Ageing, Motion Perception and the Compensation for Eye Movements.

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Abstract

Smooth pursuit over a textured background introduces full-field motion to the retinal image in the direction opposing the eye movement. If this motion is not correctly attributed to the eye movement, it can be falsely perceived as motion in the world (Haarmeier, Thier, Repnow & Petersen, 1997). In order to correctly attribute retinal motion, the visual system must compensate for the effects of eye movements on the retinal image in motion perception. Visual motion perception is important for safely navigating the environment and has been linked to difficulties experienced by older adults while driving (Conlon & Herkes, 2008; Raghuram & Lakshminarayanan, 2006) and walking (Cavanaugh, 2002). The experiments reported in this thesis were devised in order to examine the effects of ageing on the perception of illusory motion during eye movements and therefore on the ability to compensate for eye movements in motion perception. The perception of motion during smooth pursuit eye movements was assessed in adults ranging in age from 17 to 79 years. The computer based task required participants to respond to the speed and direction of motion of a large-field random dot pattern while following a moving target dot with the eyes. For this task, a magnitude estimation tool was especially designed based on the direction response method of Bennett, Sekuler and Sekuler (2007). During the experimental session an eye tracker recorded the participant's eye movements. For the purposes of analysis, four groups were defined by age. It was found that the smooth pursuit of adults from ~40 years of age was slower than that of the younger age groups. With stationary eyes, the oldest age group ranging in age from 60 to 79 years tended to overestimate the speed of the dot pattern as compared to younger observers. This tendency decreased at higher background speeds. Eye movements appeared to affect the perception of the dot field's motion more in the group of participants ranging in age from 40 to 54 years than in the younger age groups. This also seemed to be the case for participants aged over 60 when viewing horizontal motion but not vertical motion. The results of this study suggest that older observers may be less able to compensate for the effects of eye movements on the retinal image. This could potentially affect their ability to safely and confidently navigate the environment.

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Introduction

Background

The proportion of the New Zealand population over the age of sixty-five is increasing as people have less children and live longer (Statistics New Zealand, 2007). Similarly, the baby-boom cohorts of post World War II are increasingly entering old age (Statistics New Zealand, 2007). Ageing is associated with changes in the visual system that can impact upon the activities taken for granted when young. Such changes include the normal losses in visual acuity and the ability to focus on near objects and the not so normal but still relatively common changes such as cataracts and macular degeneration which can severely impact vision (Spear, 1993; Quillen, 1999). Visual changes can have their origins in the optics of the eye itself and in the neural pathways that mediate visual perception from the retina to the brain (Spear, 1993).

Impaired vision of older adults has been linked to an increased risk of falls (Lord & Dayhew, 2001) and motor vehicle crashes (Wood, 2002). Vision is thought to be especially important to older adults in maintaining postural stability as vestibular and somatosensory systems deteriorate naturally with age (Anderson, Nienhuis, Mulder & Hulstijn, 1998; Bugnariu & Fung, 2007).

An important aspect of vision is the ability to perceive motion. Motion perception in particular seems to be relevant to difficulties experienced by older adults while driving (Conlon & Herkes, 2008; Raghuram & Lakshminarayanan, 2006; Wood, 2002) and walking (Anderson et al., 1998; Cavanaugh, 2002) . The difficulties are not surprising given the centrality of motion information to speed judgements and to self-navigation and informing action (Gibson, 1950, 1958; Gibson, Olum, & Rosenblatt, 1955).

When moving about the environment, whether it is on foot or in a vehicle, there is a characteristic pattern of motion projected onto the back of the eye (the retina) (Gibson, 1950). Motion radiates out from the point of heading increasing in speed away from this point. Gibson (1950) referred to this point as the focus of expansion and theorised that a person could tell where they are going from its location. This pattern of motion is disrupted when head or eye movements are made (e.g. when following a moving object with the eyes or even fixating a stationary object on the ground while moving forward). The retinal motion generated by the eye movement is added to the retinal motion created by the observer's locomotion (Bradley, Maxwell, Andersen, Banks & Shenoy, 1996). If the sources of motion are not separated adequately, the direction of heading can be misperceived (Banks, Ehrlich, Backus & Crowell, 1996; Royden, Banks & Crowell, 1992; Royden, Crowell & Banks, 1994; Stone & Perrone, 1997; van den Berg, 1993; Warren & Hannon, 1988).

The retinal motion introduced by an eye movement is not only relevant during locomotion but also when the observer is stationary. Smooth following of a moving object with the eye will introduce motion of the background on the retina. While normally not perceived, the background can sometimes appear to move in the opposite direction to the eyes in what is known as the Filehne illusion (Filehne, 1922 as cited in Mack & Herman, 1973). Perception of the motion caused by eye movements has general ramifications for perceptual stability of the visual world (Haarmeier et al., 1997).

Eye movements and motion perception are closely linked with each having the ability to impact the other. Given the importance of motion perception for self-motion it is therefore important to understand changes with age in both eye movements and motion perception and in their combination. Such changes could have implications for the perceived stability of the visual world in old age and thus for mobility, independence and quality of life. It is also important that natural changes with age are delineated as impairments in eye movements and motion perception have been linked to Alzheimer's disease (Gilmore, Wenk, Naylor & Koss, 1994) and Schizophrenia (Hong et al., 2009). Schizophrenia has also been linked to deficits in the compensation for eye movements (Hong et al., 2009; Lindner, Thier, Kircher, Haarmeier & Leube, 2005). Therefore, in the search for markers of genetic risk for disorder, it is important that impairments due to age are not erroneously linked to pathology (Ross et al., 1999).

Changes in Motion Perception with Age

Sensitivity to Speed of Motion

The ability of older adults to perceive motion correctly is generally believed to be degraded. The elderly observer is less sensitive to motion and less able to process moving stimuli accurately. In order to be perceived as moving at all (as suggested by consistent correct judgements of stimulus motion direction), a stimulus needs to be moving faster for an older subject (~0.121 deg/s) than it does for a younger adult (~0.087 deg/s) (Snowden & Kavanagh, 2006). This holds regardless of the spatial frequency of the stimulus so that even though older adults demonstrate reduced visibility to high spatial frequencies this apparently is not the cause of their reduced ability to detect motion (Snowden & Kavanagh, 2006). When motion is detected, the ability to differentiate between stimuli of different speeds is decreased in older adults (Norman, Ross, Hawkes & Long, 2003; Raghuram, Lakshminarayanan, & Khanna, 2005; Snowden & Kavanagh, 2006). Speed discrimination thresholds may be elevated as early as 45 years of age (Bidwell, Holzman, & Chen, 2006). However, as Norman et al. (2003, p.90) point out "while it is true that there is an age-related effect upon speed discrimination it is not necessarily true that the older one gets, the poorer the ability to discriminate differences in speed". This is reflected in the thresholds of some older adults being lower than those of young adults (Norman et al., 2003; Raghuram et al., 2005). Elevated speed discrimination thresholds for older adults seem to be more prominent when the stimulus is only briefly presented (Raghuram et al., 2005).

Sensitivity to Direction of Motion

Older observers are less sensitive to differences in direction of motion of coherent random dot patterns as compared to younger adults (Ball & Sekuler, 1986). Direction sensitivity can also be measured with stimuli presenting a percentage of dots sharing a predetermined 'signal' motion in a display of otherwise randomly moving 'noise' dots (Newsome & Paré, 1988; Snowden & Kavanagh, 2006; Wojciechowski, Trick & Steinman, 1995). The minimum percentage of signal dots required to accurately perceive their global direction of motion is known as a motion coherence threshold (Newsome & Paré, 1988; Snowden & Kavanagh, 2006; Wojciechowski et al., 1995). This threshold has frequently been demonstrated to be elevated in older adults as compared to younger adults (Atchley & Andersen, 1998; Billino, Bremmer & Gegenfurtner, 2008; Snowden & Kavanagh, 2006; Tran, Silverman, Zimmerman & Feldon, 1998; Wojciechowski et al., 1995), especially in the central visual field (Atchley & Andersen, 1998; Wojciechowski et al., 1995). However, other studies have found no real difference (Mapstone, Dickerson & Duffy, 2008; Mapstone, Logan & Duffy, 2006; Mapstone, Steffenella & Duffy, 2003; Tetewsky & Duffy, 1999) or have attributed age differences mainly to elderly females (Atchley & Andersen, 1998; Gilmore, Wenk, Naylor & Stuve, 1992). From their study, Snowden & Kavanagh (2006) suggest that this decrement may be limited to slow speeds (less than around two degrees per second), although other studies have demonstrated increased thresholds with age for higher speeds of dot motion (Atchley & Andersen, 1998; Billino et al., 2008; Wojciechowski et al., 1995). Direction sensitivity has also been measured by the ability to accurately judge the common mean direction of global flow for dots moving at relatively diverse angles (Bennett et al., 2007; Dengis, Sekuler, Bennett & Sekuler, 1998). This ability is weakened in the elderly especially when the stimulus is presented very briefly (Bennett et al., 2007; Dengis et al., 1998).

Underlying Contributions to Motion Deficits in Aged Observers

Visual acuity, retinal illumination and contrast sensitivity to high spatial and temporal frequencies are known to decline with age (Elliot, Whitaker & MacVeigh, 1990; Owsley, Sekuler & Siemsen, 1983; Snowden & Kavanagh, 2006; Spear, 1993). By accounting for the differences in these mechanisms with age, studies have been able to demonstrate that age differences in motion perception go beyond such factors. This has been inferred by equating contrast of a stimulus relative to the contrast sensitivity of the subject (Norman et al., 2003), by correlating performance on motion perception tasks with measures of acuity, contrast sensitivity or luminance sensitivity (Atchley & Andersen, 1998; Gilmore et al., 1992; Norman et al., 2003; Raghuram et al., 2005; Wojciechowski et al., 1995) or by including a control group of younger observers wearing lenses which blur vision or reduce light to the eye in order to simulate normal deterioration of vision with age (Ball & Sekuler, 1986; Norman et al., 2003, Trick & Silverman, 1991 as cited in Tran et al., 1998). These studies have attributed changes in motion perception with age to changes in neural processing more specifically associated with motion perception. This is supported by evidence that the retina and lateral geniculate nucleus of old monkeys are relatively unchanged by the ageing process (Spear, 1993). These two structures are at the beginning of the visual pathway before motion processing really takes place. Instead, ageing has been linked to changes higher up in the motion processing pathway. A brief review of the visual motion processing pathway follows in order to provide a context for the forthcoming overview of cortical changes with age.

Visual Motion Processing

The Visual Motion Processing Pathway

Light reflected from objects in the world enters the eye and is projected onto its rear surface. This surface is called the retina and it is rich in sensors which detect light. Motion in the world is seen because light in the image on the retina changes over space and time. This information is passed along the optic nerve to the lateral geniculate nucleus and from there to the striate cortex also known as area V1 (Maunsell & Newsome, 1987). Cells in V1 can process the orientation, direction of motion and sometimes speed of stimuli in a very small area of the visual field (Maunsell & Newsome, 1987; Orban, 2008; Priebe, Lisberger & Movshon, 2006). Due to their limited view of the retinal image, they can generally only process motion which is orthogonal to a stimulus (e.g. bars, lines or edges) of their preferred orientation (Born & Bradley, 2005; Maunsell & Newsome, 1987; Movshon, Adelson, Gizzi & Newsome, 1983; Perrone, 2004).

The next step in the motion processing pathway is the middle temporal (MT) area (Born & Bradley, 2005; Maunsell & Newsome, 1987). This area is able to use the information provided to it by area V1 to complete more complex motion processing (Born & Bradley, 2005). It is better suited for more global motion, with MT cells being able to process stimulation from a much greater retinal area than that available to V1 cells (Born & Bradley, 2005; Gattass & Gross, 1981). Damage to this area greatly increases motion coherence thresholds even though the pattern of dots can still be seen (Newsome & Paré, 1988).

Even higher in the motion pathway, neurons in the medial superior temporal (MST) and ventral intraparietal (VIP) areas of the posterior parietal cortex are capable of responding to complex patterns of motion comprising multiple speeds and directions such as the optic flow patterns produced on the retina when an observer moves about their environment (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Britten, 2008; Duffy & Wurtz, 1991; Orban, 2008; Saito et al., 1986).

Speed Processing and its Changes with Age

Neurons in the motion processing pathway before area MST generally demonstrate preferences for relatively simple patterns of speed and direction (Britten, 2008). Preferences can be measured by way of tuning curves. A tuning curve is obtained by keeping all other stimulus parameters constant but varying the parameter of interest to observe changes in responding. Strong tuning is implied by high responding to a particular value with responses falling off sharply as the value moves away from the preferred stimulus.

The speed of a grating stimulus in degrees of visual angle per second is specified by its temporal frequency (the number of cycles per second in hertz (Hz)) divided by its spatial frequency (the number of cycles per degree of visual angle) (Perrone & Thiele, 2001; Priebe et al., 2006). On average, V1 cells in old monkey cortex are tuned to lower optimal spatial and temporal frequencies than young monkey cells (Zhang et al., 2008). For a neuron to be 'tuned' to a particular speed, it must respond preferentially to a range of different temporal and spatial frequencies such that their quotient equals the preferred speed (Perrone & Thiele, 2001; Priebe et al., 2006). A proportion of directionally selective complex cells in striate cortex (V1) and neurons in middle temporal cortex (MT) can be described as speed tuned (Perrone & Thiele, 2001; Priebe, Cassanello & Lisberger, 2003; Priebe et al., 2006).

Mendelson & Wells (2002) found that for older rats as compared to young ones, the average preferred speed across cells in the visual cortex was lower and the ability to respond to quickly flickering stimuli with synchronised bursts of firing had also degraded. They took this as evidence for a loss in temporal processing speed with age (Mendelson & Wells, 2002). In aged macaque neurons, testing with random dot patterns has generally demonstrated lower preferred speeds and wider speed tuning curves, and thus weaker speed selectivity (Yang, Zhang et al., 2009). A neuron's alteration in responding to changes in stimulus speed and the ability to discriminate “between its preferred and nonpreferred stimulus” (p.2) were degraded. (Yang, Zhang et al., 2009). The authors used these results to calculate speed discrimination thresholds and found that they related well to human psychophysical studies of elevated speed discrimination thresholds in older adults (Snowden & Kavanagh, 2006).

Direction Processing and its Changes with Age

As with speed tuning, poor direction selectivity is represented by a cell responding equally to all directions and not showing a preference for any particular direction. A preference for a particular direction is associated with high responding to that direction, decreased responding to those directions around it and lowest responding to the direction opposite it preferred direction. Both orientation and direction selectivity are reduced in the visual cortex of old monkeys (Yu, Wang, Li, Zhou & Leventhal, 2006) and cats (Hua et al., 2006). Direction selectivity is degraded in both V1 (Leventhal, Wang, Pu, Zhou & Ma, 2003; Liang et al., 2010; Schmolesky, Wang, Pu & Leventhal, 2000) and MT of aged rhesus monkeys with area MT being more severely affected (Liang et al., 2010). Due to decreases in direction selectivity, the proportion of neurons in these areas which could still be classified as directionally selective was reduced (Liang et al., 2010). Pattern neurons in MT seemed to be especially reduced with the authors suggesting that “pattern cells degrade into other cell types in old MT” (Liang et al., 2010, p.9). Pattern cells integrate the information from V1 cells and respond to the direction of movement of an object as a whole, even though its component parts are moving in different directions as specified by the motion orthogonal to their edges (Born & Bradley, 2005; Maunsell & Newsome, 1987; Movshon et al., 1983; Perrone, 2004). In order to be selective for pattern motion the input into MT needs to be tightly speed tuned (Perrone, 2004). This suggests that degradation of speed processing may begin earlier than MT in older animals.

Variability of Aged Cell Responses

Neurons respond to a preferred stimulus with a burst of rapid firing. This rate of firing decreases as the stimulus diverges further from its preferred characteristics. However, even without a stimulus present neurons will show sporadic firing. The ability to detect a stimulus relies on the differentiation of firing relative to a stimulus and that produced at baseline when there is no stimulus. (Leventhal et al., 2003; Yang et al., 2008; Yang, Liang, Li, Wang, & Zhou, 2009). In aged cats, monkeys and rats, visual cortical neurons (including V1 and MT in monkeys) exhibit decreased signal-to-noise ratios (Hua et al., 2006; Leventhal et al., 2003; Liang et al., 2010; Schmolesky et al., 2000; Wang, Xie, Li, Chen & Zhou, 2006; Wang, Zhou, Ma & Leventhal, 2005; Yang et al., 2008; Yang, Liang et al., 2009; Yang, Zhang et al., 2009; Yu et al., 2006; Zhang et al., 2008). This means that the response of these neurons to stimuli is not much different to their spontaneous baseline level of responding. Responding in general is increased in aged cells of monkeys whether it be to speed or direction stimuli or just spontaneous firing (Leventhal et al., 2003; Liang et al., 2010; Schmolesky et al., 2000; Yang, Zhang et al., 2009; Yu et al., 2006). However, baseline activity is increased disproportionately resulting in decreased signal to noise ratios. Greater variability in responding has also been exhibited in macaque V1 and MT where the response to the same stimulus is inconsistent across multiple presentations (Yang, Liang et al, 2009; Yang, Zhang et al., 2009). Consistent with these neurophysiological findings, Bennett et al. (2007) were able to use increased neural noise to account for the increase in error of perceived direction of motion exhibited by their older adults over the age of 70 years in a psychophysical study conducted with human subjects.

Reduced Inhibition

The decline in neural function with age exhibited by impaired selectivity, increased variability in responding and decreased salience of signal over background noise have been interpreted as stemming from degradation in cortical circuitry in the aged brain (Hua et al., 2006; Liang et al, 2010; Yang, Liang et al., 2009; Yang, Zhang et al., 2009). These circuits could be impaired because of changes in the structure of the connecting branches between neurons (Hua et al, 2006; Liang et al., 2010; Mendelson & Wells, 2002; Yang, Liang et al., 2009; Yang, Zhang et al., 2009). It could also be a result of reduced inhibition in the ageing brain (Hua et al, 2006; Liang et al., 2010; Yang, Liang et al., 2009; Yang, Zhang et al., 2009).

Leventhal and colleagues (2003) found that by administering the inhibitory neurotransmitter gamma-aminobutyric acid (GABA) or a GABA agonist (something that increases activity of GABA circuits) orientation and direction selectivity were much improved in V1 cells of old monkeys but not young monkeys whose cells were already strongly selective. These cells now "responded strongly to a narrow range of preferred orientations and directions and exhibited nearly no response to the nonpreferred orientations and directions" (p.814). The signal to noise ratio was also improved. With young monkeys, but not old monkeys, the administration of a GABA antagonist (something that reduces activity in GABA circuits) decreased direction and orientation selectivity and increased firing to resemble the original responding of the cells of old monkeys. A post-mortem study by Boley, Jones, Pinto and Murphy (2005, cited in Betts, Sekuler & Bennett, 2009) suggests that GABA systems in the human visual cortex may also be compromised over the age of 50 years. These results suggest that inhibition in neural circuits, perhaps mediated by GABA, degrades in old age and may be responsible for deficits in visual perception (Betts et al., 2009; Betts, Taylor, Sekuler & Bennett, 2005; Leventhal et al., 2003; Hua et al, 2006; Liang et al., 2010; Yang, Liang et al., 2009; Yang, Zhang et al., 2009).

Centre-Surround Processing

An important role of inhibition in visual cortex is in the receptive field properties of neurons (Allman, Miezin & McGuinness, 1985; Tanaka et al., 1986). Each neuron has an area of the visual field to which they respond best; known as its receptive field (Allman et al., 1985; Tanaka et al., 1986). Stimulation outside of this area can modulate the neuron's response to what is present within its receptive field (Allman et al., 1985; Tanaka et al., 1986). Put simply, increasing the size of the stimulus over and above its receptive field can increase or decrease the responding of a neuron (Allman et al., 1985; Tanaka et al., 1986; Born & Tootell, 1992). The former is the characteristic of neurons with excitatory surrounds while the latter suggests antagonistic centre-surround relationships (Allman et al., 1985; Tanaka et al., 1986; Born & Tootell, 1992). Such centre-surround relationships require communication between neurons, with "surround suppression … thought to be mediated by inhibitory interneurons" (Betts et al., 2005, p.361).

Around half of MT neurons demonstrate centre-surround antagonism (Born & Bradley, 2005). In general, the surrounds of these neurons have the most effect when the stimulus in the surround moves in the same direction and possibly at the same speed as the stimulus in the centre (Allman et al., 1985; Born & Bradley, 2005; Born & Tootell, 1992; Tanaka et al., 1986) although dependence on speed is not so clear-cut (Born & Bradley, 2005).

Tadin, Lappin, Gilroy and Blake (2003) have demonstrated what they believe to be a perceptual correlate of these centre-surround relationships in MT. Increasing the size of a high contrast stimulus renders direction discrimination more difficult suggesting an antagonistic surround effect (Tadin et al., 2003). However, lowering the contrast of the stimulus makes discriminating the direction of motion easier as stimulus size is increased (Tadin et al., 2003). This suggests a switch from spatial suppression to spatial summation at low contrast optimising the amount of information available when the stimulus is harder to see (Tadin et al., 2003). Interestingly, Betts, Taylor, Sekuler and Bennett (2005) have demonstrated that older observers are better at discriminating the direction of motion of a large high contrast stimulus than are younger observers. They suggest that ageing is associated with reduced surround suppression consistent with the hypothesis of decreased inhibitory function with age (Betts et al., 2005; Betts et al., 2009).

It is believed that centre-surround relationships provide the function of separating a figure from its background (Allman et al., 1985; Born & Bradley, 2005; Born, Groh, Zhao & Lukasewycz, 2000; Born & Tootell, 1992; Tanaka et al., 1986). Surround suppression has the effect of enhancing responding when a small stimulus differs from its surroundings and decreasing responding when stimulation is the same over a large area and is thus uninformative (Tadin & Blake, 2005). Other MT neurons displaying centre-surround summation rather than antagonism respond best to this large monotonous motion consistent with favouring a background stimulus (Born et al., 2000, Tadin & Blake, 2005). Such an interpretation of the function of MT centre-surround relationships resonates well with what is required to separate eye movements from background motion (Born et al., 2000; Pack, Grossberg & Mingolla, 2001; Tadin & Blake, 2005).

Eye Movements

Neural Processing of Eye Movements

The link between centre-surround relationships and eye movements has been demonstrated by Born and colleagues (2000). They showed that electrical stimulation of antagonistic centre-surround MT neurons of the macaque drove smooth pursuit eye movements in the direction preferred by the neuron while stimulation of summation neurons encouraged pursuit in the direction opposite to that preferred by the neuron (Born et al., 2000). The lateral region of the medial superior temporal area (MSTl), the next cortical area up the motion processing hierarchy from area MT, is also known to be involved in the control of pursuit eye movements (Krauzlis, 2004; Ilg, 2008). Like antagonistic centre-surround neurons in MT, many neurons in MSTl show preference for small stimuli and their stimulation will alter pursuit (Ilg, 2008; Komatsu & Wurtz, 1989; Newsome, Wurtz & Komatsu, 1988; Tanaka et al., 1986). The signalling of retinal slip by neurons in these areas may provide information to the oculomotor system that the eye needs to catch up to whatever it is following (Dürsteler & Wurtz, 1988; Ilg, 2008; Newsome et al., 1988). Damage to general area MST produces deficits not only in smooth pursuit eye movements but in optokinetic nystagmus (Dürsteler & Wurtz, 1988).

