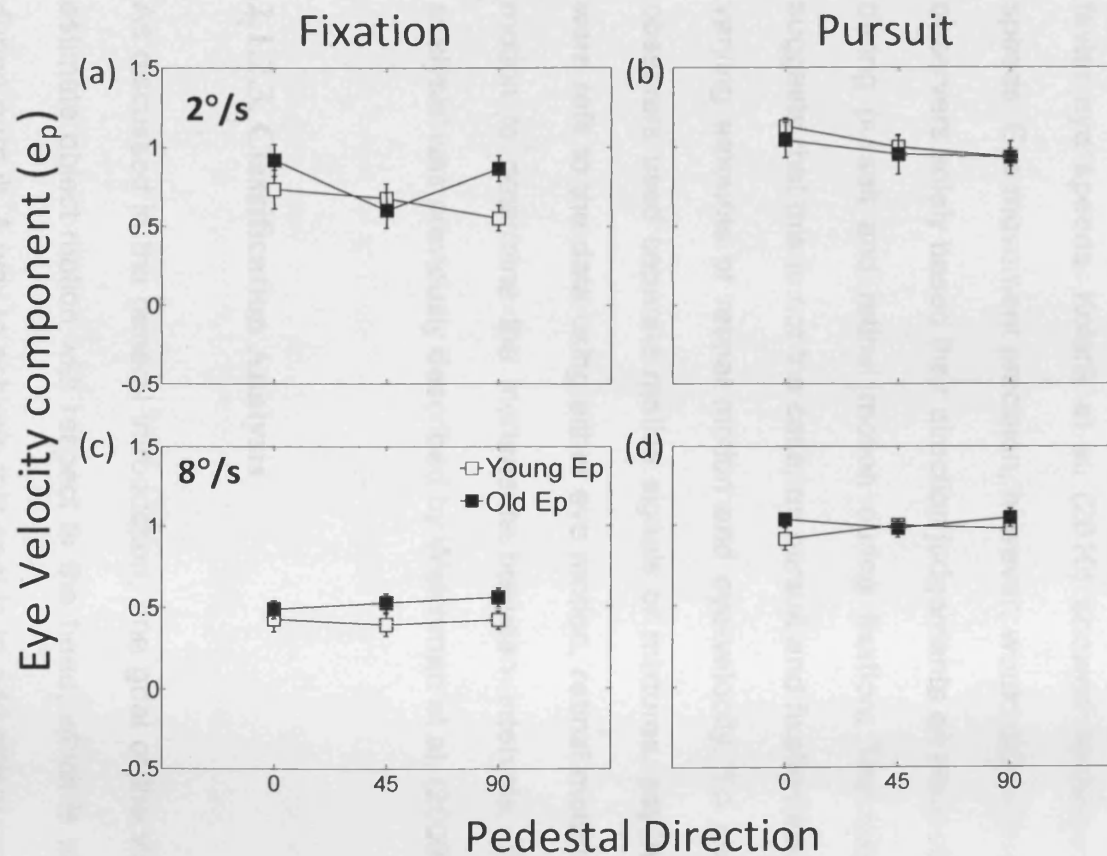


Figure 2.6. Mean eye velocity component (e_p) for stimulus speeds $2^\circ/s$ and $8^\circ/s$ during fixation and smooth pursuit. Triangles (unfilled) correspond to the younger group and triangles (filled) correspond to the older group. Error bars are ± 1 SE.

Another potential reason for the difference in eye-movement direction thresholds is the precision of pursuit and fixation. Kolarik et al. (2010) measured oculomotor accuracy and precision in older and younger observers during reflexive and deliberate eye-movement conditions. It was reported that older observers were less precise when making deliberate eye-movements at faster eye speeds. Kolarik et al. (2010) showed no effect of age at faster speeds. Eye movement precision, however, would only influence thresholds if observers solely based their direction judgements on estimates of eye velocity during pursuit and retinal motion during fixation. The eye-movement data suggests that this is not the case, as pursuit and fixation inaccuracies contain varying amounts of retinal motion and eye-velocity. To investigate whether observers used separate motion signals or mixtures, psychometric functions were refit to the data using either eye motion, retinal motion or head-centred motion to determine the increments between intervals. This 'classification analysis' was previously described by Welchman et al. (2009).

2.1.2.3. Classification Analysis

As discussed in the general introduction, one goal of the visual system is to estimate object motion with respect to the head, which is made complicated during pursuit. A way to achieve this goal is to add retinal motion to estimates of eye velocity. Welchman et al. (2009) showed that this is what observers appear to be doing when making discrimination judgements during eye movement. In a motion-in depth task, observers were asked to judge the direction of a target during vergence eye-movement. Welchman et al. (2009)

calculated the amount of retinal and eye-velocity information available on a trial-to-trial basis by subtracting the eye vergence velocity from the on-screen motion. From this, psychometric functions were constructed by plotting the direction judgements separately against retinal motion, eye-velocity estimates and their combination. For the motion-in-depth task, psychophysical judgements were best explained on the basis that observers combine both retinal motion and eye-velocity to estimate motion towards or away from them

The direction thresholds discussed above result from fitting psychometric functions to response curves determined by the difference in head-centred direction ΔD . As already noted, head-centred direction is the sum of eye-velocity and retinal motion, so the question remains whether observers' based their judgements on the combined cue or the individual motion cues in isolation. By using a similar analysis to Welchman et al. (2009), psychometric functions were re-fit to four new categories of response curves, constructed on the basis of eye speed, retinal speed, eye direction and retinal direction. The results were then compared to the original response curves constructed based on head-centred direction. It should be noted that the stimulus speed was held constant on all trials, therefore could not have been used by observers. Because ΔD differences in eye speed, retinal speed, eye direction and retinal direction are unique to each trial, a binning technique was used to re-construct the response curves. For example, to refit the psychometric functions on the basis of eye speed, the signed difference between the eye speed in interval 1 and interval 2 was determined for each trial. The eye-

speed increments were binned and the frequency of choosing interval 2 recalculated for each bin. The psychometric function was then fit to the binned data, using the bin centres as the incremental values (Freeman, Champion, Sumnall, & Snowden, 2009; Welchman et al., 2009). Goodness-of-fit was evaluated using the deviance measure suggested by (Wichmann & Hill, 2001).

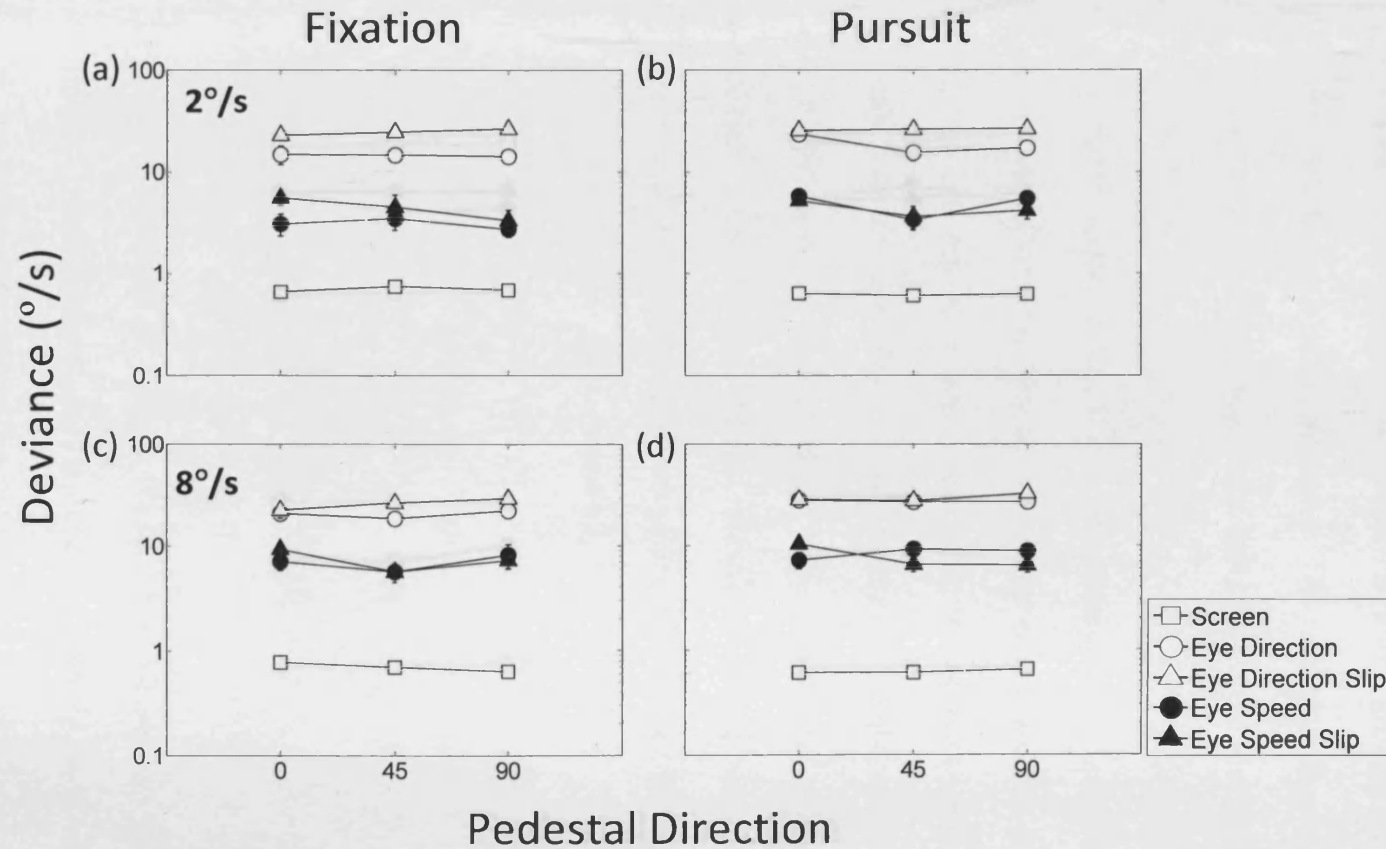


Figure 2.7. Deviance scores (best psychometric fit) for younger observers at stimulus speeds 2°/s and 8°/s during fixation and smooth pursuit. Circles and Triangles represent eye-movement and retinal slip deviance respectively with filled symbols corresponding to speed and unfilled symbols corresponding to direction. Squares correspond to screen motion deviance. Error bars are ± 1 SE

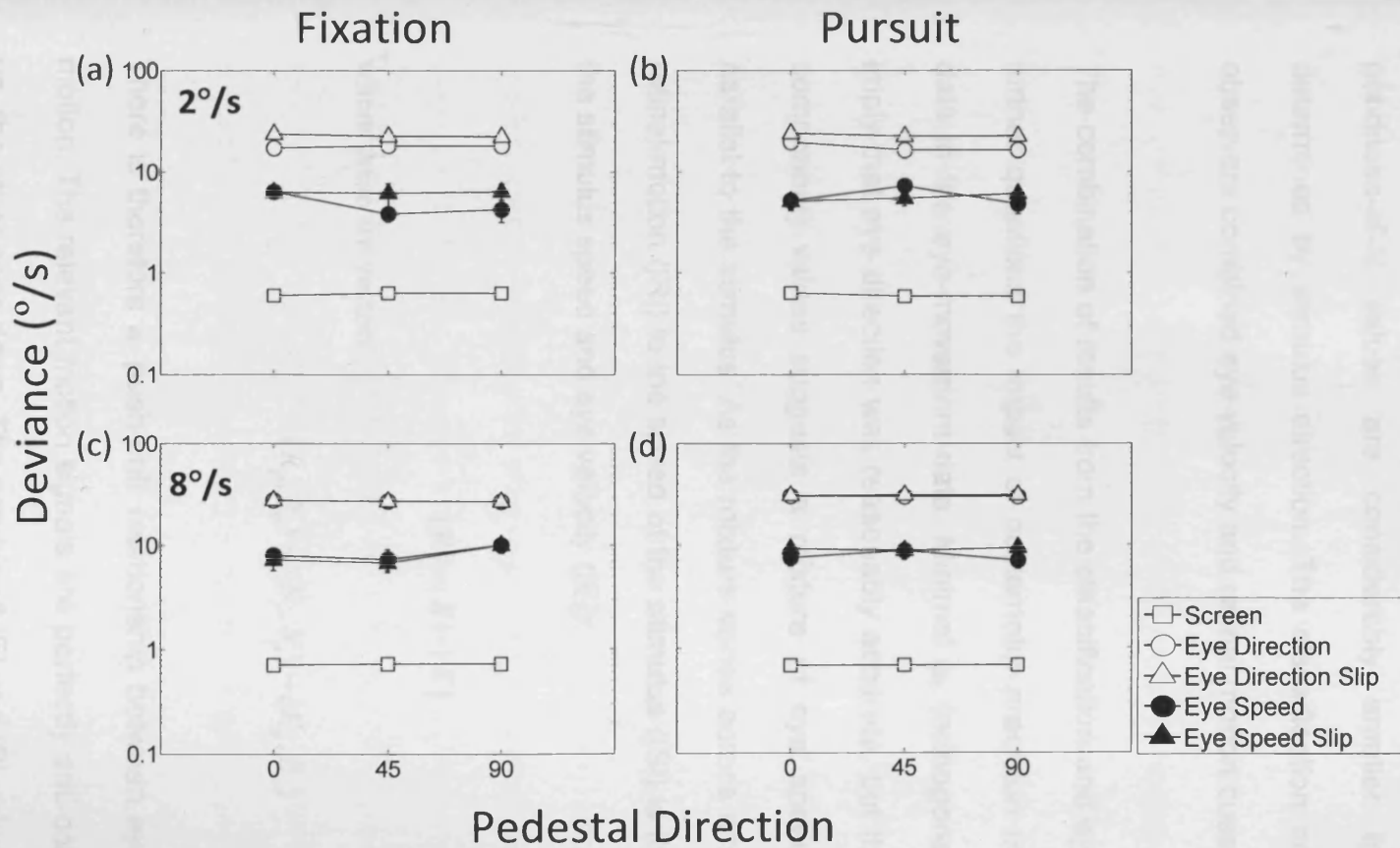


Figure 2.8. Deviance scores (best psychometric fit) for older observers at stimulus speeds 2°/s and 8°/s during fixation and smooth pursuit. Circles and Triangles represent eye-movement and retinal slip deviance respectively with filled symbols corresponding to speed and unfilled symbols corresponding to direction. Squares correspond to screen motion deviance. Error bars are ±1 SE

Figure 2.7 and 2.8 plots the goodness-of-fit for the five different motion cues considered, where a low deviance value corresponds to a better fit. The results demonstrate that for both fixation and pursuit conditions, the goodness-of-fit values are considerably smaller for response curves determined by stimulus direction. The classification analysis suggests that observers combined eye velocity and retinal motion cues in all conditions.

The combination of results from the classification and eye-movement analysis further questions the impact of oculomotor precision on the psychophysical data in the eye-movement data. Minimal e_o (orthogonal component) values imply that eye direction was reasonably accurate, but the varying e_p (parallel component) values suggests a mixture of eye speed and retinal motion parallel to the stimulus. As the mixture varies across time and conditions, the retinal motion ($|R|$) to the speed of the stimulus ($|S|$) is the difference between the stimulus speed and eye velocity ($|E|$):

$$|R| = |S| - |E| \quad (6)$$

where these are vectors

$$(R_p, R_o) = (S_p, S_o) - (E_p, E_o) \quad (7)$$

There is therefore a 'push-pull' relationship between eye velocity and retinal motion. The relevant motion signals are perfectly anti-correlated; as one goes up, the other goes down. The combined $|E|$ and $|R|$ values will always amount to the head centred stimulus speed $|S|$, which is the basis of the perceptual

judgement. As $|E|$ changes, $|R|$ changes as well, hence variability in eye movement will be counteracted by variability in retinal slip.

The general introduction proposed a second reason for differences in thresholds, namely that a difference in internal noise could account for the age effects and reduction in sensitivity during smooth pursuit. Unfortunately, due to the varying combination of retinal motion and eye-velocity during both eye-movement conditions, it is difficult to determine the sources of noise. As discussed in the introduction, Krukowski et al. (2003) compared direction thresholds during smooth pursuit and fixation and found no difference in direction sensitivity between the eye-movement conditions. They concluded that target motion was encoded during pursuit and fixation in head-centred coordinates thus creating one source of limiting internal noise within MST. However, it is also possible that a combination of separate noise sources dependent on motion cue-type and speed could also explain the results. This is supported by later studies who reported higher discrimination thresholds for pursued stimuli than fixated stimuli for speed judgements (Freeman et al. 2010) and direction of stimuli moving in depth (Welchman et al., 2009). Before examining this idea, however, we carried out the two control experiments. The first examined the influence of age-dependent changes in retinal illumination on direction discrimination. The second examined the role of relative motion, which is necessarily confounded with eye movement condition in our experiments.

2.2. Experiment 2: Luminance Control

As people get older, pupil size and the clarity of ocular media reduces. Both these factors can effectively decrease the amount of light reaching the retina by up to 66% (Weale, 1963). This questions whether the age –related changes in direction discrimination are explained by optical rather than neural changes. For example, Wright & Drasdo (1985) claimed the loss in temporal sensitivity at high flicker frequencies in older observers was the result of reduced retinal illumination. However, the mechanisms underlying flicker sensitivity may be different from that underlying direction sensitivity. Studies have shown that a reduction in retinal luminance does not explain age-related changes in other studies of motion perception. Norman et al. (2003) mimicked the optical losses present in old age by reducing retinal luminance by 0.5 log units in their younger observers, and found it did not alter speed discrimination thresholds.

Similarly, Betts et al. (2005) found no evidence that that reduced spatial suppression exhibited by older observers in a motion discrimination task could be accounted for by retinal illumination. Motion thresholds and pupil dilation were measured in a group of younger observers across a range of luminances (65 cd/m^2 , 27.3 cd/m^2 and 5.6 cd/m^2). The display luminance was manipulated by placing Neutral density filters in front of the monitor. Retinal luminance was estimated for each observer by multiplying mean monitor luminance by the individual pupil measurements. Based on these pupil diameters measurements, the two lower stimulus luminances produced retinal luminances in younger observers that were as low as or lower than retinal

illuminance experienced by older observers viewing the highest luminance. This showed that pupil dilation in younger observers fails to compensate for the reduction in luminance using ND in younger observers.

Given that, the results of Experiment 1 show that both retinal motion and eye-velocity cues contribute to direction discrimination, understanding the role of retinal illumination is important because it is unknown whether a reduction in retinal luminance can influence psychophysical performance during pursuit in older adults. To this end, the retinal luminance associated with the ageing eye was mimicked in younger observers using Neutral Density filters (ND) which reduced illumination by 50% (0.3 log units) and 75% (0.6 log units). These were compared to performance in a no-filter condition. Investigation was limited to the oblique standard direction in the slow-speed condition as this produced the greatest age effect in Experiment 1.

2.2.1. Methods

2.2.1.1. Participants

Twelve younger observers participated in the experiment aged 24 years or less (mean age 20.08 years). Again all observers had their distance visual acuity and contrast sensitivity measured prior to the main data collection using the Bailey-Lovie Log MAR chart (at 2m) and Pelli-Robson CS chart (1m) respectively (while wearing their optical correction) (see table 2.2). All observers had normal acuity and contrast sensitivity scores.

Table 2.2. Participant characteristics for younger observers in experiment 2. Age (in years) is reported as a mean followed by the standard deviation and range in parentheses. LogMAR visual acuity and Pelli-Robson contrast sensitivity scores are given as means followed by the standard deviation in parentheses. LogMAR and Pelli-Robson scores are given for binocular viewing

Experiment 2		Younger
	N	12
	Sex	2 males, 10 females
	Age	20(2.09, 18-24)
	LogMAR	0.03(0.05)
	Pelli-Robson	1.93(0.04)

2.2.1.2. Procedure

The stimuli for slow-speed oblique condition selected for investigation was identical to that used in Experiment 1. Display luminance was manipulated for the observers by placing ND filters in front of the projector lens. There were 3 conditions: ND0 (no filter), ND0.3 (50% luminance reduction) and ND0.6 (75% luminance reduction). Each observer completed six randomly ordered conditions (3 filters crossed with 2 eye movement conditions).

2.2.2. Results

2.2.2.1. Psychophysics

Figure 2.9 plots the direction discrimination thresholds for the different neutral density filters, with the results from Experiment 1 for both age groups shown on the left for comparison. The left panel corresponds to the fixation condition and right panel the pursuit condition. The difference between young and old thresholds in Experiment 1 (left hand bars in both plots) is greater than the difference between the thresholds for the ND0 and ND0.6. This suggests that retinal illumination cannot explain the ageing effect found in experiment 1. Further, the ND filter appears to have little effect on threshold in either eye-movement condition.

A 2x3 within-subjects ANOVA was carried out on the direction thresholds, with eye-movement and filter as variables. The main effect of filter was not found to be significant [$F_{2,22} = 1.141$, $p=0.338$] confirming previous observations. The ANOVA showed a significant difference between eye-movement condition [$F_{1,11} = 5.014$, $p=0.047$]. This supports findings from experiment 1, where observers found it more difficult to discriminate direction during pursuit compared to fixation.

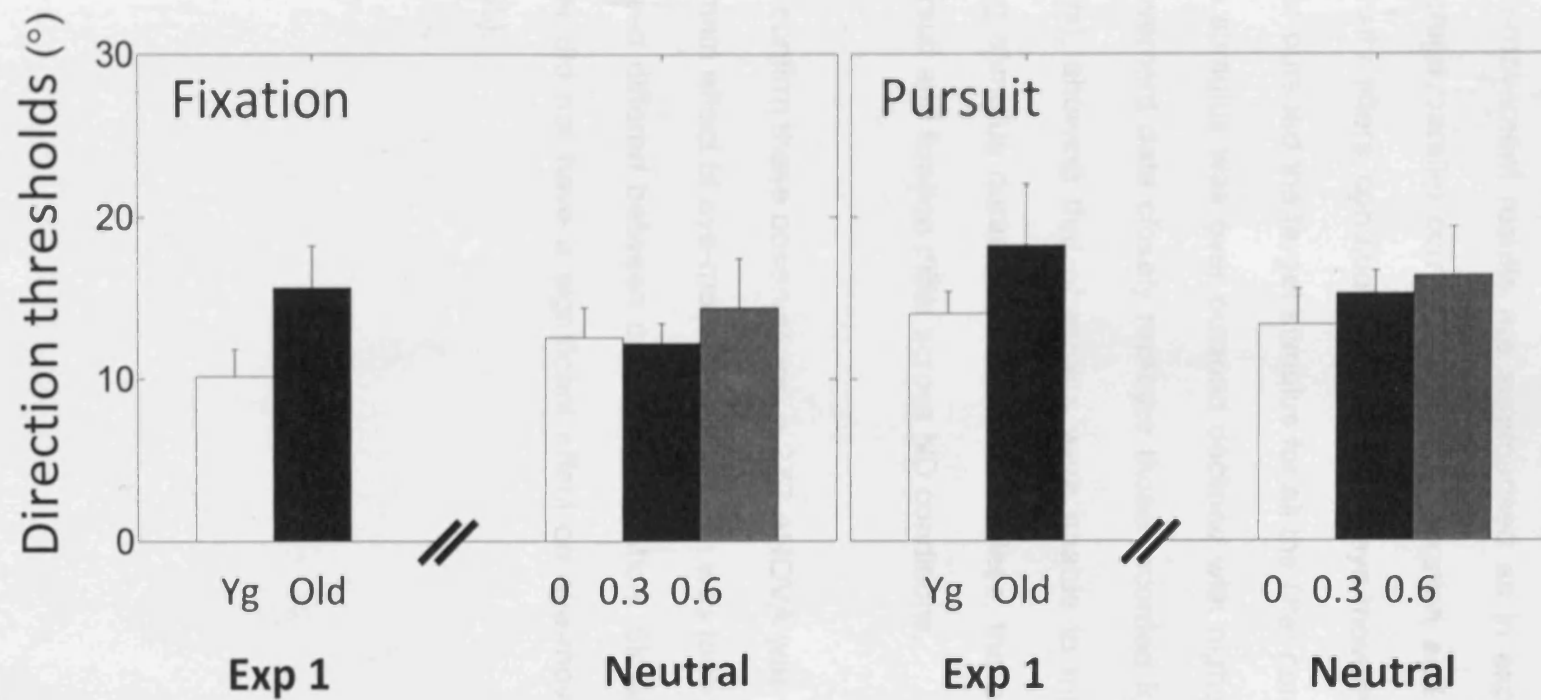


Figure 2.9. Direction discrimination thresholds for Experiment 1 (2% s) during fixation and pursuit (pedestal direction 45°) compared against younger observers direction thresholds with neutral density filters (0, 0.3, 0.6)

2.2.2.2. Eye-movements

Eye-movement results are summarised as in experiment 1. Figure 2.10 plots the average parallel component (ep) for fixation and pursuit across the three neutral density filters conditions. The pursuit eye-movement data indicate that observers over pursued the target stimulus for all the filter conditions, however amount of which the stimulus was over pursued declined with higher density filters. The fixation eye-movement data closely replicate those recorded for younger group in Experiment 1 ($2^\circ/s$), showing that observers were unable to maintain accurate fixation over the long stimulus duration (0.8s). Nevertheless, the eye-movement data suggests that pursuit and fixation differ across ND conditions.

To confirm these observations, a 2X3 ANOVA was carried out on the ep data.

A main effect of eye-movement condition was found [$F_{1,11} = 29.988$, $p = .000$], as eye speed differed between pursuit and fixation. Similar to the direction thresholds, ND filter did not have a significant effect on eye-movement results [$F_{2,22} = 2.032$, $p = .155$].