Eye Movements and Ageing

Optokinetic nystagmus is a reflexive following of large or full field motion by the eyes with subsequent saccades to re-centre fixation (Kolarik, Margrain & Freeman, 2010). The ability to accurately follow a stimulus with the eyes is often measured by the gain of the eye movement; the velocity of the eyes divided by the velocity of the stimulus they are supposed to be following. Optokinetic nystagmus gain has been shown to significantly decrease even over a decade for the adult in their late seventies (Kerber, Ishiyama & Baloh, 2006). Older adults in general have demonstrated reduced gain of optokinetic nystagmus

(Kolarik et al., 2010; Paige, 1994). The speed of optokinetic nystagmus in older adults is especially reduced at "low light levels, low contrast, and higher temporal frequencies" (Hine, Wallis, Wood & Stavrou, 2006, p.5293).

When following a small target against a background, the retinal motion of the background would serve to drive optokinetic eye movements in the opposite direction to pursuit and so needs to be suppressed (Kolarik et al., 2010). Smooth pursuit serves to keep the object followed by the eyes on the region of the retina with highest visual acuity so as to reduce blur (Krauzlis, 2004). Kolarik et al. (2010) found that older adults were less accurate than younger people in pursuing a target over a stationary background grating (but not a stationary random dot field), especially at faster target speeds. The gain of smooth pursuit has consistently been demonstrated to be decreased in older observers compared to younger observers (Kolarik et al., 2010; Moschner & Baloh, 1994; Paige, 1994; Ross et al., 1999; Sakuma, Ogino, Takahashi & Kato, 2000; Sharpe & Sylvester, 1978). However, this may only be true for target speeds of 10 degrees per second and greater (Sharpe & Sylvester, 1978) with gain differences between young and old increasing as target speed increases (Moschner & Baloh, 1994; Sharpe & Sylvester, 1978). It may also depend on the stimulus tracked. Kolarik et al. (2010) found a difference in gain with age when tracking a grating stimulus but not a field of random dots. A longitudinal study (Kerber et al., 2006) demonstrated no significant change in smooth pursuit gain for adults in their late seventies over approximately a decade. However, it did find degradation of optokinetic nystagmus and eye movements driven by interactions between visual and vestibular signals.

Older adults seem to have more variable eye movements (Kolarik et al., 2010; Moschner & Baloh, 1994) and their smooth pursuit is less accurate requiring more saccades to catch up to the target (Ross et al., 1999). The time it takes an older adult to initiate a smooth pursuit eye movement also seems to be extended (Knox, Davidson & Anderson, 2005; Sharpe & Sylvester, 1978) although age differences in latency are not always found (Sakuma et al., 2000). Sakuma et al. (2000) found reduced eye acceleration in older adults with a degraded ability to accelerate the eye in response to increasing retinal slip. They suggest that "this means that the ability to change sensory inputs into motor commands was reduced in the older group" (p.199). Deficits in eye movements with age may be a result of reduced motion detection and perception, or could be caused by degradation in several stages of the oculomotor control system such as in the muscles connected to the eyes and in cortical and subcortical areas responsible for motion processing and driving eye movements (Moschner & Baloh, 1994; Kolarik et al., 2010; Sakuma et al., 2000).

In many of the studies on motion perception with age, fixation seemed to be largely assumed and actual eye movements were not recorded (but see Atchley & Andersen, 1998; Mapstone et al., 2003; Mapstone et al., 2008; Tetewsky & Duffy, 1999). As several authors point out, stimuli were usually presented for sufficient duration to elicit eye movements (Bennett et al., 2007; Norman et al., 2003; Raghuram et al., 2005). The contribution of eye movements to changes in motion perception with age are therefore largely unknown. Tran and colleagues (1998) did measure reflexive eye movements in their young and old observers during a motion coherence task. They found an increased coherence threshold required to elicit optokinetic nystagmus in the direction of global flow with age. They also found that older observers required increased motion coherence to accurately discriminate direction of the same stimulus. However, there was no correlation between the two thresholds suggesting a dissociation between the respective mediating neural pathways (Tran et al., 1998).

Self Motion Perception

Neural Processing of Self Motion

While the lateral subdivision of MST is better suited to driving pursuit eye movements, the dorsal subdivision (MSTd) and the higher ventral intraparietal area (VIP) are associated with analysing large complex retinal motion patterns such as those produced by self-motion (Bremmer et al., 2002; Britten, 2008; Duffy & Wurtz, 1991, 1995; Orban, 2008; Saito et al., 1986; Tanaka et al., 1986). Neurons in these areas are able to integrate information over very large areas (Duffy & Wurtz, 1991; Saito et al., 1986; Tanaka et al., 1986) having receptive fields which can cover entire quadrants of the visual field or more (Duffy & Wurtz, 1991, 1995; Maunsell & Newsome, 1987). While neurons in V1 and MT have preferences for direction, neurons in MST can have preferences for a pattern consisting of many directions of motion (Britten, 2008; Duffy & Wurtz, 1991, 1995; Saito et al., 1986; Tanaka et al., 1986). Moving through the environment will produce a pattern of motion radiating out from the direction of heading where the speed of motion increases further towards the periphery. Gibson (1950) called this pattern of motion 'optic flow' and theorised that by locating the 'focus of expansion' an observer could locate where he or she was going and use the flow pattern to guide locomotion. MSTd neurons may respond to optic flow by collating the information over MT neurons responding to particular directions of motion in particular areas of the visual field (Perrone & Stone, 1994; Tanaka, Fukada & Saito, 1989). By comparing several of these optic flow “templates”, the organism can derive a representation of where it is going (Duffy & Wurtz, 1995; Perrone & Stone, 1994).

Self Motion Perception and Ageing

Unlike for translational motion (Atchley & Andersen, 1998; Billino et al., 2008; Snowden & Kavanagh, 2006; Tran et al., 1998; Wojciechowski et al., 1995) motion coherence thresholds for detecting optic flow expansion have *not* been shown to increase with age (Atchley & Andersen, 1998; Billino et al., 2008; O'Brien et al., 2001; Mapstone et al., 2003; Mapstone et al., 2006; Mapstone et al., 2008; Tetewsky & Duffy, 1999). Although thresholds increase with retinal eccentricity for both younger and older adults, optic flow detection further from central vision does not exhibit increased difficulty with advancing age (Atchley & Andersen, 1998). This suggests that older adults are perfectly able to detect radial motion characteristic of self-motion. However, the ability to use optic flow patterns to determine heading direction may not be quite so preserved with age.

Older adults are less able to discriminate the direction of heading in random dot optic flow displays depicting either straight or curved paths, needing about 1 degree more displacement than young adults to detect a change in heading direction (Warren, Blackwell, & Morris, 1989). By changing the number of dots in their optic flow stimuli Warren et al. (1989) determined that older adults, like young adults, were relying on the global structure of optic flow to determine heading and had not shifted their strategy to one of using local motion. This suggested that their ability to use global flow structure was impaired (Warren et al., 1989). In contrast, O'Brien et al., (2001) suggested that some older adults were using local motion to determine the location of the focus of expansion. In their study older adults did not demonstrate elevated motion coherence thresholds in identifying the location, either left or right of centre, of outward radial flow. However, when local motion cues in optic flow patterns were confounded by interspersing outward and inward radial flow patterns, motion coherence thresholds for the location of the focus of expansion or contraction did increase above that of young adults in around a third of the elderly adults. Other studies confirmed an increase in threshold for older adults with interleaved expansion and contraction stimuli (Mapstone et al., 2003, Mapstone et al., 2008). This suggested to the authors that these older adults were unable to use the global flow to locate the focus of expansion as young adults could (O'Brien et al., 2001; Mapstone et al., 2003; Mapstone et al., 2008). Although these studies disagree on the strategies used by older adults, they both agree on the presence of a global flow impairment in at least some older adults.

Expansion is not only a cue to heading direction. The rate of expansion can be used to estimate the time to contact of an approaching object (Andersen & Enriquez, 2006). When the time to contact is small, the rate of expansion will be high. Older observers are less able to correctly detect the imminent collision of an approaching object, being more likely than young adults to report collisions when they are not about to occur (Andersen & Enriquez, 2006). Their sensitivity is lowest when the approaching object is moving fast and has a longer time to contact and also when their own simulated motion is added to the display, suggesting a reduced ability to separate object from self motion (Andersen & Enriquez, 2006). If given more time, (i.e. if the initial distance of the object is increased) the performance of older adults can be increased but is still lower than young adults (Andersen & Enriquez, 2006).

Mapstone et al. (2006) also found differences in the abilities of older adults in interpreting optic flow expansion and object movement. They found that adults over the age of sixty were equally able to locate the heading direction depicted by optic flow expansion of a random dot field as compared to middle aged and young adults (Mapstone et al., 2006). However, older adults were generally impaired when the simulation of self-motion suggested “movement past an earth-fixed object” (p.2933) rather than into a cloud of dots (Mapstone et al., 2006). In this case the heading direction was represented by the motion and increasing size of an object out from the focus of expansion (Mapstone et al., 2006). Their performance was recovered when optic flow and object movement stimuli were combined suggesting the ability to take advantage of the most useful information present (Mapstone et al., 2006). The authors suggest that this is consistent with reduced centre-surround antagonism in ageing as optic flow occupies a large portion of the field of view and does not require centre-surround inhibition while smaller object motion can be enhanced by this processing (Mapstone et al., 2006).

Heading detection thresholds can be measured by the minimum offset of the focus of expansion from centre screen that can be located reliably. Mapstone and colleagues (2008) found that older adults had a higher heading detection threshold than younger adults for optic flow stimuli surrounded by a non overlapping annulus of stationary dots. When the outer annulus of dots moved, older adults performed even worse (Mapstone et al., 2008). In young and old adults, surrounding an optic flow stimulus with non-overlapping horizontal motion affects heading detection thresholds by causing an illusory shift of the focus of expansion (Mapstone et al., 2008). When the horizontal motion is towards the focus of expansion (i.e. if the focus of expansion is to the left of centre screen then the surrounding horizontal motion is leftwards), heading detection thresholds are decreased (Mapstone et al., 2008). When the horizontal motion is in the opposite direction to the offset of the focus of expansion, heading detection thresholds are increased (Mapstone et al., 2008). Older adults performed very badly when the surrounding motion was in the opposite direction to the focus of expansion, especially when that motion was in the near periphery. For these conditions their heading detection thresholds increased by around 3.5 degrees while younger adults' thresholds increased by less than one degree compared to their performance when the surrounding dots were stationary (Mapstone et al., 2008). This suggests that older adults had greater illusory shifts of the perceived heading in this condition (Mapstone et al., 2008). Their reduced ability to segregate different areas of motion could be due to decreased inhibition in centre-surround relationships or inability to filter out the surrounding stimulus through attention (Mapstone et al., 2008). Another interpretation of the illusory shift of the focus of expansion by uniform motion calls on the similarities between the shift of the focus of expansion in this illusion and the perceived shift in heading which occurs during eye movements (Duffy & Wurtz, 1993; Duijnhouwer, Beintema, van den Berg & van Ezel, 2006; Duijnhouwer, van Wezel & van den Berg, 2008; Pack & Mingolla, 1998).

Distortion of Self Motion Perception during Eye Movements

While moving about in the world, the eyes are rarely still. Instead they track features of the environment such as moving objects or fixate stationary objects on the ground as they approach (Britten, 2008). Moving the eyes smoothly to the right whilst heading directly forward introduces full field leftward retinal motion to the expansion stimulation produced from the forward self motion (Bradley et al., 1996). The retina receives the combination of these two flow patterns which resembles a curved path towards the right (Banks et al., 1996; Royden, 1994; Royden et al., 1992, 1994; Royden, Cahill & Conti, 2006; Warren & Hannon, 1988). To accurately recover the direction of heading, the full field motion to the left must be removed or compensated for and the heading shifted back towards the left on the retina (Banks et al., 1996; Royden et al., 1992, 1994; Royden et al., 2006; Stone & Perrone, 1997; van den Berg & Beintema, 2000; van den Berg, Beintema & Frens, 2001). Illusory shifts of the focus of expansion by full field motion may be mediated by the same mechanisms that compensate for the effects of eye movements on visual stimuli (Duffy & Wurtz, 1993; Duijnhouwer et al., 2006; Duijnhouwer et al., 2008; Pack & Mingolla, 1998). The brain may be interpreting uniform horizontal retinal motion as being due to an eye movement and attempting to compensate for it by shifting the focus of expansion opposite the direction of the perceived eye movement (in the same direction as the horizontal motion on the screen) (Duffy & Wurtz, 1993; Duijnhouwer et al., 2006; Duijnhouwer et al., 2008; Pack & Mingolla, 1998). This interpretation would suggest that older adults are overcompensating for inferred eye movements in the studies of Mapstone et al., (2008).

Compensation for Eye Movements

Eye Movements and Heading Perception

Evidence suggests that, under certain circumstances, people can recover the true heading direction on optic flow displays contaminated by a simulated eye movement by using visual information alone. These circumstances include sufficient depth cues in the scene and when the simulated eye movement is not very fast (Li & Warren, 2000; Royden et al., 1994; Royden et al., 2006; Stone & Perrone, 1997; van den Berg, 1993, 1996; Warren & Hannon, 1988). Other than this, the direction of heading generally appears grossly distorted and interpretation is consistent with movement along a curved path (Banks et al., 1996; Royden, 1994; Royden et al., 1992, 1994; Royden et al., 2006). However, when an actual eye movement is made producing the same retinal distortion people can again recover the direction of heading (Banks et al., 1996; Royden et al., 1992, 1994; Royden et al., 2006). Although information from the retina may be partly used to compensate for eye movements (Crowell & Andersen, 2001; Li & Warren, 2000; Stone & Perrone, 1997; van den Berg et al., 2001), it seems that the compensation for eye movements is very much helped by an extraretinal signal in the brain telling the visual system that an eye movement is the cause of the retinal distortion to the expansion (Banks et al., 1996; Crowell & Andersen, 2001; Li & Warren, 2000; Royden et al., 1992, 1994; Royden et al., 2006; van den Berg, 1993; van den Berg & Beitema, 2000; van den Berg et al., 2001).

Extraretinal Signals

An extraretinal signal is a source of information for visual perception which does not have its origins on the retina (Matin et al., 1982; Wertheim, 1994). Extraretinal signals can provide information about whether the body, neck, head or eyes are moving to aid interpretation of the retinal image (Sperry, 1950; von Holst & Mittelstaedt, 1971). In the mid 20th Century, von Holst and Mittelstaedt (1971) and Sperry (1950) both proposed that the visual system is able to disambiguate different sources of motion in the retinal pattern through use of a signal equivalent to the command for movement of body parts. This efference copy (von Holst & Mittelstaedt, 1971) or corollary discharge (Sperry, 1950) communicates the expected retinal stimulation from body motion which is then eliminated from the actual retinal motion with the remainder being interpreted as due to sources outside the body.

Support for the role of such an extraretinal signal in visual perception has been provided by instances where the extraretinal signal is perceived as movement despite the lack of retinal motion. For instance, pushing on the side of the eye elicits an equivalent force from the other direction to maintain fixation. This stabilising force is perceived as full-field movement of the world (Bridgeman, 1995, 2007; Bridgeman & Stark, 1991). When the eye is paralysed, an attempted eye movement can result in the perceived displacement of objects in the dark (Bridgeman, 1995; Matin et al., 1982; Stevens et al., 1976; Wurtz, 2008). In both these cases the lack of movement of the eye leaves retinal stimulation unchanged and yet motion is perceived. Motion can also be perceived when the eye does move but the retinal image remains unchanged because it is fixed on the retina. An afterimage, where staring at a bright picture adapts retinal receptors, is an example of such a case. An afterimage will appear to move about when eye movements are made in the dark (Bridgeman, 2007; Goldstein, 2002). Similarly, following a moving target with the eyes holds its image stationary on the fovea and yet the target is still perceived as moving (Goldstein, 2002). In both of these cases the eye does move but the image of the object remains fixed on the retina. These are all examples where commands to move the eye (or maintain fixation during external pressure on the eye) are not accompanied by a change in retinal stimulation and the extraretinal signal itself is perceived as movement or displacement (Bridgeman, 1995, 2007; Goldstein, 2002; Matin et al., 1982; Stevens et al., 1976).

Compensation for Eye Movements in the Brain

Compensation for the effects of eye movements during navigation requires an area of the brain that responds to optic flow stimuli characteristic of heading *and* demonstrates responding based on movements of the eyes (Andersen, Snyder, Bradley & Xing, 1997; Bradley et al., 1996). Higher motion processing areas in the dorsal stream, MSTd and VIP are well suited to this task (Andersen et al., 1997; Bremmer et al., 2002; Bremmer, 2005; Britten, 2008; Newsome et al., 1988). The tuning of MST neurons for heading direction can shift to compensate for both the speed and direction of an eye movement (Bradley et al., 1996; Shenoy, Crowell & Andersen, 2002). Some of this shift can be driven by retinal cues alone while the rest is based on extraretinal information (Shenoy et al., 2002).

Compensation for eye movements is not only important during navigation but for general perceptual stability (Andersen et al., 1997). This is revealed clearly in the case of a patient who fails completely in this ability. With every eye movement, the stationary world seems to swing against his eyes causing him to suffer vertigo (Haarmeier et al., 1997). His visual system is interpreting all retinal motion as being due to motion out in the world (Haarmeier et al., 1997). The cause of this man's deficit seems to be damage to the later stages of the motion processing pathway including an area probably equivalent to the monkey area MST (Haarmeier et al., 1997).

While neurons in area MT display behaviour more consistent with a representation of the retinal motion of the stimulus, the activity of neurons in MST is able to represent the motion of the object in space (Ilg, Schumann & Thier, 2004; Inaba, Shinomoto, Yamane, Takemura, & Kawano, 2007; Inaba & Kawano, 2009; Newsome et al., 1988). Neurons in MST have shown activity during smooth pursuit despite a lack of retinal stimulation (Ilg et al., 2004; Inaba et al 2007; Newsome et al., 1988) and preferential responding to retinal motion caused by movement of an external object rather than of the eye (Inaba et al., 2007; Sakata, Shibutani, Kawano & Harrington, 1985). Neurons in MSTd represent motion more consistent with movement in the world than movement on the retina (Inaba et al., 2007; Inaba & Kawano, 2009). It is likely that area MST receives retinal information from area MT and combines it with extraretinal information regarding eye movements (Ilg et al., 2004; Inaba et al., 2007; Inaba & Kawano, 2009; Newsome et al., 1988). The firing of MSTl neurons sensitive to the pursuit target will begin before the eye movement initiates suggesting that extraretinal information does not come from the muscles attached to the eye sensing its rotation (Ilg et al., 2004). These extraretinal signals help in perceiving the pursuit target as moving despite its lack of retinal motion (Ilg et al., 2004). An extraretinal signal for pursuit eye movement could be passed upwards from brain areas such as the brainstem involved in the generation of eye movements, or could be passed downwards from higher frontal areas such as the frontal eye fields involved in the control of eye movements (Pack et al., 2001; Sommer & Wurtz, 2008). The different perceptual effects undergone by different retinal locations during an eye movement suggests the need for different eye position signals for these areas (van Beers, Wolpert & Haggard, 2001). The concept of a single extraretinal signal may therefore be too simplified (van Beers et al., 2001).

Perrone and Krauzlis (2008) have constructed a model which specifies how the compensation for eye movements could occur within a small population of MT neurons. At each retinal image location, the activity of MT neurons preferring a range of speeds and directions can be represented by a cosine distribution of neuronal activity (Perrone & Krauzlis, 2008). If neurons tuned to different directions respond to the speed in their direction, the peak of the cosine distribution will be the speed of motion and its phase will be the direction (Perrone & Krauzlis, 2008). Negative portions of the cosine curve are mediated by inhibitory relationships between neurons tuned to opposite directions of motion (Perrone & Krauzlis, 2008). A similar distribution of activity arising from the extraretinal signal can be added to the retinal distribution and the equivalent of vector subtraction performed (Perrone & Krauzlis, 2008).

Theory Regarding Compensation for Eye Movements

Vector subtraction is needed in order to compensate for the effects of eye movements on a retinal pattern which often contains many different directions and speeds of motion (e.g. during self-motion) (Perrone & Krauzlis, 2008). The visual system needs to subtract vectors representing the retinal contribution of eye movement from total retinal motion. Subtraction of the contributing eye movement vector will not only affect the speed of perceived motion but also the direction (Becklen, Wallach & Nitzberg, 1984; Mateeff, Yakimoff, Hohnsbein & Ehrenstein, 1991; Morvan & Wexler, 2009; Perrone & Krauzlis, 2008; Souman, Hooge & Wertheim, 2005a, 2005b, 2006; Souman & Freeman, 2008; Swanston & Wade, 1988; Wallach, Becklen & Nitzberg, 1985; Wertheim, 1994).

The perceived velocity of an object in space can be calculated by adding its retinal velocity and the velocity of the eye movement, assuming the head and body are still (Morvan & Wexler, 2009; Perrone & Krauzlis, 2008; Souman et al., 2005a, 2005b, 2006; Souman & Freeman, 2008). An eye movement to the right will produce retinal motion of a stationary object to the left. These two velocities are equal and opposite; their addition should be equivalent to a cancellation of motion and the object should be perceived as stationary. However, these signals can be unbalanced. The Filehne illusion (Filehne, 1922 as cited in Mack & Herman, 1973) occurs when the stationary object is perceived as moving slightly in the direction opposite to the eye movement. Traditionally, this effect has been interpreted as resulting from the visual system underestimating the velocity of the eye movement and thus not 'cancelling' enough of the retinal motion of the stationary object (Bridgeman, 1995, 2007; De Graaf & Wertheim, 1988; Freeman & Banks, 1998; Mack & Herman, 1973, 1978; Wertheim, 1981). Freeman and Banks (1998) pointed out that the visual system may also have an inaccurate estimate of the retinal velocity at its disposal. Even for stationary eyes the perceived velocity of a stimulus changes depending on stimulus parameters such as contrast and spatial frequency despite physical (and thus retinal) velocities remaining stable (Freeman & Banks, 1998). All that can really be inferred from the Filehne illusion is that the estimate of the eye velocity is smaller than the estimate of the retinal velocity (Freeman & Banks, 1998; Freeman, 2001). Both could be overestimated, both could be underestimated, the retinal signal could be overestimated while the eye velocity could be veridical or underestimated, and so forth (Freeman & Banks, 1998; Freeman, 2001). This balance of signals can be described by the ratio between the extraretinal signal, which is the visual system's estimate of the actual eye velocity and the visual system's estimate of the retinal velocity. This 'gain ratio' is zero when no compensation for eye movements occurs while a ratio of one indicates complete compensation (Freeman, 2001; Freeman & Banks, 1998; Souman et al., 2005a, 2006).

Changing the Degree of Compensation

The Filehne illusion can be inverted, so that the direction of perceived motion is in the same direction as the eye movement, when the stimulus is of low spatial frequency (Freeman & Banks, 1998; Wertheim, 1987 as cited in Wertheim, 1994). Freeman and Banks (1998) interpreted this effect as a decrease in the visual system's estimate of retinal velocity as spatial frequency decreases (Freeman & Banks, 1998). Similarly, the Aubert-Fleischl phenomenon (Aubert, 1887 and Fleischl, 1882 as cited in Dichgans, Wist, Diener & Brandt, 1975), where the speed of a target is underestimated when pursued compared to when it passes the stationary eyes, can also be reversed at low spatial frequencies (Freeman & Banks, 1998). Freeman and Banks (1998) pointed out that although the retinal estimate when the stimulus is pursued should have no effect (because with perfect pursuit there is no retinal motion), the comparison condition where the stimulus passes the stationary eyes changes with spatial frequency (Freeman & Banks, 1998). Therefore the relationship between the two conditions will change with spatial frequency (Freeman & Banks, 1998).

Wertheim (1994) provides a different interpretation. He proposed that the visual system estimates eye velocity by supplementing the extraretinal signal with retinal and vestibular information. Motion which covers a large part of the field of view, is of relatively low spatial frequency and is generally visible for more than a brief duration, is characteristic of the retinal motion produced by eye movements and can be described as optokinetic (De Graaf & Wertheim, 1988; Wertheim, 1994). The visual system can use such retinal motion to boost the extraretinal signal and provide a composite “reference signal” for eye movement (De Graaf & Wertheim, 1988; Wertheim, 1994). Such a signal can explain reversals in the Filehne and Aubert-Fleischl phenomena with optokinetic stimuli as the reference signal becomes larger than the retinal signal (Wertheim & Bekkering, 1992; Wertheim, 1994).

It can also account for changes in perception experienced inside a rotating drum (Wertheim, 1994). If fixating a stationary point inside a drum providing optokinetic stimulation, a gradual change in perception will occur in around 5 seconds (depending on the speed of the drum) from perceiving oneself as stationary within that moving drum to a feeling of self-motion (circularvection) within a stationary drum. The lack of extraretinal signal supplied during fixation is overwhelmed by a building reference signal which cancels the retinal motion of the drum and, through its vestibular component, makes the observer feel as though they are moving instead (Wertheim, 1994).

There are conflicting results on the change with increasing age in the experience of this illusion of self-motion. Matheson, Darlington & Smith, (1998) suggested that the transition from perception of a moving drum to perception of self-motion within the stationary drum took longer in older adults. The authors posit that “a reduction in sensitivity to optokinetic stimulation, reduced reaction time, or a combination of the two” (p.2176) could have contributed to their results (Matheson et al., 1998). On the other hand Paige (1994) reported that the likelihood of experiencing circularvection and its subjective intensity increased with age. Paige (1994) attributes this to an increase in the importance of vision for self-rotation perception as vestibular inputs are degraded with age.

Sensorimotor Integration and Ageing

The integration of vision with vestibular and somatosensory systems is important for controlling posture, gait and navigation of the environment (Andersen et al., 1997; Cavanaugh, 2002; Paige, 1994). Neurons in both MSTd and VIP respond to optic flow and integrate vestibular signals while area VIP also responds to somatosensory and auditory stimuli (Andersen et al., 1997; Bremmer, 2005; Britten, 2008; Ilg et al., 2004; Kawano, Sasaki & Yamashita, 1984). Both areas are also connected to motor areas (Britten, 2008). The posterior parietal cortex thus seems to be involved in the translation of sensory information into actions (Andersen et al., 1997).

Studies have proposed that older adults are not as capable as younger adults in tasks requiring sensorimotor integration (Berard, Fung, McFadyen and Lamontagne, 2008; Bugnariu & Fung, 2007; O'Connor, Loughlin, Redfern & Sparto, 2008). Evidence suggests that due to natural degradation of the vestibular and somatosensory systems with age, older adults rely on visual information more than young people to regulate balance and posture, control locomotion and maintain head stabilisation (Anderson et al., 1998; Bugnariu & Fung, 2007; Cavanaugh, 2002; Cromwell, Newton & Forrest, 2002; Huitema et al., 2005). Eye movements controlled by visual and/or vestibular input (i.e. when the head also moves) have been shown to degrade with age and this has been tentatively linked to poorer visual stability and postural control (Kerber et al., 2006; Paige, 1994). Adults from at least the age of 44 exhibit a greater reliance on vision for maintaining posture (Poulain & Giraudet, 2008). When visual and somatosensory or vestibular information is discordant, older adults show greater postural instability (Bugnariu & Fung, 2007; Matheson, Darlington & Smith, 1999a). The elderly may also not be as capable as younger and middle aged adults in using visual cues to reduce sway (Fransson, Kristinsdottir, Hafstrom, Magnusson & Johansson, 2004; Kristinsdotter, Fransson & Magnusson, 2001).

The presentation of changes in optic flow to people while they walk will cause them to change their walking speed to resolve the conflict between visual and somatosensory information from the joints and muscles (Prokop, Schubert & Berger, 1997). Compared to younger adults, older adults have shown greater modulations of walking response to optic flow disturbances (Beschorner, McGowan, Redfern, Sparto & Cham, 2009) with removal of visibility of the ground, which provides higher velocity rate of expansion information (Anderson et al., 1998); and during a concurrent visually demanding task (Bock, 2008) suggesting a greater reliance on vision while walking (Anderson et al., 1998; Beschorner et al., 2009; Bock, 2008). Data on the ability of older adults to use optic flow cues to guide navigation while walking are conflicting. Berard et al. (2008) found that older adults were unable to use optic flow in a virtual reality world to alter their walking direction in the physical world. To do this they would have had to ignore conflicting information from other systems, such as the vestibular and somatosensory systems, and rely solely on visual information which they did not seem able to do (Berard et al., 2008). However, in another virtual reality study, Chou et al., (2009) found no difference between young and old adults in their ability to use differences in optic flow speed and asymmetry to change walking speed and direction suggesting that "older adults are able to integrate optic flow information into the multimodal system to monitor their walking speed and heading direction in much the same manner as younger adults" (p.230).

Differences between young and older adults in the influence of visual perturbations on posture and locomotion may be linked to processing speed (Huitema et al., 2005; O'Connor, Loughlin et al., 2008). Huitema et al. (2005) conducted a study where old, middle aged and young participants wore prism glasses that laterally shifted their view. This had the effect that, when required to walk towards a target, instead of heading straight for it the participants followed a curved trajectory. Immediately on removal of the glasses the young and middle aged participants were better able to correct their heading and follow the quickest linear route to the target. The older participants however continued to follow the curved path for a while. The authors suggested that not only were older adults less able to use vestibular and somatosensory cues to override any lasting effect the glasses had on their vision they needed more time to adapt which could be linked to general slowed processing (Huitema et al., 2005). Older adults exhibit greater head sway in response to changing optic flow and habituate to its repeated exposure slower than younger adults (O'Connor, Loughlin et al., 2008). This habituation requires that the relative visual contribution to postural control is lessened (O'Connor, Loughlin et al., 2008). The authors suggest that "differences between older and young adults may indicate that older adults reduce the relative visual feedback gain at a slower rate than young adults, reflecting changes in central sensory integration with age" (p.390).

Changes in Processing Speed with Age

Visual and cognitive processing speed in general is considered to be slowed in aged adults (Di Lollo, Arnett & Kruk, 1982; Salthouse, 1996; Salthouse & Madden, 2008). This can be inferred from performance on tests requiring rapid response or processing of stimuli only briefly presented (Di Lollo et al., 1982; Salthouse & Madden, 2008). The gap between performance of younger and older adults on motion direction (Bennett et al., 2007; Dengis et al., 1998) and speed discrimination (Raghuram et al., 2005) performance seems to narrow with longer stimulus duration. This suggests difficulties with temporal integration (Raghuram et al., 2005) that can be alleviated when an older adult has more time to process a stimulus (Bennett et al., 2007; Dengis et al., 1998; Raghuram et al., 2005). An increase in smooth pursuit latency with age may also suggest less efficient motion processing or general slowing (Knox et al., 2005). A decrease in the speed of visual processing is suggested by increased reaction time to motion onset in the aged when effect of stimulus parameters such as contrast and motor slowing are removed (Porciatti, Fiorentini, Morrone & Burr, 1999). However, by measuring the pattern of electric potentials through the scalp Roggeveen, Prime and Ward

(2007) suggest that the slowed reaction time of the elderly is primarily due to slowed motor processing.

Slowed information processing has been linked to deficient communication between brain areas as inferred by studies of white matter integrity (Salthouse & Madden, 2008). There is evidence for increases in response latency, reduction in information processing rate and delay of transfer of information between cortical areas in the visual cortex of both aged rats (Wang et al., 2006) and monkeys (Wang et al., 2005). Langrová, Kuba, Kremláček, Kubová and Vít (2006) found that the visual evoked potential to radial and linear motion in humans showed a steady prolongation of latency from around age 20 onwards.

Duration and Compensation for Eye Movements

While processing speed impacts upon the perception of briefly visible stimuli, the duration of presentation itself impacts upon the perception of the Filehne illusion. A background stimulus briefly displayed for less than half a second will result in a substantial Filehne illusion while a longer presentation weakens the Filehne illusion (De Graaf & Wertheim, 1988; Mack & Herman, 1978; Wertheim, 1994). For a background dot moving vertically while the eyes pursue a horizontally moving object, the error of perceived direction away from the vertical decreases with longer presentation time (Souman et al., 2005b). Souman et al. (2005b) tested the idea that the visual system's estimate of eye velocity increased over time. Presenting the background stimulus earlier in the pursuit path should theoretically cause a greater illusion than a stimulus presented later in the eye's transit if the extraretinal signal increases over time (Souman et al., 2005b). This effect did not occur, suggesting that duration has its effect on compensation through other means. Souman et al. (2005b) suggested that compensation was altered by a change in estimated retinal velocity over time and in the build up of the retinal contribution to the composite reference signal estimating eye movement.

Compensation for Eye Movements and Ageing

It appears that the effect of duration on the Filehne illusion depends on the age of the observer (Wertheim & Bekkering, 1992; Freeman, Naji & Margrain, 2002). For young subjects there is a weakening of the Filehne illusion with increasing stimulus duration until at 1200 milliseconds the illusion is even slightly inverted (Wertheim & Bekkering, 1992). Wertheim & Bekkering (1992) discovered that adults older than around 45 years demonstrated a strongly inverted Filehne illusion for brief durations of 150 ms that diminished with longer times until it resembled the slight inverse illusion of the younger subjects. In other words, the background for older observers appeared to move in the same direction as the eye at short durations. This suggested to the authors that, even for brief durations, older adults had a reference signal larger than their retinal signal while for younger observers the reference signal grew until it was larger than retinal signal only at the longest duration (Wertheim & Bekkering, 1992). As eye movements across age groups were equivalent, the authors interpreted their results as being due to an increase in retinal signal across time for older adults rather than a decrease in reference signal (Wertheim & Bekkering, 1992). An undersized retinal signal at brief durations was supported by a decreased ability with age to detect motion of a stimulus briefly presented during fixation so that “the distance between the threshold for motion to the right and to the left indeed increased slightly with age” (Wertheim & Bekkering, 1992, p.2383).

Exploring these findings, Freeman et al. (2002) found a similar trend concerning age and duration with older observers becoming more similar to younger observers at long durations. Younger observers showed a relatively strong Filehne illusion at both short and longer durations. For their older observers, a weak Filehne illusion at the brief duration of 200 ms became more similar to the strong Filehne illusion of younger participants at 700 ms. Only a small minority of their older observers experienced an inverted Filehne illusion. Freeman et al. (2002) were able to partially explain their results with the finding that older participants had a slower pursuit than their younger counterparts. Slower pursuit would mean less retinal motion of a stationary stimulus and thus less illusory motion to report if that retinal motion is under-compensated (Freeman et al., 2002). However, on investigating the Aubert-Fleischl phenomenon, which presumably results from similar compensation mechanisms to the Filehne illusion, there was no difference between the perceptions of young and old participants despite the fact that older participants still demonstrated slower pursuit in this condition than the younger subjects (Freeman et al., 2002).

From these results they concluded that there is no obvious account of how ageing affects the ability of the visual system to compensate for eye movements and how this is related to the duration of the stimulus (Freeman et al., 2002). Theoretically ageing could have its influence on the retinal signal, the extra-retinal signal, and/or in the process of combining the two.

Summary and Experimental Aims

Ageing is associated with several changes concerning visual motion processing. Psychophysical studies of speed and direction perception have demonstrated decrements in performance of older observers which are consistent with neurophysiological evidence for less selective and noisier responding in the middle temporal area of aged monkeys. Eye movements, which are intricately linked with motion processing in the brain have been shown to slow with age. Changes with age in tasks demonstrating sensorimotor integration and higher order motion perception useful for self-navigation have also been found. This suggests less effective processing in higher visual motion processing areas of the brain, including human area MST, for at least some older adults. While neurons in MT respond more to retinal motion, neurons in MST show responding which suggests that the effect of eye movements on the retinal image are being taken into account.

If both areas, MT and MST (human equivalents) are operating less effectively in at least some older adults, as suggested by psychophysical and neurophysiological studies, then it can be expected that the compensation for eye movements which likely involves both areas is also operating less effectively (especially if there is a general reduction in efficiency of communication within and between cortical circuits in the aged brain).

This thesis aims to explore the effect of age on the ability to compensate for eye movements. The results of the studies by Wertheim and Bekkering (1992) and Freeman and colleagues (2002) exploring age effects on the Filehne illusion, and also in the latter case the Aubert-Fleischl phenomenon, are inconclusive. As Freeman et al., (2002) point out, differing stimuli between their study and that of Wertheim and Bekkering (1992) and different methods for each illusion in their own study, could be masking interactions between age and duration on the ability to compensate for eye movements. Disagreements between the studies on the strength of the Filehne illusion and in the accuracy of eye movements with ageing also need to be resolved (Freeman et al., 2002). The Filehne illusion and Aubert-Fleischl effect are also only two points on the continuum of motion perception during pursuit eye movements (Freeman, 2001). Between a background stimulus which is stationary and one which is moving at the same speed as the eyes there are a range of speeds of motion which need the removal of eye movement effects in order to be perceived veridically; not to mention motion which is in a different direction to the eye movement (Freeman, 2001, Perrone & Krauzlis, 2008; Souman et al., 2005a, 2005b).

Since, in the prior studies, the greatest difference between young and old adults was found for the shortest presentation times of background stimuli the focus of this thesis will be on brief exposure. A breakdown of the compensation mechanism with age is likely to be most salient with a short presentation time.

The aims of the experiment reported in this thesis are as follows:

1. To design a simple and intuitive method for measuring perceived velocity across a range of eye and background velocities, enabling an estimate of both the Filehne illusion and Aubert-Fleischl phenomenon in the same subjects with the same method.
2. To examine the presence of a change in motion perception with age when the eyes are stationary.
3. To examine the presence of a change in eye movements with age.
4. To replicate the results of Wertheim and Bekkering (1992) and Freeman et al. (2002) by showing that the performance of older adults is consistent with a larger degree of compensation (even to the extent of an inverse Filehne illusion) at the short duration used.
5. To investigate changes with age in the ability to compensate for eye movements for a range of directions and speeds of motion.

It is hoped that by furthering the investigation into the effects of age on the Filehne and Aubert-Fleischl phenomena; and by extending the range of speeds and directions of motion examined during pursuit with older adults; a clearer picture of the changes with age in the ability to compensate for eye movements will emerge. Both retinal motion and eye movement signals are compared within the visual system in order to accurately perceive motion. By studying this process for the relatively simple combinations of background and eye velocities to be covered in this thesis, it is hoped that insights will be gained into potential neural changes with age and difficulties experienced by older adults in moving about their environment.

Chapter Two
General Methods

In order to measure the perceived velocity of a background stimulus during pursuit eye movements, a method was designed which could provide estimates of a range of background velocities during a range of eye movement velocities in a relatively short space of time. In motion perception studies with older adults, speed perception is generally measured by presenting two successive or concurrent stimuli and asking the observer to compare their speeds (Norman et al., 2003; Snowden & Kavanagh, 2006). The presentation of successive stimuli would theoretically double the experimental time to cover a given range of stimulus velocities. Concurrent stimuli could influence each other's perception (Snowden & Kavanagh, 2006) and would involve dividing attention between the target dot and two background stimuli for the present task. Similarly, studies on the perception of a range of background velocities during eye movements have used two intervals. The first interval presents a background stimulus during a pursuit eye movement and asks the observer to match or adjust its speed and/or direction to an interval where the eye is stationary (Freeman, 2001; Souman et al., 2006; Turano & Massof, 2001). The adjustment of the second interval to match the first would require extended viewing which could influence the perception of its speed and in turn the relative speed of the first interval (Raghuram et al., 2005). As Souman et al. (2006) point out, it is important to measure both perceived speed and direction at the same time because perception can change from trial to trial. It was decided magnitude estimation would be a relatively simple, intuitive and quick method for satisfying the requirements of the experiment. It does not involve repeatedly comparing two conditions and can provide estimates of perceived velocity for different combinations of background and eye velocities with the same method. Magnitude estimation methods have been used effectively to assess the amplitude of displacement of sinusoidal motion during head movements (Li, Adelstein & Ellis, 2009) and the perceived speed of an optic flow field while walking (Durgin, Gigone, & Scott, 2005). On the downside, magnitude estimation is potentially less precise than matching tasks as it is subject to individual biases (Poulton, 1979).

Method

Participants

A total of 34 individuals participated in this study. Table 2.1 shows the age and gender distribution of the participants.

Table 2.1

Age and gender distribution of participants.

Age	Female	Male	Total (N = 34)
17-24	11	3	14
25-29	2	1	3
30-34	2	-	2
35-39	1	1	2
40-44	-	-	-
45-49	2	1	3
50-54	1	3	4
55-59	-	-	-
60-64	1	-	1
65-69	1	1	2
70-74	1	-	1
75-79	1	1	2

Both paper and online advertisements (Appendix A) were used to recruit participants from undergraduate and postgraduate psychology courses, staff members at the University of Waikato, members of the Recreation Centre on the University Campus and visitors of local community centres for aged citizens. Seventeen of the participants were first year psychology students who received partial course credit as reimbursement while all other participants received book voucher(s) in exchange for their participation.

All participants completed a small questionnaire on ocular and general health (Appendix B). Four females over the age of sixty reported early or mild cataracts, one of whom also reported mild macular degeneration. One female participant younger than 24 reported experiencing dizziness in the past month. Participants who would normally wear eyeglasses or contact lenses at the viewing distance required were asked to wear them for the experiment. The data of one participant aged between 17 and 24 was excluded due to malfunction of the eye-tracker and so the data of 33 participants remained for analysis.

All experimental protocols adhered to the procedures outlined by the Waikato University Psychology Research and Ethics Committee.

Apparatus

Stimuli were displayed on a 19”Dell M992 Trinitron CRT monitor with a resolution of 1600 x 1200 at a refresh rate of 75 Hz. The field of view of the display was 34.5° horizontal by 25.9° vertical. The presentation of stimuli and collection of responses were custom programmed using the Psychophysics and Video Toolboxes (Brainard, 1997; Pelli, 1997) in Matlab 7.1 (The Mathworks, 2005). These were run on a Dell OptiPlex 755DT. Although stimuli were presented binocularly, an Eyelink 1000 Desktop mounted infrared video-based eye tracker (Eyelink 1000, 2010) recorded the movements of the right eye only at a sampling rate of 1000 Hz. A Dell OptiPlex 760 Minitower running 32 bit Windows XP SP2 hosted the Eyelink tracker.

The head of the participant was kept steady through the use of a desk mounted forehead and chin rest at a distance of 57 cm from the display monitor such that the centre of the screen was at eye height. Participants responded by using a computer mouse. The experiment was completed in a windowless room with the lights extinguished, the sole illumination coming from the monitors displaying the stimuli and eye tracker menu system. The latter was positioned off to the right of the participant and faced away from them. The walls of the room surrounding the apparatus were painted black to reduce ambient light.

Data were analysed in the R language and environment for statistical computing (R Development Core Team, 2009) using the lme4 package (Bates &

Maechler, 2009).

Stimuli

Stimuli consisted of a target dot of 0.22º diameter and a background dot pattern which subtended 34.5º horizontally and 25.9º vertically and consisted of 200 dots of 0.12º diameter. Background dots had a luminance of approximately 6.6 cd/m^{-2} while the target dot had a higher luminance of 10 cd/m^{-2} on average. Dot luminances were low to prevent the perception of residual streaks following dot motion. Both were presented against a dark grey background with an approximate luminance of 0.75 cd/m^{-2}. The Weber contrast for the background pattern was 7.8 while the target dot had a Weber contrast of 12.3 (Moulden et al., 1990 as cited in Snowden & Kavanagh, 2006). Luminances were measured by use of a Minolta Chroma Meter CS-100 on circular areas of 4.5º diameter. To effectively mask the presence of background dots in the area immediately surrounding the target dot, a circular area of 1º diameter with the same luminance as the background screen surrounded the target dot and moved with it. Prior to the presentation of dot stimuli, a cross with horizontal and vertical arms of 0.22º length was present in the centre of the screen to encourage fixation.

The response screen consisted of a small circle of 0.12º diameter in the centre of the screen and the outlines of five concentric circles increasing in size out from the centre. These outlines had radii of 0.41º (19 pixels) to 6.6º (304 pixels) with each being twice the radius of the one inside it. The luminance of these response circles was approximately 6.6 cd/m^{-2}.

Procedure

Participants completed a training condition before undertaking the experimental condition. The lights were turned on for around a minute between each condition and between each part of a condition to minimize dark adaptation.

Trials. Trials in both the training and experimental conditions followed the same structure. For the first 500 ms a large white rectangle (25.9º x 17.3º) was flashed on the screen to help prevent dark adaptation and the persistence of after-images from the previous trial. A fixation cross then appeared in the centre of the dark grey screen and remained for 1500 ms. This was then replaced by the target dot. The target either appeared in the centre of the screen if it was to remain stationary throughout the trial or appeared to the left or right of centre screen if it was to move during the trial. Other than stationary, the possible velocities of the target dot were 4 and 8 degrees per second to the left or right. The path of the target was always horizontal at eye height through the centre of the screen. The target appeared in a location such that it passed through the centre of the screen at the midpoint of its motion path. This was 1.9º of visual angle to the left or right of centre if it moved at 4º/s and 3.8º degrees of visual angle out from centre if its speed was to be 8º/s.