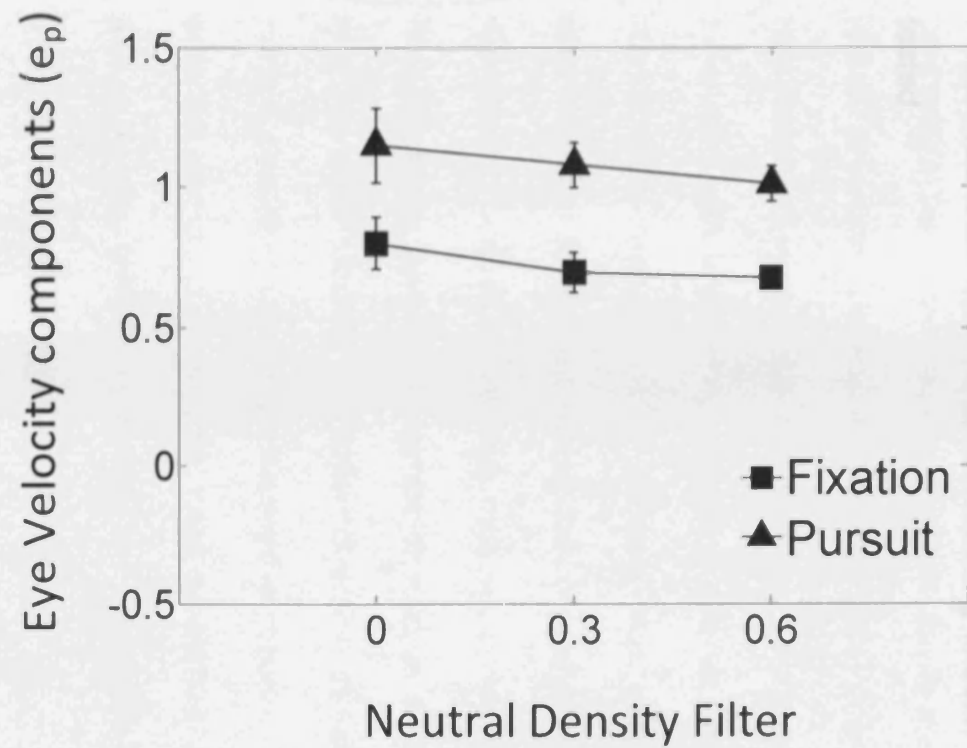


Figure 2.10. Mean eye velocity component (e_p) across neutral density filter (0, 0.3, 0.6) for stimulus speeds $2^\circ/s$ during fixation and smooth pursuit. Triangles correspond to the fixation condition and squares correspond to pursuit condition.

In summary, the luminance control experiment demonstrated that the age-related decline in direction sensitivity at slow stimulus speeds cannot be explained by an age-related reduction in retinal luminance. This supports previous motion discrimination studies using fixation stimuli (Ball & Sekuler, 1986; Norman et al., 2003). Furthermore, pursuit thresholds were higher than fixation thresholds replicating experiment 1. The eye-movement data showed that observers had difficulty maintaining fixation for all neutral density filters tested.

2.3. Experiment 3: Relative Motion

Relative motion is another possible explanation for the psychophysical differences found between fixation and pursuit during the direction discrimination task. To control eye-movements during the fixation condition, a stationary dot was placed in the centre of the moving random-dot stimuli. This provided the observers with an obvious source of relative motion, in direct contrast to the pursuit condition where the fixation point and stimuli window moved in unison. Smeets & Brenner (1994) in a reaction time study showed that observers were quicker at detecting a moving target at slow speeds when presented with a stimulus containing relative motion. In a similar trend, the results from experiment 1 showed that observers had lower direction discrimination thresholds during fixation (when relative motion was present) than during pursuit (no relative motion), again only at a slow speed of 2°/s. This suggests that the existence of relative motion in the fixation condition may have contributed to a lower direction threshold when compared to the pursuit condition for the slow-speed condition. In order to investigate this potential confound, observers were presented with two fixation conditions, one containing relative motion (as in Experiment 1) and another containing no relative motion, at slow and fast speeds.

2.3.1. Methods

2.3.1.1. Participants

Twelve younger observers participated in the experiment aged 21 years or less (mean age 18.75 years). Again all observers had their visual acuity and

contrast sensitivity measured prior to the main data collection using the Bailey-Lovie Log MAR chart (at 2m) and Pelli-Robson CS chart (1m) respectively (while wearing their optical correction) (see table 2.3). All observers had normal acuity and contrast sensitivity scores.

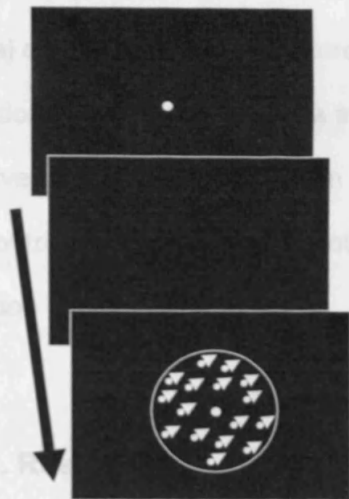
Table 2.3. Participant characteristics for younger observers in experiment 3. Age (in years) is reported as a mean followed by the standard deviation and range in parentheses. LogMAR visual acuity and Pelli-Robson contrast sensitivity scores are given as means followed by the standard deviation in parentheses. LogMAR and Pelli-Robson scores are given for binocular viewing

Experiment 3		Younger
	N	12
	Sex	1 males, 11 females
	Age	18.8(2.09, 18-21)
	LogMAR	0.0(0.009)
	Pelli-Robson	1.86 (0.1)

2.3.1.2. Procedure

A two-alternative forced-choice procedure was used to determine discrimination thresholds for the oblique standard direction of 45° at two different speeds (2°/s and 8°/s). As in Experiment 1, stimuli consisted of dots (0.1° radius, density of 1.5 dot/deg²) randomly positioned within a circular aperture (5° radius). In all conditions, a fixation point (0.2° radius) was presented for 0.5s in the centre of the screen. This was followed by blank screen, for which the duration was randomised across trials (0-0.4s) to

A. Relative



B. No relative

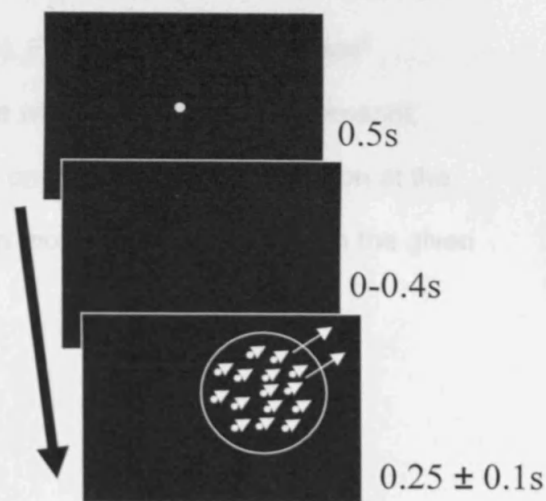


Figure 2.11. Schematic diagrams of the sequence of the visual stimuli for relative motion task . Initial fixation point presented for 0.5s followed by randomised delay (0-0.4s) and random dot pattern (0.25s±0.1s).

A. *Relative*: Fixation point centred in random dot display throughout presentation duration.

B. *No relative*: Fixation point disappears during random dot display. Observers asked to maintain fixation in position of initial fixation point.

prevent anticipatory eye-following responses. The random dot stimulus then appeared for $0.25\text{s} \pm 0.1\text{s}$. For the 'relative motion' condition a random dot pattern moved behind a fixed window with a stationary fixation point placed central of the stimulus (see figure 2.11a). For the 'no relative motion' condition, no fixation point was available while the stimulus was present; observers were asked to remain fixated on the initial fixation position at the start of trial while the random dot pattern moved with the window in the given direction (see Figure 2.11b).

2.3.2. Results

2.3.2.1. Psychophysics

Figure 2.12 plots the direction discrimination thresholds for the 'relative motion' and 'no relative motion' conditions during slow and fast speeds. No difference in direction discrimination thresholds between relative and no-relative motion conditions were observed for $2^\circ/\text{s}$ and $8^\circ/\text{s}$. As in experiment 1, an effect of stimulus speed is also evident, whereby increasing the stimulus speed produced lower direction thresholds irrespective of 'relative' and 'no relative motion' conditions.

Both these observations were confirmed with a 2X2 within subjects ANOVA. A significant main effect of speed was found [$F_{1,11} = 39.626$, $p = .000$], where direction thresholds decreased with increasing stimulus velocity. No significant difference was found between relative and non-relative motion conditions [$F_{1,11} = 0.163$, $p = .694$]. These results imply that relative motion

present in the fixation condition does not explain the different direction discrimination thresholds found in experiment 1 for pursuit and fixation at 2°/s. Smeets & Brenner (1994) observed higher reaction times to 'no relative' versus 'relative' motion onset for stimulus velocities of 1°/s and lower. At stimulus velocity 2°/s, Smeets & Brenner (1994) appeared to show no difference in reaction time between relative and no-relative motion conditions. This supports findings from the current experiment.

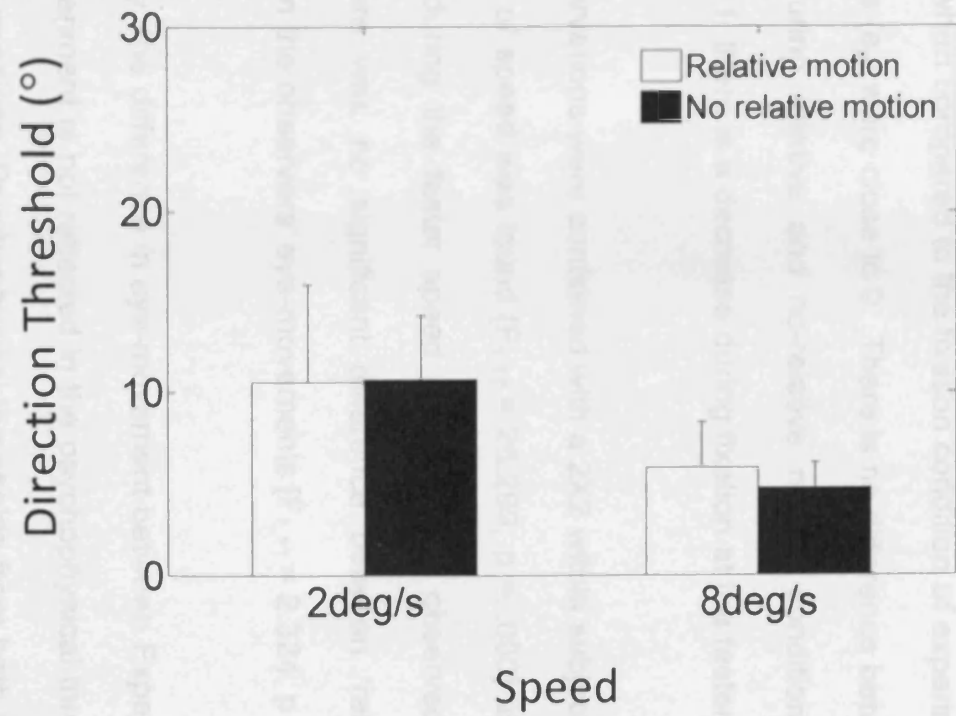


Figure 2.12. Mean direction discrimination thresholds for stimulus speeds 2°/s and 8°/s during relative and no relative motion conditions. Error bars are ± 1 SE.

2.3.2.2. Eye-movements

Figure 2.13 plots the mean parallel component (e_p) for 'relative motion' and 'no relative motion' conditions across speeds (2°/s and 8°/s). Due to the shorter stimulus presentation, a substantial reduction in eye-movement was found for both conditions when compared to the fixation condition of experiment 1. The eye-velocity components (e_p) were close to 0. There is no difference between the eye-movement recorded during relative and no-relative motion conditions. Further, as seen in experiment 1, there is a decrease during fixation at the faster speed.

These observations were confirmed with a 2X2 within subjects ANOVA. A significant main effect of speed was found [$F_{1,11} = 26.299$, $p = .000$] as observers moved their eyes less during the faster speed condition. As observed in the psychophysical results, there was no significant difference between 'relative' and 'no relative' conditions in the observers' eye-movements [$F_{1,11} = 2.324$, $p = .156$].

Interestingly, the difference in eye-movement between Experiment 1 and the relative motion experiment is not reflected in the psychophysical thresholds recorded for the slow speed condition. Psychophysical thresholds from both experiments averaged to ~10°. The fast speed however, shows a slight reduction in the direction thresholds for the relative motion experiment (~ 6°) when compared to experiment 1.

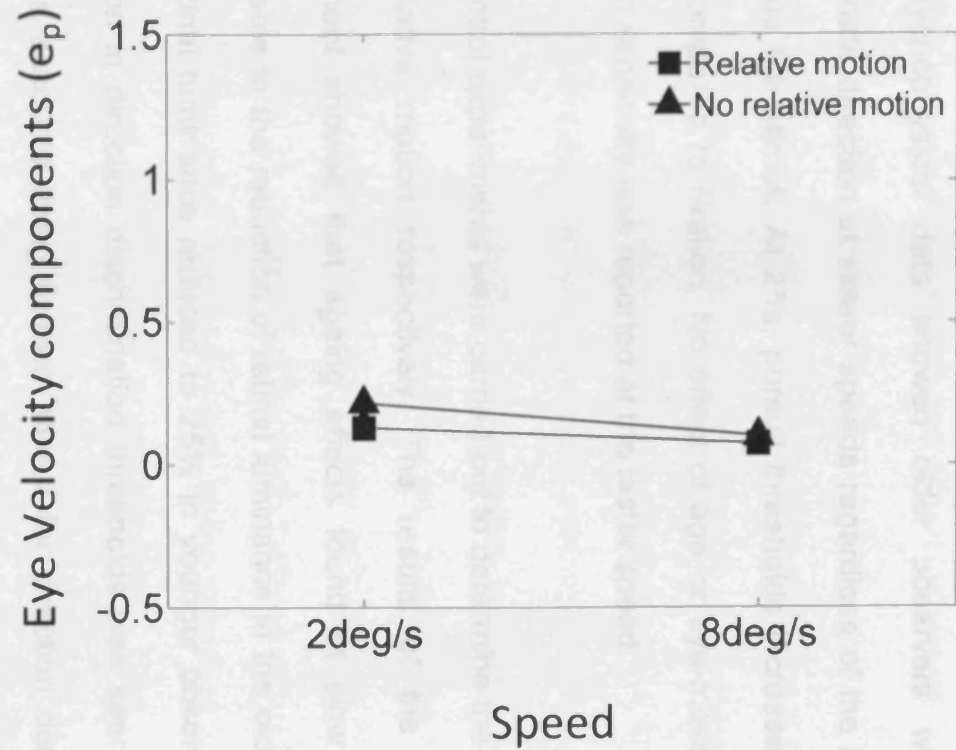


Figure 2.13. Mean eye velocity component (e_p) across stimulus speeds 2°/s and 8°/s during relative and no relative motion condition. Squares correspond to the relative motion condition and triangles correspond to no relative motion condition

2.4. Discussion

The studies reported here aimed to investigate age-related change in direction motion sensitivity during two types of eye movements, smooth pursuit and fixation. To do this, direction discrimination thresholds were measured in old and young observers using stimulus speeds of 2°/s and 8°/s. The psychophysical data showed older observers were less able to discriminate direction at slower speeds regardless of the instruction to fixate or pursue the stimuli. At 2°/s, pursuit thresholds increased for all observers when compared to fixation. No effect of age or eye-movement condition for direction sensitivity was reported at the faster speed.

Two control experiments were carried out to determine the effect of luminance and relative motion respectively. The results of the luminance control experiment showed that ageing effects found at slow speeds were not attributable to the reduction of retinal luminance in the older observers. Even with retinal luminance reduced to 25% in younger observers, no significant reduction in direction discrimination thresholds was seen. This agrees with previous accounts using fixation stimuli for direction discrimination (Ball & Sekuler, 1986) and speed discrimination (Norman et al. 2003).

Relative motion in the fixation condition was another potential confound that may have explained the psychophysical differences found between eye-movement conditions. Smeets & Brenner (1994) reported a significant reduction in reaction times to motion onset for stimulus, which contained

relative motion compared to stimulus with no-relative motion at slow speeds. Experiment 3 found no difference in discrimination thresholds between relative or no-relative conditions regardless of slow or fast speeds. This implies that eye-movement or age-related differences observed in the current direction discrimination study were not the result of relative motion. The results therefore, are attributable to the two other sources of motion information, namely retinal motion and eye-velocity cues.

One limitation to the experimental set-up is that it cannot completely preclude head-movements. Although assumed small, if translational head movements occurred then this would have added a component of image motion. There are several ways in which the visual system can compensate for head-movements, including vestibular-ocular reflex, feedback from neck preceptors and efference copy, either from the command signaling from the head-movements, or compensatory eye-movements (Harris, 1994). The effect of head-movement on motion discrimination during head movement is not well known, however there is evidence that motion detection is less optimal during head-movements (van Damme & van de Grind, 1996; Swanston & Wade, 1988).

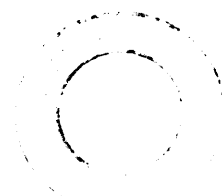
In the introduction, oculomotor control and internal noise were discussed as potential factors that could lead to differences between fixation and smooth pursuit direction sensitivity. The eye movement analyses from experiment 1 (section 2.1.2.2) suggest that oculomotor control is not able to explain the findings. The eye-movement data showed no effect of age or direction, results

which were inconsistent with the direction discrimination thresholds. The psychophysical findings demonstrated effects of age at the slower speed of 2°/s and direction effects for all conditions with one exception; older observers at faster speed of 8°/s. Eye movement precision also fails to explain the direction threshold differences between eye-movement conditions as this argument assumes that separate motion signals dominate direction sensitivity during fixation and smooth pursuit. Instead, the eye-movement data suggested that both old and young observers had access to varying quantities of retinal and extra-retinal motion signals across conditions. Classification analysis demonstrated that observers combined these cues to make their judgements. This agrees with Welchman et al. (2009) who showed that direction discrimination thresholds during a motion in depth task were best predicted using both retinal motion and eye-velocity cues. Eye-movement data also suggests that any variation in the magnitude of extra-retinal signal was offset by changes in the retinal slip: as one went up, the other went down. In these circumstances, combining signals therefore shields observers from any changes in extra-retinal signals linked to imprecise pursuit.

As mentioned in the introduction, this chapter aimed to address two separate issues 1) the effect of eye-movement condition on direction sensitivity and 2) ageing effects on direction sensitivity. These are now discussed in turn.

Direction sensitivity and eye-movement condition

At low speeds, the psychophysical differences reported between the two eye-movement conditions could not be attributed to differences in oculomotor



control. These results imply that internal noise from two motion cues is at the source of the psychophysical differences between pursuit and fixation conditions in the direction discrimination task. Classification analysis demonstrated that observers made direction judgements using head-centred motion for both pursuit and fixation conditions. Hence, both age groups combined retinal and extra-retinal motion cues. Furthermore, the proportion of each motion cue varied depending on the eye-movement condition. During pursuit, the extra-retinal motion was larger than the retinal motion, however during fixation, the eye-movement results suggests there is more extra-retinal motion during slow stimulus speeds and approximately equal amounts of retinal and extra-retinal during fast stimulus speeds.

Given this information, there are two possible sources of noise that could explain the psychophysical differences found between pursuit and fixation. The first suggests that a combination of retinal and extra-retinal signal noise dominates all conditions, supporting the previous account by Krukowski et al. (2003). In their study, they directly compared direction discrimination for fixation and smooth pursuit but found no difference in performance between the two eye-movement conditions. One suggestion for the similar thresholds was the presence of retinal slip in a percentage of the pursuit trials with low pursuit accuracy. They therefore divided the pursuit trials into low (78 %) and high gain (101%) groups but found no difference between the direction thresholds for the two subsets of trials. Krukowski et al. argued that pursuit and fixation direction thresholds are robust to changes in the proportion of retinal and extra-retinal input. This supports findings from the classification

analysis carried out in the current experiment. The authors proposed that target motion was encoded for both eye-movement conditions in head-centred co-ordinates, thus creating one source of limiting internal noise. MST was suggested as the location of this noise because evidence suggests that some neurons in MST encode head-centred motion (Newsome, Wurtz, & Komatsu, 1988). Given that Krukowski et al. (2003) presented their stimulus at 10°/s, their psychophysical results are consistent with our findings for the fast speed condition (8°/s). However, while a combined internal noise source could explain why no effect of eye-movement was found at fast speeds, it does not explain the differences in thresholds found at the slow speed. Therefore, it is unlikely that combination noise can explain this effect at the slow stimulus speed, given that noise at the combination stage does not reflect the inputs themselves. Combination noise could vary or decrease as a function of speed, however as discussed by Krukowski et al., it is difficult to see how this noise varies with the relative proportions of input signals. Further, it fails to explain other accounts where lower motion sensitivity was found during pursuit when compared to fixation (Freeman et al., 2010; Welchman et al., 2009).

For these reasons it is unlikely that the combined noise hypothesis is able to explain psychophysical differences found here between pursuit and fixation at slow speeds. The other possible explanation is that extra-retinal and retinal noise at the input stage limits performance. Given that for both eye-movement conditions; direction sensitivity improves as function of speed, in order to

model direction sensitivity, one would need to clarify the relationship between the noise sources and stimulus speed.

Direction sensitivity and age

Previous research has concentrated on retinal motion sensitivity. As outlined in the introduction, psychophysical and physiological evidence suggests that this ageing effect is due to an increased level of neuronal noise. Recently, Bennett et al. (2007) modelled age-related decline in a direction identification and judgement task, by increasing internal noise by a fixed amount, or combining this added noise with an increase in channel bandwidth. Bennett et al.'s internal noise model, combined with neurophysiological evidence showing decreased MT cellular activity and GABA inhibition, provide a good account of why retinal motion sensitivity reduces in older adults. However, similar to Krukowski et al. (2003), the study was limited to one stimulus speed (6°/s) and the fixed level of internal noise cannot explain the lack of age-effects found in experiment 1 at higher speeds. Furthermore, the model is limited to retinal motion sensitivity and thus offers no insight into age-related decline during smooth pursuit. Combining the results from experiment 1 with findings from Krukowski (2003) and Bennett (2007), one could conclude that there is a significant relationship between how speed and levels of internal noise vary not only as function of eye-movement condition but also age.

Stimulus Speed

The results suggest that stimulus speed plays an influential role in psychophysical performance for both young and old observers during fixation and pursuit. The fixation results support previous findings (Pasternak and Merigan, 1984; De Bryun & Orban, 1988; Ball and Sekuler, 1987), all of which report significant decreases in direction discrimination thresholds at low stimulus speeds. Both De Bryun & Orban (1988) and Ball & Sekuler (1987) found that as speed increased, direction sensitivity improved. In these studies, the sensitivity increase asymptoted at stimulus speeds of around 8-10°/s. Pasternak & Merigan (1984) found that improvements in direction discrimination thresholds levelled off at slower speeds around 2°/s. More recently, in a motion coherence task, Snowden & Kavanagh (2006) showed that both younger and older adults were less able to discriminate motion at slower speeds (<1°/s). They also found that older observers were less sensitive than younger observers. However, at the faster speeds the age-related deficit disappeared. The results of the current study agree with these findings. Increasing stimulus speed eradicated age-related reduction in direction sensitivity during fixation evident at the slow speeds. The same effects were evident in the pursuit condition. Both younger and older observers' direction sensitivity improved at faster pursuit speeds and the age effect found between young and old participants disappeared. This implies a positive correlation between stimulus speed and direction sensitivity irrespective of age or eye-movement condition.

In the general introduction, evidence for independent slow and fast motion channels were discussed in terms of retinal motion (e.g. van der Smagt et al, 1999). Different mechanisms or underlying neural substrates for slow and fast temporal processes may explain the effect of speed on direction discrimination in old and young observers during fixation. However, similar discrimination curves were shown for both fixation and smooth pursuit conditions, whether there exists a slow and fast channel for the processing of extra-retinal motion during pursuit remains unknown. This issue of slow and fast temporal process is complicated by the fact that in both pursuit and fixation, the observers combine both retinal and extra-retinal information.

Oblique Effect

Similar to Krukowski et al. (2003) experiment 1 showed a weak 'oblique effect' for old and younger observers during both fixation and smooth pursuit. This replicates psychophysical findings in a variety of motion perception tasks (Ball & Sekuler, 1980; Coletta, Segu, & Tiana, 1993; Gros, Blake, & Hiris, 1998). In addition, for younger observers the oblique effect did not vary as a function of speed in both eye-movement conditions. This has been reported previously for direction sensitivity during fixation (Ball & Sekuler, 1987, Gros et al. 1998). Neurophysiological evidence suggests that fewer cells are tuned to oblique representations within the early visual cortex such as V1 (Li et al., 2003; Mansfield, 1974), which has been supported using neuroimaging techniques (Furmanski & Engel, 2000). MT and possibly MST are also associated with the oblique anisotropies. For instance, Heeley & Buchanan-Smith (1992), in a study using drifting plaids, recorded lower directional acuity scores for plaids

that drifted in an oblique direction, despite the plaid consisting of cardinal direction components. This implies that pattern cells, which are located further along the visual pathway in MT and MST, are also subject to the oblique effect (Movshon et al., 1986). Unlike MT, the direction selective receptive fields in a percentage of MST cells are defined in head-centred coordinates. Given that head-centred motion cues were used during fixation and pursuit, this suggests that the observed oblique effect during both eye-movements conditions corresponds with activity in MST.

Summary

The experiments in this chapter successfully replicated previous accounts of age-related decline in motion perception during fixation, and demonstrated for the first time that both old and young observers' motion sensitivity during pursuit is subject to decline. Most pertinent to the findings is these effects were limited to a slow stimulus speed. Interestingly, the results also showed that eye-movement accuracy have little impact on the performance of observers during either eye-movement condition. Combined noise hypothesis as suggested by Krukowski et al. (2003) fails to account for the higher direction thresholds during pursuit at slow speeds. This suggests that changes to retinal and extra-retinal noise at the input stage may explain psychophysical differences in direction discrimination between eye-movement conditions.