After its appearance, the target dot remained stationary for 1000 ms to help the participants acquire it prior to pursuit. For the following period of 400 ms it would then move at its specified speed back towards the centre of the screen, or if stationary, remain fixed in the centre of the screen.

After this period of establishing pursuit the background dot pattern appeared moving at its specified velocity for 160 ms while the target dot continued its motion course. Each trial presented a different random constellation of background dots. Possible background motions included stationary and speeds of 1, 2, 4, 8 and 16º/s leftwards, rightwards and straight up. The target dot reached the centre of the screen midway through background exposure. The background then disappeared and the target dot continued to move for 400 ms to help keep pursuit eye movements stable. The target dot disappeared and was replaced by the response screen and a cross shaped cursor in the centre of the screen.

Training condition. The aim of the training condition was to introduce participants to the method of responding employed in the study. The method was based on the one used in the study of Bennett et al. (2007) on the effects of ageing on motion direction discrimination. In their study participants used a circle to communicate the perceived direction of motion by moving a cursor to a point on the circle best representing the direction seen (Bennett et al., 2007). The present study extended this method by having a different circle represent each speed of motion.

The present method required participants to use the circles presented on the response screen as a measure for speed by moving a cursor on or between the circle outlines to communicate a speed and direction judgement. Clicking in the centre of the screen would correspond to a judgement of no motion. Each circle outline corresponded to one of the possible background speeds. The first circle outline represented a speed of one degree per second while clicking on the largest circle corresponded to reporting a perception of very fast motion (16º/s). The angle of the set cursor position out from the centre of the screen corresponded to a direction of motion judgement (0º = rightwards, 180º = leftwards and 90º = upwards).

In the training condition the target dot always remained stationary in the centre of the screen. The background dot pattern moved coherently towards the right (0º) at one of five possible speeds (1, 2, 4, 8 or 16º/s) or was stationary (0º/s).

Training was made up of three parts and eye movements were not monitored. Participants received standardised instructions prior to the commencement of trials (Appendix C). In the first part of training the background pattern speed started at 0º per second on the first trial and increased for each subsequent trial so all background speeds between 0 and 16º/s were presented. When the response screen appeared at the end of each trial the computer controlled cursor stayed in the centre of the screen for 500 ms and then appeared at the correct position on the circle representing the speed of motion. It remained there for 2000 ms at which point the next trial began. Two complete cycles of the range of speeds were presented.

The second part of the training condition required the participant to practice responding while also being provided with feedback. The entire range of background speeds was presented in the same random order for every participant. Each speed was presented twice. In this part of training the participant was required to click the left mouse button on the circle, or between the circles, depending on how fast they perceived the background pattern to be moving. Once their response was recorded, feedback was provided in the form of a computer controlled cursor in the shape of a hand appearing to point at the correct circle. On completion, a plot appeared relating the participant's response to the background speed.

The third part of training was the same as the second part except feedback was not provided at the end of each trial. The plots which appeared at the end of part two and three were compared to make sure the participant was improving in their responding. In part three, if the slope of the best-fit regression line which related their responses to the true speed of the background dots was outside the range of 0.8 to 1.2 and the correlation between speed and response was less than 0.5 the participants were asked to repeat the entire training condition.

The training condition lasted between twenty minutes and an hour depending on how accurate and confident the participant was with the method. Verbal feedback, explanation and encouragement were provided throughout training.

Experimental condition. In the experimental condition the target dot moved to the right (0°) or left (180°) and had speeds of 0, 4, or 8°/s. The background moved coherently either towards the right (0°), left (180°) or upwards (90°) at possible speeds of 1, 2, 4 or 8°/s or remained stationary (0°/s). Due to there being a speed of 0°/s for each direction of target and background motion, there were more trials where the target or background were stationary than there were for each other speed. The extra target stationary trials helped to determine perception of motion without interference by eye movement, and the extra background stationary trials helped to anchor the responses to background motion and determine the occurrence of the Filehne illusion.

At the start of the experimental condition the eye tracker was calibrated to the participant's eye movements. This took around five to ten minutes. Participants received standardised instructions before beginning the experiment (Appendix C). They were asked to keep their eyes on the target dot and judge the speed and direction of the background dot pattern. For each participant, the experimental condition was separated into three sections in which each different combination of target and background velocity was presented once. Each section had a different random order of trials and lasted around 10 minutes. Participants were given the opportunity to rest for up to ten minutes between sections. Before beginning the next section, a demonstration of the circle corresponding to each speed (as per the first part of the training condition with a single cycle) was presented in order to keep the speed representations fresh in the participant's mind. The entire experimental condition lasted between 30 minutes and an hour and no feedback was given during the trials or rest periods.

Measures

Participants responded by clicking the left mouse button on or between the response circles. The location of the mouse click was recorded by the computer in x and y coordinates out from the centre of the screen in pixels. The (x, y) values were converted to degrees per second by dividing their magnitude (in pixels) by 19 pixels (the radius of the 1°/s circle on the response screen). Clicking rightwards from centre produced positive responses in the x coordinate while clicking left from centre produced negative values. Likewise, a positive response value in the y coordinate was provided by clicking up from the centre of the screen and a negative response by clicking below the centre. The x and y coordinates were converted into a vector (V_R, θ_R) where V_R in degrees per second was taken to reflect the participant's perception of background speed and θ_R its direction. In the remaining parts of this thesis, 'response velocity' refers to either the horizontal or vertical component of this vector depending on the context.

Speed and direction of eye movement was calculated offline from the eye tracker data. The change in eye position in both x and y coordinates was smoothed with a Gaussian filter (standard deviation of five) and the average speed over the 160 ms of background exposure was taken for each coordinate. The x and y components were converted into a vector (V_E, θ_E) which represented the participant's eye velocity. In the remainder of this thesis, 'eye velocity' refers to the horizontal component of this vector. Blinks and saccades were detected by the Eyelink software where saccades were defined as an eye velocity exceeding 30 degrees per second and acceleration of 8000 $°/s^{-2}$.

Data Analysis

Eye blinks and saccades are inconsistent with smooth pursuit. If such eye movements were detected to occur during the background exposure (or within 15 ms either side), that trial was removed from further analysis. A total of 16.5% of trials were removed due to blinks or saccades. This left some participants with less than the full number of data points.

Participants were grouped according to their age for the purposes of analysis. This grouping can be seen in Table 2.2. Due to age groups being unequal in size, the presence of missing data and the extra trials for stationary target and background, the experimental design was unbalanced and required an analytical technique which could take this into account.

Table 2.2

Age range and gender distribution of age groups.

Age Group (years)	1 (17-24)	2 (25-39)	3 (45-54)	4 (60-79)
Female	10	5	3	4
Male	3	2	4	2
Total	13	7	7	6

Statistical Modelling

The approach to data analysis was required to not only deal with unbalanced data but also with correlated observations within participants. The following is a discussion of the statistical approach (and its underlying theory) chosen to tackle these issues within this thesis.

The aims of this study were to ascertain the relative influence of target and background motion and age group on eye velocity and response velocity. Linear regression approaches these questions by examining how much of the variation in eye or response velocity is explained by the predictor variables. However, doing such a regression assumes the independence of model residuals (Hoffman & Rovine, 2007). In this study, the outcomes of eye and response velocity were measured several times for each participant over multiple conditions. These repeated measures are more likely to be related within a person than between people (Hoffman & Rovine, 2007; Zuur, Ieno, Walker, Saveliev & Smith, 2009). Such correlation between measures violates the assumption of independence of observations (Everitt & Hothorn, 2006; Field, 2009; Galwey, 2006; Hoffman & Rovine, 2007; Zuur et al., 2009). Repeated measures are nested within participants which, being a lower-level unit, are nested within age groups which are the higher level units (Field, 2009; Hoffman & Rovine, 2007; Zuur et al., 2009).

Since differences between age groups and not between participants was of primary interest in this study, a possible analysis which could deal with the unbalanced data and the repeated measures involved a two stage analysis (Faraway, 2006; Hoffman & Rovine, 2007; Zuur et al., 2009). First linear regression of the outcome variable on the explanatory variables for each participant would be performed and then the regression coefficients compared over age groups with a second linear regression. However, this would not be the most efficient use of information as all the data for one person is summarised by a single parameter and the second analysis models this data only indirectly (Faraway, 2006; Hoffman & Rovine, 2007; Zuur et al., 2009). It also does not recognise "the differential reliability of the individual regression estimates" (Hoffman & Rovine, 2007, p.102). In other words, equal weight is given to each participant irrespective of the goodness of fit of the first stage linear regression. Instead, these two stages can be combined in a single mixed model to make the most of all the data provided (Faraway, 2006; Zuur et al., 2009). Hoffman and Rovine (2007) say this type of model "can be conceptualised as a series of interrelated regression models that explain sources of variance at multiple levels of analysis" (p.102). Mixed models estimate model parameters based on *all* of the available data using maximum likelihood principles which are robust when data is missing at random (Hoffman & Rovine, 2007; Schafer & Graham, 2002). Trials removed in the present study due to blinks and saccades could be considered to be missing at random as their removal did not depend on the outcome variables of either speed of smooth pursuit or response to the background (Schafer & Graham, 2002). The data in this study were therefore analysed using linear mixed models.

Mixed Models

Mixed models are named as such because they contain both fixed and random effects (Galwey, 2006). Fixed effects are estimates for the average response for the group of individuals and are expected to be shared by individuals (Cheng, Edwards, Maldonado-Molina, Komro & Muller, 2010; Galwey, 2006; Hoffman & Rovine, 2007; Zuur et al., 2009). If there are differences between age groups in the present study there will be an interaction between age and other fixed effects.

The random effects describe how much participants vary from the group mean for the intercept and slope in the relationship of interest (Cheng et al., 2010; Galwey, 2006; Zuur et al., 2009). Without them, "systematic variation ends up in the residuals, leading to potentially biased inference" (Zuur et al., 2009, p.109). The random effects and residual error are assumed to be normally distributed with a mean of zero (Cheng et al., 2010; Galwey, 2006; Zuur et al., 2009). Residuals also need to be checked for violations of the assumptions of independence and homogeneity of variance (Cheng et al., 2010; Zuur et al., 2009).

Model specification. Following recommendations by Zuur and colleagues (2009) and Cheng et al. (2010), model specification followed a top-down strategy. An alpha level of 0.05 was used as the significance criterion for all statistical tests.

Graphical analysis and theory informed the construction of a "*beyond optimal* model" (Zuur et al., 2009, p.121). This is a model with all possible predictors and their interactions in the fixed effects (Cheng et al., 2010; Zuur et al., 2009). Once this was chosen, to evaluate whether random effects parameters were justified a series of likelihood ratio tests was conducted on nested mixed models (fit by restricted maximum likelihood) which involved increasingly complex random effects and their correlations (Zuur et al., 2009). The difference in log likelihood between the models with and without the terms was compared to a Chi square distribution, the degrees of freedom being the number of added parameters (Faraway, 2006).

Once the random effects structure was determined, the significance of fixed effects were estimated. Age group was treated as a factor and the parameter estimates for age groups were compared via treatment contrasts with age group one as the base level (Faraway, 2006). Due to the hierarchical nature and ongoing development of mixed model theory, the number of degrees of freedom for testing the t-statistic is uncertain when estimating the significance of the parameter estimates of the fixed effects (Baayen, 2008; Faraway, 2009). In general with a large sample size, the higher the t-value above 2.00 in absolute value, the more confident one can be that the parameter estimate can be considered significant at the .05 level (Baayen, 2008; Faraway, 2009). Instead of using t-values, the significance of fixed effects was estimated using log-likelihood testing. Fixed effects were tested by conducting likelihood ratio tests on two nested mixed models (fit by maximum likelihood) which differed only in their fixed effects (Faraway, 2006; Zuur et al., 2009).

Beginning with third order interactions, each fixed effect parameter in the *beyond optimal* model was removed and the model refit (Zuur et al., 2009). Likelihood ratio tests were conducted to compare the model with and without the parameter to confirm that its inclusion was justified (Zuur et al., 2009). The p-value generated by this test is generally underestimated for fixed effects (Faraway, 2006). Therefore, parametric bootstrapping with one thousand simulations was conducted to check p-values which were only marginally significant (Faraway, 2006). If any simulations failed to converge these were removed from the number of simulations used to calculate the p-value.

If a fixed effect did not significantly improve the model it was removed. However, if an interaction was significant, intercepts and main effects were retained (Cheng et al., 2010; Zuur et al., 2009). The values of the Akaike Information Criterion (AIC) were also compared to select the best-fitting model. The AIC weighs the improved fit of a model against its complexity. Smaller values of the AIC imply better models (Faraway, 2006; Zuur et al., 2009).

All values of likelihood ratio tests and AIC reported for the fixed effects are in comparison to the final selected model when non-significant fixed effects were added or significant ones were removed. Higher order terms which were not significant are compared to the model when necessary lower order terms were added. Likewise, the significance of lower order terms is demonstrated with regards to the model not containing higher order terms.

Model diagnostics. Wilkinson and the APA Task Force on Statistical Inference (1999) point out that “statistical tests of models are often more robust than our statistical tests of assumptions” (p.598). Model diagnostics were thus conducted first and foremost by graphical analysis. Assumptions were checked by inspecting plots of the residuals against each explanatory variable and the fitted values of the model and looking for patterns and spread (Faraway, 2005, 2006, Zuur et al., 2009). If the residual error of a model was proportional to target or background velocity, weights were applied to the model to counter the effect such that the weighting of the observation increased as the variance decreased (Faraway, 2005). On reaching the optimal un-weighted model, weights were calculated and the optimal weighted model was found. The final model was reached using weights recalculated from the residuals of the optimal weighted model. Normality was assessed by using quantile-quantile plots (QQ-plot) of the residuals and the random effects in conjunction with the Shapiro-Wilk normality test (Faraway, 2005, 2006). The QQ-plots compare true values with “ideal” normal observations (Faraway, 2006, p.14) where normality can be assumed if the points on the QQ-plot lie along a straight line (Faraway, 2005, 2006; Zuur et al., 2009).

Chapter Three
Analysis One - Pursuit Gain

Hypotheses

The ability of people to smoothly follow a moving object with their eyes can be quantified as their pursuit gain. Pursuit gain is measured by dividing the velocity of the eyes by the velocity of the object with which they are attempting to keep pace. A ratio of one means that the eye is pursuing the target perfectly. In this study, participants were presented with target speeds of four and eight degrees per second to the left and right as well as a stationary target.

Based on the literature reviewed regarding the ability of older adults to accurately pursue a moving object (Kolarik et al., 2010; Moschner & Baloh, 1994; Paige, 1994; Ross et al., 1999; Sakuma et al., 2000; Sharpe & Sylvester, 1978), two hypotheses have been generated with respect to age.

Firstly, it is expected that pursuit gain will decrease with age. The second hypothesis is that this difference between age groups will be greater at higher speeds of the target.

Method

Mixed Model

Pursuit gain can be described by the slope of the regression of eye velocity on target velocity (both horizontal). Perfect smooth pursuit at all target speeds would have a slope of one and an intercept of zero.

Random effects. Participants were included in the analysis as random effects. Each participant completed three repetitions of each condition. A person's ability to track the target is likely to be more similar within each repetition than between repetitions. It was therefore decided to include the factor repetition nested within participant as random effects.

Fixed effects. The main fixed effects included in the analysis were target velocity and age group. Background velocity and repetition number were added as fixed effects of interest. Background velocity was entered to assess competition between target and background in determining pursuit speed.

Repetitions can be ordered in time so that for each participant, repetition three followed repetition two which was after repetition one. Repetition as a continuous variable was entered in order to determine changes such as slowing from fatigue.

Preliminary Analysis and Weights

Preliminary analysis showed that residual variance increased with target speed. Weights were applied to the model to counter this effect. Weights were calculated as one over the variance of the residuals at each absolute value of target velocity. At this stage three outlying points were also removed. These were more than six standard deviations from the mean of the residuals and occurred when the eye was moving in the opposite direction to the target.

Results

The means and standard deviations of eye velocity at each target velocity for each repetition within age group are presented in Table 3.1. Negative values are movement leftwards, while positive sign indicates rightwards.

Table 3.1

Mean eye velocity (and standard deviation) at each target velocity for each repetition (rep) within age group.

		Target velocity (°/s) *M (SD)*				
Age group	Rep	-8	-4	0	4	8
One (n^a = 3232)	1	-5.94 (2.34)	-3.30 (1.11)	0.03 (0.52)	3.44 (1.21)	6.16 (2.19)
	2	-5.53 (2.32)	-3.19 (1.20)	0.04 (0.55)	3.18 (1.40)	5.38 (2.32)
	3	-5.01 (2.62)	-2.77 (1.45)	-0.03 (0.52)	2.87 (1.26)	4.95 (2.54)
Two (*n* = 1372)	1	-6.98 (1.02)	-4.02 (0.83)	-0.01 (0.47)	3.80 (0.86)	7.07 (1.13)
	2	-7.18 (1.38)	-3.88 (0.89)	-0.02 (0.48)	3.83 (0.84)	7.02 (1.33)
	3	-6.18 (2.01)	-3.42 (1.16)	0.03 (0.54)	3.41 (0.96)	5.43 (2.09)
Three (*n* = 1633)	1	-3.99 (2.05)	-2.42 (1.13)	0.00 (0.47)	3.12 (1.08)	4.86 (2.11)
	2	-3.57 (2.34)	-2.23 (1.27)	0.11 (0.54)	2.63 (1.37)	3.81 (2.65)
	3	-3.18 (2.33)	-2.16 (1.52)	0.08 (0.56)	2.69 (1.47)	3.87 (2.44)
Four (*n* = 1197)	1	-3.40 (2.12)	-2.14 (1.57)	-0.00 (0.46)	2.21 (1.38)	2.80 (1.95)
	2	-2.34 (1.74)	-2.02 (1.35)	-0.04 (0.49)	1.98 (1.20)	2.12 (1.72)
	3	-2.23 (2.04)	-1.69 (1.35)	-0.05 (0.56)	1.62 (1.09)	2.20 (1.94)

Note. Negative values indicate leftwards motion. *N* = 7434.

[a] *n* refers to number of observations in each age group.

The examination of means of eye speed by target speed for each group suggest that in the older groups especially, eye speed is much the same for a target moving at four degrees per second as it is for target motion of eight degrees per second. This would result in a smaller pursuit gain at the larger target speed and thus the need for a quadratic term in the model of eye speed against target speed. A quadratic term for target speed was added to the *beyond optimal* model which included all interactions relevant to the analysis. It was as follows:

$$Pursuit = AgeGroup \times (\alpha + \beta_1 Target + \beta_2 Target^2 + \beta_3 Repetition$$
$$\beta_4 Background + \beta_5 |Target| + \beta_6 Target \times Repetition$$
$$+ \beta_7 Background \times |Target|) + \varepsilon$$

where

Pursuit	=	eye velocity in degrees per second
AgeGroup	=	age group factor with four levels
Target	=	target velocity (º/s)
Target²	=	target velocity squared multiplied by the sign of target velocity (º/s)
Background	=	background velocity (º/s)
Repetition	=	repetition number as a continuous variable
ε	=	error

Random Effects

Testing the change in log-likelihood for the addition of successive random effects resulted in the following model when significant random effects were retained:

$$Pursuit_{ijk} = AgeGroup_i \times (\alpha + \beta_1 Target_{ijk} + \beta_2 Target_{ijk}^2 + \beta_3 Repetition_{ij}$$
$$+ \beta_4 Background_{ijk} + \beta_5 |Target_{ijk}| + \beta_6 Target_{ijk} \times Repetition_{ij}$$
$$+ \beta_7 Background_{ijk} \times |Target_{ijk}|)$$
$$+ a_i + a_{ij} + b_i Target_{ijk} + b_{ij} Target_{ijk} + b_i |Target_{ijk}| + b_i Target_{ijk}^2 + \varepsilon_{ijk}$$

Subscripts *i, j,* and *k* denote participant, repetition number and observation within repetition respectively. Thus, $Pursuit_{ijk}$ is the eye velocity for observation *k,* within repetition *j,* for participant *i.*

The Akaike Information Criterion (AIC) for this model was 21490 when fit using maximum likelihood and 21491 when fit using restricted maximum likelihood.

The AIC for the model with only a random intercept for participant was 24087. All tests were conducted on models fit using restricted maximum likelihood. The likelihood ratio test indicates that introducing a participant random effect for slope of eye velocity on target velocity ($b_i Target_{ijk}$) significantly improved the model, $\chi^2(1) = 2347.20$, $p < 0.001$, AIC = 21742, as did entering the quadratic term $b_i Target^2_{ijk}$, $\chi^2(1) = 15.48$, $p < 0.001$, AIC = 21729. The absolute value of target velocity (i.e. the target speed) was included as a participant random effect ($b_i|Targeti_{jk}|$) to assess asymmetry in the slope of eye on target velocity associated with relative strength of left and right eye movements. It also significantly improved the model, $\chi^2(1) = 65.29$, $p < 0.001$, AIC = 21665. Adding the variation in the slope of target velocity against eye velocity as a random effect for repetition within person ($b_{ij} Target_{ijk}$) significantly improved the model, $\chi^2(1) = 178.08$, $p < 0.001$, AIC = 21491.

The participant random effect of slope for target velocity did not significantly covary with the intercept for participant, $\chi^2(1) = 1.72$, $p = 0.19$, AIC = 21491. Nor did the quadratic term covary with the intercept and linear slope, $\chi^2(2) = 3.10$, $p = 0.21$, AIC = 21492, or the absolute value of target velocity covary with the intercept, linear and quadratic terms for participant, $\chi^2(3) = 0.57$, $p = 0.90$, AIC = 21497. Adding correlation between intercept and target slope for repetition within participant also did not produce a significantly better fit, $\chi^2(1) = 0.45$, $p = 0.50$, AIC = 21492.

Fixed Effects

Fixed effect terms which did not significantly improve the fit of the model were removed. This left the following model which was taken as the final model:

$$\begin{gathered} Pursuit_{ijk} = AgeGroup_i \times (\alpha + \beta_1 Target_{ijk} + \beta_2 Target^2_{ijk} + \beta_4 Background_{ijk}) \\ + \beta_3 Repetition_{ij} + \beta_5 |Target_{ijk}| + \beta_6 Target_{ijk} \times Repetition_{ij} \\ + \beta_7 Background_{ijk} \times |Target_{ijk}| \\ + a_i + a_{ij} + b_i Target_{ijk} + b_{ij} Target_{ijk} + b_i |Target_{ijk}| + b_i Target^2_{ijk} + \varepsilon_{ijk} \end{gathered}$$

This model (fit using maximum likelihood) had an AIC of 21478. The parameter estimates of the fixed effects can be seen in Table 3.2.

Table 3.2.

Parameter estimates of the fixed effects with their standard errors and t-values for the model representing pursuit gain.

	Estimate	Std. error	*t* value[a]
α	0.032	0.028	1.13
$AgeGroup\,2$	-0.017	0.04	-0.426
$AgeGroup\,3$	0.062	0.038	1.62
$AgeGroup\,4$	-0.036	0.041	-0.874
$\beta_1 Target_{ijk}$	0.98	0.041	24
$\beta_2 Target_{ijk}^2$	-0.019	0.003	-6.5
$\beta_3 Repetition_{ij}$	-0.0087	0.0089	-0.979
$\beta_4 Background_{ijk}$	0.014	0.0022	6.46
$\beta_5 \lvert Target_{ijk} \rvert$	0.0051	0.0061	0.845
$AgeGroup\,2 : \beta_1 Target_{ijk}$	0.19	0.07	2.65
$AgeGroup\,3 : \beta_1 Target_{ijk}$	-0.08	0.067	-1.2
$AgeGroup\,4 : \beta_1 Target_{ijk}$	-0.22	0.07	-3.06
$AgeGroup\,2 : \beta_2 Target_{ijk}^2$	-0.008	0.0055	-1.46
$AgeGroup\,3 : \beta_2 Target_{ijk}^2$	-0.016	0.0052	-3.13
$AgeGroup\,4 : \beta_2 Target_{ijk}^2$	-0.022	0.0055	-3.93
$\beta_6 Target_{ijk} \times Repetition_{ij}$	-0.061	0.0067	-9.05
$\beta_7 Background_{ijk} \times \lvert Target_{ijk} \rvert$	0.0021	0.00079	2.71

Note. Number of observations: 7434, groups: Repetition, 99; Participant, 33

[a] Due to uncertainty over the degrees of freedom (Baayen, 2008; Faraway, 2009), p-values are not presented. Instead, significance values for fixed effects are given by the likelihood ratio tests in text.

Age group. The interactions between age group and target velocity, $\chi^2(3) = 14.96$, p = 0.0018, AIC = 21492, and the quadratic term, $\chi^2(3) = 10.74$, p = 0.013, AIC = 21483, significantly improved the fit of the model. The latter was checked via parametric bootstrapping which returned a still significant p-value of 0.008. Compared to age group one ($\beta_1 Target_{ijk}$ = 0.98), the slope of target velocity against eye velocity increased for age group two (*AgeGroup 2 :* $\beta_1 Target_{ijk}$ = 0.19) , decreased slightly for age group three (*AgeGroup 3 :* $\beta_1 Target_{ijk}$ = -0.08) and decreased more for age group four ($AgeGroup\ 4 : \beta_1 Target_{ijk}$ = -0.22). The quadratic term became more negative with age from $\beta_2 Target^2_{ijk}$ = -0.02 for age group one, to a reduction of 0.022 to this term for age group four ($AgeGroup\ 4 : \beta_2 Target^2_{ijk}$ = -0.022). In general, as age group increased, pursuit gain was lower especially at higher target speeds.

Age group did not significantly interact with absolute target velocity (i.e target speed) in determining eye velocity, $\chi^2(3) = 6.35$, $p = 0.096$, AIC = 21478, indicating that age groups did not have different slopes of eye on target speed for leftwards and rightwards target motion. Parametric bootstrapping was used to check this p-value as it was near significance but it remained greater than 0.05 (0.15).

Background. The interaction of background velocity with the absolute value of target velocity, $\chi^2(1) = 4.11$, $p = 0.043$, AIC = 21480, significantly improved the model. This p-value was still significant after being checked by parametric bootstrapping ($p = 0.02$).

Eye velocity increased slightly with background velocity ($\beta_4 Background_{ijk}$ = 0.014). However the background velocity interacted with target speed in determining eye velocity by the addition of a small amount to the slope of eye on target velocity ($\beta_7 Background_{ijk} \times |Target_{ijk}|$ = 0.0021). This had the effect of increasing the slope of eye on target velocity when background and target were moving in the same direction but decreasing the slope when they were moving in opposite directions.

Age group did not interact with background velocity in determining eye velocity, $\chi^2(3) = 7.32$, $p = 0.062$, AIC = 21477. Parametric bootstrapping was used to check this p-value as it was near significance but it remained greater than 0.05 (0.19).

Age group did not interact with target speed and background velocity in determining eye velocity, $\chi^2(3) = 1.04$, $p = 0.79$, AIC = 21481.

Repetition. The interaction between target velocity and repetition significantly improved the fit of the model, $\chi^2(1) = 34.95$, $p < 0.001$, AIC = 21511. As repetition increased, the slope of eye against target velocity decreased ($\beta_6 Target_{ijk} \times Repetition_{ij}$ = -0.061).

There was no difference between age groups in the change in speed of eye movements over repetitions. Interactions of age group and repetition, $\chi^2(3)$ = 2.56, p = 0.46, AIC = 21482, and age group, target velocity and repetition, $\chi^2(3)$ = 1.36, p = 0.71, AIC = 21486, did not significantly improve the model.

The fitted model predictions and the mean eye velocity for each repetition within each age group can be seen in Figure 3.1 for a stationary background. For all age groups, Figure 3.1. depicts a decrease in eye speed as repetition number increases.

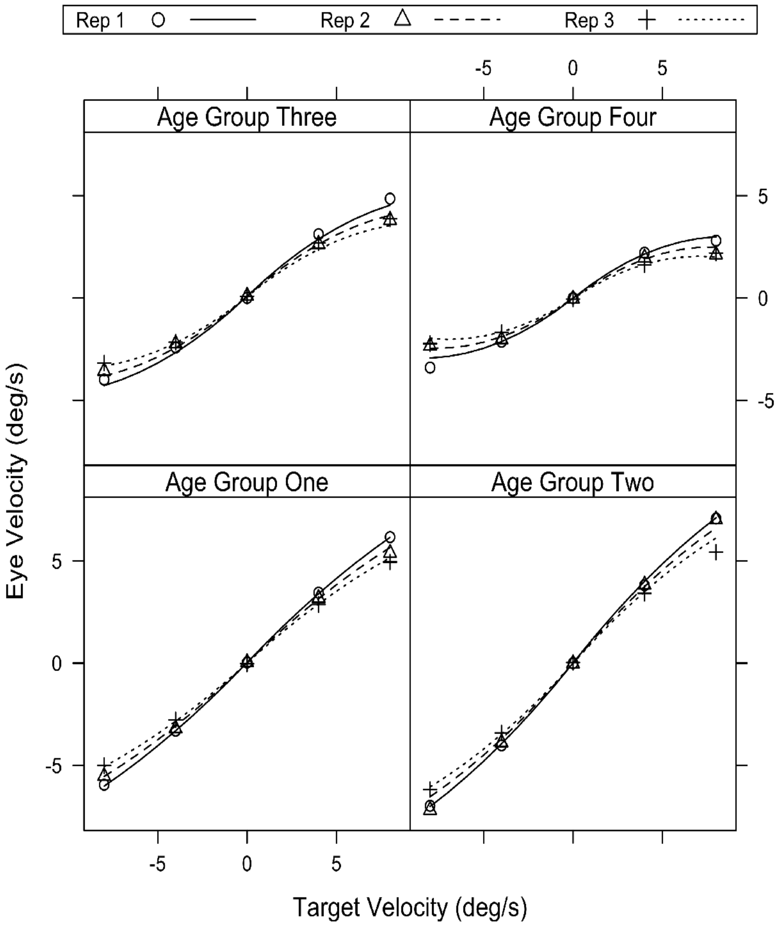

Figure 3.1. Actual and predicted eye velocities for each age group at each target velocity and repetition. Symbols represent actual mean eye velocities for each repetition within age group while lines constitute model predictions.

Figure 3.2 presents, for the middle repetition and each background velocity, the fitted model predictions against the actual mean eye velocity (at each target velocity) for each age group.

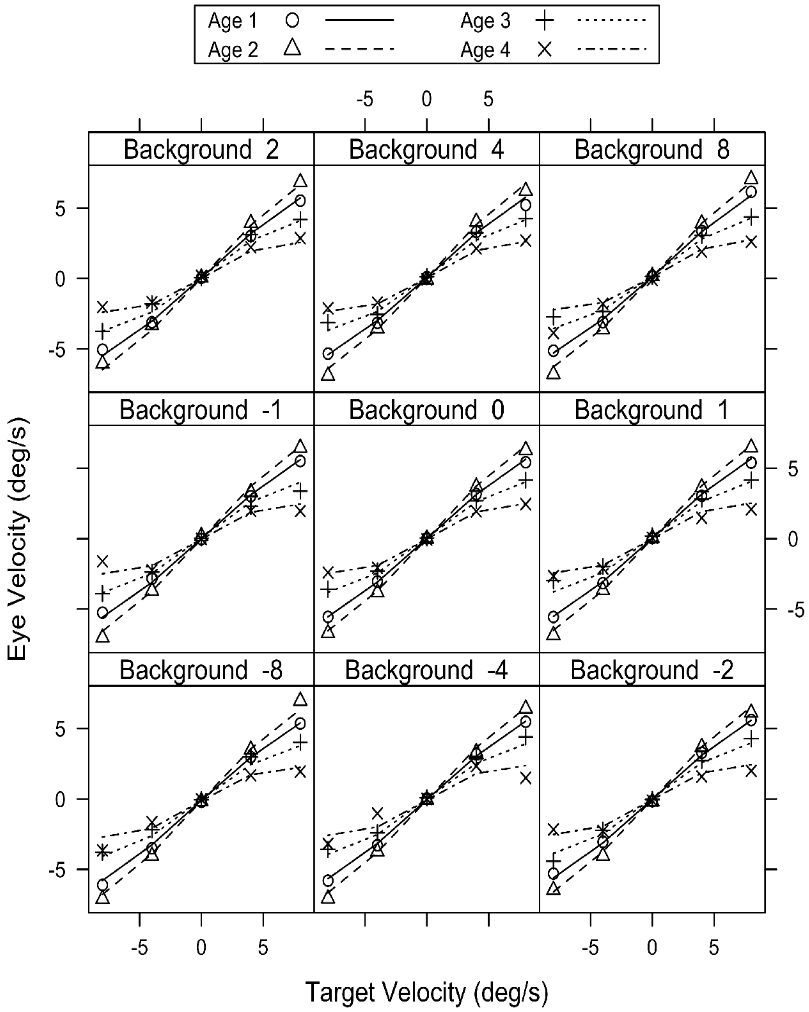

Figure 3.2. Actual and predicted eye velocities for each age group at each background and target velocity for repetition two. Symbols denote the actual mean eye velocity for each age group while lines represent the predicted eye velocity from the model. Background velocity is in deg/s.

In Figure 3.2., for each velocity of background motion, the slope of the relationship between eye and target velocity decreases with age. Although the interaction between background velocity and target speed was significant, a change in the slope of eye on target velocity dependant on background velocity is not readily apparent (Figure 3.2).

Random Effects and Residuals

The variances and standard deviations of the random effects can be seen in Table 3.3. Inspection of the QQ-plot of the normalised residuals suggested minor deviations from the assumption of normality (Appendix D). Residuals showed non extreme skewness (-0.11) and kurtosis of 1.3 above that of a normal distribution. Of the random effects, all but the intercept for repetition within person (a_i Shapiro-Wilk = 0.96, p < 0.01) could be assumed to be normally distributed (Appendices, E & F). The plot of the square root of the absolute value of the residuals against the fitted values of the model suggests heteroscedasticity (Appendix G). There is less variance in the residuals for eye movements falling between target speeds presumably because there is less data between target speeds.

Table 3.3.

Random effects variances and standard deviations for the model representing pursuit gain.

Groups	Name	Variance	*SD*
Repetition	$b_{ij} Target_{ijk}$	0.0024	0.049
Repetition	a_{ij}	0.0011	0.033
Participant	$b_i \lvert Target_{ijk} \rvert$	0.00097	0.031
Participant	$b_i Target_{ijk}^2$	7.8e-05	0.0089
Participant	$b_i Target_{ijk}$	0.018	0.13
Participant	a_i	0.0047	0.069
Residual		0.55	0.74

Note. Number of observations: 7434, groups: Repetition, 99; Participant, 33.

Scientific notation is used for very small values.

Discussion

In support of hypothesis one, older observers demonstrated decreased smooth pursuit gain in comparison with younger participants. Keeping all other variables constant (i.e. background velocity, repetition number and target direction), the difference predicted by the mixed model between a group of observers aged less than 25 and a group of participants aged 60 and over was a reduction in pursuit gain of ~0.3 at a target speed of four degrees per second and ~0.4 at a target speed of eight degrees per second. Young participants demonstrated a predicted pursuit gain of ~0.9 and ~0.82 at target speeds of four and eight respectively while participants in the oldest age group showed smooth pursuit gains of ~0.6 and ~0.42. For the studies of age effects on the ability to compensate for eye movements in motion perception, the present results agree more closely with those of Freeman et al. (2002) than the results of Wertheim and Bekkering (1992). For a background stimulus duration comparable to the present study of 200ms, Freeman et al. (2002) reported a pursuit gain of around 0.3 for their older group and 0.8 for their younger group for a target speed of 10º/s. These gains are similar to the values generated from the mixed model of ~0.82 and ~0.42 for youngest and oldest groups respectively at a target speed of 8 degrees per second in the present study. Whether young or old, all participants in the study of Wertheim and Bekkering (1992) are reported to have similar pursuit gain at a target speed of 12º/s with a mean of 0.86 over all subjects. It is commonly reported however that smooth pursuit gain is lower for older observers (Kolarik et al., 2010; Moschner & Baloh, 1994; Paige, 1994; Ross, et al., 1999; Sakuma et al., 2000; Sharpe & Sylvester, 1978) and so the present results are consistent with the general literature.

While the smooth pursuit gain of younger observers remained relatively stable as target speed increased, for those observers in the middle-aged and older age groups an increase in target speed meant a decrease in smooth pursuit gain. This is consistent with hypothesis two which stated that the difference between young and older observers in pursuit gain should become more apparent at higher target speeds. Kolarik et al (2010) found small differences between young and old in pursuing a target dot over a large stationary grating stimulus, but not a dot field stimulus, with differences between age groups increasing as target speeds rose from around 5º/s to 40º/s. Although differences in gain between age groups were not significant for pursuit over a dot field, the trend was similar to that demonstrated for pursuit over a grating (Kolarik et al., 2010). For a single dot stimuli without a background, Sharpe and Sylvester (1978) found that the difference between young and old observers was not apparent at a target velocity of 5º/s but increased for target velocities of 10º/s and greater. Similarly, Moschner and Baloh (1994) found a widening gap between young and old for target velocities of around 11º/s and higher, 11º/s being the lowest speed measured. The target speeds of four and eight degrees per second used in the present study are slightly lower than the target speeds found in the literature on age effects on smooth pursuit. Testing a greater range of target speeds would provide more information on the differences between age groups in smooth pursuit gain.

Freeman et al. (2002) reported similar smooth pursuit gains whether the background had the same or different velocity to the target for both young and old groups. It is well known in the literature however, that a background stimulus present during pursuit eye movements will cause a change in the ability to track a target depending on the speed and direction of the background (Spering & Gegenfurtner, 2007a, 2007b; Suehiro et al., 1999; Yee, Daniels, Jones, Baloh & Honrubia, 1983) and especially if the background is attended to (Kerzel, Souto & Ziegler, 2008). There was a very slight tendency to follow the background in the present study which was not significantly different for age groups. Overall, as background velocity increased, eye velocity increased by ~1.4% of background velocity. Target speed and direction mediated the effect of background on eye velocity. When target and background velocity were moving in the same direction, the pursuit gain (slope) increased while opposite directions of target and background motion were associated with a decrease in pursuit gain. The effect in the present study ranged from a change of 0.13 to the slope when background and target were both moving at eight degrees per second (decrease when in opposite directions, increase when same direction) down to an alteration of only 0.03 to the slope when target and background had speeds of four degrees per second. Although statistically significant, the effect is so small as to be practically insignificant and is not even visibly apparent on the model plot for each background velocity (Figure 3.2).

Other studies have also reported an improvement in smooth pursuit gain when a background is perturbed in the direction of the target (Spering & Gegenfurtner, 2007a, 2007b; Suehiro et al., 1999). However, many studies report little or no change in eye velocity when the background perturbation is in the opposite direction to the target (Spering & Gegenfurtner, 2007a, 2007b; Suehiro et al., 1999). Where, in the present study, the background *appeared* briefly, the background in these studies was present for the entire trial and *changed* its velocity briefly. The background velocity before the perturbation had an effect on the change in eye movement after perturbation onset (Spering & Gegenfurtner, 2007a, 2007b; Suehiro et al., 1999). Also, prior studies suggest eye velocity changes after around 70-100ms after background perturbation onset. In the present study eye velocity is averaged over the entire background period of 160ms. A change in eye velocity occurring in the present study would most probably begin in the latter half of the background stimulus period and would be diminished when the eye velocity is averaged over the entire background period. These differences between the present study and results reported in the literature could explain the different effects found for background.

It is important to note that although background velocity had a marginal effect, the target speed and direction was the primary driver of pursuit eye movements. It can therefore be assumed in later analyses that participants were following the target with their eyes as required, even though older age groups were following at a slower speed than younger groups. All participants tired at the same rate such that their pursuit gain decreased for each successive group of trials. The gain decreased by around 0.12 between the first and last set of trials. The decrease suggests that the experimental time should be limited further to prevent fatigue.

Chapter Four
Analysis Two – Retinal Motion Perception

Hypotheses

Sensitivity to the speed and direction of object motion when the eyes are not moving can be inferred to be due to processing of retinal information alone. Extra-retinal signals for the velocity of smooth pursuit are not relevant for veridical motion perception in this case.

The literature suggests a decrease in sensitivity to differences in speed of retinal motion in older adults (Norman et al., 2003; Raghuram et al., 2005; Snowden & Kavanagh, 2006) as early as 45 years of age (Bidwell et al., 2006). In the present study speed discrimination ability can be inferred by the slope of the relationship between background and response velocity (Scialfa, Guzy, Leibowitz, & Tyrrell, 1991). The hypothesis is therefore that retinal speed discrimination will decrease with age.

This chapter is divided into two parts. The first will present the model for response velocity when the background is moving to the left or the right. The second part deals with responding when the background is moving upwards.

Horizontal Motion

Method

Mixed Model

In order to analyse the processing of retinal motion, a subset of the data was taken where the target was stationary and the eye speed to either the left or right was between 0 and 0.5 degrees per second inclusive. Trials where the background was moving upwards were also removed. The mixed model regresses horizontal response velocity on horizontal background velocity.

Random effects. Participant was included in the model as a random effect.

Fixed effects. Other than background velocity, age group was the only fixed effect used in the analysis.

Preliminary Analysis and Weights

Pearson product-moment correlations were calculated between background and response velocity for each participant. Only two participants generated correlation coefficients which were not significantly different from zero (0.09, $p = 0.65$ and 0.25, $p = 0.21$). Both these participants were females aged over 60 years. One reported early cataracts while the other reported both mild cataract in one eye and mild macular degeneration in the other. As these two participants showed no relationship between the background movement and their responding they were removed from the analysis.

Of the remaining observations, a single outlying response for a stationary background was removed from further analysis.

Preliminary analysis showed that residual variance increased with background speed. Weights were applied to the model to counter this effect. The weights used to reach the final model were calculated as:

$$variance = \alpha + \beta_1\, absolute\ value(Background) + \beta_2\, Background^2$$
$$weight = 1/variance$$

where

α = 0.11

β_1 = 0.66

β_2 = 0.10

Results

Response velocity means and standard deviations are presented for each age group and each background velocity in Table 4.1. Positive values indicate rightwards motion while the negative sign implies leftwards movement.

Table 4.1

Mean response velocity (and standard deviation) for each age group at each velocity of horizontal background motion.

	Age group			
Background velocity (°/s)	One ($n^a = 561$)	Two ($n = 251$)	Three ($n = 271$)	Four ($n = 155$)
-8	-7.17 (3.80)	-8.02 (3.86)	-7.02 (5.97)	-7.69 (5.44)
-4	-2.30 (1.50)	-2.58 (1.34)	-2.94 (3.51)	-3.94 (3.37)
-2	-1.13 (1.31)	-1.62 (1.12)	-1.48 (1.62)	-2.53 (1.03)
-1	-0.73 (0.63)	-0.91 (0.86)	-0.65 (0.83)	-2.19 (1.99)
0	0.05 (0.28)	-0.03 (0.11)	0.05 (0.31)	-0.25 (0.65)
1	0.71 (0.59)	0.59 (0.53)	0.45 (0.67)	1.49 (1.93)
2	1.31 (0.94)	1.25 (0.66)	1.59 (1.65)	2.96 (2.83)
4	2.56 (1.72)	2.39 (1.02)	2.31 (3.78)	4.67 (3.33)
8	6.89 (4.03)	7.43 (3.27)	7.40 (4.35)	9.63 (5.13)

Note. Negative values indicate leftwards motion. $N = 1238$.

[a] *n* refers to number of observations in each age group.

Graphical analysis and inspection of the means suggested the need for a quadratic term for background in the model. The *beyond optimal* model was as follows:

$$Response = AgeGroup \times (\alpha + \beta_1 Background + \beta_2 Background^2 + \beta_3 |Background|) + \varepsilon$$

where

Response	=	response velocity in degrees per second
AgeGroup	=	age group with four levels
Background	=	background velocity (°/s)
Background^2	=	background velocity squared multiplied by the sign of background velocity (°/s)

|*Background*|	=	absolute value of background velocity i.e. background speed (°/s)
ε	=	error

Random Effects

Testing the change in log-likelihood for the addition of successive random effects resulted in the following model when significant random effects were retained:

$$Response_{ij} = AgeGroup_i \times (\alpha + \beta_1 Background_{ij} + \beta_2 Background_{ij}^2 + \beta_3 |Background_{ij}|) + a_i + b_i Background_{ij} + \varepsilon_{ij}$$

Subscripts *i* and *j* denote participant and observation within participant respectively. Thus, $Response_{ij}$ is the response velocity for observation *j* for participant *i.*

The Akaike Information Criterion (AIC) was 3756.8 for the model with the only random effect being the intercept for participant. Likelihood ratio testing indicated that adding the participant random effect for the slope of response against background velocity $b_i Background_{ij}$ significantly improved the model, $\chi^2(1) = 144.21$, $p < 0.001$, AIC = 3614.6. Adding a random effect representing difference between people in the quadratic term $b_i Background^2_{ij}$ did not significantly improve the model, $\chi^2(1) = 1.40$, $p = 0.24$, AIC = 3615.2. The absolute value of background velocity (i.e. the background speed) was tested as a participant random effect $b_i|Background_{ij}|$ to assess difference in the slope between responding to left and right background motion. It did not significantly improve the model, $\chi^2(1) = 1.08$, $p = 0.30$, AIC = 3615.5. The intercept and slope did not covary for participants, $\chi^2(1) = 0.27$, $p = 0.60$, AIC = 3616.3.