3. Trajectory-matching

Direction discrimination is known to improve with stimulus speed (Pasternak & Merigan, 1984; De Bruyn & Orban, 1988; Ball & Sekuler, 1987). Furthermore, observers have also been shown to be more sensitive to directions moving along the cardinal axes compared to oblique axes, often referred to as the 'Oblique effect' (Ball & Sekuler, 1987; De Bruyn & Orban, 1988; Gros et al., 1998; Pasternak & Merigan, 1984). Both these results were replicated in the direction discrimination task in chapter 2, for both age groups and eye-movement conditions. Experiment 4 in Chapter 3 investigated whether these sensitivity differences generalised to a 'trajectory-matching' task. For this task, observers rotated the orientation of a line stimulus so that it matched the trajectory of motion of a dot pattern viewed in fixation and pursuit conditions. Observer performance was evaluated in two ways. Firstly, direction precision was defined as the variability in error between stimulus trajectory and trajectory-matches across trials (variable error). Secondly, observers' accuracy was calculated as the average trajectory estimate error (constant error).

3.1. Methods

3.1.1. Participants

Twenty-four observers participated in the experiment, 12 older than 60 years (mean age 67.5 years), and 12 aged 20 years or less (mean age 19.25

years). As in previous experiments both young and old observers had their distance visual acuity and contrast sensitivity measured prior to the main data collection using the Bailey-Lovie Log MAR chart (at 2m) and Pelli-Robson CS chart (1m) respectively (see table 3.1). All observers had normal acuity and contrast sensitivity scores.

Table 3.1. Participant characteristics for younger and older observers in experiment 4. Age (in years) is reported as a mean followed by the standard deviation and range in parentheses. LogMAR visual acuity and Pelli-Robson contrast sensitivity scores are given as means followed by the standard deviation in parentheses. LogMAR and Pelli-Robson scores are given for binocular viewing

Experiment 4		Younger	Older
	N	12	12
	Sex	1 males, 11 females	7 males, 5 females
	Age	19.3(0.97, 18-21)	67.5(4.40, 61-75)
	LogMAR	0.01(0.02)	0.04(0.05)
	Pelli-Robson	1.93(0.04)	1.88(0.10)

3.1.2. Stimuli

The stimuli for the trajectory-matching task were the same as experiment 1, apart from the following difference. After the presentation of the stimulus, an arrow appeared on-screen (see figure 3.1). Participants estimated the trajectory of the stimulus by rotating the arrow using the arrows keys on a keyboard.

3.1.3. Procedure

On each trial, observers were presented with one interval of stimulus motion, moving in one of eight possible directions (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°) and two possible speeds (2°/s and 8°/s). Following the stimulus presentation, an arrow appeared on-screen. The observer's task was to rotate this arrow using arrow keys on a keyboard to indicate as accurately as possible the perceived trajectory of the stimulus motion. A space-bar press recorded the observer's trajectory-match and initiated the next trial. The starting orientation line of the arrow in each trial was random (360°) to avoid bias.

In each condition (fixation and smooth pursuit), there were 160 trials, all randomly presented. Each condition contained 10 replications of the eight directions (4 ordinal, 4 cardinal) for slow and fast speeds (2°/s and 8°/s). Pursuit and fixation conditions were run in two separate sessions, the order of which was randomised between participants. Before the start of each session, the observers were informed of the type of eye-movement to use in the subsequent session. Each observer carried out each condition just once, with each testing session lasting about 40 minutes.

Variable error (equivalent to an observer's sensitivity to direction) was calculated as the standard deviation of trajectory estimate error. The latter was defined as the angular difference between the stimulus trajectory and the trajectory match made by the observer. Constant error (equivalent to an observer's bias) was calculated as the mean trajectory estimate error. The

variable and constant error were calculated for the eight directions and then collapsed into two direction conditions, cardinal (0° , 90° , 180° , 270°) and

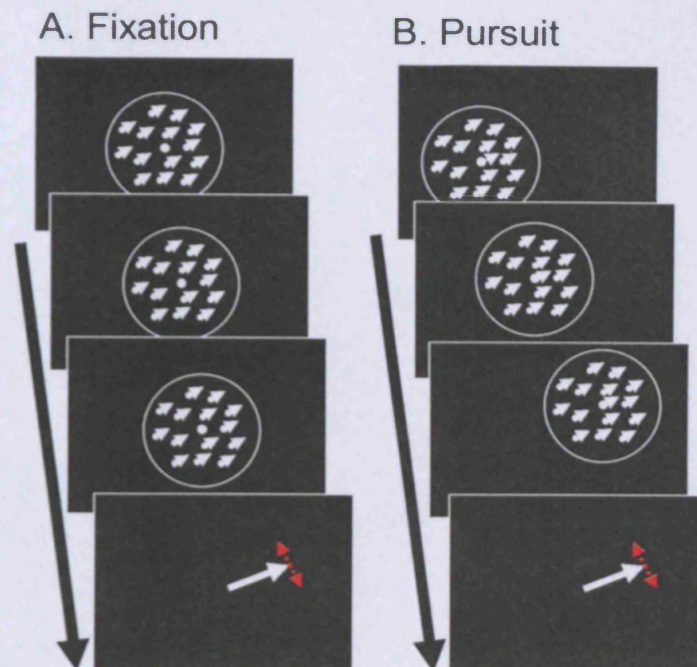


Figure 3.1. Schematic diagrams of the sequence of the visual stimuli for trajectory matching task. **A. Fixation:** participants fixated their eyes on the stationary point in the centre and judged the direction of the surrounding random dot pattern for $0.8s \pm 0.1$. **B. Pursuit:** participants judged the direction of the random dot pattern whilst pursuing the centre fixation point for $0.8s \pm 0.1$. The random dot pattern was present throughout the entire trial. After the pattern was presented, an arrow appeared on-screen. Participants reported the direction of the stimulus by rotating the arrow using the arrows keys on a keyboard. Space-bar press recorded the trajectory match and initiated the next trial.

oblique (45° , 125° , 225° , 315°). Figure 3.2 illustrates an example of trajectory match variability and bias for one observer across a series of trials. In this example, the trajectory matches for the oblique direction 315° were more variable than the cardinal direction 0° , as there was a larger standard deviation in trajectory estimate error. The greater the variable error, the less precise the observer is at correctly identifying the direction of the target stimulus. The constant error measures the observer bias, which in the example is positive for both directions. This indicates a bias, where the trajectory matches were made anticlockwise of the target. A negative trajectory estimate error implies bias clockwise of target.

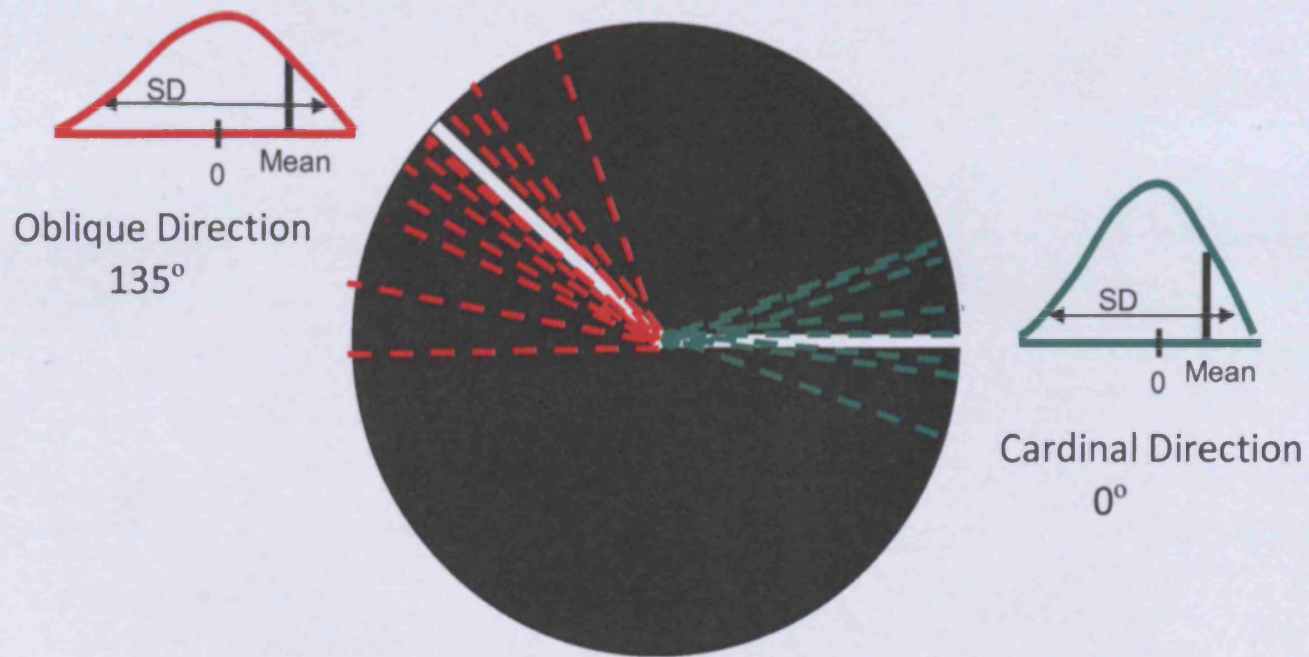


Figure 3.2. Variable error (measure of sensitivity) calculated as the standard deviation (SD) across *trajectory estimate error* (trajectory match - trajectory direction) over a series of trials. Constant error (observer's bias) calculated as the mean *trajectory estimate error* across trials

3.2. Results

3.2.1. Variable Error

Variable error for oblique and cardinal motion during fixation and pursuit in old and young observers are summarized in figure 3.3. The two eye-movement conditions are plotted individually for speed with 2°/s (top row) and 8°/s (bottom row). Variable error decreased with stimulus speed for both younger and older adults, as well as for cardinal and oblique conditions. Variable error was also greater during smooth pursuit compared to fixation at slow speeds. Older observers' were less precise at trajectory matching compared to younger observers in all conditions. There was however one exception, when both age groups performed equally when oblique angles were presented during fixation at slow speeds. Finally, there was larger variability in trajectory matching for the oblique directions for both speeds

These observations apart from an age effect were supported by statistical analysis. A 2X2X2X2 ANOVA, was carried out on the variable error scores, with age as the between-subject variable and the eye movement condition, stimulus speed and direction condition as within-subject variables. A significant main effect was reported for direction condition, revealing an oblique effect for all aged observers during both stimulus speeds [$F_{1,22} = 34.809$, $p = 0.000$]. The effect of speed was also significant [$F_{1,22} = 95.888$, $p = 0.000$], as was the main effect of eye-movement condition [$F_{1,22} = 14.027$, $p = 0.01$]. Variable error was higher during pursuit compared to fixation, at the slow speed only. This observation was confirmed with a significant interaction

between eye-movement and speed [$F_{1,22} = 28.280$, $p = 0.000$]. No significant effect of age was found [$F_{1,22} = 2.386$, $p = 0.137$], despite the trend visible in figure 3.3.

Further investigation into the eye-movement and speed interaction was carried out using separate 2X2X2 [Age, Speed and Direction] ANOVAs on the pursuit and fixation conditions. Speed effects were observed during both fixation [$F_{1,22} = 36.259$, $p = 0.000$] and smooth pursuit [$F_{1,22} = 83.274$, $p = 0.000$] eye-movement conditions. As illustrated in figure 3.3, variable error decreased at 8°/s for both young and old observers. A significant main effect of direction condition was found for both eye-movement conditions [Fixation: $F_{1,22} = 33.214$, $p = 0.000$] [Pursuit: $F_{1,22} = 19.414$, $p = 0.000$]. This indicates an oblique effect for fixation and smooth pursuit. No significant age effect was found during fixation [$F_{1,22} = 1.614$, $p = 0.217$] or smooth pursuit [$F_{1,22} = 2.309$, $p = 0.143$].

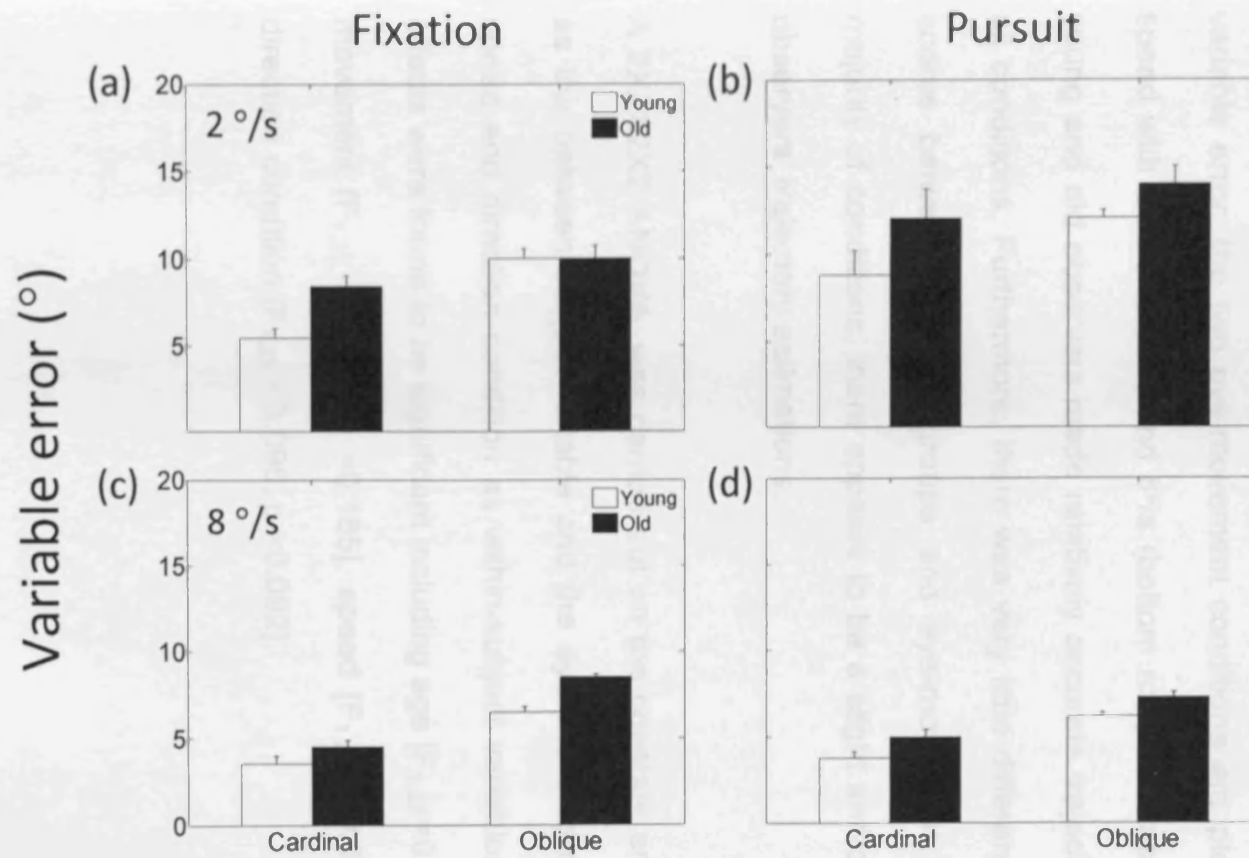


Figure 3.3. Mean Variable error (°) for young and old observers in trajectory matching task during Fixation and smooth pursuit. Error bars are ±1 SE.

3.2.2. Constant Error

Figure 3.4. plots the constant error scores for oblique and cardinal direction conditions during fixation and pursuit in old and young observers. As with the variable error, the two eye-movement conditions are plotted individually for speed with 2°/s (top row) and 8°/s (bottom row). It was observed that both young and old observers made relatively accurate trajectory matches across all conditions. Furthermore, there was very little difference in constant error scores between the age groups and eye-movement conditions. For the majority of conditions, there appears to be a slight anti-clockwise bias in the observers' trajectory estimations.

A 2X2X2X2 ANOVA, was carried out on the constant error scores, with age as the between-subject variable and the eye movement condition, stimulus speed and direction condition as within-subject variables. None of the main effects were found to be significant including age [$F_{1,22} = 0.002$, $p = 0.965$], eye-movement [$F_{1,22} = 1.872$, $p = 0.185$], speed [$F_{1,22} = 0.059$, $p = 0.811$], and direction condition [$F_{1,22} = 3.096$, $p = 0.092$].

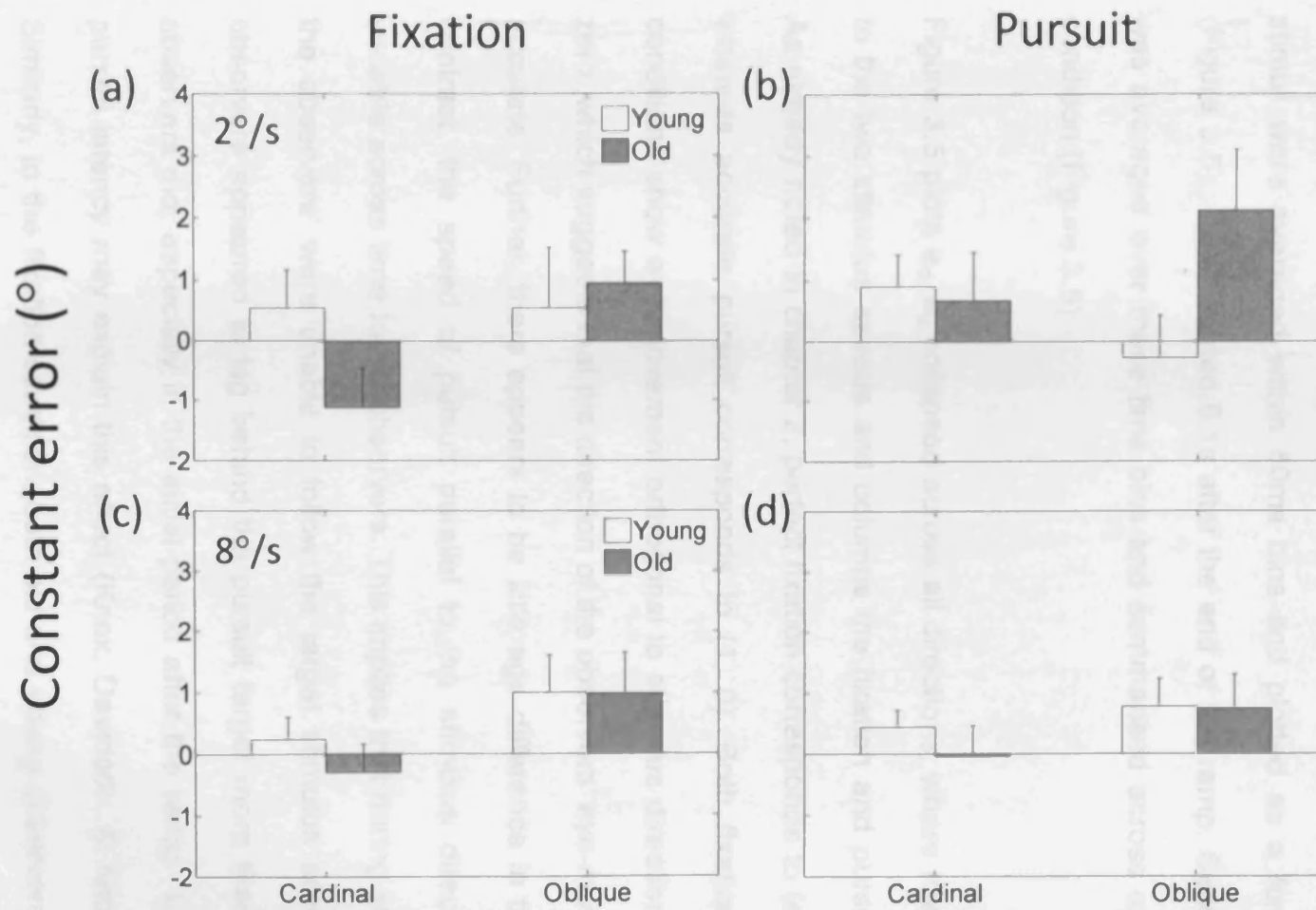


Figure 3.4. Mean constant error (°) for young and old observers in trajectory matching task during fixation and smooth pursuit. Error bars are ±1 SE.

3.2.3. Eye-movements

As in chapter 2, the eye-movement data was analysed in two ways. Firstly the normalised components (e_p, e_o) of eye velocity parallel and orthogonal to the stimuli were averaged within 50ms bins and plotted as a function of time (Figure 3.5). Time started 0.1s after the end of the ramp. Secondly, e_p data was averaged over these time bins and summarised across age group and condition (Figure 3.6).

Figure 3.5 plots e_o, e_p collapsed across all directions, where rows correspond to the two stimulus speeds and columns the fixation and pursuit conditions. As already noted in chapter 2, perfect fixation corresponds to $(e_p, e_o) = (0, 0)$ whereas accurate pursuit corresponds to $(1, 0)$. Both fixation and pursuit conditions show eye-movement orthogonal to stimulus direction (e_o) close to zero, which suggests that the direction of the observers' eye-movements were accurate. Further, there appears to be little age difference in the e_o data. In contrast, the speed of pursuit parallel to the stimulus direction (e_p) was variable across time for all observers. This implies that during smooth pursuit, the observers' were unable to follow the target stimulus accurately. Older observers appeared to lag behind the pursuit target more than the younger observers did, especially in the initial period after the ramp. Longer smooth pursuit latency may explain this effect (Knox, Davidson, & Anderson, 2005). Similarly, in the fixation condition, both old and young observers were unable to maintain accurate fixation. Eye speed for older adults' was faster compared to younger adults during the fixation condition.

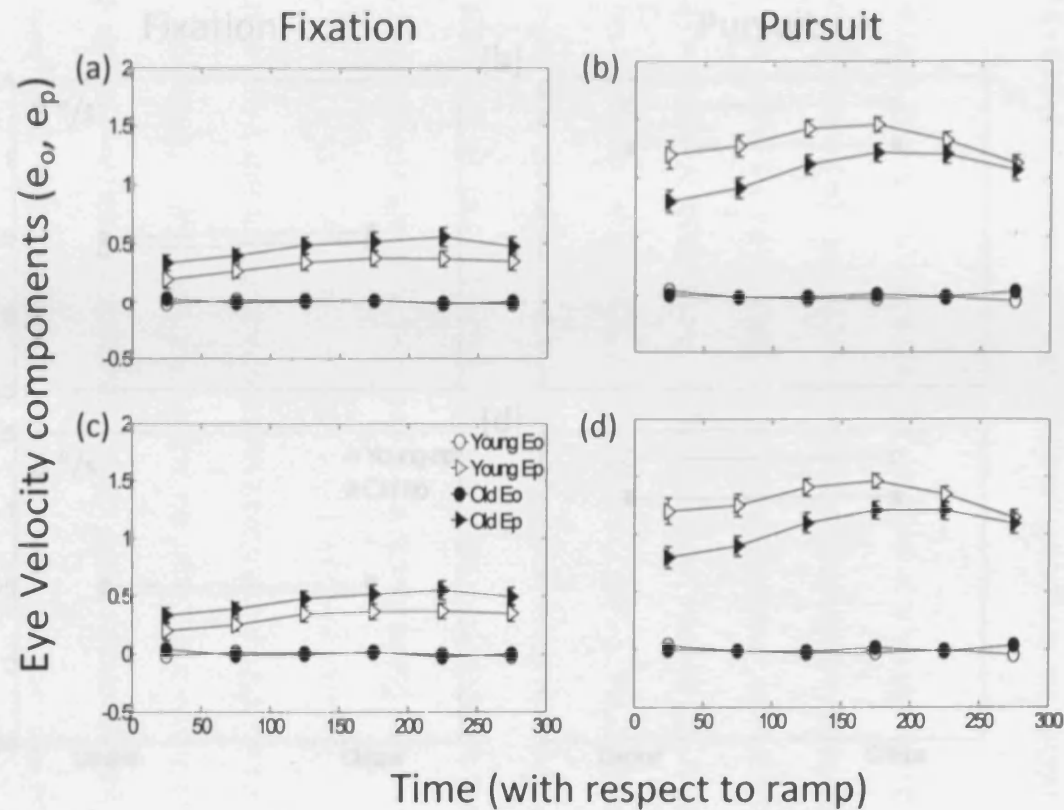


Figure 3.5. Normalised components of eye velocity (e_p, e_o) parallel and orthogonal to the direction of stimulus motion as a function of time (50ms bins) collapsed across all target directions. Eye-movement accuracy is shown for stimulus speeds $2^\circ/s$ and $8^\circ/s$ during fixation and smooth pursuit. Circles (unfilled) and triangles (unfilled) correspond to e_o and e_p respectively for the younger group. Circles (filled) and triangles (filled) correspond to e_o and e_p respectively for the older group. Error bars are ± 1 SE.

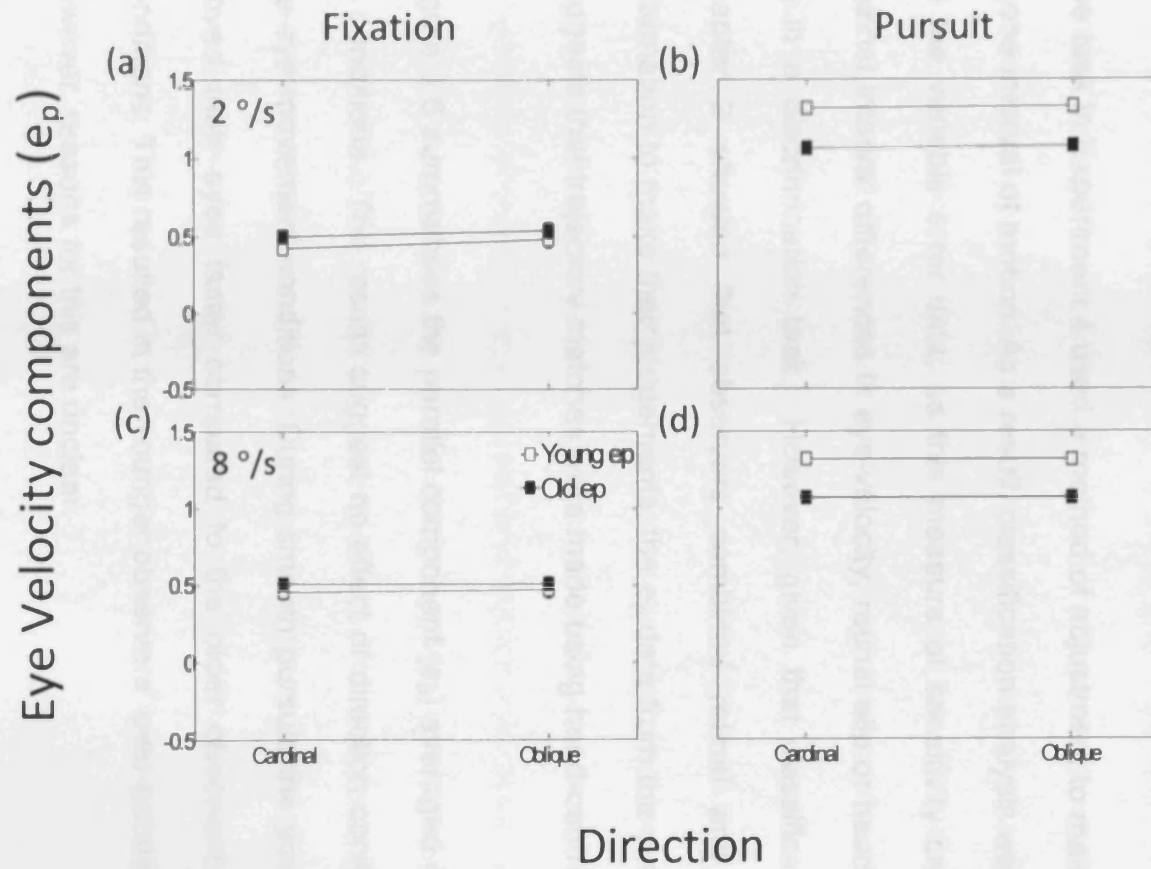


Figure 3.6 . Mean eye velocity component (e_p) for stimulus speeds $2^\circ/s$ and $8^\circ/s$ during fixation and smooth pursuit.

Squares (unfilled) correspond to the younger group and squares (filled) correspond to the older group. Error bars are ± 1 SE.

The eye-movement results show a similar pattern to those reported in experiment 1, where observers failed to maintain accurate fixation and pursuit eye-movement. As argued in Chapter 2, this suggests that during fixation and smooth pursuit, observers had access to both retinal and eye-movement information when making direction judgements. In addition, the mix of retinal motion and eye-velocity depended on time, eye-movement condition and age.

The task in Experiment 4 used a method of adjustment to match the trajectory of one interval of motion. As a result, classification analysis was not performed on the variable error data, as this measure of sensitivity cannot be plotted against interval differences in eye-velocity, retinal slip or head-centred motion as in a discrimination task. However, given that classification analysis in chapter 2 showed that observers combined retinal and eye-movement information to make their judgements, the e_p data from the current experiment suggests that trajectory matches were made using head-centred motion.

Figure 3.6 summarises the parallel component (e_p) averaged over time across all conditions. The results suggest no effect of direction condition in either of the eye-movement conditions. During smooth pursuit, the younger observers' moved their eyes faster compared to the older observers in both speed conditions. This resulted in the younger observers' over-pursuing the stimulus; however, reasons for this are unclear.

Again, eye-movement accuracy fails to account for variable error results, which suggests little relationship between eye-movement accuracy and performance.

A 2X2X2X3 [age, speed, eye-movement condition and direction] ANOVA, was carried out on the e_p values, with age and speed as the between-subject variable and eye-movement condition and direction as within-subject variables. Despite the difference in e_p values between old and young observers during smooth pursuit, age was not reported as a main effect [$F_{1, 22} = 1.567$, $p=0.224$]. No significant difference was found for direction condition, therefore there was no difference in the e_p values between cardinal and oblique directions [$F_{1, 22} = 2.461$, $p=0.131$]. The effect of eye-movement condition was also significant [$F_{1, 22} = 122.353$, $p=0.000$]. This confirms observation from figure 3.5, that while observers failed to maintain accurate fixation in both slow and fast conditions, there remains a significant difference in e_p values between smooth pursuit and fixation eye-movement conditions. A significant interaction was also found between eye-movement condition and age [$F_{1, 22} = 5.836$, $p=0.024$]. This resulted from age groups having similar eye-movements during the fixation conditions, but during pursuit, the younger observers over pursued the stimulus compared to the older group.

3.3. Discussion

In experiment 4, variable and constant error was measured for a range of cardinal and oblique direction stimuli in a trajectory-matching task using old

and young observers. Each direction was presented at two speeds; 2°/s and 8°/s. The variable error results correlate with three findings in direction discrimination thresholds in experiment 1. Firstly, variable error decreased as stimulus speed increased. Secondly, higher variable error was reported for oblique directions compared to cardinal direction. Thirdly, variable error increased during smooth pursuit compared to fixation. All these results apply to both age groups. Despite an age-related trend similar to experiment 1, the effect of age was not significant. The constant error results showed that observers of all ages made relatively accurate trajectory matches across all conditions, with no effect of age-group or eye-movement condition.

As noted for psychophysical thresholds in the direction discrimination experiment, variable error in the trajectory-matching task appears to decrease with increased stimulus speed for both eye-movement conditions. This finding is also in line with previous accounts of direction discrimination for retinal presented stimuli (Ball & Sekuler, 1987; DeBruyn & Orban, 1988; Pasternak & Merigan, 1984). Furthermore, the oblique effect observed in variable error during smooth pursuit and fixation, supports Krukowski et al. (2003) findings with direction discrimination thresholds. In the trajectory-matching task, the oblique effect was evident across the slow and fast stimulus speeds, which also correlates with direction discrimination thresholds from previous studies (Ball & Sekuler, 1987; Gros et al., 1998).

One limitation to this study is that there is no evidence to show that the observers did not do the task by realizing that the directions were restricted to

eight possible directions, despite precautions taken to ramp the stimulus and randomize both speed and direction. If however the observers did perform the task by identifying the eight possible directions, it fails to explain the significant difference in variable error between slow and fast stimulus speeds and eye-movement condition that is consistent with the direction discrimination task.

Overall, the trajectory-matching task provides support that the results from experiment 1 can generalise to another direction judgement task. In particular, it emphasises the role of stimulus speed in direction sensitivity for both old and young observers regardless of eye-movement condition. Additional evidence was given to the presence of the oblique effect during both pursuit and fixation, irrespective of stimulus speed.

4. Speed Discrimination

As discussed in the general introduction, retinal speed sensitivity is known to decline in older age (Norman et al., 2003; Raghuram et al., 2005; Snowden & Kavanagh, 2006). Similar to reports on direction discrimination, the effect of age on retinal speed discrimination are considered a product of age-related cortical changes in brain areas associated to motion processing, particularly MT. Yang et al. (2009) investigated the effects of ageing on speed-tuning curves in cortical area MT of macaque visual cortex. They compared 107 young and 88 old MT cells across a range of measures. Results showed that the speed-tuning curves for the older MT cells were more broadly tuned than younger cells, thus less selective for speed. In addition, spontaneous activity was greater in the older cells, decreasing the signal: noise ratio when compared to younger cells. Both changes to tuning and increased noise were shown to reduce retinal speed sensitivity in macaques monkeys. Yang et al. (2009) also observed that predicted speed discrimination thresholds increased approximately linearly with speed for both age groups, replicating previous findings (Nover, Anderson, & DeAngelis, 2005; Snowden & Kavanagh, 2006).

In younger observers, speed sensitivity has been shown to decline for pursued stimuli compared to fixated stimuli (Freeman et al., 2010). Furthermore, speed thresholds increased for faster stimulus speeds during both eye-movement conditions. However, research regarding speed sensitivity in older observers is limited to retinal motion when the eyes are fixated. In chapter 2, observers of all ages had higher direction discrimination

thresholds for pursued stimuli compared to fixated stimuli at slow speeds. Furthermore, the direction thresholds increased for older observers in both eye-movement conditions. Therefore, the aim of this chapter was to compare speed discrimination thresholds between young and old observers during smooth pursuit and fixation. As in the earlier chapters, two questions were addressed. Firstly, do speed thresholds increase for pursued stimuli compared to fixated stimuli as evidenced by Freeman et al. (2010). Secondly, are older observers less sensitive to speed in both fixation and smooth pursuit discrimination tasks?

4.1. Methods

4.1.1. Participants

Forty-two observers participated in the speed discrimination experiment, 21 older than 60 years (mean age 68 years), and 21 aged 26 years or less (mean age 20 years). As in previous experiments both young and old observers had their distance visual acuity and contrast sensitivity measured prior to the main data collection using the Bailey-Lovie Log MAR chart (at 2m) and Pelli-Robson CS chart (1m) respectively (see table 4.1). All observers had normal acuity and contrast sensitivity scores.

Table 4.1. Participant characteristics for younger and older observers in speed discrimination experiment 5. Age (in years) is reported as a mean followed by the standard deviation and range in parentheses. LogMAR visual acuity and Pelli-Robson contrast sensitivity scores are given as means followed by the standard deviation in parentheses. LogMAR and Pelli-Robson scores are given for binocular viewing.

Experiment 5		Younger	Older
	N	21	21
	Sex	7 males, 14 females	12 males, 9 females
	Age	20.0(2.47, 18-26)	68.0(6.67, 61-83)
	LogMAR	0.01(0.03)	0.06(0.10)
	Pelli-Robson	1.94(0.05)	1.82(0.14)

4.1.2. Stimuli

As for experiment 1-4, stimuli for the speed discrimination task consisted of random dot patterns. In each pattern, dots (0.1° radius, density of 1 dot/ $^\circ$ ²) were randomly positioned within a circular aperture (8° radius), with a fixation point (0.2° radius) located in the centre. The instructions for each eye-movement condition were the same as previous experiments, except the observers were asked to judge the speed of the surrounding pattern.

In both eye-movement conditions, the stimulus speed was linearly ramped over the first 0.3s. The ramp aimed to minimise the amount of retinal slip available to the observer that corresponded to the target speed. The ramp started at the zero and increased linearly over time until it reached the interval's target speed. The target speed was then presented for 0.5s. Similar

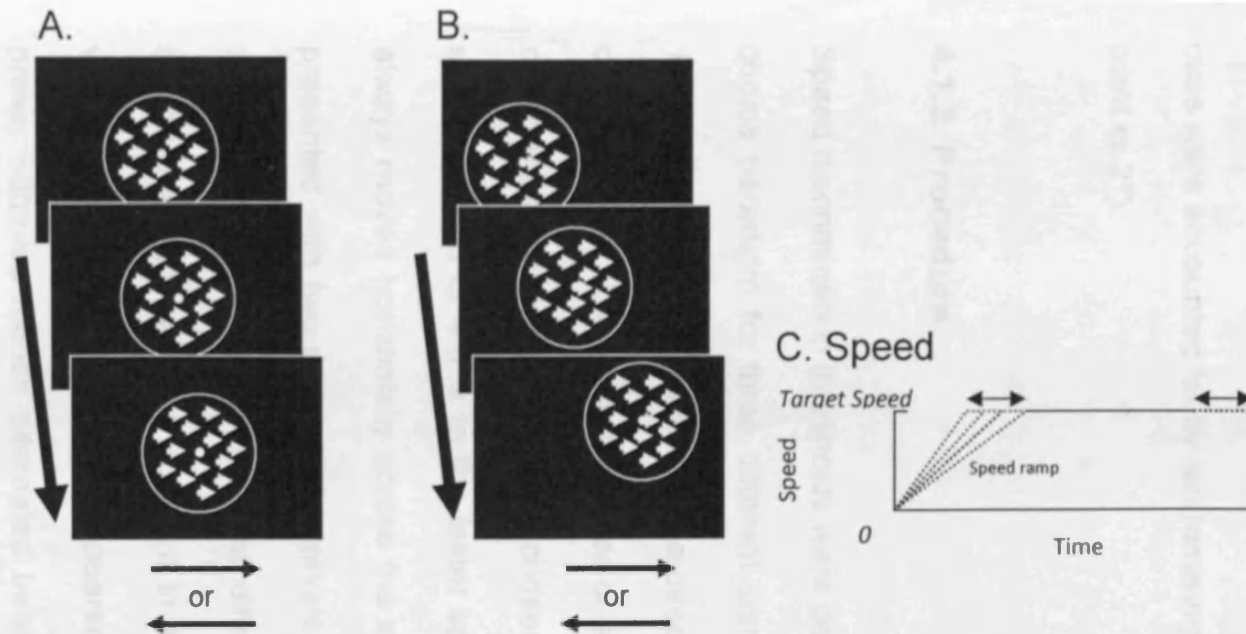


Figure 4.1. Schematic diagrams of the sequence of the visual stimuli for speed discrimination task . **A. Fixation:** participants fixated their eyes on the stationary point in the centre and judged the speed of the surrounding random dot pattern for $0.8s \pm 0.1$. **B. Pursuit:** participants judged the speed of the random dot pattern whilst pursuing the centre fixation point for $0.8s \pm 0.1$. The random dot pattern was present throughout the entire trial. **C. Speed Ramp:** the direction of the stimulus was linearly ramped before it reached target speed ($S \pm \Delta S$) in order to reduce the amount of retinal motion available to the observer during the pursuit condition. The duration of the linear ramp was then randomised from trial to trial ($0.3s \pm 0.025$)

to the direction discrimination experiment, the time where the stimulus speed was ramped was randomised (± 0.025 s). The time during which the stimuli was ramped ranged from 0.275s to 0.325s (see inset to Fig.4.1). Furthermore, the overall stimulus presentation was randomised (± 0.1 s), which aimed to prevent observers judging the target speed from position cues. Other position cues were accounted for by randomising the position of the starting fixation point ($\pm 2^\circ$).

4.1.3. Procedure

Speed discrimination thresholds were determined using a 2-alternative-forced-choice paradigm for three different standard speeds ($S = 4.8^\circ/\text{s}$, $9.6^\circ/\text{s}$ and $19.2^\circ/\text{s}$). As was the case with the direction discrimination experiments in the chapter 2 and 3, a limited number of speeds were investigated due to time constraints. Three speeds were chosen that increased in octaves from the slowest speed of $4.8^\circ/\text{s}$ to the faster speeds of $9.6^\circ/\text{s}$ and $19.2^\circ/\text{s}$. Stimuli always moved horizontally across the screen. For each trial, observers were presented with two sequential intervals of stimulus motion, one moving at a standard speed (S) and one that differed from the standard ($S \pm \Delta S$). The standard speed was held constant in any one session. The observer's task was to choose which interval appeared to move faster using mouse-button press. Stimulus motion alternated between leftward and rightward direction following each button press.

The speed difference between the two intervals (ΔS) was adjusted logarithmically within two randomly interleaved 1-up 1 down staircases (Kaernbach, 1991). As in the direction discrimination task, ΔS increased by three step sizes following each incorrect response and decreased by one step size following each correct response. Each staircase was designed to converge on the 75% correct responses and terminate after eight reversals. Pursuit, fixation and control conditions were run in separate sessions, yielding nine types of trials (3 conditions X 3 standard directions). The order of the nine conditions was randomised, with a break in between to explain the type of eye-movement to use in the subsequent session. Each observer carried out each condition just once, with each testing session lasting about an hour.

The linear ramp at the start of the stimulus presentation was designed to reduce retinal slip information related to the target speed. However, the observers could still have access to the ramp motion. To rule out the possibility that this initial retinal ramp motion was used to make speed judgements in the pursuit condition, a control was run in addition to the fixation and pursuit conditions. In the control condition, the participants were shown the initial portion of the fixation trials where the motion was linearly ramped and randomized in duration. The procedure was identical to the pursuit and fixation conditions outlined above.

4.1.4. Psychophysical analysis

As described for the direction discrimination thresholds in Chapter 2, the speed discrimination thresholds were calculated using Probit analysis (Finney, 1971). The JND was computed by subtracting ΔS at 75% from ΔS at 50%, which in this case referred to the amount of additional stimulus needed to increase speed discrimination rate from 50% to 75% on the fitted psychometric function. Again, the frequency of choosing interval 2 was plotted against the signed difference ΔS between the two intervals.

4.1.5. Eye-movement recording and analysis

For the speed discrimination experiment, eye-movements were recorded at a sample rate of 60Hz, using a head-mounted video eye-tracker (ASL Series 5000). Note that this is a different eye tracker from that used in the earlier experiments. As in Chapter 2, calibration was carried out prior to each recording using a 3-by-3 grid of points projected on the screen. The eye-movement analysis and saccade detection were also performed using the same techniques described in the direction discrimination task.

Recall that in the direction experiments, eye movement accuracy was based on two components (e_o, e_p), which allowed a standardised eye movement measure for stimuli that changed in direction. Stimulus motion in the current speed discrimination experiment was always horizontal, so the analysis of eye movements was restricted to using the data from the horizontal channel of the

eye tracker (i.e. E_x). This is equivalent to the parallel component e_p used in the direction discrimination experiments and is the standard way of analysing experiments confined to a single stimulus direction (e.g. Freeman, 1999; 2000; 2007; Freeman, Champion, Sumnall, & Snowden, 2009). Horizontal eye speeds were converted to gains by dividing by the appropriate stimulus speed.

In the speed discrimination task, eye-movement accuracy was calculated as a gain (eye speed/ target speed). A pursuit gain of 1 indicates that the observer pursued the stimulus target accurately. A pursuit gain of less or more than one indicates that the observer under pursued and over pursued the target respectively. In the fixation condition, target speed was zero; therefore, accuracy was reported as eye speed/ stimulus speed. A fixation gain of zero indicates the observer maintained perfect fixation. A fixation gain greater than zero indicates an observer moving their eyes to follow the stimulus.

4.2. Results

4.2.1. Psychophysics

Speed discrimination thresholds are summarised in figure 4.2 for old and young observers during fixation and smooth pursuit. Speed sensitivity decreased with increased stimulus speed in both age groups, however the effect was more pronounced for the pursued stimuli. Furthermore, observers of all ages were worse at discriminating speed during smooth pursuit compared to fixation. This supports findings by Freeman et al. (2010).

Importantly, there appears to be little effect of age. In the pursuit condition, older observers are more sensitive than younger observers to the medium standard speed (9.6°/s). However, this appears to be an anomalous finding, given there was no effects of age at the slower or faster standard speeds.

A 2X2X3 (age, eye-movement condition and speed) ANOVA, with age as the between-subjects variable and condition and speed as within-subject

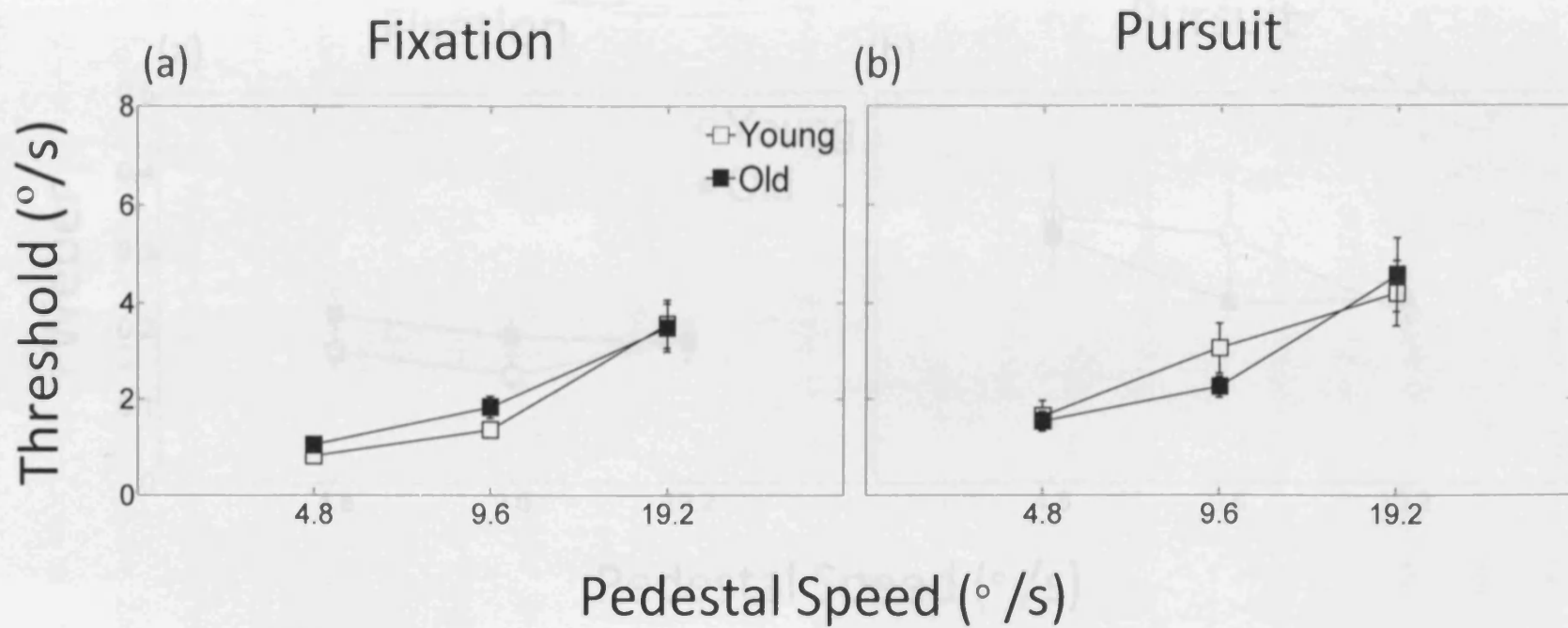


Figure 4.2. Mean speed discrimination thresholds for pedestal speeds 4.8°/s, 9.6°/s 19.2°/s during fixation and smooth pursuit. Squares (unfilled) correspond to the younger group and squares (filled) correspond to the older group. Error bars are ±1 SE.

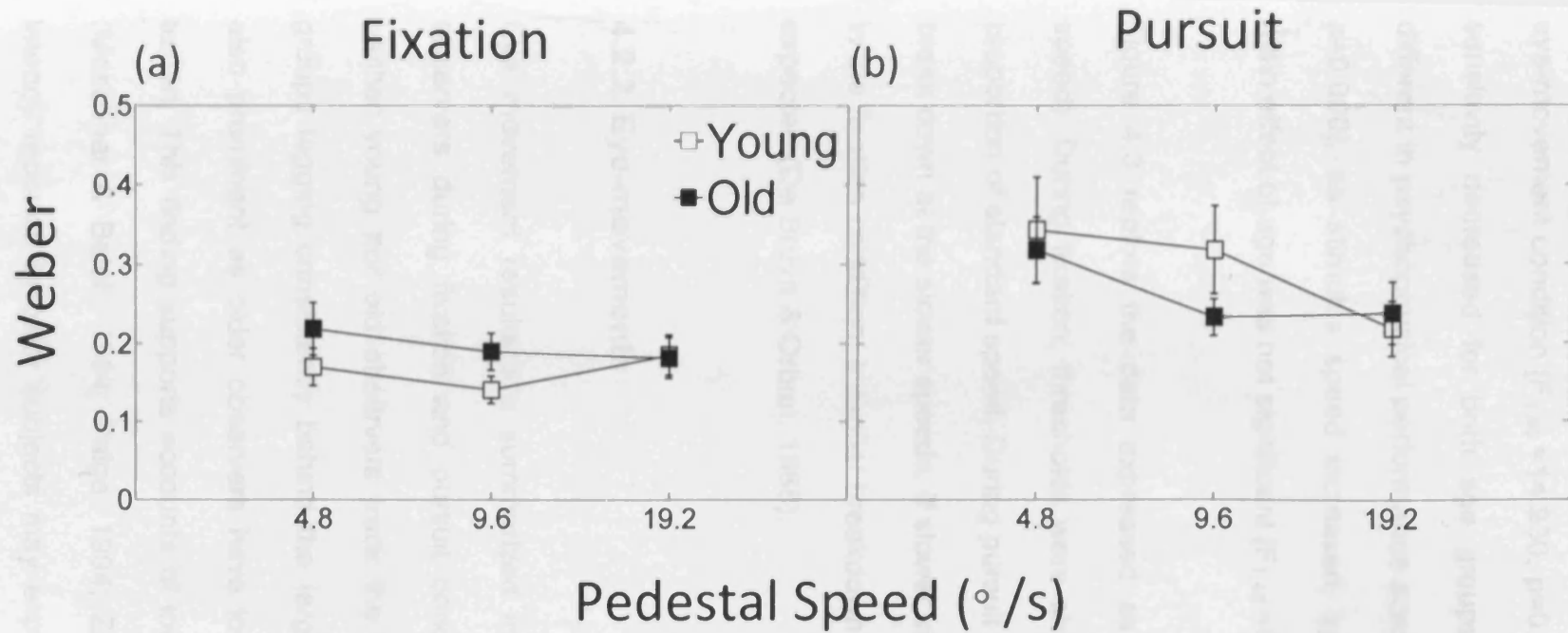


Figure 4.3. Weber fractions for pedestal speeds 4.8°/s, 9.6°/s 19.2°/s during fixation and smooth pursuit. Squares (unfilled) correspond to the younger group and squares (filled) correspond to the older group. Error bars are ± 1 .

variables confirms these observations. A significant main effect was found for eye-movement condition [$F_{1,40} = 14.930$, $p = 0.000$] where during pursuit, speed sensitivity decreased for both age groups. There was also a significant difference in psychophysical performance across stimulus speed [$F_{2,80} = 47.448$, $p = 0.000$], as stimulus speed increased, speed sensitivity decreased. The main effect of age was not significant [$F_{1,40} = 0.003$, $p = 0.955$].

Figure 4.3 replots the data expressed as Weber fractions (JND/pedestal speed). During fixation, thresholds were shown to be approximately a fixed proportion of standard speed. During pursuit however, Weber's law appears to break down at the slower speeds. If slower standard speeds were investigated in the fixation condition, a similar breakdown of Weber's law would have been expected (De Bruyn & Orban, 1988).

4.2.2. Eye-movements

Eye movement results are summarized in Figure 4.4 for young and old observers during fixation and pursuit conditions. In the pursuit condition, neither young nor old observers track the target accurately, with both age groups lagging consistently behind the target velocity. An age difference is also prominent as older observers have lower pursuit gains for all speeds tested. This finding supports accounts of low pursuit gain in older observers (Moschner & Baloh, 1994; Paige, 1994; Zackon & Sharpe, 1987). Pursuit latency reported in older subjects may explain this age effect (Knox et al., 2005). In the fixation condition, the older observers are less able to maintain

accurate fixation when compared to the younger observers, particularly at the slower speeds.