Fixed Effects

Fixed effect terms which did not significantly improve the fit of the model were removed. This left the following model which was taken as the final model:

$$Response_{ij} = AgeGroup_i \times (\alpha + \beta_1 Background_{ij} + \beta_2 Background_{ij}^2) + a_i + b_i Background_{ij} + \varepsilon_{ij}$$

This model (fit using maximum likelihood) had an AIC of 3614.1. The estimated coefficients of the fixed effects can be seen in Table 4.2 along with their standard errors and *t*-values:

Table 4.2.

Parameter estimates of the fixed effects for horizontal retinal motion perception with their standard errors and t-values.

	Estimate	Std. error	*t* value[a]
α	0.045	0.025	1.81
$AgeGroup\,2$	-0.092	0.044	-2.1
$AgeGroup\,3$	-0.02	0.044	-0.46
$AgeGroup\,4$	-0.25	0.053	-4.73
$\beta_1 Background_{ij}$	0.53	0.064	8.34
$\beta_2 Background_{ij}^2$	0.039	0.0066	5.96
$AgeGroup\,2:\beta_1 Background_{ij}$	0.031	0.12	0.27
$AgeGroup\,3:\beta_1 Background_{ij}$	0.022	0.11	0.203
$AgeGroup\,4:\beta_1 Background_{ij}$	0.93	0.14	6.78
$AgeGroup\,2:\beta_2 Background_{ij}^2$	0.0052	0.012	0.433
$AgeGroup\,3:\beta_2 Background_{ij}^2$	0.0075	0.011	0.668
$AgeGroup\,4:\beta_2 Background_{ij}^2$	-0.089	0.014	-6.43

Note. Number of observations: 1238, groups: Participant, 31

[a] Due to uncertainty over the degrees of freedom (Baayen, 2008; Faraway, 2009), p-values are not presented. Instead, significance values for fixed effects are given by the likelihood ratio tests in text.

Age group. The interaction of age group and the absolute value of background velocity (i.e. background speed) was nearly significant, $\chi^2(3) = 7.19$, p

= 0.066, AIC = 3614.1, and so was checked via parametric bootstrapping which gave a significant p-value (0.004). Age groups one ($\beta_3|Background_{ij}|$ = -0.008), two ($AgeGroup\ 2 : \beta_3|Background_{ij}|$ = -0.030) and three ($AgeGroup\ 3 : \beta_3|Background_{ij}|$ = -0.025) demonstrated no real difference between the slope of response on background velocity for leftwards as compared to rightwards motion. Age group four had a slope of response on background velocity 0.12 higher for rightwards as compared to leftwards motion ($AgeGroup\ 4 : \beta_3|Background_{ij}|$ = 0.13). Despite this, including the interaction increased the AIC by a point over the final model and so it was removed to keep the final model as simple as possible. On average, participants did not demonstrate significantly different slopes of response on background velocity for left and rightwards motion $\beta_3|Background_{ij}|$, $\chi^2(1) = 0.013$, p = 0.91, AIC = 3615.3.

Without the effect of age on the quadratic background term, Age group did not significantly interact with the linear background velocity in determining response, $\chi^2(3) = 6.71$, p = 0.082, AIC = 3629.2. It did however significantly interact with the quadratic term, $\chi^2(3) = 21.92$, p < 0.001, AIC = 3629.2, in improving the fit of the model. Being the highest order term, lower order interactions (including age group by linear background) and main effects were retained. The linear slope of response velocity against background velocity increased with age from 0.53 for age group one ($\beta_1 Background_{ij}$ = 0.53) to 1.46 for age group four ($AgeGroup\ 4 : \beta_1 Background_{ij}$ = 0.93). Compared to age group one, the quadratic term of age groups two and three increased very marginally ($AgeGroup\ 2 : \beta_1 Background^2_{ij}$ = 0.0052, $AgeGroup\ 3 : \beta_1 Background^2_{ij}$ = 0.0075) while that of age group four decreased ($AgeGroup\ 4 : \beta_1 Background^2_{ij}$ = -0.089).

The predictions of the final model against the mean response velocity for each background velocity and age group can be seen in Figure 4.1.

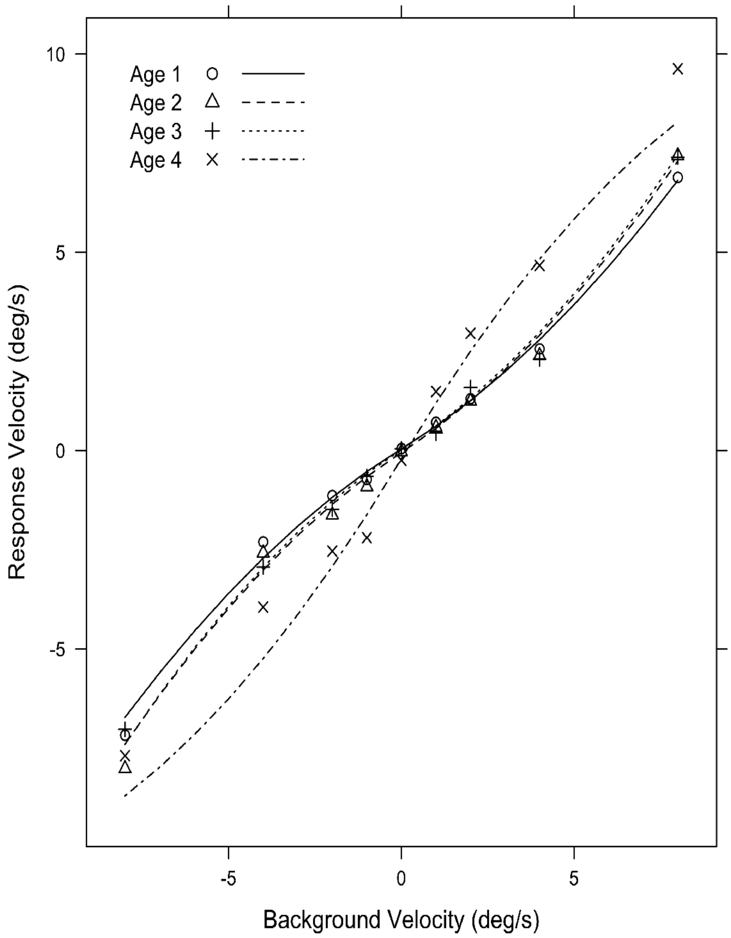

Figure 4.1. Actual and predicted response velocities for each age group at each velocity of horizontal background motion. Symbols represent actual mean response velocities for each age group while lines constitute model predictions.

In Figure 4.1., up to a background speed of around 4 deg/s, the slope of response on background velocity is steeper for the oldest age group as compared to the first three age groups. This indicates an increased sensitivity to differences in the speed of motion for this age group.

Model Residuals and Random Effects

Random effect variances and standard deviations can be seen in Table 4.3. Inspection of QQ-plots of the normalised residuals suggested deviation from the assumption of normality (Appendix H). Residual error showed marginal skew

(0.11) and excess kurtosis of 6.5 compared to a normal distribution (Shapiro-Wilk = 0.89, $p < 0.001$). The random effect representing variation in intercept between participants could not be assumed to be normally distributed (a_i ; Shapiro-Wilk = 0.77, $p < 0.001$; Appendix I) as it had skew of 2.1 and kurtosis of 6.1 above that of a normal distribution. This was because most participants had an intercept very close to zero but a few participants had higher intercepts reaching up to ~0.2 in absolute value. More importantly, the random effect for the slope of response velocity on background velocity could be assumed to be normally distributed ($b_i Background_{ij}$; Shapiro-Wilk = 0.96, $p = 0.33$; Appendix I). Plots of the residuals demonstrated mild heteroscedasticity (Appendix J).

Table 4.3.

Random effects variances and standard deviations for the model representing horizontal retinal motion perception.

Groups	Name	Variance	*SD*
Participant	a_i	0.0038	0.061
Participant	$b_i Background_{ij}$	0.037	0.19
Residual		0.43	0.66

Note. Number of observations: 1238, groups: Participant, 31.

Vertical Motion

Method

Mixed Model

For this analysis only the upward background direction was included. These data were analysed by regressing vertical response velocity on vertical background velocity.

Random effects. Participant was included in the model as a random effect.

Fixed effects. Other than background velocity, age group was the only fixed effect used in the analysis.

Preliminary Analysis and Weights

Pearson product-moment correlations were calculated between background and response velocity for each participant. The correlation coefficients for two participants were less than 0.4 and not significantly different from zero (-0.008, $p = 0.98$ and 0.26, $p = 0.25$). These were the same two female participants aged over 60 who were removed from the horizontal motion analysis. A further participant's correlation coefficient was not significantly different from zero but it exceeded 0.4 in value (0.43, $p = 0.11$). Like the previous two participants, this participant was also a female aged over 60 years who reported mild cataracts. It was decided to retain the third participant's data because their correlation was high enough to warrant its inclusion despite it being non significant. The data of the other two participants was removed from the analysis as it was unlikely to be from the same population as the retained data. A single participant aged between 17 and 24 had a significant correlation coefficient of -0.78 ($p < 0.001$). This participant's data was also removed from the analysis.

Preliminary analysis showed that residual variance increased with background speed. Weights were applied to the model to counter this effect. Two data points were removed at this point which were more than five standard deviations from the mean of the residuals of the optimal weighted model. The weights used to reach the final model were recalculated as:

$$variance = \alpha + \beta_1 \, absolute\ value(Background)$$
$$weight = 1 / variance$$

where

α = 0.09

β_1 = 1.20

Results

Response velocity means and standard deviations for each age group and background velocity are presented in Table 4.4. Positive values indicate upwards motion while the negative sign implies downwards movement.

Table 4.4

Mean response velocity (and standard deviation) for each age group at each velocity of vertical background motion.

	Age group			
Background velocity (°/s)	One (n^a = 252)	Two (n = 125)	Three (n = 139)	Four (n = 66)
0	0.03 (0.14)	-0.04 (0.18)	-0.01 (0.10)	0.13 (0.29)
1	1.00 (0.56)	1.09 (0.56)	1.15 (0.77)	2.17 (0.97)
2	1.94 (1.05)	1.71 (0.57)	2.10 (1.66)	2.71 (1.77)
4	4.36 (2.34)	3.36 (1.67)	4.79 (3.14)	6.48 (3.26)
8	9.74 (4.80)	9.46 (3.17)	10.88 (4.15)	9.09 (5.82)

Note. Negative values indicate downwards motion. N = 582.

[a] n refers to number of observations in each age group.

The *beyond optimal* model was as follows:

$$Response = AgeGroup \times (\alpha + \beta_1\, Background + \beta_2\, Background^2) + \varepsilon$$

where

Response	=	response velocity in degrees per second
AgeGroup	=	factor for age group with four levels
Background	=	background velocity (°/s)
Background^2	=	background velocity squared (°/s)
ε	=	error

Random Effects

Testing the change in log-likelihood for the addition of successive random effects resulted in the following model when significant random effects were retained:

$$Response_{ij} = AgeGroup_i \times (\alpha + \beta_1 Background_{ij} + \beta_2 Background_{ij}^2) + b_i Background_{ij} + b_i Background_{ij}^2 + \varepsilon_{ij}$$

Subscripts *i* and *j* denote participant and observation within participant respectively. Thus, $Response_{ij}$ is the response velocity for observation *j* for participant *i*.

The AIC for the model including only an intercept for participant in the random effects was 1633.55. Likelihood ratio testing indicated that the participant random effect for slope of response against background velocity $b_i Background_{ij}$ significantly improved the model, $\chi^2(1) = 106.43$, $p < 0.001$, AIC = 1529.13. There was no variation between participants in the intercept term, $\chi^2(1) = 0$, $p = 1$, and so it was eliminated from the model at this stage (AIC = 1527.13). The quadratic term for background velocity $b_i Background^2_{ij}$ significantly improved the model, $\chi^2(1) = 14.58$, $p < 0.001$, AIC = 1514.55, as did the correlation between the linear and quadratic background terms, $\chi^2(1) = 9.65$, $p = 0.0019$, AIC = 1506.90.

Fixed Effects

Likelihood ratio testing indicated that none of the fixed effects could be removed due to non-significance. The final model was therefore the same as above:

$$Response_{ij} = AgeGroup_i \times (\alpha + \beta_1 Background_{ij} + \beta_2 Background_{ij}^2) + b_i Background_{ij} + b_i Background_{ij}^2 + \varepsilon_{ij}$$

The AIC of this model when fit using maximum likelihood was 1506.42. The estimated coefficients of the fixed effects can be seen in Table 4.5 along with their standard errors and *t*-values.

Table 4.5

Parameter estimates of the fixed effects for vertical retinal motion perception with their standard errors and t-values.

	Estimate	Std. error	*t* value[a]
α	0.028	0.02	1.37
$AgeGroup\,2$	-0.054	0.035	-1.53
$AgeGroup\,3$	-0.038	0.034	-1.12
$AgeGroup\,4$	0.11	0.042	2.56
$\beta_1\,Background_{ij}$	0.87	0.095	9.17
$\beta_2\,Background_{ij}^2$	0.044	0.015	2.93
$AgeGroup\,2:\beta_1\,Background_{ij}$	-0.087	0.17	-0.523
$AgeGroup\,3:\beta_1\,Background_{ij}$	0.20	0.16	1.23
$AgeGroup\,4:\beta_1\,Background_{ij}$	0.95	0.20	4.75
$AgeGroup\,2:\beta_2\,Background_{ij}^2$	0.0046	0.026	0.176
$AgeGroup\,3:\beta_2\,Background_{ij}^2$	-0.0088	0.025	-0.349
$AgeGroup\,4:\beta_2\,Background_{ij}^2$	-0.14	0.032	-4.46

Note. Number of observations: 582, groups: Participant, 30

[a] Due to uncertainty over the degrees of freedom (Baayen, 2008; Faraway, 2009), p-values are not presented. Instead, significance values for fixed effects are given by the likelihood ratio tests in text.

Age group. Age group significantly interacted with the quadratic term, $\chi^2(3) = 8.5452$, p = 0.036, AIC = 1508.96, in improving the fit of the model. The significance of this term was checked via parametric bootstrapping which gave a similar significant p-value (0.037). Being the highest order term, all lower order interactions and main effects were retained. Without the age effect on the quadratic term, the effect of age group on the linear slope of background was not significant, $\chi^2(3) = 2.69$, p = 0.44, AIC = 1505.65.

The linear slope of response velocity against background velocity increased with age from 0.87 for age group one ($\beta_1 Background_{ij}$ = 0.87) to 1.82 for age group four (*AgeGroup 4:* $\beta_1 Background_{ij}$ = 0.95). Compared to age group one ($\beta_2 Background^2_{ij}$ = 0.044), there was no real change in the quadratic term for age groups two and three (*AgeGroup 2:* $\beta_2 Background^2_{ij}$ = 0.0046, *AgeGroup 3:* $\beta_2 Background^2_{ij}$ = -0.0088) while that of age group four was lower (*AgeGroup 4:* $\beta_2 Background^2_{ij}$ = -0.14).

The predictions of the final model can be seen in Figure 4.2 along with the mean response velocity at each background velocity for the age groups.

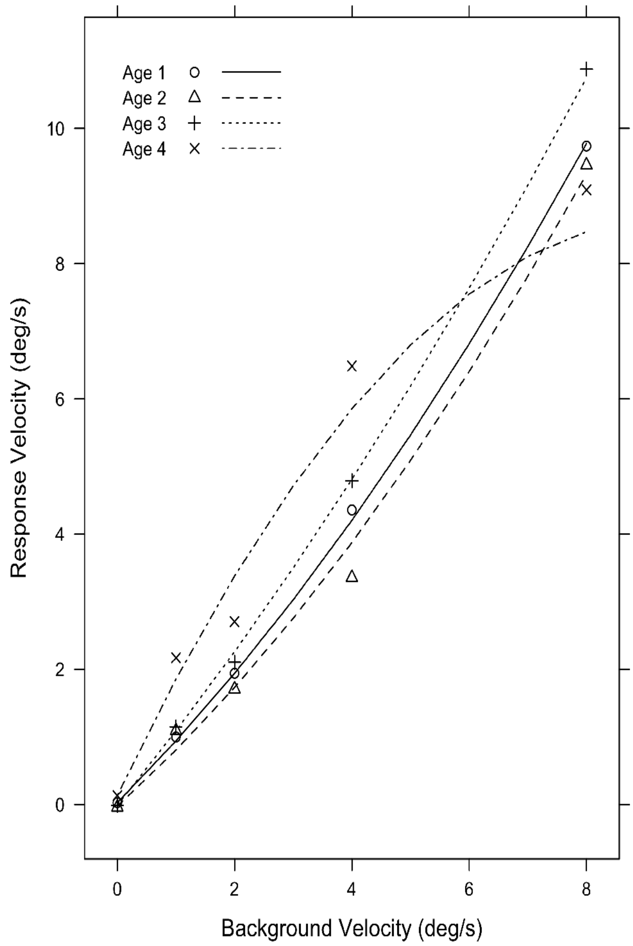

Figure 4.2. Actual and predicted response velocities for each age group at each velocity of vertical background motion. Symbols represent actual mean response velocities for each age group while lines constitute model predictions.

As in Figure 4.1., the slope relating response speed to background speed is steeper for the oldest age group as compared to the first three age groups before a background speed of 4 deg/s.

Model Residuals and Random Effects

Random effects variances and standard deviations can be seen in Table 4.6. Residual variance showed slight skewness (0.77) and kurtosis of 3.62 above that of a normal distribution. It could not be assumed to be normally distributed (Shapiro-Wilk = 0.93, p < 0.001; Appendix K). The random effect representing variation between participants in the slope of background against response velocity showed slight variation from a normal distribution (Shapiro-Wilk = 0.91, p = 0.018; Appendix L). The quadratic term could be assumed to be normally distributed (Shapiro-Wilk = 0.99, p = 0.98; Appendix L). Residual variance showed slight heteroscedasticity (Appendix M).

Table 4.6.

Random effects variances and standard deviations for the model representing vertical retinal motion perception.

Groups	Name	Variance	*SD*	Correlation
Participant	$b_i Background_{ij}$	0.083	0.29	
Participant	$b_i Background^2_{ij}$	0.0021	0.045	-0.717
Residual		0.24	0.49	

Note. Number of observations: 582, groups: Participant, 30.

Discussion

It was hypothesised that older adults would demonstrate decreased sensitivity to differences in speed compared to younger adults. Support for the hypothesis would be demonstrated, in this study, by a lower slope of response velocity against background velocity for the older adults. In contrast, the group of oldest adults demonstrated a slope higher than that of the younger groups up to a background speed of four degrees per second when the background moved horizontally. The first three age groups demonstrated similar slopes. Between each successive background velocity, the slope predicted by the model for the oldest age group was higher than one up to a background speed of 4º/s. For this age group the slope ranged from ~1.41 between a stationary background and a background speed of one degree per second down to ~1.16 between background speeds of two and four degrees per second. Between the background speeds of 4 and 8º/s the slope was approximately 0.86. In comparison, the youngest age group had slopes ranging from ~0.57 between a stationary background and background speed of one degree per second up to ~0.76 between the background velocities of 2 and 4º/s. Their highest slope was between speeds of 4 and 8º/s being approximately 1.00. Therefore, in the present study, support for the hypothesis was only garnered between the background speeds of four and eight degrees per second when the background moved to the left or right.

The pattern of results was similar when the background moved vertically. The slope for the youngest age group grew from ~0.91 to ~1.40 as background speed increased while the slope for the oldest age group shrank from ~1.72 to ~0.67 as background speed increased. Again, the oldest age group only had a lower slope than the youngest age group when the background moved between four and eight degrees per second.

The results of the present study are in opposition to the general literature which reports a decrease in speed discrimination ability for older adults as compared to younger adults (Bidwell et al., 2006; Norman et al., 2003; Raghuram et al., 2005; Scialfa et al., 1991; Snowden & Kavanagh, 2006). Several factors could explain this discordance. Firstly, the present study involved very small groups of participants. In particular, the oldest age group consisted of only four participants after the data of two further older participants was removed from the analysis. This is compared to fourteen participants in the youngest age group and seven in both the middle age groups. The study should be repeated on a larger number of participants with more equal group sizes.

The data of the two older participants was removed from the analysis because they failed to exhibit a correlation between their responding and the background velocity. In other words, their ability to discriminate speeds was very low if not non-existent. The model would not have been able to fit these data, but it suggests that for the present study the group of older participants was split into two groups; those who could not do the task at all, and those who could and exhibited increased sensitivity to differences in speed compared to the younger participants. Put together, the average ability to discriminate changes in velocity may well have been lower than the younger age group at least for some background speeds.

This highlights further differences between the present study and those in the literature. The two participants whose data was removed both reported having early cataracts and one reported mild macular degeneration. Of those older participants remaining a further two female participants reported early cataracts. In general, the studies in the literature demonstrated much more rigorous controls on the ocular health of their participants. It was decided not to exert ocular health criteria on participation in this case in order to optimise the number of participants. Eye health may have had an effect on the results obtained for the oldest age group.

A further difference between the present study and those in the literature is the methodology employed. The present study used a magnitude estimation type task to measure perceived speed with speed discrimination ability inferred from the slope of response on background velocity. Reported studies have focused explicitly on speed discrimination ability by obtaining the threshold for detection of a change in speed of motion. Their results for speed discrimination are likely to be more accurate than the present study.

Scialfa et al. (1991) evaluated the effect of age on the perceived speed of passing motor vehicles in a manner more similar to the present study than those assessing speed discrimination ability more specifically. Although they found a shallower slope of response on actual velocity for older participants they also found, like the present study, that relative to younger participants, older participants were more likely to overestimate speed for lower velocities and underestimate speed at higher velocities.

The non-linear relationship between response and background speed was very similar for the first three age groups in this study (ranging in age from 17 to 54 years). As background speed increased, response speed increased slowly at first but then more rapidly at higher background speeds. This relationship is similar to that described by an expansive power function. Studies in the literature regarding the relationship between perceived and actual speed have used power functions to describe their results, unlike the present study where a quadratic polynomial was employed in order to retain a linear model. While some of these studies have reported expansive power functions (Freeman, 2001; Scialfa et al., 1991; Souman & Freeman, 2008), others have described linear (Kennedy, Yessenow, & Wendt, 1972 as cited in Scialfa et al., 1991) or even compressive power functions (Algom & Cohen-Raz, 1984; Rachlin, 1966; Turano & Massof, 2001). Compressive power functions are more akin to the behaviour demonstrated by the oldest age group where slope decreases as actual background velocity increases. The behaviour of the first three age groups is in agreement with some studies using similar dot pattern stimuli but multiple eye movement speeds (Freeman, 2001; Souman & Freeman, 2008; except Turano & Massof, 2001). It is important to note that the relationships in the present study are the average within a group of similarly aged participants. Individuals may demonstrate compressive, expansive, or linear type relationships.

Age group four demonstrated a slightly higher slope of response on background speed for rightwards motion as compared to leftwards motion. On average though, the slope of response on background speed did not differ significantly for left and rightwards motion. This suggests that although leftward motion was not practised, participants were generally able to effectively apply the method of responding to different directions of motion. This is supported by the similarity between the non-linear relationships found for the horizontal motion and the vertical motion for each age group. The consistency of the relationship between the first three age groups in both horizontal and vertical motion cases also suggests that the method worked well.