Statistical analysis confirmed these observations. A 2X2X3 (age, condition and speed) ANOVA, was performed on the pursuit gains with age as the between-subject variable and the condition and speed as within-subject variables. This showed a significant main effect of age [$F_{1,40} = 5.694$, $p=0.022$], where older observers had less accurate eye-movement gains. This was particularly evident during the pursuit condition which resulted in a close to significant interaction between eye-movement and age [$F_{1,40} = 5.255$, $p=0.067$]. There was also a significant effect of speed [$F_{2,80} = 15.471$, $p=0.000$], with gains decreasing for faster speeds during both eye-movement conditions. Unsurprisingly, a main effect of eye-movement condition was also found [$F_{1,40} = 781.373$, $p=0.000$].

Similar to the direction discrimination experiment and the trajectory estimation experiment, the eye-movement results in experiment 4 were not consistent with some of the psychophysical findings. While psychophysical thresholds show no effects of age, the eye-movement results indicate a significant difference between younger and older adults. Thus, eye-movement accuracy cannot explain the speed discrimination thresholds obtained for younger and older observers. Further, both eye-movement conditions contained varying mixtures of retinal and extra-retinal motion due to an inability to keep eyes stationary in the fixation condition and with pursuit gains less than 1 in the pursuit condition. As discussed in chapter 1, this does not easily implicate

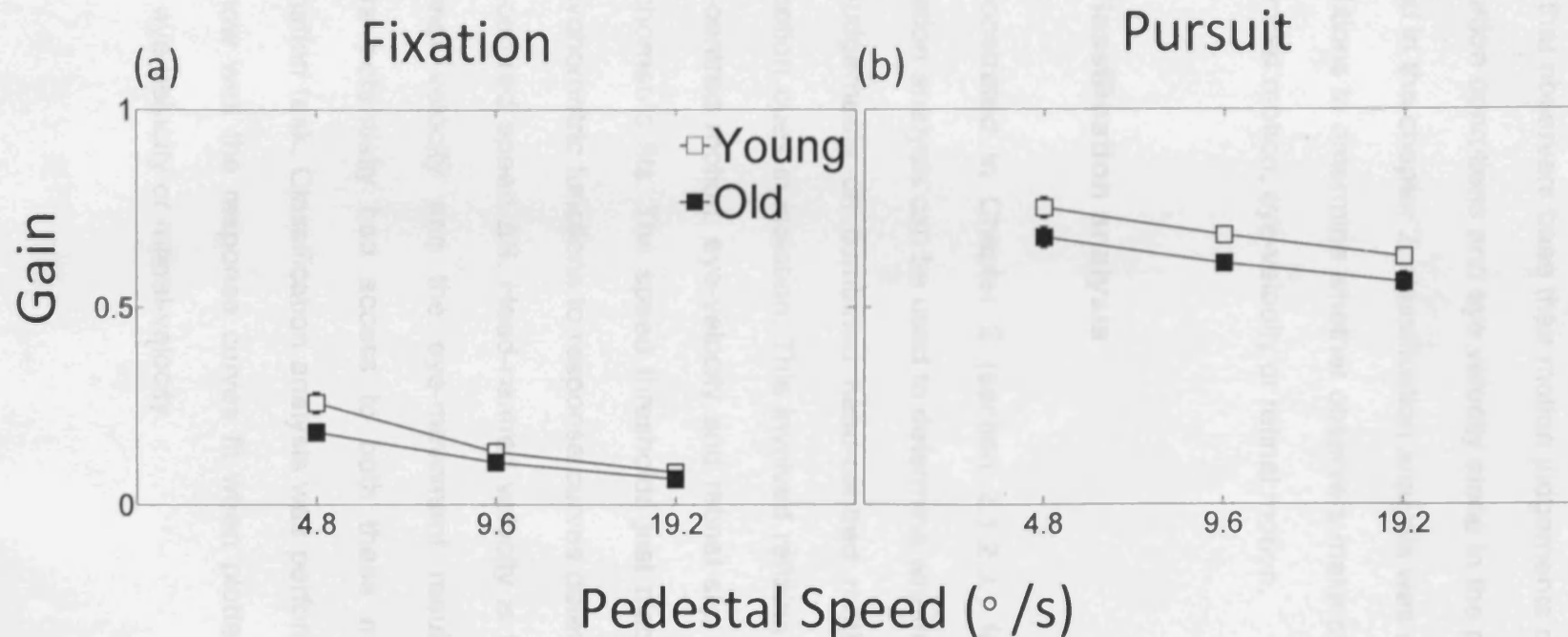


Figure 4.4. Mean pursuit gain for pedestal speeds 4.8°/s, 9.6°/s 19.2°/s during fixation and smooth pursuit. Squares (unfilled) correspond to the younger group and squares (filled) correspond to the older group. Error bars are ± 1 SE.

eye-movement precision as a reason for the psychophysical findings found. In order to compare the precision of fixation and pursuit, you would need to assume that observers base their motion judgements on retinal motion alone in the fixation conditions and eye velocity alone in the pursuit condition. As described in the chapter 2, classification analysis was carried out on each of the conditions to determine whether observers make speed judgements using head-centred motion, eye-velocity or retinal motion.

4.2.3. Classification analysis

As demonstrated in Chapter 2 (section 2.1.2.3.) for direction thresholds, classification analysis can be used to determine whether observers' base their motion judgements on combined head-centred motion or eye-velocity and retinal motion cues in isolation. This involved refitting psychometric functions to head-centred motion, eye-velocity and retinal slip and comparing each of the psychometric fits. The speed thresholds just discussed are the result of fitting psychometric functions to response curves determined by the difference in head-centred speed ΔS . Head-centred velocity is the sum of eye velocity and retinal velocity and the eye-movement results give evidence that observers potentially had access to both these motion cues during the discrimination task. Classification analysis was performed on the speed data, to see how well the response curves fit when plotted against head-centred velocity, eye-velocity or retinal-velocity.

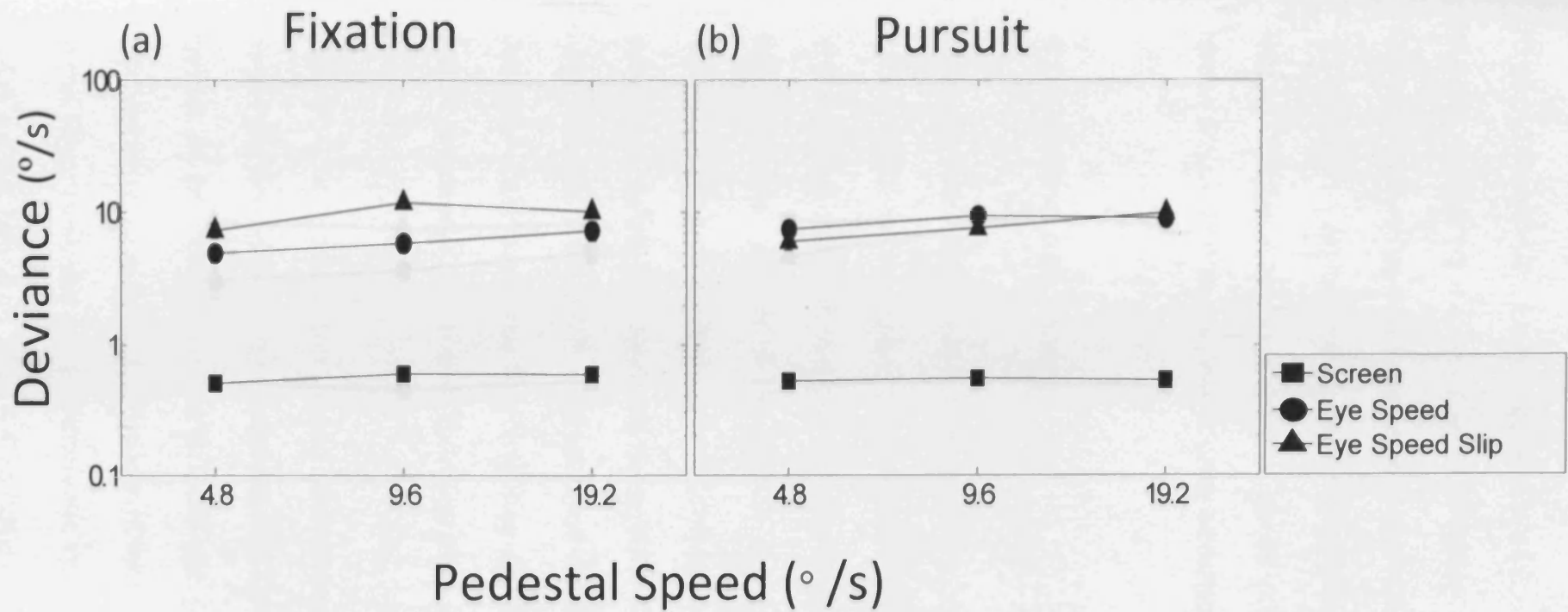


Figure 4.5. Deviance scores (best psychometric fit) for younger observers at pedestal speeds 4.8°/s, 9.6°/s 19.2°/s during fixation and smooth pursuit. Circles and Triangles represent eye-movement and retinal slip deviance respectively. Squares correspond to screen motion deviance. Error bars are ± 1 SE

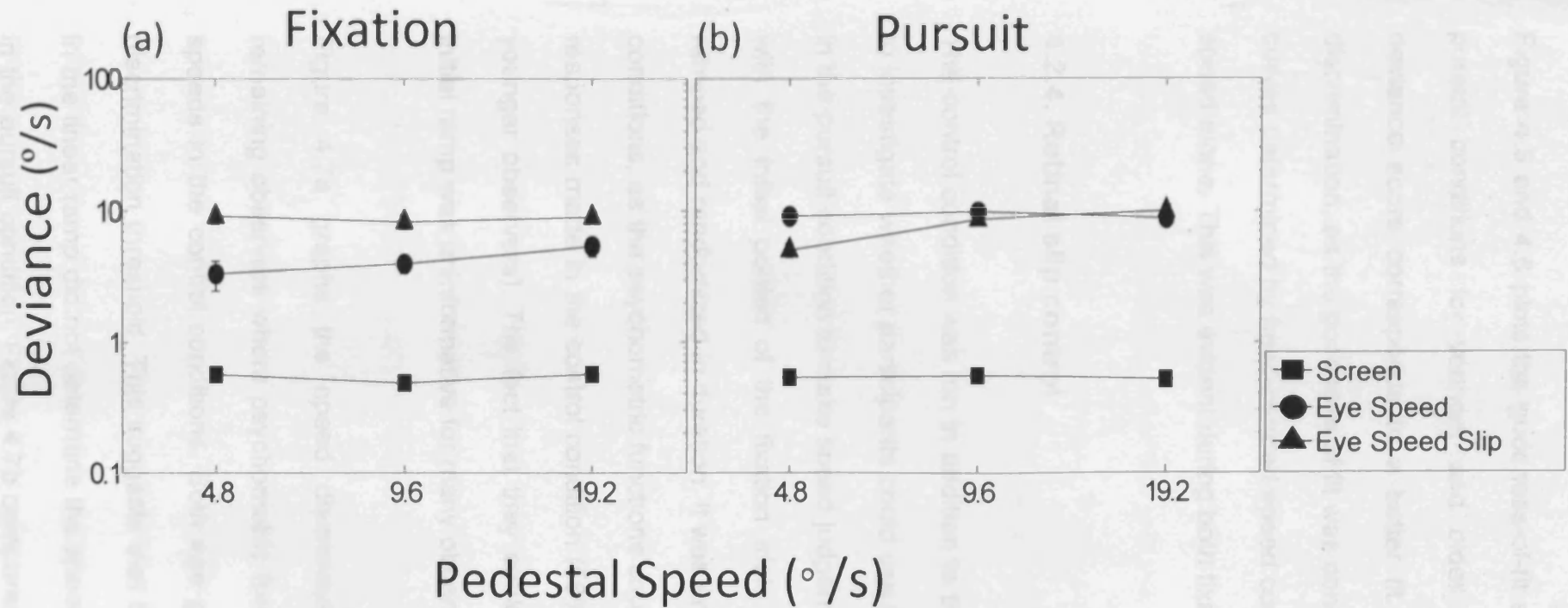


Figure 4.6. Deviance scores (best psychometric fit) for older observers at pedestal speeds 4.8°/s, 9.6°/s 19.2°/s during fixation and smooth pursuit. Circles and Triangles represent eye-movement and retinal slip deviance respectively. Squares correspond to screen motion deviance. Error bars are ± 1 SE

Figure 4.5 and 4.6 plots the goodness-of-fit scores derived from fixation and pursuit conditions for younger and older observers respectively. A low deviance score corresponds to a better fit. The results replicate direction discrimination, as the goodness of fit was considerably better for the response curves determined by head-centred speed compared to eye-speed and retinal speed alone. This was evident during both fixation and smooth pursuit.

4.2.4. Retinal slip control

The control condition was run in addition to the fixation and pursuit conditions to investigate whether participants could use the initial retinal motion available in the pursuit condition to make speed judgements. Observers were presented with the initial portion of the fixation trials where the motion was linearly ramped and randomized in duration. It was analysed separately from the main conditions, as the psychometric functions could not be fit to the majority of the responses made in the control condition (58% of older observers and 34% of younger observers). The fact that they could not is good evidence that the initial ramp was uninformative for many observers.

Figure 4.7a graphs the speed discrimination thresholds found for the remaining observers where psychometric function could be fit to all pedestal speeds in the control conditions. Both age groups show a large increase in discrimination threshold. This suggests that the initial retinal motion available in the linear ramp did not determine the speed sensitivity thresholds observed in the pursuit condition. Figure 4.7b compares the fixation thresholds from the

main experiment with the thresholds in the control condition for the same observers who could perform the task. Speed thresholds were lower in the fixation condition from the main experiment compared to the control.

To support these findings, a 2X2X3 (age, eye-movement and speed) mixed ANOVA, was performed on the speed discrimination thresholds. The between subject variable was age and the within-subject variables were condition (fixation vs. control) and speed. There was a significant main effect of condition [$F_{1,21} = 30.744$, $p=0.000$], where observers showed reduced speed sensitivity during the control compared to the original fixation condition. A significant difference in stimulus speed was also found [$F_{2,42} = 28.423$, $p=0.000$]. However as this was only apparent in the control condition, it led to a significant interaction between age, condition and speed [$F_{2,42} = 3.423$, $p=0.042$]. Further investigation into each condition separately, using a 2X3 ANOVA confirmed a significant main effect of speed in the control condition [$F_{2,42} = 13.446$, $p=0.000$] and fixation condition [$F_{2,42} = 28.850$, $p=0.000$]. As the majority of the observers could not perform the control task, and those that could show a large drop in speed sensitivity, this suggests that the observers were relying predominately on motion information after the ramp.

Figure 4.8a plots the eye-movement gains calculated for the percentage of participants that could complete the control condition, and Figure 4.8b plots the pursuit gains for the same observers during the fixation condition. For both conditions, observers were unable to maintain perfect fixation, although the discrepancy was larger in the fixation condition compared to the control. This

was most evident at the slowest speed of 4.8°/s. The difference in fixation eye-movement gain would be due to the comparative length of the stimulus presentation in each condition, ~800ms in the fixation compared to ~300ms in the control. The ideal presentation time for fixation stimuli is approximately 200ms, before people begin to move their eyes. No age difference was apparent in the pursuit gains for both conditions and during fixation and pursuit condition eye-movement accuracy improved with increasing stimulus speed.

To confirm these observations, A 2X2X3 (age, condition and speed) ANOVA, was performed on the pursuit gains, with age as the between-subject variable and the condition (fixation vs. control) and speed as within-subject variables, A significant main effect was found for condition [$F_{1,22} = 9.248, p=0.006$] and speed [$F_{2,42}=20.361, p=0.000$].

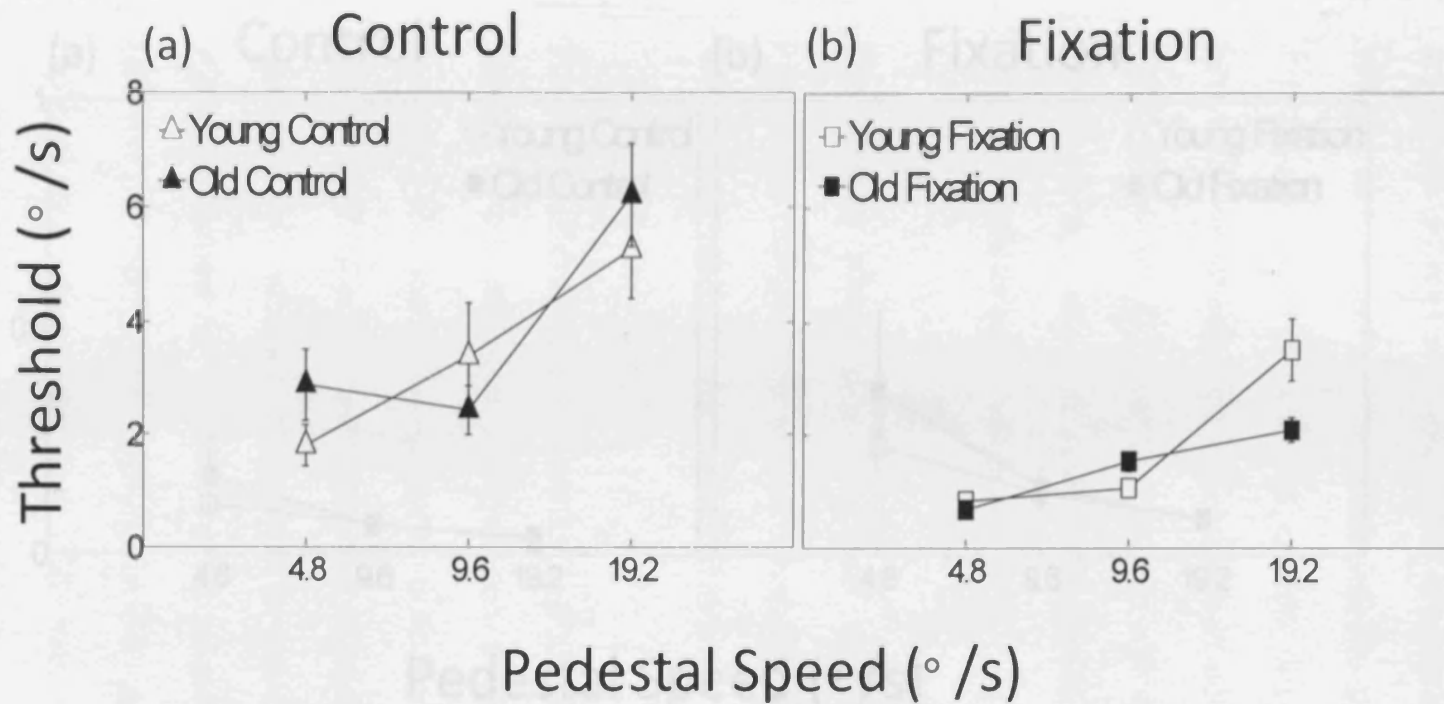


Figure 4.7. Mean speed discrimination thresholds for % of participants who completed (a) control task and (b) corresponding fixation condition . Unfilled symbols correspond to the younger group and filled correspond to the older group. Error bars are ± 1 SE.

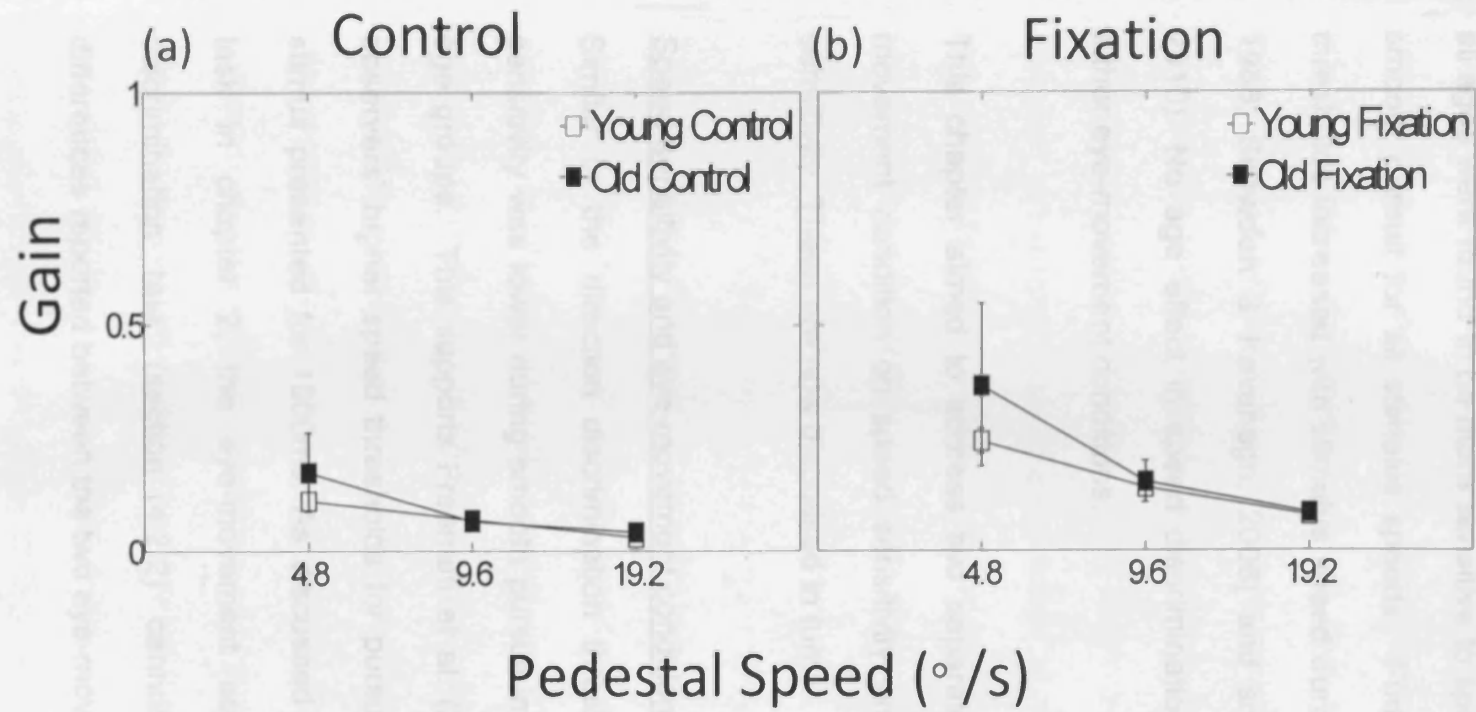


Figure 4.8. Mean pursuit gains for % of participants who completed (a) control task and (b) corresponding fixation condition . Unfilled symbols correspond to the younger group and filled correspond to the older group. Error bars are ± 1 SE.

4.3. Discussion

Experiment 5 investigated age-related changes in speed discrimination during two types of eye movements, smooth pursuit and fixation. Observers of all ages were found to be more sensitive to speed during fixation compared to smooth pursuit for all stimulus speeds. Furthermore, speed discrimination thresholds increased with stimulus speed during fixation (De Bruyn & Orban, 1988; Snowden & Kavanagh, 2006) and smooth pursuit (Freeman et al. 2010). No age effect in speed discrimination thresholds was reported for either eye-movement conditions.

This chapter aimed to address two separate issues 1) the effect of eye-movement condition on speed sensitivity and 2) ageing effects on speed sensitivity. These are now discussed in turn.

Speed sensitivity and eye-movement condition

Similar to the direction discrimination thresholds in experiment 1, speed sensitivity was lower during smooth pursuit in comparison to fixation for both age groups. This supports Freeman et al. (2010) who reported in younger observers' higher speed thresholds for pursued stimuli compared to fixated stimuli presented for 1000ms. As discussed for the direction discrimination task in chapter 2, the eye-movement accuracy data from the speed discrimination task (section 4.2.2) cannot explain the psychophysical differences reported between the two eye-movement conditions.

For example, the eye-movement results showed an effect of age, which was inconsistent with the psychophysical findings. Equally, eye-movement precision could not account for the increased speed thresholds in speed discrimination, as already noted, this argument makes the assumption that retinal and extra-retinal motion dominates speed sensitivity during fixation and smooth pursuit respectively. This was not the case, as demonstrated by the eye-movement data. Observers of all ages had access to both retinal and extra-retinal motion during both eye-movement conditions. Furthermore, classification analysis demonstrated that observers combined the retinal and extra-retinal motion during the speed discrimination task. This implies that any variation in the magnitude of extra-retinal signal was offset by changes in the retinal slip. Therefore, as with direction discrimination task, the combination of motion signals protected observers from changes in extra-retinal motion associated with imprecise pursuit.

The significant difference in smooth pursuit and fixation speed thresholds, confirms Freeman et al. (2010) speed discrimination findings, as well as direction discrimination results (experiment 1) and direction thresholds for a motion-in depth task (Welchman et al. 2009). Furthermore, it supports conclusions from experiment 1, namely that combination noise hypothesis (Krukowski et al. 2003) fails to explain the speed thresholds difference between eye-movement conditions. As pointed out by Krukowski et al., combination noise must be independent of the individual input noise for retinal and extra-retinal signals. If this were the case, the combination noise hypothesis would predict similar thresholds for smooth pursuit and fixation

which was not found. This again suggests that the internal noise limiting motion thresholds is located at the input of the combination stage.

Another piece of evidence against the combination noise hypothesis is that unlike the direction discrimination thresholds, the speed thresholds increase with faster stimulus speeds. The results therefore show opposing relationships between input noise and subsequent speed and direction thresholds. This further complicates how retinal and extra-retinal input noise and motion sensitivity could be modelled as a function of speed.

Speed sensitivity and age

The results from experiment 5 do not replicate previous studies that have shown that retinal motion sensitivity declines as a function of age during fixation (Bidwell et al., 2006; Norman et al., 2003; Snowden & Kavanagh, 2006). The duration of stimulus presentation may have been a contributing factor to the lack of age-related deficit in experiment 5, as speed sensitivity is thought to be particularly dependent on temporal summation, where speed sensitivity increases with greater presentation time (De Bruyn & Orban, 1988). Other previous accounts of ageing effects in speed discrimination had shorter stimulus durations than the current experiment. For instance, Bidwell et al. (2006) in a 2-AFC velocity discrimination task reported age-related decline during fixation for speeds 3.6°/s, 10°/s and 26.3°/s with a presentation time which lasted approximately 300ms. Furthermore, Snowden and Kavanagh (2006) in presenting their speed stimulus for approx. 500ms found significant age-related decline in speed discrimination for 0.125°/s, 1°/s and 8°/s.

Furthermore, Raghuram et al. (2005) presented a pair of first-order drifting luminance gratings at two durations of 500ms and 1000ms. While they reported a pronounced age-effect for the shorter duration of 500ms, they observed that this age-effect close to disappeared when they increased the stimulus duration to 1000ms for both 2°/s, and 8°/s pedestal speeds. However, they also compared different luminance levels and found that the age effect at longer durations declined less for scotopic compared to mesopic trials. The luminance of stimuli in experiment 5 was more akin to scotopic levels. In addition, Norman et al. (2003), reported ageing effects for speed discrimination for 1.22°/s, 5.48°/s, and 24.34°/s, allowed unlimited stimulus presentation. Therefore, it is somewhat unclear from the psychophysical evidence whether stimulus duration is an important factor in reported age effects in speed discrimination.

It should be noted however that, there is physiological evidence to suggest that age-related deficits in the extrastriate visual pathway (Liang et al., 2008; Yang et al., 2009) can be overcome by integrating motion signals over a longer period of time. Vaina, Cowey, Jakab, & Kikinis (2005) compared patients with extrastriate visual cortex damage against controls in a speed discrimination task. They investigated the observers' ability to integrate local motion signals to detect the speed of global motion in two different conditions. The first condition, the dots moved in complete random motion, therefore speed discrimination was computed by a local computation. In the second condition all the dots moved the same throughout the duration of the trial. Observers, who exhibited speed sensitivity deficits in random dot task,

presented no deficit when the stimuli moved consistently over the course of 22 frames (1000 ms). Furthermore, Cohen & Newsome (2009) demonstrated that while MT neurons are limited by their own response noise when encoding stimulus direction, by integrating neural activity over a long period of time these neurons yield became more sensitive as the noise was averaged over time. This would suggest that if age-related decline during retinal motion sensitivity is linked to deficits in the motion pathway, temporal integration might influence observers' ability to discriminate speed differences. It may also explain why speed sensitivity was similar for old and young participants in this particular study.

Speed sensitivity and stimulus speed

In contrast to the direction sensitivity, the speed thresholds reported here were shown to steadily increase as a function of speed. This supports previous accounts with fixated stimuli (DeBruyn & Orban, 1988). Similar results have been reported using single targets (McKee, 1981). Snowden & Kavanagh (2006) reported decreased speed sensitivity for both young and old observers for stimulus speeds that increased from 0.125°/s to 8°/s. The same pattern was evident for older subjects in the current experiment. Furthermore, speed sensitivity during smooth pursuit also declined with increased stimulus speed for both younger and older observers.

Weber fractions

Notably, the Weber fractions reported in experiment 5 were comparably higher than fractions reported in previous speed discrimination studies (eg. De

Bryun & Orban, 1988; Snowden & Kavanagh, 2006). A possible reason for this increase in Weber fractions is the presence of the accelerating speed ramp in the current experiment. Snowden & Braddick (1991) have shown that subjects have higher optimal discrimination thresholds when asked to modulate between changes in velocity within one interval compared to when subjects discriminate between two separate constant velocities. When velocities altered between two values without an intervening interval, the optimal performance was shown to be five times higher. Furthermore, when subjects were asked to modulate changes in velocity, there was 250ms presentation time of constant velocity. This was longer than the presentation time given when subjects were asked to discriminate between two constant velocities. Despite the difference in time, subjects still found it more difficult to distinguish changes in velocity in the same interval. This finding supports previous accounts that subjects are not sensitive to acceleration (Gottsdanker, 1956).

Summary

The speed discrimination experiment in this chapter replicated previous accounts that observers find it more difficult to discriminate speed during smooth pursuit compared to fixation. Furthermore, experiment 5 demonstrated for the first time that this effect is evident across old and young observers. In contrast to previous studies, no age-related decline in speed sensitivity was found during fixation. Reasons for this contradiction is unclear, however the long stimulus duration may have been a factor. Again, as discussed for direction discrimination (experiment 1), the eye-movement

results appears to have little impact on the speed discrimination thresholds for all observers during smooth pursuit and fixation eye-movement. Furthermore, the combined noise hypothesis as suggested by Krukowski et al. (2003) could not explain the higher speed thresholds during pursuit. As with direction discrimination, the remaining hypothesis that may explain these findings is changes to retinal and extra-retinal noise at the input stage.

5. Motion Coherence

Along with other aspects of visual function, there is evidence of age-related decline in retinal motion coherence levels. Coherence thresholds increase in older adults for both slow ($5.8^{\circ}/s$ - $6.6^{\circ}/s$) (Billino, Bremmer, & Gegenfurtner, 2008; Trick & Silverman, 1991) and fast speeds ($28^{\circ}/s$) (Wojciechowski et al., 1995). Whereas previous studies tested one speed only, Snowden and Kavanagh (2006) examined motion coherence thresholds across range of stimulus speeds within the same set of young and old observers. They found that an age-related deficit was limited to slow speeds of less than $1^{\circ}/s$. The rate of motion coherence decline in the older adults has also proven to vary, with studies reporting declines of 1% per decade (Trick & Silverman, 1991) to 0.4% per decade (Tran et al., 1998).

Motion coherence sensitivity has been linked to the directional tuning of MT cells (Albright & Stoner, 2002), specifically pattern cells that encode global motion (Huk & Heeger, 2002). Liang et al. (2008), in a single-cell recording study, compared the proportion of component and patterns MT cells in old and young macaque monkeys using drifting sinusoidal gratings and plaid patterns composed of two overlapping sinusoidals. Age-related degradation in direction sensitivity was observed for all cells, but the effect was most prominent for pattern cells, where the proportion of cells declined significantly. Liang et al. (2008) suggested that age-related reduction in GABA in MT was responsible for the latter effect. As others have argued, reducing GABA weakens the inhibition mechanism used to suppress the response of pattern cells to the

individual plaid components (Rust et al., 2006; Rust et al., 2005). This would explain why pattern cells in the older macaques are less tuned to the direction of plaid motion.

Human subjects with damage to the brain area homologous to primate MT show comparable global motion deficits with damage to the brain area homologous to primate MT (Schenk & Zihl, 1997). Moreover, MST lesions in macaque monkeys produce a profound deficit in motion coherence performance while leaving remaining visual functions intact (Newsome & Pare, 1988). Electrical stimulation of MST neurons (Celebrini & Newsome, 1994) has been shown to bias a monkey's perception of motion coherence by increasing the probability that dot motion appears to move in the stimulated neurons' preferred direction with increased coherence. This implies a strong association between neural activity in MT and MST and retinal motion coherence sensitivity (Newsome, Britten, & Movshon, 1989).

As with speed and direction sensitivity, our understanding of motion coherence is limited to stationary fixation. Chapter 5 aimed to investigate the role of smooth pursuit in the ability to detect coherent motion in younger and older observers. Previous research has shown that imprecise and inaccurate eye movement can negatively affect dynamic visual acuity. Haarmeier & Their (1999) compared dynamic visual acuity thresholds between a group of healthy subjects and two groups of patients exhibiting catch-up saccades and saccadic intrusion respectively. Subjects were asked to judge orientation of the Landolt C gap during pursuit. The pursuit thresholds were then compared

against thresholds where the subjects' eyes remained fixated. Haarmeier & Their (1999) observed significantly higher dynamic acuity thresholds in the two patient groups with pursuit disorders. These findings were explained by an increase in retinal position error due to inaccurate and imprecise eye-movements. Such inaccuracies allowed the target to slip from the fovea producing a consequent decrease in visual acuity. Similar explanations have been offered for the loss of acuity in congenital nystagamus patients. For example, Chung & Bedell (1995) simulated the retinal effects of a repetitive eye wobble known as congenital nystagamus and found visual acuity in normal observers declined in the presence of the simulated noise.

Older observers are known to compensate for reduced pursuit velocity (Spooner et al., 1980) with an increased frequency of catch-up saccades (Ross et al., 1999). Along with increased latency during smooth pursuit initiation (Knox et al. 2005), these pursuit inaccuracies could lead to a decline in motion coherence sensitivity in the older observers, similar to the patient group in Haarmeier & Their (1999) study. Using similar methods to Haarmeier & Their (1999), experiment 6 compared fixation and smooth pursuit in a motion detection task using younger and older observers. Participants were asked to pursue a target point horizontally and judge whether the random dot pattern that appeared surrounding the target point contained signal motion. In each trial, the random dot pattern contained both signal and noise dots, however the percentage of signal dots was varied to obtain the observer's motion coherence threshold. Results were compared to a fixation condition.

Two directions of motion were investigated, one where signal motion moves collinear with pursuit and another where the signal motion moves orthogonal with pursuit. Inaccurate pursuit produces collinear retinal slip; therefore, the aim of presenting the collinear and orthogonal signal motion was to establish whether collinear retinal slip interfered more with collinear signal detection compared to orthogonal signal detection, as suggested by Haarmeier & Their (1999) results.

5.1. Methods

5.1.1. Participants

Twenty-six observers participated in the experiment, 13 older than 60 years (mean age 67.70 years), and 13 aged 27 years or less (mean age 20.4 years). Distance visual acuity and contrast sensitivity was measured prior to the main data collection using the Bailey-Lovie Log MAR chart (at 2m) and Pelli-Robson CS chart (1m) respectively (while wearing their optical correction)(see Table 5.1). All observers had normal acuity and contrast sensitivity scores.

Table 5.1. Participant characteristics for younger and older observers in experiment 6. Age (in years) is reported as a mean followed by the standard deviation and range in parentheses. LogMAR visual acuity and Pelli-Robson contrast sensitivity scores are given as means followed by the standard deviation in parentheses. LogMAR and Pelli-Robson scores are given for binocular viewing

Experiment 5		Younger	Older
	N	13	13
	Sex	5 males, 8 females	9 males, 4 females
	Age	20.4(2.53, 18-27)	67.7(2.89, 64-73)
	LogMAR	0.01(0.02)	0.04(0.06)
	Pelli-Robson	1.95(0.06)	1.89(0.09)

5.1.2. Stimuli

Stimuli consisted of dots (0.1° radius, density of $0.1 \text{ dot}^\circ\text{2}$) randomly positioned within a circular aperture (8° radius). The random dot pattern presented contained 256 dots, each of which lifespan lasted random (36Hz). A fixation point (0.1° radius) was centred within the random dot pattern. In the 'fixation' condition, the participants were instructed to fixate their eyes on a central stationary point, whilst determining whether the surrounding random dot pattern contained signal or noise dots (see Fig 5.1a). In the 'pursuit' condition, the participants pursued the dot pattern and again were asked to determine the surrounding random dot pattern contained signal or noise dots (see Fig 5.1b).

As illustrated in figure 5.1, the surrounding random dot pattern appeared for $0.3s \pm 0.1$ in both conditions. During the pursuit condition, the target dot appeared to the left or right of the screen (alternate trials). The participant pursued the single target for $0.3s \pm 0.1$ before the stimulus dots appeared. The participant continued to track the target dot during the stimulus presentation until the target dot disappeared from screen. During the fixation condition, the target dot appeared for $0.3s \pm 0.1$ before stimulus dots appeared. The observer remained fixated until the stimulus dots disappeared and the single target dot disappeared from screen. Both the pursuit and fixation conditions lasted for 0.9s. For all the trials, dot speed remained at $2^\circ/s$ while pursuit speed was set at $4^\circ/s$.

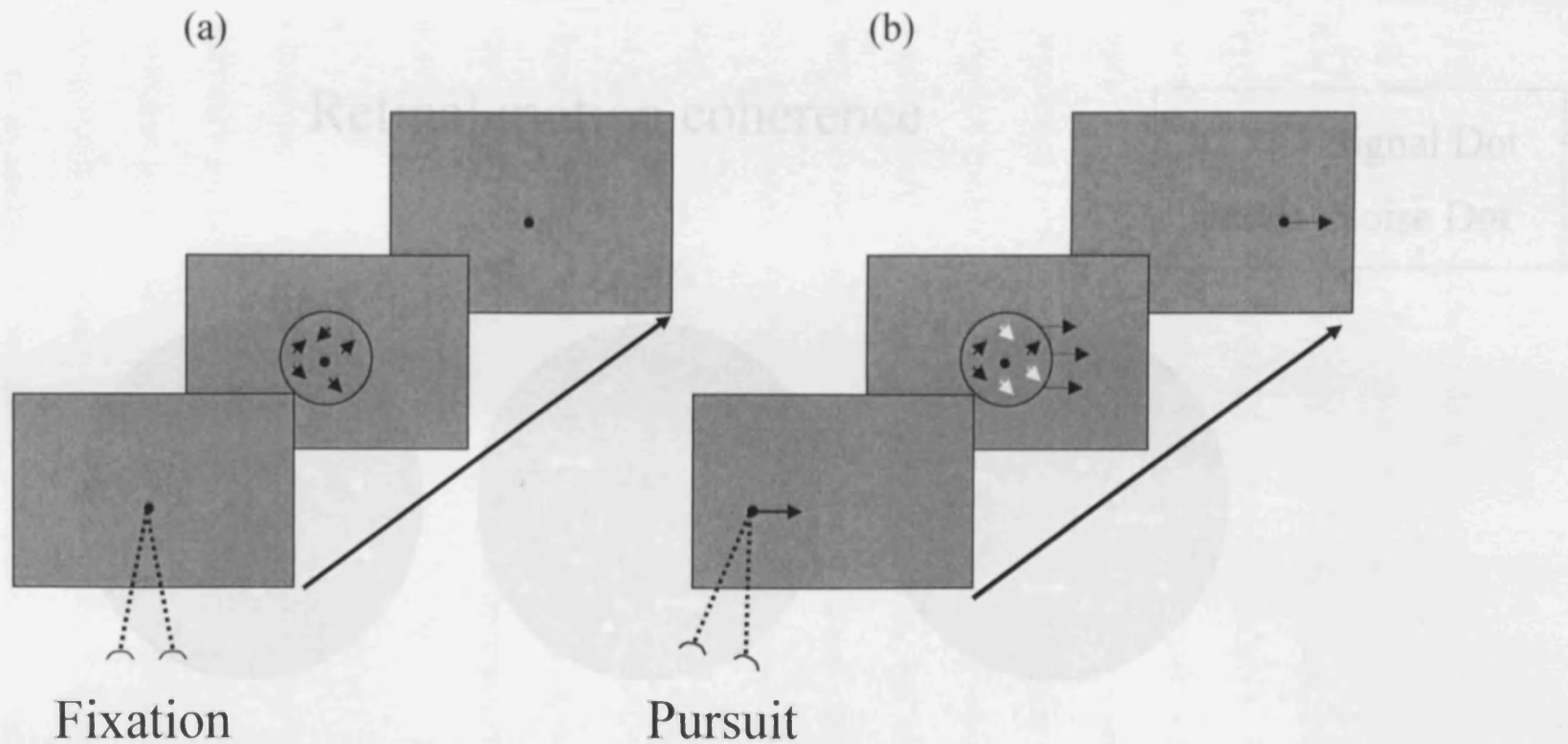


Figure 5.1. Schematic diagrams of the sequence of the visual stimuli for motion coherence task. (a) Fixation paradigm. The participants fixated their eyes on the stationary point in the centre and judged the motion coherence of the surrounding random dot pattern for $0.3s \pm 0.1$ (b) Pursuit paradigm. The participants judged the direction of the random dot pattern whilst pursuing the target point for $0.9s$ (dot pattern for $0.3s \pm 0.1$).

Figure 5.1. Schematic diagrams of the sequence of the visual stimuli for motion coherence task. (a) Fixation paradigm. The participants fixated their eyes on the stationary point in the centre and judged the motion coherence of the surrounding random dot pattern for $0.3s \pm 0.1$ (b) Pursuit paradigm. The participants judged the direction of the random dot pattern whilst pursuing the target point for $0.9s$ (dot pattern for $0.3s \pm 0.1$).

Retinal motion coherence

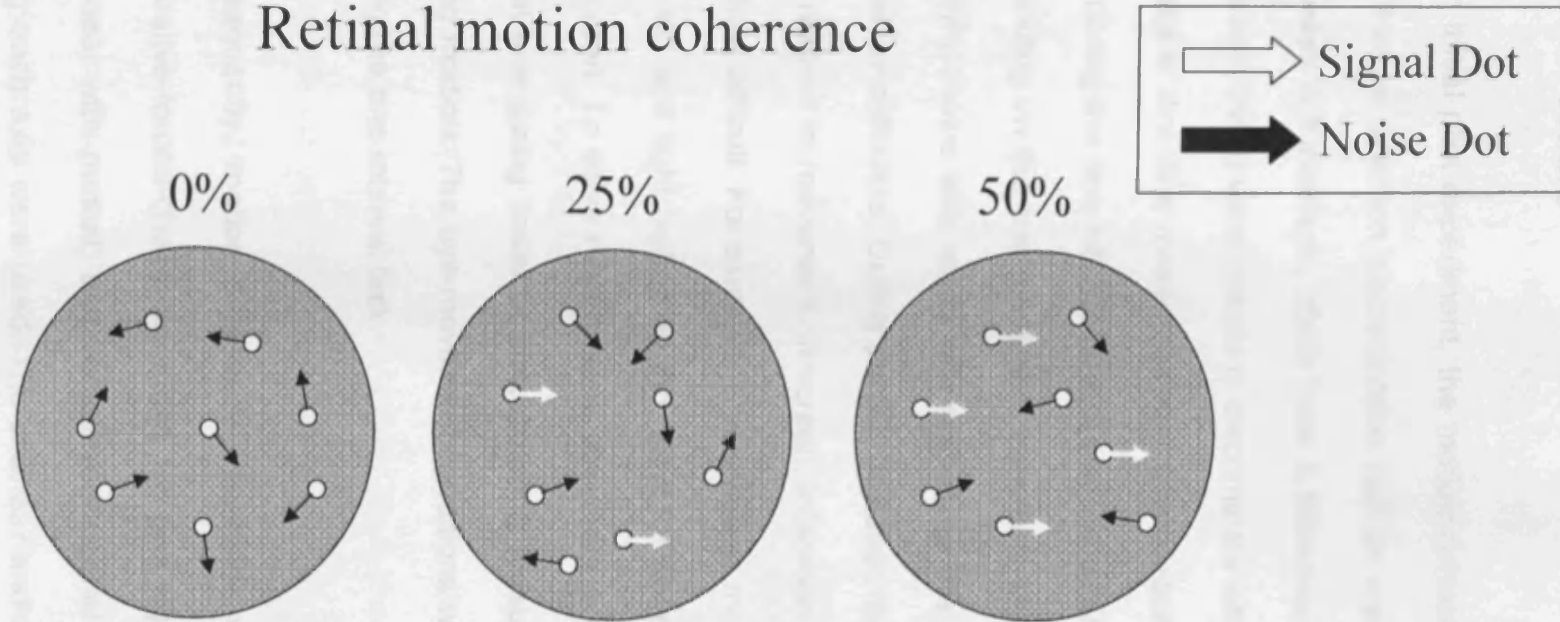


Figure 5.2. Example of a random-dot motion stimulus of variable motion coherence. Stimulus strength is varied by changing the proportion of dots moving coherently in a single direction.

5.1.3. Procedure

In an initial pilot experiment, the motion coherence task was presented as a one interval direction discrimination task as reported in previous studies (e.g. Snowden & Kavanagh, 2006; Trick & Silverman, 1991). Results showed that observers (N=3) were unable to discriminate left from right signal motion when the signal direction moved collinear with pursuit. A possible reason for this is that during the one interval task, it was difficult to explain the left/right 'choice' depending on the eye-movement condition. During the fixation condition, the left/right choice was made with respect to the retina and/or fixation point, in retinal co-ordinates. During pursuit however, the left/right 'choice' was made with respect to movement on screen, in screen co-ordinates, which proves to be more difficult. For example, if pursuit was moving to the right at fast speed, then left and right motion on the retina for slow signal speeds is always right on screen. To solve this problem, observers would have to judge whether the signal was going faster or slower during pursuit, in contrast, to the left/right during fixation. The eye-movement conditions would therefore be confounded during the one interval task.

Consequently, motion coherence thresholds were determined using a 2-alternative-forced-choice paradigm for two signal dot directions, horizontal (collinear with pursuit) and vertical (orthogonal with pursuit). Both directions along each axis were used. The collinear and orthogonal and collinear trials were presented in separate conditions. On each trial, observers were presented with two sequential intervals of stimulus motion, one containing

signal dots moving in a coherent direction, and another containing noise dots moving in random directions (see figure 5.1). The subject's task was to identify which of two intervals contained coherent motion using mouse button press.

The percentage signal displayed in the signal interval was adjusted logarithmically within two randomly interleaved 1-up 1 down staircases (Kaernbach, 1991). Each staircase was designed to converge on the 75% correct responses and terminate after eight reversals. Pursuit and fixation conditions were run in separate sessions, yielding four types of trials (2 conditions X 2 signal dot directions). The order of the four conditions were randomised, providing the observers with a break in-between sessions. Each observer carried out each condition once, with each testing session lasting about an hour.

5.1.4. Psychophysical Analysis

As with the previous chapters, motion coherence thresholds were determined using Probit analysis (Finney, 1971). Response curves were constructed by plotting the frequency of choosing interval 2 as a function % signal (see figure 5.2 for example of retinal motion coherence). Percentage correct results ranged from 0% to 100%. The coherence threshold was calculated by subtracting percentage signal correct at 75% from percentage signal correct at 50%. This indicates the amount of additional percentage signal needed to increase a participant's motion detection rate from 50% to 75% on the fitted psychometric function.

5.1.5. Eye-movement analysis

Eye position was sampled at a rate of 1000Hz using a video-based eye tracker mounted on the chin-and-forehead rest (SR Eyelink 1000). The same calibration method as experiment 1 was performed in experiment 6. Saccadic detection and removal was carried out on the X and Y channels using the Cartesian co-ordinates (E_x , E_y) method outlined in experiment 1 (see figure 2.2 for further details).

Eye-movement accuracy was calculated as a gain (eye speed/ target speed), using the data from the X channel of the eye tracker (i.e. E_x). As described in the speed discrimination chapter, a pursuit gain of 1 indicates accurate pursuit of the target stimulus. A gain greater or less than one implies overpursuing and underpursuing of the target, respectively. For the fixation condition, target speed was zero; therefore, accuracy was reported as eye speed/ stimulus speed. Perfect fixation required a gain of zero, anything greater than zero implies observers were moving their eyes in response to the stimulus speed.

5.2. Results

5.2.1. Psychophysics

Motion coherence detection thresholds for detecting signal from noise motion during fixation and pursuit in old and young observers are summarized in figure 5.3. The age groups are plotted individually, with each bar representing a combination of eye-movement condition and signal direction. The results suggest that for the two signal directions (collinear and orthogonal) observers were more sensitive at detecting coherent motion during fixation compared to smooth pursuit. Older observers also exhibit higher motion coherence thresholds than young observers, though this seems isolated to the pursuit condition. Further, observers were less sensitive at detecting coherent motion when signal direction was collinear with eye-movement.

These observations were supported by a 2X2X2 (age, eye-movement condition and signal direction) mixed ANOVA, with age as the between-subject variable and the eye movement condition and signal direction as within-subject variables. Significant main effects were reported for eye-movement condition [$F_{1,24} = 56.879$, $p=0.000$] and age [$F_{1,24} = 8.262$, $p=0.008$]. A significant eye-movement*age interaction [$F_{1,24} = 11.868$, $p=0.002$] was also found, which on inspection of the figure suggests that the age effect was located to the pursuit condition. Most interestingly, a significant interaction was found between eye-movement*signal direction [$F_{1,24} = 25.273$, $p=0.000$]. From the Figure, it appears that both old and young observers had

greater difficulty detecting collinear signal compared to orthogonal during pursuit only.