A final comment is that due to the duration being constant across trials, the distance travelled by the background dots was confounded with their speed; those going faster travelled further. Participants could therefore have been judging the background motion based on its distance or its speed of motion (Snowden & Kavanagh, 2006). Further research will be needed where duration is varied to disentangle speed and distance effects in order to clarify whether age differences are better explained in terms of speed or distance judgements.

Chapter Five
Analysis Three – Compensation for Eye Movements

Moving the eyes will introduce opposing retinal motion. Without any ability to compensate for the effect of the eye movement, all retinal motion will be seen as motion in the world (Haarmeier et al., 1997). The Filehne illusion occurs when a stationary background is perceived to move in the opposite direction to a pursuit eye movement (Mack & Herman, 1973). If the eyes follow a target and a background stimulus moving at the same speed and in the same direction, the underestimation of the speed of the stimuli when compared to their perception with stationary eyes is known as the Aubert-Fleischl phenomenon (Dichgans et al., 1975). These phenomena represent two points on a continuum regarding the compensation for the effects of eye movement on the retinal image (Freeman, 2001). With imperfect compensation, erroneous motion perception will not only occur for a stationary background or one moving with the eyes but for all intervening speeds of background motion (Freeman, 2001). Background motion at different directions to the eye movement will also be affected (Freeman, 2001; Souman et al., 2005a, 2005b).

This chapter is divided into two parts. The first will present the model for response velocity when the background is moving horizontally. The second part deals with responding when the background is moving upwards.

Horizontal Motion

Hypotheses

The degree of ability to compensate for the effect of eye movements on the retinal image can be inferred from the change in responding to the same background motion when the eyes move in pursuit of a target object at different speeds (Turano & Massof, 2001). Without full compensation, a component of motion in the opposite direction to the eye movement will be present in the perception of background motion. As the eye speed increases, the speed of this 'backward' motion should increase. This relationship can be described by the equation (Freeman, 2001; Souman et al., 2005a):

$$\textit{Perceived Background Speed} = \beta_1 \textit{Actual Background Speed} + \beta_2 \textit{Eye Speed}$$

If there is a complete inability to compensate for eye movements, then β_2 should be negative one, while with perfect compensation it should be zero (Freeman, 2001; Souman et al., 2005a). Wertheim and Bekkering (1992) and Freeman et al. (2002) found that older adults perceived a smaller or inverse Filehne illusion when compared to younger adults. Based on these findings, the hypothesis is that older adults will show higher compensation than younger adults. In other words the β_2 of older adults should be closer to zero than that of younger adults.

Method

Mixed Model

For this analysis, a subset of the data was taken which included only those observations where the background moved to the left or right.

Random effects. Participant and repetition as a factor were included in the random effects of the model.

Fixed effects. The main fixed effects consisted of background velocity, eye velocity and age. A quadratic term for background velocity was included in the model as the retinal analysis suggested that response velocity was not linearly related to background velocity. The effect of repetition as a continuous variable was assessed in order to determine changes over time. Target velocity was not included in the analysis as it was collinear with eye velocity.

Preliminary Analysis and Weights

Only two participants generated correlation coefficients between background and response velocity which were not significantly different from zero (-0.02, $p = 0.82$ and 0.151, $p = 0.099$). These participants were both female and aged over 60 years. One reported early cataracts while the other reported both mild cataract in one eye and mild macular degeneration in the other. Since the analysis was designed to concentrate on those participants who could reliably respond to the background motion, these two participants were removed from the data set.

Preliminary analysis showed that residual variance increased with background speed. Weights were applied to the model to counter this effect. At this stage, a single outlying point exceeding 10 standard errors from the mean of the residuals was removed from the analysis. The weights used to reach the final model were calculated as:

$$variance = \alpha + \beta_1 \, absolute\ value(Background) + \beta_2 \, Background^2$$
$$weight = 1 / variance$$

where

α = 0.63

β_1 = 1.00

β_2 = 0.08

Results

The means and standard deviations of response velocity at each target velocity, background velocity and age group are presented in Table 5.1 and Table 5.2. Negative values of velocity indicate leftwards motion while positive values indicate rightwards motion. To keep tables at a reasonable size, response velocity for leftwards background motion can be seen in Table 5.1 while response for rightwards motion can be seen in Table 5.2.

Table 5.1

Mean response velocity (and standard deviation) for each age group and target velocity at each background velocity of leftwards horizontal motion.

		Background velocity (°/s) *M (SD)*				
Age group	Target (°/s)	-8	-4	-2	-1	0
One (n^a = 2156)	-8	-6.51 (4.23)	-2.76 (3.24)	-0.75 (1.81)	-0.13 (1.05)	-0.04 (1.34)
	-4	-5.46 (2.46)	-2.77 (2.40)	-1.17 (1.91)	-0.20 (1.57)	-0.03 (0.64)
	0	-6.94 (4.20)	-2.31 (2.04)	-1.16 (1.20)	-0.75 (0.63)	0.03 (0.26)
	4	-8.66 (4.70)	-2.64 (2.59)	-0.78 (1.50)	-0.16 (1.08)	0.21 (0.82)
	8	-9.30 (5.45)	-2.90 (3.79)	-1.45 (2.64)	0.07 (1.86)	0.41 (1.92)
Two (*n* = 922)	-8	-5.37 (2.56)	-1.77 (1.57)	-1.14 (2.44)	0.02 (0.73)	0.31 (0.67)
	-4	-5.22 (2.27)	-2.52 (1.26)	-0.98 (0.73)	-0.64 (0.60)	-0.13 (0.54)
	0	-7.34 (4.30)	-2.50 (1.85)	-1.44 (1.10)	-0.81 (0.81)	-0.03 (0.10)
	4	-10.25 (4.59)	-4.00 (2.22)	-0.77 (1.21)	-0.52 (0.97)	0.02 (0.44)
	8	-10.05 (6.18)	-4.51 (4.26)	-1.28 (1.56)	0.12 (2.54)	-0.06 (0.57)
Three (*n* = 1096)	-8	-5.85 (6.48)	-2.31 (2.88)	-0.53 (1.55)	-0.28 (1.98)	0.16 (1.23)
	-4	-5.78 (5.56)	-2.11 (4.11)	-1.18 (1.99)	-0.73 (2.79)	0.09 (1.27)
	0	-7.34 (5.67)	-3.15 (3.10)	-1.39 (1.51)	-0.82 (0.91)	0.03 (0.27)
	4	-7.64 (4.82)	-2.66 (1.72)	-2.18 (2.36)	-1.03 (1.58)	-0.31 (0.98)
	8	-9.68 (8.29)	-4.20 (4.99)	-1.03 (2.27)	-1.12 (1.59)	-0.71 (1.05)
Four (*n* = 546)	-8	-6.71 (8.47)	-4.53 (4.24)	-1.08 (2.77)	-0.63 (1.15)	0.41 (0.63)
	-4	-6.89 (5.37)	-6.19 (3.75)	-2.29 (3.94)	0.03 (0.66)	0.07 (0.74)
	0	-8.88 (5.56)	-4.38 (3.24)	-2.64 (1.88)	-2.38 (2.10)	-0.17 (0.70)
	4	-6.69 (4.47)	-3.90 (2.69)	-2.55 (5.23)	-0.92 (1.10)	-1.00 (1.37)
	8	-10.61 (4.57)	-5.90 (4.50)	-3.22 (3.84)	-3.35 (3.39)	0.11 (0.97)

Note. Negative values of velocity indicate leftwards motion while positive values indicate rightwards motion. *N* = 4720.

[a] *n* refers to number of observations in each age group.

Table 5.2

Mean response velocity (and standard deviation) for each age group and target velocity at each background velocity of rightwards horizontal motion.

		Background velocity (º/s) *M (SD)*			
Age group	Target (º/s)	1	2	4	8
One (n^a = 2156)	-8	0.50 (1.84)	1.09 (1.76)	2.98 (4.59)	9.52 (5.41)
	-4	0.06 (1.49)	0.60 (1.41)	2.77 (2.36)	7.64 (4.98)
	0	0.74 (0.71)	1.24 (0.83)	2.55 (1.61)	7.18 (3.89)
	4	0.46 (0.66)	1.31 (1.59)	2.29 (1.75)	3.46 (4.95)
	8	0.52 (0.94)	0.90 (1.27)	2.70 (2.55)	6.19 (4.35)
Two (*n* = 922)	-8	0.58 (1.23)	1.36 (2.29)	4.44 (4.78)	11.05 (5.27)
	-4	0.62 (1.07)	1.20 (1.51)	4.00 (2.50)	9.45 (4.56)
	0	0.67 (0.55)	1.34 (0.64)	2.35 (0.99)	7.47 (3.23)
	4	0.34 (0.43)	0.84 (0.65)	1.52 (1.06)	4.31 (1.83)
	8	1.01 (1.61)	0.70 (0.78)	1.22 (0.82)	4.67 (1.72)
Three (*n* = 1096)	-8	0.66 (1.46)	1.16 (1.73)	3.57 (4.89)	9.25 (6.66)
	-4	0.32 (0.78)	1.01 (1.20)	2.91 (4.79)	8.82 (6.14)
	0	0.45 (0.60)	1.49 (1.51)	2.22 (3.14)	8.09 (4.48)
	4	0.00 (0.89)	0.61 (1.77)	1.96 (2.01)	4.73 (5.26)
	8	-0.62 (1.02)	-0.34 (1.63)	0.67 (2.24)	8.30 (4.76)
Four (*n* = 546)	-8	0.95 (0.73)	3.00 (3.58)	5.72 (4.72)	8.40 (7.43)
	-4	0.57 (0.96)	2.46 (2.51)	3.26 (2.73)	9.48 (5.38)
	0	1.94 (2.58)	3.15 (2.95)	4.19 (3.37)	9.37 (5.32)
	4	0.51 (0.89)	2.69 (3.93)	6.01 (5.59)	7.18 (4.64)
	8	0.03 (1.05)	0.66 (2.16)	4.71 (4.74)	9.98 (4.26)

Note. Negative values of velocity indicate leftwards motion while positive values indicate rightwards motion. $N = 4720$.

[a] *n* refers to number of observations in each age group.

The *beyond optimal* model was as follows:

$$Response = AgeGroup \times (\alpha + \beta_1 Background + \beta_2 Background^2 + \beta_3 Eye + \beta_4 |Background| + \beta_5 Repetition + \beta_6 Eye \times |Background| + \beta_7 Eye \times |Background^2| + \beta_8 Background \times Repetition + \beta_9 Eye \times Repetition + \beta_{10} Background \times Eye \times Repetition) + \varepsilon$$

where

Response	=	response velocity in degrees per second
AgeGroup	=	factor for age group with four levels
Background	=	background velocity (°/s)
Background²	=	background velocity squared multiplied by the sign of background velocity (°/s)
Eye	=	eye velocity (°/s)
|*Background*|	=	absolute value of background velocity (i.e. background speed) (°/s)
Repetition	=	repetition number as a continuous variable
ε	=	error

Random Effects

Testing the change in log-likelihood for the addition of successive random effects resulted in the following model when significant random effects were retained:

$$Response_{ijk} = AgeGroup_i \times (\alpha + \beta_1 Background_{ijk} + \beta_2 Background^2_{ijk} + \beta_3 Eye_{ijk} + \beta_4 |Background_{ijk}| + \beta_5 Repetition_{ij} + \beta_6 Eye_{ijk} \times |Background_{ijk}| + \beta_7 Eye_{ijk} \times |Background^2_{ijk}| + \beta_8 Background_{ijk} \times Repetition_{ij} + \beta_9 Eye_{ijk} \times Repetition_{ij} + \beta_{10} |Background_{ijk}| \times Pursuit_{ijk} \times Repetition_{ij}) + a_i + a_{ij} + b_i Background_{ijk} + b_{ij} Background_{ijk} + b_i Background^2_{ijk} + b_i |Background_{ijk}| + b_i Eye_{ijk} + b_{ij} Eye_{ijk} + b_i Eye_{ijk} \times |Background_{ijk}| + \varepsilon_{ijk}$$

Subscripts i, j, and k denote participant, repetition number and observation within repetition respectively. Thus, $Response_{ijk}$ is the response velocity for observation k, within repetition j, for participant i.

The AIC was 14575.6 for the model with the sole random effect being the intercept for participant a_i. A significant change in log-likelihood was demonstrated with the addition of the participant random effect for the slope of response against background velocity $b_iBackground_{ijk}$, $\chi^2(1) = 502.91$, $p < 0.001$, AIC = 14074.6, and its quadratic term $b_iBackground^2_{ijk}$, $\chi^2(1) = 39.50$, $p < 0.001$, AIC = 14037.1. Adding the participant random effect representing change in response by eye velocity b_iEye_{ijk} also significantly improved the model, $\chi^2(1) = 25.78$, $p < 0.001$, AIC = 14013.4, as did the interaction between eye velocity and background speed $b_iEye_{ijk} \times |Background_{ijk}|$, $\chi^2(1) = 24.39$, $p < 0.001$, AIC = 13993.2.

Repetition intercept a_{ij} did not significantly improve the model, $\chi^2(1) = 0.23$, $p = 0.63$, AIC = 13994.9. The slopes of response against background $b_{ij}Background_{ijk}$, $\chi^2(1) = 48.60$, $p < 0.001$, AIC = 13948.3, and eye velocity $b_{ij}Eye_{ijk}$, $\chi^2(1) = 36.90$, $p < 0.001$, AIC = 13913.4, did significantly improve the model and so the intercept was retained. The interaction between eye velocity and background speed $b_{ij}Eye_{ijk} \times |Background_{ijk}|$ for repetition did not significantly improve the model, $\chi^2(1) = 1.33$, $p = 0.25$, AIC = 13916.1.

Participant intercept a_i, $b_iBackground_{ijk}$, $b_iBackground_{ijk}$, and $b_iEye_{ijk} \times |Background_{ijk}|$ were correlated (all $p < 0.05$) while repetition a_{ij}, $b_{ij}Background_{ijk}$ and $b_{ij}Eye_{ijk}$ were not (all $p > 0.05$).

Fixed Effects

The effects of repetition were tested first. While some were significant, they were not retained for the final model in order to keep it as simple as possible. They will however be addressed in the text. Age effects were then tested and removed if not significant. This left the following model which was taken as the final model:

$$
\begin{aligned}
Response_{ij} = AgeGroup_i \times (\alpha + \beta_1 Background_{ijk} + \beta_2 Background^2_{ijk} + \beta_3 Eye_{ijk}) \\
+ \beta_4 Eye_{ijk} \times |Background_{ijk}| + \beta_5 Eye_{ijk} \times |Background^2_{ijk}| \\
+ a_i + a_{ij} + b_i Background_{ijk} + b_{ij} Background_{ijk} + b_i Background^2_{ijk} \\
+ b_i |Background_{ijk}| + b_i Eye_{ijk} + b_{ij} Eye_{ijk} + b_i Eye_{ijk} \times |Background_{ijk}| + \varepsilon_{ijk}
\end{aligned}
$$

The AIC of this model when fit using maximum likelihood was 13867.7. The estimated coefficients of the fixed effects can be seen in Table 5.3 along with their standard errors and *t*-values.

Table 5.3

Parameter estimates of the fixed effects with their standard errors and t-values for the model regarding compensation for eye movements with horizontal background motion.

	Estimate	Std. error	*t* value[a]
α	0.091	0.12	0.787
$AgeGroup\,2$	-0.061	0.21	-0.292
$AgeGroup\,3$	-0.24	0.2	-1.22
$AgeGroup\,4$	-0.22	0.25	-0.882
$\beta_1\,Background_{ijk}$	0.37	0.16	2.32
$\beta_2\,Background^2_{ijk}$	0.065	0.018	3.63
$\beta_3\,Eye_{ijk}$	0.038	0.023	1.68
$\beta_4\lvert Background_{ijk}\rvert$	-0.048	0.042	-1.16
$\beta_5\lvert Background^2_{ijk}\rvert$	0.0063	0.006	1.04
$AgeGroup\,2:\beta_1\,Background_{ijk}$	0.0055	0.27	0.0201
$AgeGroup\,3:\beta_1\,Background_{ijk}$	0.14	0.26	0.548
$AgeGroup\,4:\beta_1\,Background_{ijk}$	1.1	0.32	3.33
$AgeGroup\,2:\beta_2\,Background^2_{ijk}$	-0.0052	0.031	-0.168
$AgeGroup\,3:\beta_2\,Background^2_{ijk}$	-0.0084	0.03	-0.284
$AgeGroup\,4:\beta_2\,Background^2_{ijk}$	-0.1	0.037	-2.73
$AgeGroup\,2:\beta_3\,Eye_{ijk}$	-0.044	0.039	-1.13
$AgeGroup\,3:\beta_3\,Eye_{ijk}$	-0.11	0.04	-2.78
$AgeGroup\,4:\beta_3\,Eye_{ijk}$	-0.13	0.058	-2.28
$\beta_6\,Pursuit_{ijk}\times\lvert Background_{ijk}\rvert$	-0.0041	0.013	-0.302
$\beta_7\,Pursuit_{ijk}\times\lvert Background^2_{ijk}\rvert$	-0.0053	0.0017	-3.16

Note. Number of observations: 4720, Groups: repetition, 93; participant, 31.

[a] Due to uncertainty over the degrees of freedom (Baayen, 2008; Faraway, 2009), p-values are not presented. Instead, significance values for fixed effects are given by the likelihood ratio tests in text.

Repetition. The interaction of repetition, eye velocity and background speed significantly improved the model, $\chi^2(1) = 5.71$, $p = 0.017$, AIC = 13863.9, as did the interaction of repetition and background velocity, $\chi^2(1) = 10.14$, $p = 0.0015$, AIC = 13873.1. The former was checked via parametric bootstrapping which returned a still significant p-value ($p<0.001$). On average, the slope of response on background speed increased with repetition ($\beta_8 Background_{ijk} \times Repetition_{ij} = 0.076$) and for a given background speed, the slope of response on eye velocity became more negative with repetition ($\beta_{10}|Background_{ijk}| \times Eye_{ijk} \times Repetition_{ij} = -0.01$).

The effect of repetition did not differ by age group. The four way interaction of age group, repetition, absolute background velocity and pursuit velocity was not significant, $\chi^2(3) = 3.29$, $p = 0.35$, AIC = 13879.3. Repetition also did not interact with age group and background velocity, $\chi^2(3) = 0.60$, $p = 0.90$, AIC = 13876.6, or age group and eye velocity, $\chi^2(3) = 1.99$, $p = 0.57$, AIC = 13866.2.

Age group. Without the effect of age on the quadratic background term, age group did not significantly interact with the linear background velocity in determining response velocity, $\chi^2(3) = 4.48$, $p = 0.21$, AIC = 13873.7. It did however significantly interact with the quadratic term, $\chi^2(3) = 12.03$, $p = 0.0073$, AIC = 13873.7, in improving the fit of the model. Being the highest order term, the age effect on the linear slope was retained. The linear slope of response velocity against background velocity increased with age from 0.37 for age group one ($\beta_1 Background_{ijk} = 0.37$) to 1.47 for age group four ($AgeGroup\ 4 : \beta_1 Background_{ijk} = 1.1$) when the eyes were stationary. While the quadratic terms of age groups one, two and three were positive and much the same (~0.065), the quadratic term of age group four was slightly negative (-0.035) ($\beta_2 Background^2_{ijk} = 0.065$; $AgeGroup\ 4 : \beta_2 Background^2_{ijk} = -0.1$).

The interaction between age group and pursuit velocity was significant, $\chi^2(3) = 17.95$, $p < 0.001$, AIC = 13879.7. The slope of response velocity against eye velocity for a stationary background decreased with age from 0.038 for age group one ($\beta_3 Eye_{ijk} = 0.038$) to -0.092 for age group four ($AgeGroup\ 4 : \beta_3 Eye_{ijk} = -0.13$).

Age group did not significantly interact with pursuit velocity and background speed squared $\beta_5 Eye_{ijk} \times |Background^2_{ijk}|$, $\chi^2(3) = 6.02$, $p = 0.11$, AIC

= 13872.7, nor did it determine the change in slope for response against eye velocity at each background speed $\beta_4 Eye_{ijk} \times |Background_{ijk}|$, $\chi^2(3) = 1.90$, p = 0.59, AIC = 13872.8.

The predicted response velocities from the model can be seen plotted against eye and background velocity in Figures 5.1 and 5.2. The predictions of the fitted model and actual mean response velocities for each age group can be seen in Figures 5.3 and 5.4.

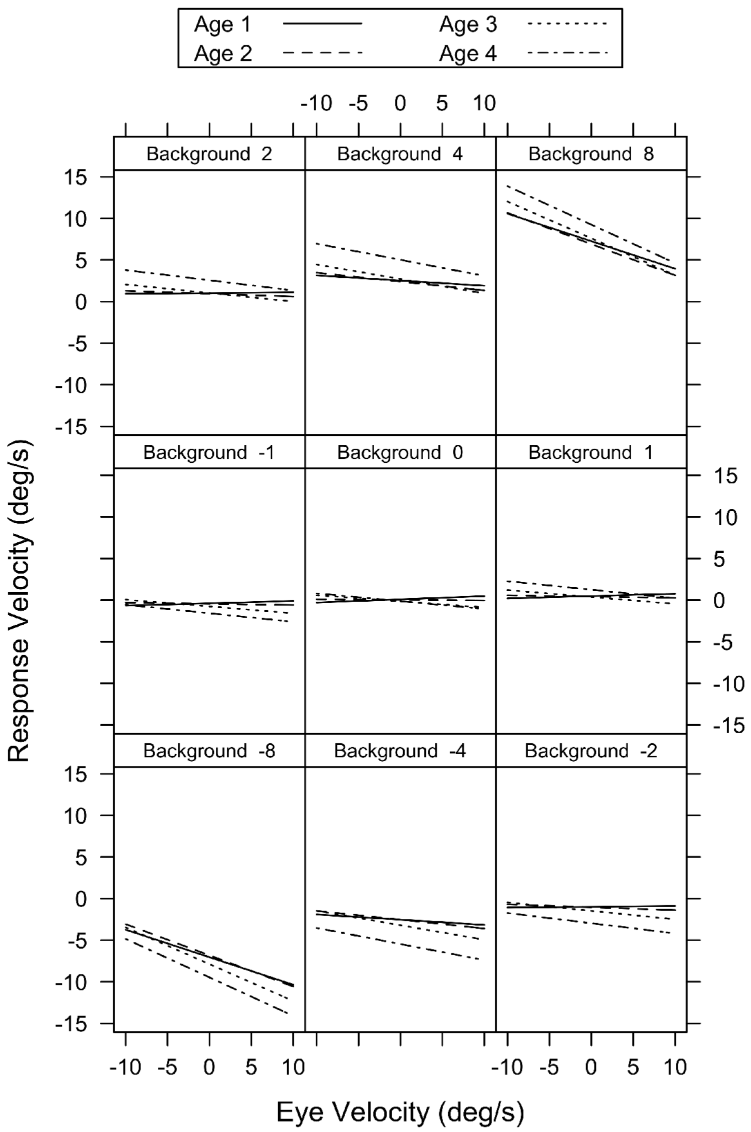

Figure 5.1. Predicted response velocity against eye velocity for each age group at each horizontal background velocity.