Further analysis investigated each of eye-movement conditions separately using 2X2 mixed ANOVAs. For the pursuit condition, there was a significant effect of signal direction [$F_{1,24} = 10.418$, $p=0.004$], where collinear signal motion produced higher coherence thresholds compared to orthogonal signal

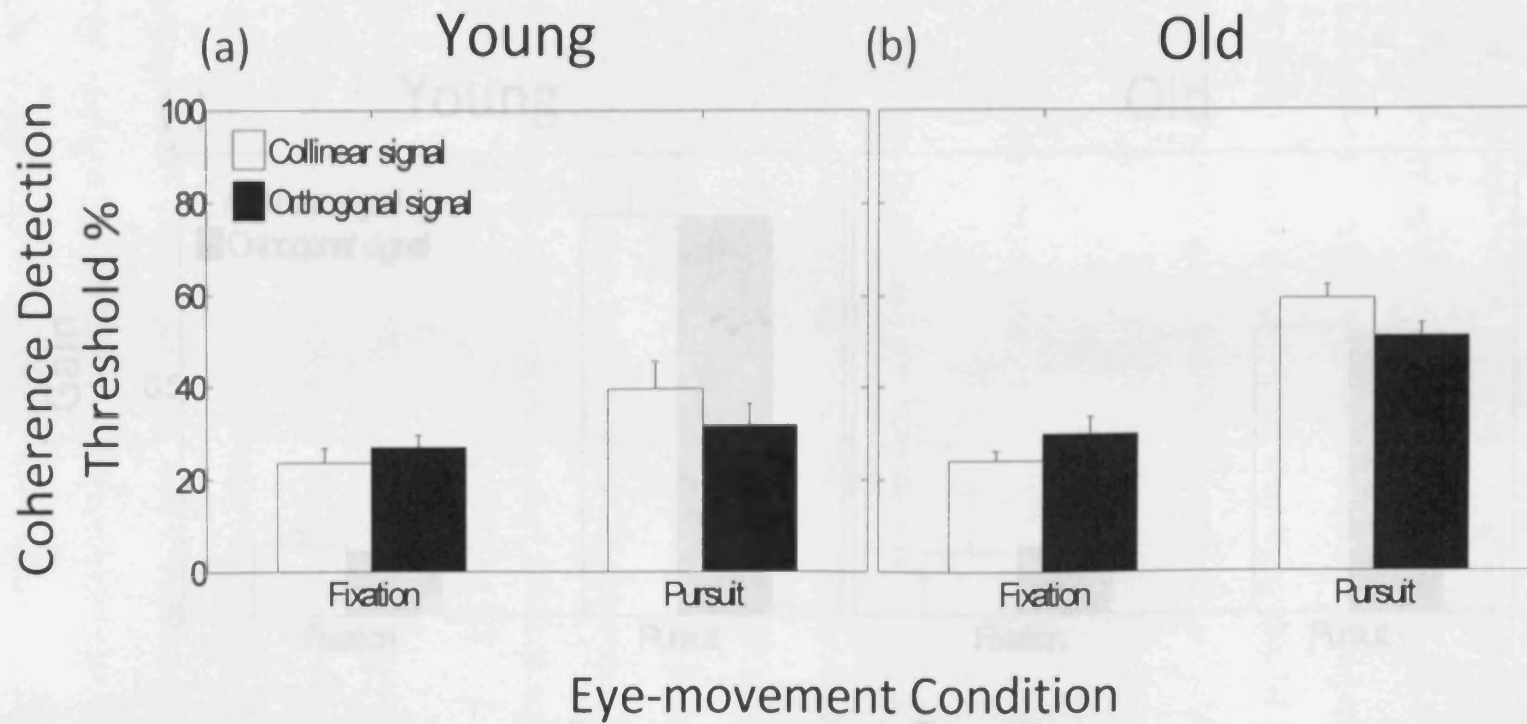


Figure 5.3. Mean detection thresholds for fixation and pursuit conditions in (a) younger (b) older observers. White columns correspond to the collinear signal and black columns correspond to orthogonal signal. Error bars are ± 1 SE.

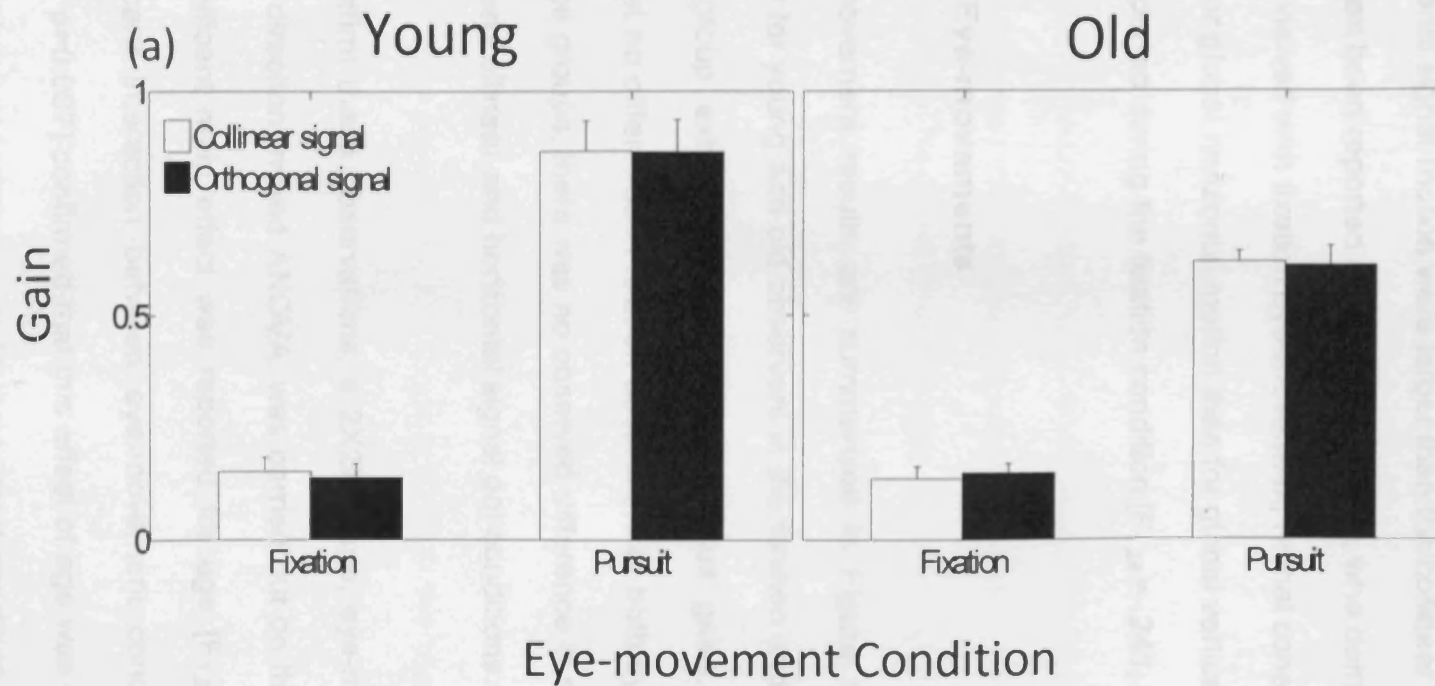


Figure 5.4. Eye-movement gain for fixation and pursuit conditions in (a) younger (b) older observers. White columns correspond to the collinear dot signal and black columns correspond to orthogonal dot signal. Error bars are ± 1 SE.

motion. The age effect was again confirmed during the pursuit condition [$F_{1,24} = 13.659, p=0.001$]. For fixation the signal direction was close to significant [$F_{1,24} = 4.228, p=0.051$], however in this case, coherence thresholds for the orthogonal signal motion were larger than the collinear thresholds. A similar trend has been reported by Raymond (1994), who demonstrated that for stimuli viewed with fixation eye-movement, retinal coherence thresholds were lower for global horizontal motion than for global vertical motion. No age effect was reported during the fixation condition [$F_{1,24} = .241, p=0.628$].

5.2.2. Eye-movements

Eye movement results are summarized in Figure 5.4. The mean gain is plotted for young and old observers in the fixation and pursuit conditions. The older group exhibited lower smooth pursuit gains. However, the results suggest no difference in fixation accuracy. For both eye-movement conditions and age groups, there was no observed difference in eye-movement accuracy between collinear and horizontal signal dot conditions.

To confirm these observations, a 2X2X2 (age, eye-movement condition and signal direction) mixed ANOVA, was carried out on the eye-movement gains. A significant main effect was reported for age [$F_{1,24} = 8.723, p=0.007$]. A significant interaction between eye-movement condition and age [$F_{1,24} = 8.756, p=0.007$] confirmed that this effect of age was due to the less accurate gains of the older observers in the pursuit condition only. No main effect of signal direction was found [$F_{1,24} = 0.022, p=0.884$], while eye-movement gains

for fixation and smooth pursuit condition were significantly different. [$F_{1,24} = 212.753$ $p=0.000$].

In the present experiment, the age-related decline in motion coherence sensitivity during smooth pursuit was accompanied by lower pursuit gains. This implies that smooth pursuit eye-movements were less accurate in older observers. A possible explanation for the difference in thresholds between young and old observers is due to the retinal slip from the inaccurate horizontal pursuit. Retinal slip, when added to the signal and noise dot vectors, changes the physical velocity of the dots. This is shown schematically in Figure 5.5. The figure assumes pursuit to the right. Examples of noise dots are shown in red and signal dots are shown in yellow (the difference between 'with' and 'against' is discussed below). The retinal slip vector produced by inaccurate horizontal smooth pursuit (gain <1) is shown by black arrows. These combine with the signal and noise dots to produce the green vectors labelled 'vector sum'. The green vectors therefore show the actual retinal motions delivered to the observer. When the horizontal retinal slip vector is added to the noise dots, the result is to shift the direction of the noise dots closer to the direction of the signal dots. This is likely to make detecting coherent motion harder. The figure also shows that 50% of the trials in the experiment contained signal dots moving 'against' the pursuit target and 50% moved 'with' the pursuit target. Therefore, the relationship between slip-modulated noise and signal dots also depends on the direction of the signal. As can be seen in the schematic, for 'with' trials, the signal speed increases,

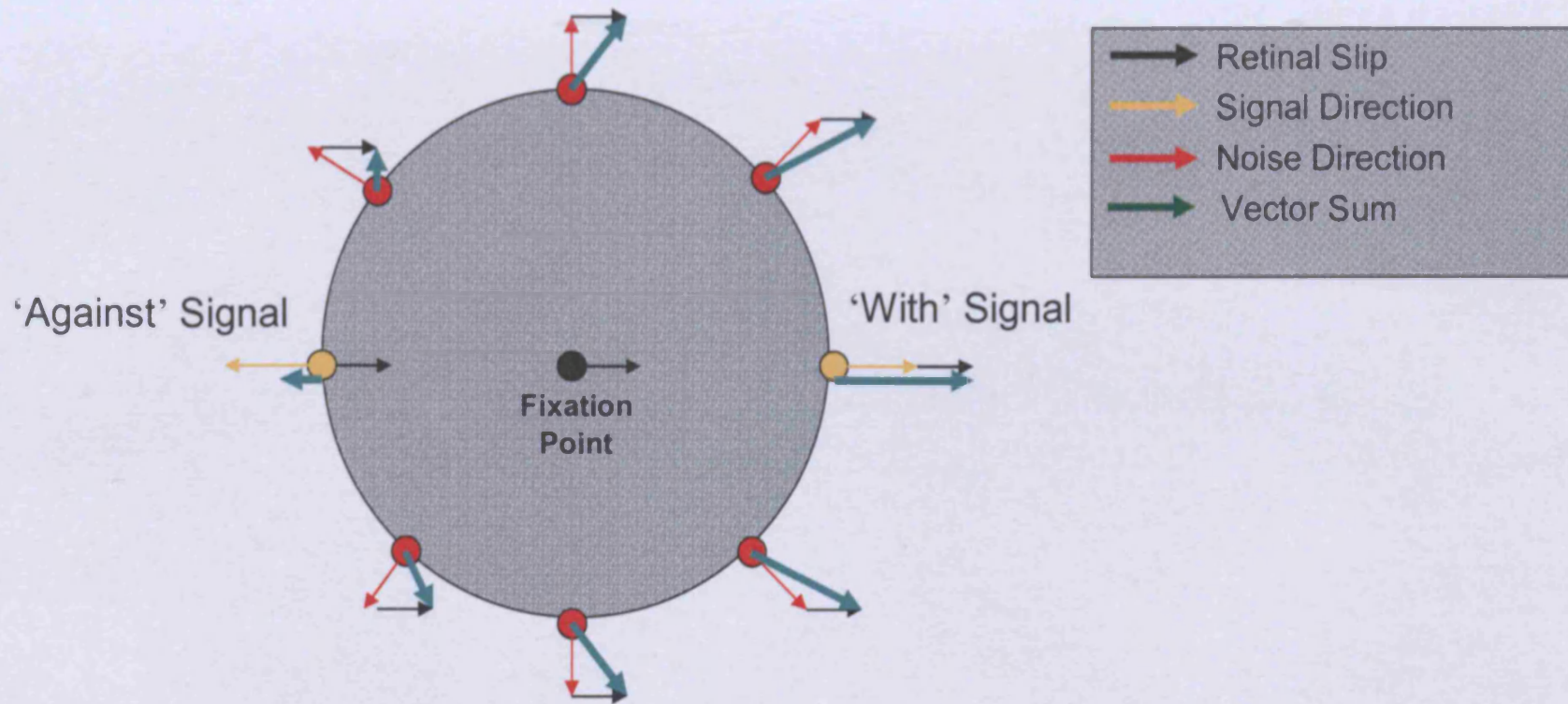


Figure 5.5. For 50% of trials, the signal motion was moving in the same direction as the pursuit target, while in the remaining trials the signal motion moved in an opposite direction to the pursuit target. During inaccurate pursuit, ($gain < 1$), when the signal direction and the eye move in opposite directions, motion on the retina is less than when signal direction and eye move together .

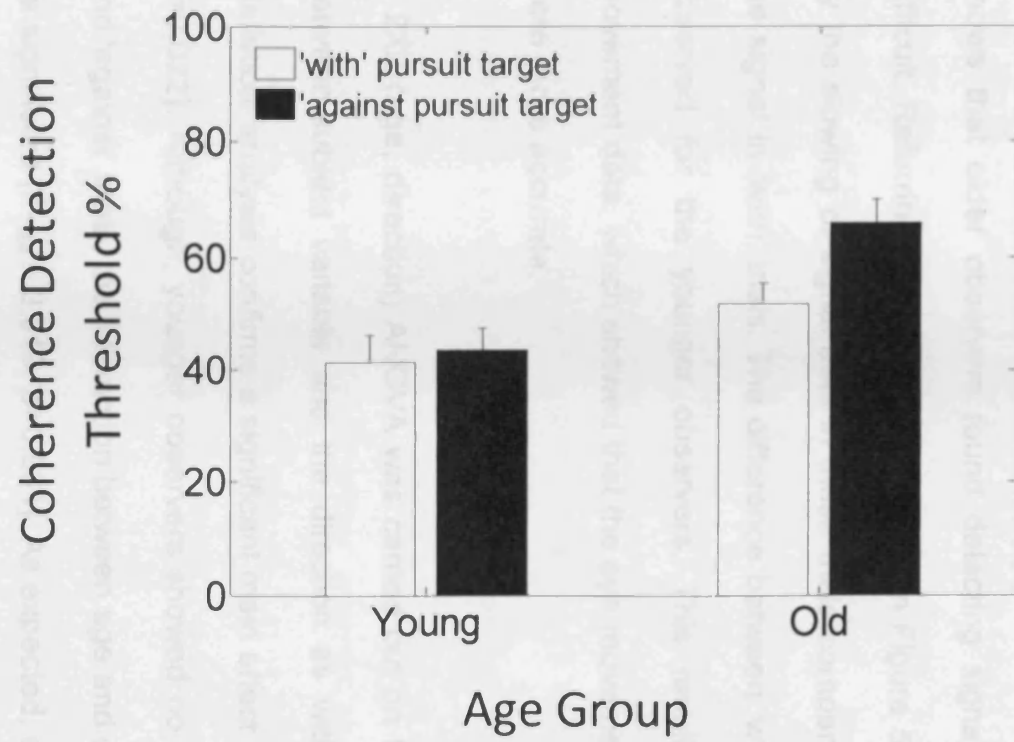


Figure 5.6. Mean detection thresholds for the pursuit condition in young and old observers. White columns correspond to coherence thresholds when the signal direction moved ‘with’ the pursuit target and black columns correspond to thresholds when the signal direction moved ‘against’ the pursuit target. Error bars are ± 1 SE.

as indicated by the green vector shown on the right of the schematic. However, for 'against' trials the signal speed decreases.

Comparing thresholds for 'with' and 'against' trials is therefore one way to test the retinal-slip hypothesis further. Figure 5.6 plots the detection thresholds for these different types of pursuit trial in younger and older observers. The result shows that older observers found detecting signal in 'against' trials more difficult. Referring back to the schematic in Figure 5.5, this can be explained by the slowing of signal dots in these trials compared to the speeding up of the signal in 'with' trials. The difference between 'with' and 'against' was not observed for the younger observers. This result maps on to the eye-movement data, which showed that the eye movements of younger observers were more accurate.

A 2X2 (age, direction) ANOVA was carried out on the data, with age as the between-subject variable and the direction as within-subject variable. The statistical analysis confirms a significant main effect of direction [$F_{1,24} = 6.000$, $p=0.022$]. Although, younger observers showed no difference between 'with' and 'against' trials, the interaction between age and direction was not found to be significant [$F_{1,24} = 3.319$, $p=0.081$]. As expected, an main effect of age was also observed [$F_{1,24} = 11.566$, $p=0.002$]. These results indicate that older observers' find it more difficult to detect coherent motion during collinear pursuit for dot stimuli that travel 'against' the pursuit target versus 'with'.

5.3. Discussion

Motion coherence thresholds are known to decline in older observers during fixation (Billino et al. 2008; Trick & Silverman, 1991; Snowden & Kavanagh, 2006). Experiment 6 investigated whether a similar age-related deficit occurred when motion stimulus was pursued. Motion coherence thresholds were compared between younger and older adults during fixation and smooth pursuit eye-movement. For both age groups, there was an increase in detection thresholds during smooth pursuit, an effect that was more pronounced in older observers. During fixation, no difference was found between age group and eye-movement condition. The effect of signal direction was also investigated. Observers were presented with horizontal signal motion moving collinear to pursuit, and vertical signal motion moving orthogonal to pursuit. Coherence thresholds indicated that younger and older adults found it more difficult to detect coherent motion when it was collinear with eye-movement direction. Further analysis showed that the decline in collinear motion detection during smooth pursuit increased for older observers when signal dot motion and pursuit target moved in opposite directions.

Contrary to previous findings, no age-related deficit in motion coherence sensitivity was reported during fixation (Billino et al., 2008; Gilmore et al., 1992; Trick & Silverman, 1991; Wojciechowski et al., 1995). A possible reason for the discrepancy is the particular dot speed studied. Snowden and Kavanagh (2006) measured motion coherence thresholds for a range of dot speed in old and young observers and only observed age-related increase in motion coherence thresholds for speeds of 1°/s or lower. However, other

studies have reported ageing effects in motion coherence tasks for stimulus speeds ranging from 5.5 to 28°/s (Billino et al., 2008; Gilmore et al., 1992; Trick & Silverman, 1991; Wojciechowski et al., 1995). Snowden & Kavanagh (2006) argue that an ageing effect in motion coherence is difficult to generalise to all speeds, when the previous studies presented only a single speed. Snowden & Kavanagh (2006) suggested that variation to luminance and stimulus eccentricity across studies may have changed motion coherence at some speeds but not others. By presenting identical stimuli at different speeds to the same observers, it is possible that Snowden & Kavanagh's (2006) results give a better indication of the relationship of stimulus speed and motion coherence.

During pursuit, observers of all ages found it more difficult to detect collinear compared to orthogonal signal motion. One explanation for this finding is that retinal slip caused by the inaccurate eye-movements (gain <1) was added to signal and noise dots vectors. This produced a change to the physical velocity of the dots on the retina. In the collinear condition, when horizontal retinal slip was added to the noise dots, the direction of the noise dots shifted closer to the direction of the horizontally moving signal dots. This would have made it more difficult to differentiate signal dots from noise dots, compared to the orthogonal condition where the signal dots moved vertically.

Extra-retinal signals could also explain the increase in detection thresholds during collinear signal motion. As discussed in previous chapters, head-centred motion is a combination of extra-retinal and retinal image motion. In

order to recover head-centred motion during pursuit, the extra-retinal signal acts to compensate for the additional retinal motion caused by the eye-movement. The extra-retinal signal hypothesis, however assumes that access to motion information can only occur beyond this point of compensation. Freeman et al. (2009) addressed whether observers had direct access to retinal motion during smooth pursuit. In a 2-AFC speed discrimination task, they varied the correlation between retinal motion and head-centred motion. The observers' responses were plotted separately against retinal speed, head-centred speed and the relative motion between the pursuit target and the stimulus. Results showed that observers based their speed judgements on relative motion even when they were provided trial to trial feedback on the actual retinal motion in stimuli. It therefore remains unknown whether observers have direct access to motion signals prior to compensation.

Older observers showed a larger increase in detection thresholds during smooth pursuit. This finding aligns with the retinal slip hypothesis, as their eye-movements were less accurate compared to the younger observers. Consequently, the retinal slip added to the signal and noise dots vectors was greater. This would have shifted the noise dots even closer to the direction of the horizontal moving signal dots, making signal motion harder to detect for the older observers. In further support of the retinal slip hypothesis, older observers were less sensitive to coherence motion in the collinear condition when the signal motion moved in an opposite direction to the pursuit target. As mentioned in the eye-movement results section (5.2.2), when pursuit is in the direction of the signal dots, retinal slip causes the retinal motion of signal

dots to increase. In contrast, when signal dots and the eye move in the opposite direction, retinal slip causes signal dots to slow down. Therefore, in the 'with' condition, when the pursuit target and the signal motion moved in the same direction, signal dots speeded up compared to the slowing of signal dots in the 'against' condition. The slower signal dots proved harder to detect for the older observers. The younger observers showed no difference in coherence thresholds between the 'with' and 'against' conditions, which correlates with their more accurate smooth pursuit eye-movement.

As discussed in section 5.1.3. the motion coherence task was not presented as a one interval direction discrimination task as in a pilot study observers (N=3) were unable to discriminate left from right signal motion when the signal direction moved collinear with pursuit. However, it could also be argued that the two-interval motion coherence task carried out in the main experiment did not sufficiently measure motion coherence, as it was possible for observers to carry out the task without integrating local dot motion. An alternative solution could be to ask observers to judge the direction of motion of stimuli moving at 45-degree angles. This would prevent the problems caused by collinear pursuit.

To conclude, the experiment in this chapter demonstrated for the first time that motion coherence declines in both old and young observers during pursuit compared to fixation. In particular, observers of all ages were less sensitive to coherence motion when the signal dots moved collinear with the smooth pursuit eye-movement. This effect was shown to decline further with

older age. Retinal slip due to inaccurate eye-movements could explain these findings, however further investigation is necessary to discount the role of extra-retinal signals.

6. General Discussion

6.1. Summary Findings

The primary aim of this thesis was to investigate extra-retinal and retinal motion sensitivity as function of age. Previous research has shown that retinal motion sensitivity declines in older adults across a range of psychophysical tasks, including direction (Ball & Sekuler, 1987), speed (Bidwell et al., 2006; Norman et al., 2003; Raghuram et al., 2005; Sciafla et al., 1987, 1991; Snowden & Kavanagh, 2006) and motion coherence (Billino et al., 2008; Gilmore et al., 1992; Snowden & Kavanagh, 2006; Trick & Silverman, 1991; Wojciechowski et al., 1995). In order to determine whether there is a similar age-related decline in extra-retinal motion sensitivity, motion sensitivity was compared between smooth pursuit and fixation across young and old observers.

In experiment 1, direction discrimination thresholds were measured in old and young observers using stimulus speeds of 2°/s and 8°/s. The psychophysical data showed older observers were less able to discriminate direction at slower speeds regardless of the instruction to fixate or pursue the stimuli. At the slower stimulus speed, observers found it more difficult to discriminate the direction of pursued stimuli compared to fixated stimuli. At the faster speed, both age and eye-movement effects disappeared. This latter finding does not agree with a number of studies that have reported age-related decline during fixation at fast-stimulus speeds (Ball & Sekuler, 1986; Bennett et al, 2006).

Previous research, however, has shown that direction discrimination improves with increased stimulus speed during fixation (Ball & Sekuler, 1987; De Bryun & Orban, 1988). This was shown in experiment 1 for both fixation and pursued stimuli. Furthermore, both old and young observers were less sensitive to oblique directions compared to cardinal directions. The oblique effect was evident in both fixation and smooth pursuit conditions replicating Krukowski et al. (2003). The oblique effect was also shown across a range of stimulus speeds ($2^\circ/\text{s}$ & $8^\circ/\text{s}$), which was previously shown for fixated stimuli (Ball & Sekuler, 1987). Classification analysis was carried out to determine which motion signals observers were using to make the direction judgements. The analysis involved refitting psychometric functions to head-centred motion, eye-velocity and retinal motion and examining the goodness-of-fit. Results showed that observers combined retinal and extra-retinal motion signals to discriminate direction.

Experiment 2 assessed whether the age-effect at slow stimulus speeds was a result of the decrease in retinal luminance in older observers. Reduced retinal luminance showed no effect on motion sensitivity in younger observers, supporting previous accounts for fixated stimuli (Betts et al., 2005; Norman et al., 2003). Furthermore, experiment 3, demonstrated that lower direction discrimination thresholds during fixation at slow speeds were not the product of relative motion in the fixation condition. Experiment 4 replicated the findings of experiment 1 using a trajectory-matching task. Results showed a decline in trajectory-estimation during pursuit for slow speeds only. This reiterates that

stimulus speed is an important factor in direction sensitivity for both young and old adults. An oblique effect was also observed during both eye-movement conditions.

Experiment 5 investigated age-related changes in speed discrimination during smooth pursuit and fixation. A number of studies have also shown that there is a decline in retinal speed discrimination in older observers (Bidwell et al., 2006; Norman et al., 2003; Snowden & Kavanagh, 2006). This however was not replicated in experiment 5, which found no effect of age on speed discrimination for either eye-movement conditions. Similar to the direction discrimination results, speed discrimination improved during fixation compared to smooth pursuit for all pedestal speeds tested. In contrast, however to the direction discrimination thresholds, the speed discrimination thresholds in experiment 5 increased with faster stimulus speeds. This supports previous studies using fixated (De Bryun & Orban, 1988; Norman et al. 2003; Snowden & Kavanagh, 2006) and pursued stimuli (Freeman et al. 2010). Again, classification analysis demonstrated that during the speed discrimination task, observers combined retinal and extra-retinal motion cues to make speed judgements. A control condition in experiment 5 showed that retinal slip at the beginning of the pursuit trials was uninformative for discriminating speed.

Experiment 6 compared motion coherence detection thresholds in younger and older adults during fixation and smooth pursuit eye-movement. Observers of all ages showed poorer detection during smooth pursuit compared to

fixation; however, this effect was larger in older observers. During fixation, motion coherence thresholds have also been shown to decrease with age, both for slow (Billino et al., 2008; Trick & Silverman, 1991) and fast speeds (Wojciechowski et al., 1995). Results from experiment 6 do not support these findings, as no effect of age-related decline for fixated stimuli. Two directions of motion were investigated, one where signal motion moves collinear with pursuit and another where the signal motion moves orthogonal with pursuit. During pursuit, there was an effect of signal direction, with young and old observers finding it more difficult to detect coherent motion when it was collinear with eye-movement direction. In addition, the decline in collinear motion detection during smooth pursuit increased for older observers when signal dot motion and pursuit target moved in opposite directions. During fixation, the coherence thresholds for the orthogonal signal motion were slightly larger than the collinear thresholds. This trend supports Raymond (1994), who demonstrated that for stimuli viewed during fixation, retinal coherence thresholds were lower for global horizontal motion than for global vertical motion.

6.2. Summary Conclusions

6.2.1. Why pursuit influences motion discrimination?

In an attempt to understand ageing effects on motion sensitivity, it is first necessary to understand factors that may have influenced motion thresholds with or without pursuit. In both the speed and direction discrimination experiments, observers of all ages were poorer at discriminating pursued

stimuli than fixated stimuli. In the general introduction, three suggestions were made that could account for possible differences in motion sensitivity between pursuit and fixation. Firstly, the eye-movement effect may be due to oculomotor control, with imprecise pursuit eye-movement leading to noisier extra-retinal signals. A second option is the level of internal noise at the input stage is greater for extra-retinal signals than retinal signals. Thirdly, internal noise computed at the stage where motion signals combine may limit motion thresholds, as suggested by Krukowski et al. (2003). The following paragraphs will argue that results from experiment 1 and 4 fail to support that oculomotor control or combined noise limit motion discrimination.

Oculomotor control

Classification analysis revealed that both younger and older observers combined motion signals regardless of the eye-movement condition being tested. This is a sensible strategy because it allows observers to estimate the head-centred motion of the stimulus, which when head and body are fixed, equates to the velocity on the screen in the experiments. The fact that signals were combined questions whether imprecise pursuit could explain the differences between eye-movement conditions. In speed and direction experiments, pursuit eye-movement orthogonal to the stimulus motion was minimal; therefore the observers only considered pursuit eye-movement parallel to the direction of stimulus. Further, the eye-movement results revealed that observers either under-pursued or were reasonably accurate, thus an increase in eye-movement speed would have been accompanied with a decrease in retinal slip. It therefore follows that as the magnitude of the

extra-retinal signal varied, the corresponding retinal slip varied. The motion signals were perfectly anti-correlated as the combined extra-retinal and retinal values always amounted to the head centred stimulus motion. This protected the observer from any changes in extra-retinal signals linked to imprecise pursuit.

Internal Noise – Combination V's Input?

Combined noise hypothesis suggested by Krukowski et al. (2003) argues that motion discrimination is limited by noise at the stage where motion signals combine. According to Krukowski et al. (2003), combination noise is independent of the individual input noise for retinal and extra-retinal signals; therefore, it would predict similar thresholds for both eye-movement conditions. Results from experiment 1 and 4 suggest that motion sensitivity is not limited by combination noise as suggested Krukowski et al. (2003). The direction discrimination results from experiment 1 are consistent with the combination noise hypothesis at fast speeds. At slow speeds however, both young and old observers found it more difficult to discriminate direction for fixated stimuli compared to pursued stimuli. Similarly, in the speed discrimination task, results showed that observers discriminated speed better during fixation compared to pursuit for all standard speeds tested.

The evidence presented in this thesis therefore suggests that input noise from the motion signals limits performance. As demonstrated in experiments 1, 4 and 5, stimulus speed appears to have a significant role on how input noise increases or decreases as a function of motion judgement (speed versus

direction). To model performance, one would need to specify how those noise sources change as a function of speed. In visual perception, it is noted that the subjective discrimination thresholds are scaled non-linearly with stimulus intensity. For example, Weber's law states that the difference in stimulus intensity that can be discriminated by an observer is proportional to the absolute stimulus strength. Weber's law can be modelled using a fixed, speed-independent noise, combined with a non-linear transducer (Zanker, 1995). Any departure from Weber's law at slow speeds can then be accounted for by modifying the non-linearity (Stocker & Simoncelli, 2006). However, Freeman et al (2010) showed that combining variable noise and a linear transducer also models performance well. A similar debate exists in the contrast discrimination literature, where different combinations of noise and transducer are able to model contrast discrimination data equally well (Georgeson & Meese, 2006). With two inputs, as implicated by the data in Chapter 2 and 4, the problem is exacerbated – potentially there may exist different transducers for retinal and extra-retinal signals, and also different noise-speed relationships as well.

6.4.2. Why pursuit influences motion coherence?

In the motion coherence task, evidence suggests that an increase in detection thresholds during pursuit is due to retinal slip from inaccurate eye-movements. As argued in Chapter 5, the retinal slip created by both young and older observers adds to the signal and noise dot vectors, causing the physical velocity of the dots to change on the retina. In the collinear condition,

the addition of horizontal retinal slip to the noise dots therefore shifted their actual direction so it became closer to the horizontally moving signal dots. This resulted in horizontal signal dots being more difficult to differentiate from the noise dots compared to the vertical signal dots in the orthogonal condition. One way to test this theory further is to compare collinear and orthogonal signal motion conditions during vertical eye-movement. This would determine whether vertical retinal slip causes a similar increase in motion coherence thresholds when signal motion moves collinearly compared to the orthogonal moving signals.

The extra-retinal signal may also be involved in the increase in coherence detection thresholds during pursuit. As discussed in detail in previous chapters, head-centred motion is a combination of extra-retinal and retinal image motion. The extra-retinal signal compensates for retinal motion caused by the eye-movement, to recover head-centred motion during pursuit. An assumption of an extra-retinal signal hypothesis is motion information can only be accessed after this point of compensation. Whether the results from experiment 6 are best explained by the retinal slip or extra-retinal hypothesis is unclear. One way to determine this is to present observers with a motion coherence stimulus analogous to the fixation condition in experiment 6. In one condition, movement would be introduced to the fixation stimulus to simulate retinal slip. This movement could be controlled to match retinal slip from previous pursuit trials. The detection thresholds from condition 1 could then be compared to a second condition where the stimulus remained stationary with no retinal slip. Both conditions in this experiment would not contain any

smooth pursuit eye-movement and thus would eliminate the effect of extra retinal signals. If observers found it more difficult to detect coherent motion when retinal slip was present, this would suggest that the retinal slip hypothesis rather than the extra-retinal hypothesis, best explains the pursuit effect in experiment 6.

6.3. Implications and future directions

The evidence presented in this thesis contributes to a greater understanding of the comparable effects of ageing on motion discrimination and detection during smooth pursuit and fixation. Studies have shown that observers have lower motion thresholds for pursued stimuli compared to fixation across a variety of psychophysical tasks. How these findings apply to real world situations needs to be investigated further. For all the experiments in this thesis, random dot stimuli were presented in a dark room to prevent observers from using reference cues in estimating eye-velocity. This was to encourage the observers to use extra-retinal information alone in their motion judgements. In real life, however, observers are usually part of a busy environment, surrounded by reference objects, both static and moving. For example, when walking down a city street, we can see tall buildings lined on the left and right, with cars and people moving in various directions. In this instance, when an observer pursues a single car, the pursuit system has to override a stabilisation reflex to the static background buildings to maintain contact with the moving target. Kolarik et al (2010) measured eye-movement control in a group of younger and older observers as they pursued a small

target moving over a stationary background. Results showed that older observers were less accurate and less precise in tracking the pursuit target compared to younger observers, particularly at faster stimulus speeds. While tracking over static background objects has been shown to make the eye movement worse, static objects can also promote the use of visual solutions in interpreting retinal motion during tracking. Whether smooth pursuit of a target over backgrounds increase or decrease age-related differences in retinal and extra-retinal motion sensitivity have yet to be explored.

Ageing effects for both fixation and smooth pursuit eye-movement were shown to be dependent on stimulus speed. Experiment 1 demonstrated that direction sensitivity declined for older observers at slow speeds but not at high speeds. This finding does not agree with Ball & Sekuler (1986), who reported age-related decline for discriminating between same and different directions at stimulus speed 10°/s. A possible explanation for this difference in results is the stimulus duration, which in the case of Ball & Sekuler (1986) is shorter at 500ms compared to 800ms in experiment 1. One of the aims of this thesis was to compare pursuit and fixation conditions. As a result, it was necessary to present equal stimulus durations for fixation and pursued stimuli. Bennett et al. (2007) found that the precision of direction judgements for stimulus speed of 6°/s improved significantly as stimulus duration increased from 75 to 470 ms. Stimulus duration was not directly investigated in the experiments in the thesis, but appears to play an important role on motion discrimination performance regardless of age. Furthermore, De Bryun & Orban (1988) measured speed and direction discrimination thresholds for a large range of

stimulus speeds, showing that retinal motion sensitivity changes as a function of speed. In the thesis, motion sensitivity thresholds during smooth pursuit were limited to a small number of speeds. By extending the range of the stimulus speeds, this would gain greater insight into how smooth pursuit and fixation motion sensitivity thresholds compare as a function of speed. Future research is open to exploring the role of stimulus parameters such as duration and speed in ageing effects during motion perception.

In the general introduction, the effect of gender on motion sensitivity was discussed, where there is some evidence to suggest that retinal motion sensitivity is lower in older women compared to older men (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Gilmore et al., 1992; Norman et al, 2003; Raghuram et al., 2005). However, evidence also suggests that there is no difference in motion sensitivity thresholds between men and women (Billno et al., 2008; Owsley et al., 1983; Tran et al., 1998). Meanwhile, whether there are gender effects for motion sensitivity during smooth pursuit remains unresolved. The experiments in this thesis were not designed to investigate this, and thus lacked the appropriate power to address the issue. Despite this, given that an age effect in smooth pursuit motion discrimination was found, the possible effect of gender on smooth pursuit motion perception should be carried out in future projects.

In conclusion, the studies in this thesis highlight the importance of measuring eye-movements during psychophysical motion judgements. It was demonstrated that observers of all ages found it difficult to control eye-

movements accurately during fixation and smooth pursuit. In the motion coherence experiment, retinal slip caused by inaccurate eye-movements during pursuit may have caused a decline in detection threshold for younger and older observers. In the discrimination experiments classification analysis revealed that observers of all ages combine both motion signals to make speed and direction judgements, regardless of instructed eye-movement. This is problematic when making associations between motion thresholds and the precision of retinal and extra-retinal signals. As the eye movement data suggests, the inaccuracies of fixation and pursuit mean that both conditions contain mixtures of retinal and extra-retinal motion. To explore further, how extra-retinal and retinal motion sensitivity changes as a function of age, future research needs to address how to model retinal and extra-retinal inputs with relation to speed and direction sensitivity.

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APPENDIX A: CHAPTER 2 STATISTICAL TABLES

A. Statistical results from experiment 1 (direction discrimination). A 2X2X2X3 (age, speed, eye-movement and direction) mixed ANOVA [repeated], was performed on the directional discrimination thresholds. Age and speed were defined as the between-subject variables and eye-movement condition and direction as within-subject variables.

Experiment 1	df	F	Sig.	Eta. Sq
Eye-movement	1,43	2.585	.115	.057
Direction	2,86	11.508	.000*	.211
Speed	1,43	24.494	.000*	.363
Age	1,43	1.188	.282	.027
Eye-movement*Speed	1,43	6.529	.014*	.132
Eye-movement*Age	1,43	2.183	.147	.048
Eye-movement*Speed*Age	1,43	.215	.646	.005
Direction*Speed	2,43	.704	.497	.016
Direction*Age	2,43	1.450	.246	.033
Direction*Speed*Age	2,43	.630	.535	.014
Speed*Age	1,43	1.942	.171	.043
Eye-movement*Direction	2,43	.002	.998	.000
Eye-movement*Direction*Speed	2,43	.124	.993	.003
Eye-movement*Direction*Age	2,43	.396	.674	.009
Eye-movement*Direction*Speed*Age	2,43	.428	.653	.010

B. Statistical results from experiment 1 (direction discrimination). A 2X2X3 (age, eye-movement and direction) mixed ANOVA [repeated] was performed on the direction thresholds for 2°/s and 8°/s respectively. Age was the between-subject variable and the eye movement condition and direction were within-subject variables.

Experiment 1 (2°/s)	df	F	Sig.	Eta. Sq
Eye-movement	1,21	5.654	.027	.204
Direction	2,42	3.265	.048	.129
Age	1,21	4.614	.043	.173
Eye-movement*Age	1,21	.643	.431	.028
Direction * Age	2,42	.356	.702	.016
Eye-movement * Direction	2,42	.056	.945	.003
Eye-movement * Direction * Age	2,42	.324	.725	.015

Experiment 1 (8°/s)	df	F	Sig.	Eta. Sq
Eye-movement	1,21	.508	.484	.024
Direction	2,42	9.234	.000	.305
Age	1,21	.014	.906	.001
Eye-movement*Age	1,21	.429	.519	.020
Direction * Age	2,42	2.364	.106	.101
Eye-movement * Direction	2,42	.068	.934	.003
Eye-movement * Direction * Age	2,42	.198	.821	.009

C. Statistical results from experiment 1 (direction discrimination). A 2X2X2X3 (age, speed, eye-movement and direction) mixed ANOVA [repeated], was performed on the Eye-velocity component (e_p) data. Age and speed were defined as the between-subject variables and eye movement condition and direction as within-subject variables.

Experiment 1	df	F	Sig.
Eye-movement	1,43	133.358	.000*
Direction	2,86	1.454	.239
Speed	1,43	9.444	.004*
Age	1,43	2.277	.139
Eye-movement*Speed	1,43	13.425	.001*
Eye-movement*Age	1,43	2.953	.093
Eye-movement*Speed*Age	1,43	.883	.353
Direction*Speed	2,43	2.458	.092
Direction*Age	2,43	1.196	.307
Direction*Speed*Age	2,43	.516	.599
Speed*Age	1,43	.166	.686
Eye-movement*Direction	2,43	.949	.391
Eye-movement*Direction*Speed	2,43	.016	.656
Eye-movement*Direction*Age	2,43	1.104	.336
Eye-movement*Direction*Speed*Age	2,43	4.756	.011*

D. Statistical results from experiment 2 (Low luminance). A 2X3 (Eye-movement, Filter) ANOVA [repeated], was performed on the direction discrimination threshold data.

Experiment 2	df	F	Sig.	Eta. Sq
Filter	2,22	1.141	.338	.094
Eye-movement	1,11	5.014	.047*	.313
Filter*Eye-movement	2,22	1.032	.373	.086

E. Statistical results from experiment 2 (Low lumiance). A 2X2 (Filter, eye-movement) ANOVA [repeated], was performed on the Eye-velocity component (e_p) data.

Experiment 2	df	F	Sig.
Filter	2,22	2.032	.155
Eye-movement	1,11	29.988	.000*
Filter*Eye-movement	2,22	.168	.846

F. Statistical results from experiment 3 (Relative Motion). A 2X2 (Motion Type, Speed) ANOVA [repeated], was performed on the direction discrimination threshold data.

Experiment 3	df	F	Sig.	Eta. Sq
Motion Type	1,11	.163	.694	.015
Speed	1,11	39.626	.000*	.783
Motion Type*Speed	1,11	.599	.455	.052

G. Statistical results from experiment 3 (Relative Motion). A 2X2 (Motion Type, Speed) ANOVA [repeated], was performed on the on the Eye-velocity component (e_p) data.

Experiment 3	df	F	Sig.
Motion Type	1,11	2.324	.156
Speed	1,11	26.299	.000*
Motion Type*Speed	1,11	1.452	.253

APPENDIX B: CHAPTER 3 STATISTICAL TABLES

A. Statistical results from experiment 4 (trajectory matching). A 2X2X2X2 (age, eye-movement, speed and direction) mixed ANOVA [repeated], was performed on the variable error results. Age was defined as the between-subject variable and the eye movement condition, stimulus speed and direction as within-subject variables.

Experiment 4	df	F	Sig.	Eta Sq
Eye-movement	1,22	14.027	.001*	.389
Speed	1,22	95.888	.000*	.818
Direction	1,22	34.809	.000*	.613
Age	1,22	2.386	.137	.093
Eye-movement*Age	1,22	.075	.787	.003
Speed*Age	1,22	.089	.768	.004
Direction*Age	1,22	1.437	.243	.061
Eye-movement*Speed	1,22	28.280	.000*	.562
Eye-movement*Speed*Age	1,22	.000	.997	.060
Eye-movement*Direction	1,22	.062	.806	.003
Eye-movement*Direction*Age	1,22	.091	.760	.004
Speed*Direction	1,22	.220	.644	.010
Speed*Direction *Age	1,22	2.167	.155	.090
Eye-movement* Speed*Direction	1,22	1.800	.193	.076
Eye-movement* Speed*Direction*Age	1,22	.071	.792	.003

B. Statistical results from experiment 4 (trajectory matching). A 2X2X2 (age, speed and direction) mixed ANOVA [repeated], was performed on the fixation and pursuit variable error results respectively. Age was defined as the between-subject variable and stimulus speed and direction as within-subject variables.

Fixation (Exp 4)	df	F	Sig.	Eta Sq
Speed	1,22	36.259	.000*	.622
Direction	1,22	33.214	.000*	.602
Age	1,22	1.614	.217	.068
Speed*Age	1,22	0.103	.752	.005
Direction *Age	1,22	1.006	.327	.044
Speed*Direction	1,22	.765	.391	.034
Speed*Direction*Age	1,22	1.568	.224	.067

Pursuit (Exp 4)	df	F	Sig.	Eta Sq
Speed	1,22	83.274	.000*	.791
Direction	1,22	19.414	.000*	.469
Age	1,22	2.309	.143	.095
Speed*Age	1,22	0.037	.848	.002
Direction *Age	1,22	1.033	.320	.045
Speed*Direction	1,22	1.500	.234	.064
Speed*Direction*Age	1,22	.389	.539	.017

C. Statistical results from experiment 4 (trajectory matching). A 2X2X2X2 (age, eye-movement, speed and direction) mixed ANOVA [repeated], was performed on the constant error results. Age was defined as the between-subject variable and the eye movement condition, stimulus speed and direction as within-subject variables,.

Experiment 4	df	F	Sig.	Eta Sq
Eye-movement	1,22	1.872	.185	.078
Speed	1,22	0.059	.811	.003
Direction	1,22	3.096	.092	.123
Age	1,22	0.002	.965	.000
Eye-movement*Age	1,22	3.594	.071	.140
Speed*Age	1,22	0.932	.345	.041
Direction*Age	1,22	3.289	.083	.130
Eye-movement*Speed	1,22	2.056	.166	.085
Eye-movement*Speed*Age	1,22	3.696	.068	.144
Eye-movement*Direction	1,22	1.899	.182	.079
Eye-movement*Direction*Age	1,22	.063	.804	.003
Speed*Direction	1,22	0.109	.745	.005
Speed*Direction *Age	1,22	2.099	.161	.087
Eye-movement* Speed*Direction	1,22	0.140	.712	.066
Eye-movement* Speed*Direction*Age	1,22	0.073	.790	.003

D. Statistical results from experiment 4 (trajectory matching). A 2X2X2X2 (age, eye-movement, speed and direction) mixed ANOVA [repeated], was performed on the Eye-velocity components (e_p). Age was defined as the between-subject variable and the eye movement condition, stimulus speed and direction as within-subject variables.

Experiment 4	df	F	Sig.
Eye-movement	1,22	122.353	.000*
Direction	1,22	2.461	.131
Speed	1,22	.077	.784
Age	1,22	1.567	.224
Eye-movement*Speed	1,22	.071	.793
Eye-movement*Age	1,22	5.836	.024*
Eye-movement*Speed*Age	1,22	3.317	.082
Direction*Speed	1,22	9.835	.005*
Direction*Age	1,22	.072	.790
Direction*Speed*Age	1,22	.039	.845
Speed*Age	1,22	.784	.385
Eye-movement*Direction	1,22	1.116	.302
Eye-movement*Direction*Speed	1,22	1.574	.223
Eye-movement*Direction*Age	1,22	.113	.740
Eye-movement*Direction*Speed*Age	1,22	.033	.857

APPENDIX C: CHAPTER 4 STATISTICAL TABLES

A. Statistical results from experiment 5 (speed discrimination). A 2X2X3 (age, eye-movement and speed) mixed ANOVA [repeated], was performed on the speed discrimination thresholds. Age was defined as the between-subject variable and the eye movement condition and speed as within-subject variables.

Experiment 5	df	F	Sig.
Eye-movement	1,40	14.930	.000*
Speed	2,80	47.558	.000*
Age	1,40	.003	.955
Eye-movement*Speed	2,80	.454	.636
Eye-movement*Age	1,40	.644	.427
Eye-movement*Speed*Age	2,80	1.337	.269
Speed*Age	2,80	.190	.827

B. Statistical results from experiment 4 (speed discrimination). A 2X2X3 (age, eye-movement and speed) mixed ANOVA [repeated], was performed on the weber fractions. Age was defined as the between-subject variable and the eye movement condition and speed as within-subject variables,.

Experiment 5	df	F	Sig.	Eta Sq
Eye-movement	1,40	18.260	.000*	.313
Speed	2,80	5.222	.007*	.115
Age	1,40	0.090	.765	.002
Eye-movement*Speed	2,80	2.937	.059	.068
Eye-movement*Age	1,40	1.767	.191	.042
Eye-movement*Speed*Age	2,80	1.322	.270	.032
Speed*Age	2,80	0.384	.682	.010

C. Statistical results from experiment 4 (speed discrimination). A 2X2X3 (age, eye-movement and speed) mixed ANOVA [repeated], was performed on the eye-movement gains. Age was defined as the between-subject variable and the eye movement condition and speed as within-subject variables.

Experiment 5	df	F	Sig.
Eye-movement	1,40	781.373	.000*
Speed	2,80	15.471	.000*
Age	1,40	5.694	.022*
Eye-movement*Speed	2,80	1.310	.276
Eye-movement*Age	1,40	5.255	.027*
Eye-movement*Speed*Age	2,80	.004	.702
Speed*Age	2,80	.784	.284

D. Statistical results from experiment 5 (Control speed discrimination). A 2X2X3 (age, eye-movement and speed) mixed ANOVA [repeated], was performed on the speed discrimination thresholds. Age was defined as the between-subject variable and the condition and speed as within-subject variables.

Experiment 5	df	F	Sig.	Eta Sq
Condition	1,21	36.774	.000*	.637
Speed	2,42	28.423	.000*	.575
Age	1,21	.001	.981	.000
Condition*Speed	2,42	2.115	.133	.092
Condition*Age	1,21	1.130	.300	.051
Condition*Speed*Age	2,42	3.423	.042*	.140
Speed*Age	2,42	.585	.563	.027

E. Statistical results from experiment 5 (Control speed discrimination). A 2X3 (age and speed) mixed ANOVA [repeated], was performed on the speed discrimination thresholds for the control condition only.

Experiment 5 (Control)	df	F	Sig.	Eta Sq
Speed	2,42	13.446	.000*	.390
Speed*Age	2,42	1.328	.270	.059
Age	1,21	0.220	.644	.010

F. Statistical results from experiment 5 (Fixation speed discrimination). A 2X3 (age and speed) mixed ANOVA [repeated], was performed on the speed discrimination thresholds for the fixation condition only.

Experiment 5 (Fixation)	df	F	Sig.	Eta Sq
Speed	2,42	28.850	.000*	.579
Speed*Age	2,42	6.020	.005*	.233
Age	1,21	1.509	.233	.067

G. Statistical results from experiment 5 (Control speed discrimination). A 2X2X3 (age, eye-movement and speed) mixed ANOVA [repeated], was performed on the eye-movement gains. Age was defined as the between-subject variable and the condition and speed as within-subject variables,

Experiment 5	df	F	Sig.
Condition	1,21	9.248	.006*
Speed	2,42	20.361	.000*
Age	1,21	0.320	.577
Condition*Speed	2,42	2.374	.105
Condition*Age	1,21	1.780	.196
Condition*Speed*Age	2,42	1.213	.308
Speed*Age	2,42	0.281	.756

APPENDIX D: CHAPTER 5 STATISTICAL TABLES

A. Statistical results from experiment 6 (motion coherence). A 2X2X2 (age, eye-movement and dot signal) mixed ANOVA [repeated], was performed on the coherence detection thresholds. Age was defined as the between-subject variable and the eye movement condition and dot signal as within-subject variables,

Experiment 6	df	F	Sig.	Eta Sq
Eye-movement	1,24	56.879	.000*	.703
Dot signal	1,24	0.830	.371	.033
Age	1,24	8.262	.008*	.256
Eye-movement* Dot signal	1,24	25.273	.000*	.513
Eye-movement*Age	1,24	11.868	.002*	.331
Eye-movement* Dot signal *Age	1,24	0.292	.594	.012
Dot signal *Age	1,24	0.052	.822	.022

B. Statistical results from experiment 6 (Motion Coherence). A 2X2 (age and dot signal) mixed ANOVA [repeated], was performed on the Motion coherence thresholds for the pursuit condition only.

Experiment 6 (Pursuit)	df	F	Sig.	Eta Sq
Dot Signal	1,24	10.418	.004	.303
Dot Signal *Age	1,24	.008	.929	.269
Age	1,24	13.659	.001	.363

C. Statistical results from experiment 6 (Motion Coherence). A 2X2 (age and dot signal) mixed ANOVA [repeated], was performed on the Motion coherence thresholds for the fixation condition only.

Experiment 6 (Fixation)	df	F	Sig.	Eta Sq
Signal	1,24	4.228	.051	.150
Signal * Age	1,24	2.690	.609	.269
Age	1,24	0.241	.628	.010

D. Statistical results from experiment 5 (motion coherence). A 2X2X2 (age, eye-movement and dot signal) mixed ANOVA [repeated], was performed on the pursuit gains. Age was defined as the between-subject variable and the eye movement condition and dot signal as within-subject variables.

Experiment 6	df	F	Sig.
Eye-movement	1,24	212.753	.000*
Dot signal	1,24	0.022	.884
Age	1,24	8.723	.007*
Eye-movement* Dot signal	1,24	0.030	.863
Eye-movement*Age	1,24	8.756	.007*
Eye-movement* Dot signal *Age	1,24	0.432	.517
Dot signal *Age	1,24	0.096	.759

E. Statistical results from experiment 5 (motion coherence). A 2X2 (age *direction) mixed ANOVA [repeated], was performed on the pursuit condition motion coherence thresholds. Age was defined as the between-subject variable and direction (with vs against) as within-subject variables.

Experiment 6 (With versus Against)	df	F	Sig.
Direction	1,24	6.000	.022*
Direction * Age	1,24	3.319	.081
Age	1,24	11.566	.002*