In Figure 5.1. the Filehne illusion can be seen in the middle segment representing the predicted change in response velocity with eye movement for a stationary background. As can be seen, the slope of the relationship between response and eye velocity is ever so slightly positive for age groups one and two and negative for age groups three and four. This suggests a Filehne illusion for the older participants but an inverse Filehne illusion for the younger participants where the background seemed to move fractionally with the eye. As the background speed increases the slopes for all age groups become increasingly negative and the intercept for age groups three and four become steadily higher in absolute response velocity as compared to the younger age groups. This has the effect of bringing the relationships between eye and response velocity closer together for the four age groups when eye and background are moving in the same direction (Aubert-Fleischl phenomenon). The Aubert-Fleischl phenomenon can be seen for example in the top right segment of Figure 5.1 representing a background velocity of 8º/s. All age groups underestimate the speed of the background at an eye velocity of 8º/s as compared to their estimate for a stationary eye (0º/s). For each segment, a slope of zero for response against eye velocity indicates perfect compensation for eye movements while a negative slope implies under-compensation for the effects of eye movements.

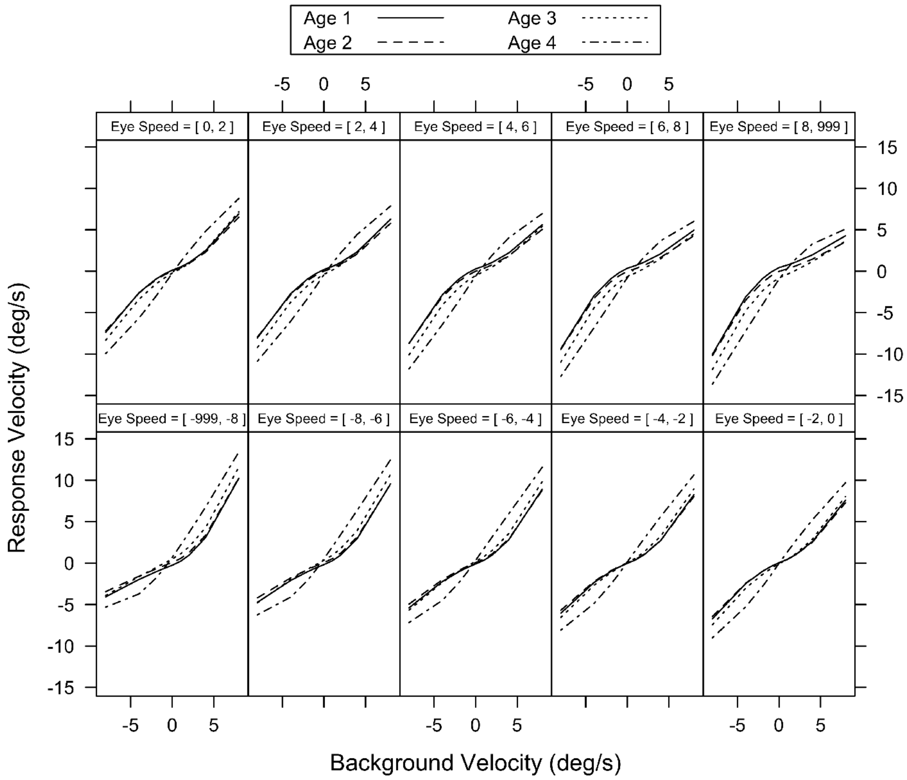

Figure 5.2. Predicted response velocity against horizontal background velocity for each age group at each interval of measured eye velocity.

In Figure 5.2. the predicted relationship between background and response velocity can be seen for each interval of measured eye movement. For eye speeds between -2 and 2º/s (top left and bottom right segments), the relationships between response and background speed for each age group are practically identical to those found in the analysis of retinal motion perception (Figure 4.1). As eye speed increases, the relationship between response and background speed for each age group flattens out when eye and background move in the same direction. For eye and background motion in opposite directions, the slope increases.

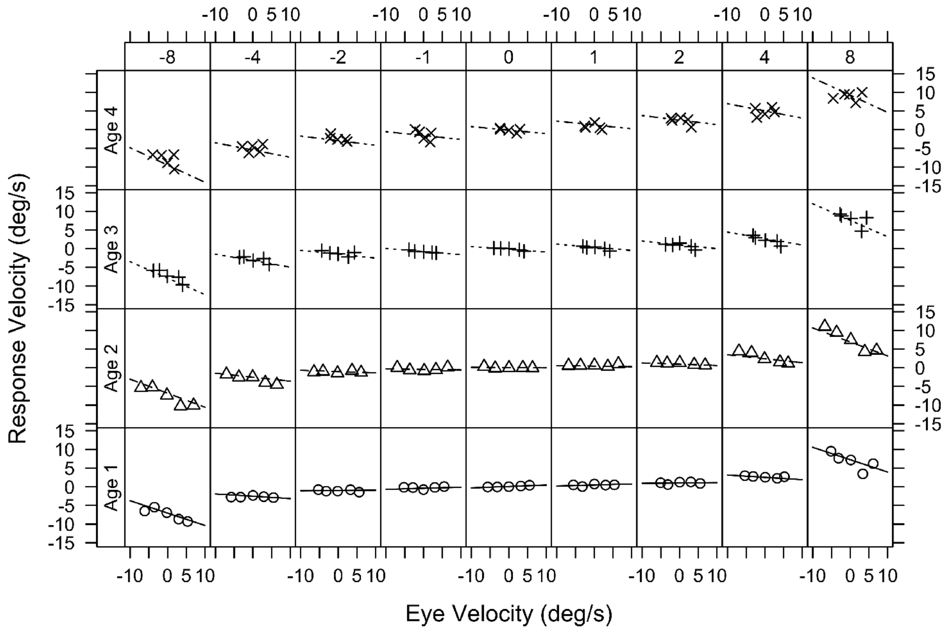

Figure 5.3. Actual and predicted response velocities against eye velocity for each age group and horizontal background velocity. Symbols represent the actual mean response velocities for each age group at the mean eye velocity for each target velocity. Lines constitute model predictions. Columns correspond to background velocities and rows to age groups.

The actual mean response velocities for each age group depicted in Figure 5.3. are for each background velocity against the mean eye velocity at each target velocity. As can be seen, the model predictions appear to represent the pattern portrayed by the means quite well for the first three age groups. The fourth age group has a more variable distribution of mean response velocities and a restricted range of eye velocities. This may have affected the model fit.

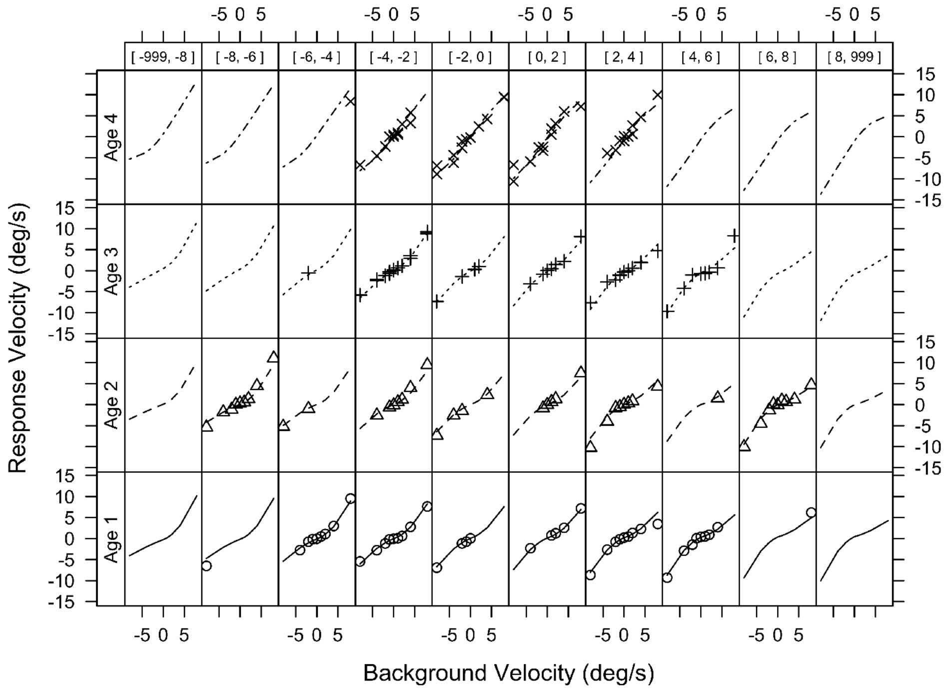

Figure 5.4. Actual and predicted response velocities against horizontal background velocity for each age group and interval of eye velocity. Symbols represent the actual mean response velocities for each age group at the mean eye velocity for each target velocity. Lines constitute model predictions. Rows correspond to age groups and columns to intervals of eye velocity. The far left and far right columns represent mean eye speeds of 8°/s and beyond.

The actual mean response velocities in Figure 5.4 are the same as presented in Figure 5.3. In Figure 5.4. there are segments without any actual mean response velocities, especially for the oldest age group. This is because there were no mean eye velocities in the range represented by these segments at any of the target velocities.

Model Residuals and Random Effects

Variance and standard deviation of the random effects can be seen in Table 5.4. Residual error showed slight skew (0.50) and extreme excess kurtosis of 9.3 compared to a normal distribution (Shapiro-Wilk = 0.88, $p < 0.001$; Appendix N). The intercept (Shapiro-Wilk = 0.95, $p < 0.001$) and slope of response against eye velocity (Shapiro-Wilk = 0.89, p < 0.001) in the repetition random effects (Appendix O) demonstrated distributions which were both slightly leptokurtic (excess kurtosis of 4.8 and 2.9 respectively). The random effect representing variation in intercept between participants (Appendix P) could not be assumed to be normally distributed (Shapiro-Wilk = 0.73, p < 0.001) as it had skew of 2.4 and kurtosis of 9.5 above that of a normal distribution. This was mainly due to one outlying participant with an intercept of 1.1 where everyone else had intercepts very close to zero. The residuals demonstrated mild heteroscedasticity (Appendix Q).

Table 5.4.

Random effects variances and standard deviations for the model representing compensation for eye movements with horizontal motion.

Groups	Name	Variance	*SD*	Correlations			
Repetition	$b_{ij} Eye_{ijk}$	0.0094	0.097				
	$b_{ij} Background_{ijk}$	0.048	0.22				
	a_{ij}	0.01	0.1				
Participant	$b_i Eye_{ijk}$	0.0014	0.038				
	a_i	0.15	0.39				
	$b_i Background_{ijk}$	0.36	0.6	-0.427			
	$b_i Background^2_{ijk}$	0.0042	0.065	0.495	-0.768		
	$b_i \lvert Background_{ijk} \rvert$	0.0029	0.054	0.191	-0.926	0.855	
	$b_i Eye_{ijk} \times b_i Background_{ijk}$	0.0016	0.04	-0.036	-0.293	-0.294	0.072
Residual		1.8	1.3				

Note. Number of observations: 4720, Groups: repetition, 93; participant, 31.

Vertical Motion

Hypotheses

When a background stimulus moves upwards and the eyes move horizontally the degree of compensation for eye movement can be inferred from the extent of the horizontal component of the response (Souman et al., 2005a, 2005b). This is because smooth pursuit will introduce retinal motion in the opposite direction to the eyes (Souman et al., 2005a, 2005b). If this motion is not compensated by an extra-retinal signal, the background should appear to move at a diagonal opposite the eyes rather than straight up (Souman et al., 2005a, 2005b). This relationship is represented in Figure 5.5.

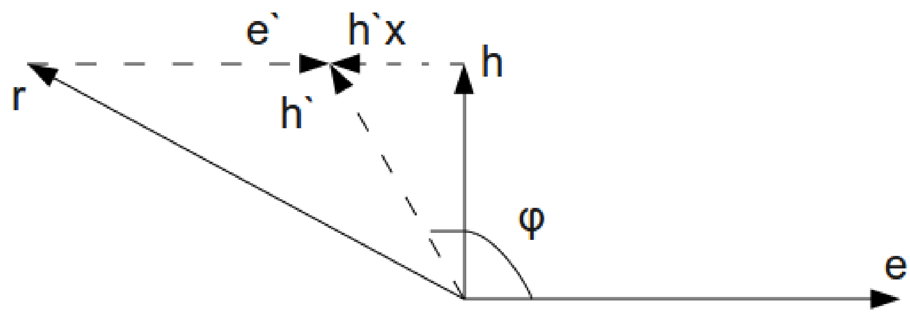

Figure 5.5. Vector representation of the compensation for eye movements with vertical background motion. Vector **e** represents eye velocity. Vector **h** represents the velocity of the background stimulus relative to the head (i.e. on the screen) while **r** represents its velocity on the retina. Primed symbols are estimates of these velocities by the visual system. Figure adapted from "Perceived motion direction during smooth pursuit eye movements" by J. L. Souman, I. T. C. Hooge, and A. H. Wertheim, 2005a, *Experimental Brain Research, 164,* p.377.

In Figure 5.5. the eye movement (**e**) causes the background (**h**) to move diagonally opposite the eyes on the retina (**r**). Subtracting the estimate of the eye velocity (vector **e`**) from the retinal velocity (**r**) gives the estimated velocity of the background relative to the head (**h`**) (Souman et al., 2005a). This representation assumes that the velocity of retinal motion is estimated perfectly (Souman et al., 2005a). If eye velocity is underestimated (**e`**) the background will be perceived to move at an angle (**φ**) opposite the eyes (Souman et al., 2005a). The horizontal component (**h`x**) of the perceived background velocity (**h`**) is the retinal motion induced by the eye movement which is left over after the estimate of eye velocity (**e`**) has been removed (Souman et al., 2005b). It is this horizontal component (**h`x**) that is used as the response velocity in the following analysis of compensation for eye movements with vertical background motion.

The hypothesis based on the literature (Wertheim & Bekkering, 1992; Freeman et al., 2002) is that older adults will show greater compensation than younger adults (i.e. **h'x** will be smaller for older age groups).

Method

Mixed Model

For this analysis, a subset of the data was taken which included only those observations where the background moved upwards. The mixed model regressed the horizontal component of response velocity on vertical background velocity and horizontal eye velocity. The coefficient for eye velocity gives an indication of compensation ability as for the earlier analysis with horizontal motion.

Random effects. Participant and repetition within participant were included in the model as random effects.

Fixed effects. The main fixed effects consisted of background velocity, eye velocity and age as a factor. Repetition as a continuous variable was tested as a fixed effect of interest. Target velocity was not included in the analysis as it was collinear with eye velocity.

Preliminary Analysis and Weights

All of the participants generated correlation coefficients between the vertical components of response and background velocity which were significantly different from zero (all $p < 0.01$). However, the two females in the oldest age group who were removed from the prior analysis on compensation for eye movements with horizontal motion and in the retinal analyses of *Chapter Four* were also removed here to keep the analyses comparable. This was justified because although significant, their correlation coefficients were only 0.37 ($p = 0.0022$) and 0.36 ($p = 0.004$) where all other participants had correlation coefficients exceeding 0.60. A female participant aged between 17 and 24 years demonstrated a correlation of -0.80 ($p < 0.001$). Since the analysis was designed to concentrate on those participants who could reliably and correctly respond to the background motion, this participant's data was also removed from the data set.

Preliminary analysis showed that the residuals were leptokurtic and their variance increased with background speed. Instead of using weights as in prior analyses, the signed square root transformation of the response and predictors were used to improve the distribution of the residuals. There were complications in the back transformation of values either side of zero when the intercept was not at the origin. Because of this, the data for left and right eye movements were pooled as there was no reason to believe the compensation for eye movements would be different for these opposite directions of eye movement with vertical background motion. A single outlying point exceeding six standard errors from the mean of the residuals was removed from the analysis.

Results

The means and standard deviations of response velocity at each target velocity, background velocity and age group are presented in Table 5.5. Negative values of response velocity indicate a response in the opposite direction to the eye movement while positive values indicate the same direction. Negative values of target velocity indicate leftwards target motion while positive values are rightwards target motion.

Table 5.5.

Mean response velocity (and standard deviation) at each target velocity, background velocity and age group for vertical background motion.

		Background velocity (°/s) *M (SD)*				
Age group	Target (°/s)	0	1	2	4	8
One (n^a = 994)	-8	-0.19 (1.22)	-0.20 (0.78)	0.30 (1.04)	0.14 (1.22)	0.66 (2.02)
	-4	0.03 (1.01)	-0.13 (0.88)	0.01 (0.88)	0.07 (0.90)	0.38 (1.35)
	0	0.08 (0.54)	-0.04 (0.14)	-0.01 (0.12)	-0.01 (0.32)	0.01 (0.38)
	4	0.12 (0.71)	-0.24 (0.95)	-0.60 (1.09)	-0.47 (1.24)	-1.68 (2.44)
	8	0.21 (0.96)	0.23 (1.84)	-1.00 (1.22)	-1.04 (1.99)	-2.36 (2.81)
Two (*n* = 449)	-8	-0.43 (0.82)	-0.27 (1.36)	0.63 (0.99)	0.83 (1.37)	2.89 (3.14)
	-4	0.03 (0.68)	0.15 (0.55)	0.40 (0.67)	0.62 (1.38)	1.12 (1.23)
	0	0.01 (0.17)	-0.01 (0.10)	-0.03 (0.14)	-0.02 (0.25)	-0.08 (0.31)
	4	0.12 (0.32)	0.00 (0.57)	-0.43 (0.79)	-0.89 (1.54)	-2.28 (2.63)
	8	0.09 (0.77)	-0.33 (0.41)	-0.72 (1.36)	-1.83 (1.83)	-2.74 (3.35)
Three (*n* = 538)	-8	0.10 (0.98)	0.66 (1.43)	0.86 (1.56)	1.83 (2.12)	2.11 (2.64)
	-4	-0.12 (0.76)	0.50 (1.21)	1.06 (1.79)	0.90 (2.18)	1.02 (2.38)
	0	-0.22 (1.05)	0.05 (0.64)	-0.06 (0.64)	-0.05 (0.60)	-0.05 (0.88)
	4	-0.32 (0.75)	-0.61 (1.52)	-1.13 (1.59)	-1.98 (2.48)	-1.24 (1.79)
	8	0.10 (1.26)	-1.48 (1.83)	-1.83 (2.71)	-2.00 (2.55)	-2.36 (3.07)
Four (*n* = 270)	-8	0.51 (0.68)	0.61 (1.31)	0.20 (0.40)	0.09 (0.22)	0.06 (1.04)
	-4	-0.38 (0.81)	0.11 (1.74)	0.93 (3.16)	0.01 (0.15)	-0.04 (0.27)
	0	-0.08 (0.56)	-0.04 (0.19)	0.03 (0.20)	-0.20 (0.33)	-0.10 (0.62)
	4	-0.04 (1.02)	-0.43 (0.62)	-0.72 (1.13)	-0.31 (1.25)	-0.11 (0.52)
	8	-1.00 (2.95)	-0.71 (0.85)	-0.60 (1.30)	-0.65 (0.93)	-0.45 (1.25)

Note. Negative values of response velocity indicate a response in the opposite direction to the eye movement while positive values indicate the same direction. Negative values of target velocity indicate leftwards target motion while positive values are rightwards target motion. *N* = 2251.

[a] n refers to number of observations in each age group.

The *beyond optimal* model was as follows:

$$Response = AgeGroup \times (\alpha + \beta_1 Eye + \beta_2 Background + \beta_3 Repetition$$
$$+ \beta_4 Eye \times Background + \beta_5 Background \times Repetition + \beta_6 Eye \times Repetition$$
$$+ \beta_7 Background \times Eye \times Repetition) + \varepsilon$$

where

Response	=	signed square root of absolute value of response velocity in degrees per second. Negative values indicate motion in the opposite direction to the eye movement, while positive values indicate eye and response motion in the same direction.
AgeGroup	=	factor for age group with four levels
Eye	=	square root of absolute value of eye velocity (º/s)
Background	=	square root of background velocity (º/s)
ε	=	error

Random Effects

Testing the change in log-likelihood for the addition of successive random effects resulted in the following model when significant random effects were retained:

$$Response_{ijk} = AgeGroup_i \times (\alpha + \beta_1 Eye_{ijk} + \beta_2 Background_{ijk} + \beta_3 Repetition_{ij}$$
$$+ \beta_4 Eye_{ijk} \times Background_{ijk} + \beta_5 Background_{ijk} \times Repetition_{ij}$$
$$+ \beta_6 Eye_{ijk} \times Repetition_{ij} + \beta_7 Background_{ijk} \times Eye_{ijk} \times Repetition_{ij})$$
$$+ b_i Eye_{ijk} + b_i Eye_{ijk} \times Background_{ijk} + \varepsilon_{ijk}$$

Subscripts *i*, *j*, and *k* denote participant, repetition number and observation within repetition respectively. Thus, $Response_{ijk}$ is the response velocity for observation *k*, within repetition *j*, for participant *i*.

The model with only the intercept for participant a_i in the random effects had an AIC of 4891.9. A significant change in log-likelihood was demonstrated with the addition of the participant random effect for the slope of response against background velocity $b_i Background_{ijk}$, $\chi^2(1) = 92.59$, $p < 0.001$, AIC = 4801.3, and eye velocity $b_i Eye_{ijk}$, $\chi^2(1) = 47.17$, $p < 0.001$, AIC = 4756.1. The interaction between eye and background velocities also significantly improved the fit of the model $b_i Eye_{ijk} \times Background_{ijk}$, $\chi^2(1) = 141.98$, $p < 0.001$, AIC = 4616.2. When the slope of response on eye velocity and the interaction term were included, the participant random effects for intercept and the main effect of background velocity no longer explained any of the variance. They were thus removed as the real variables of interest were the eye velocity and the interaction which explained more of the variance. The slope of horizontal response on vertical background velocity was not expected to explain any variance as over all the eye velocities it should average to zero for all participants.

None of the random effects for repetition within participant significantly improved the model and there was no significant covariation between participant random effects (all $p > 0.05$).

Fixed Effects

The effects of repetition were tested first and removed and then age effects were tested and removed if not significant. This left the following model which was taken as the final model:

$$
\begin{aligned}
Response_{ijk} = AgeGroup_i \times (& \alpha + \beta_1 Eye_{ijk} + \beta_2 Background_{ijk} \\
& + \beta_3 Eye_{ijk} \times Background_{ijk}) \\
& + b_i Eye_{ijk} + b_i Eye_{ijk} \times Background_{ijk} + \varepsilon_{ijk}
\end{aligned}
$$

This model (fit using maximum likelihood) had an AIC of 4607.4. The estimated coefficients of the fixed effects can be seen in Table 5.6 along with their standard errors and *t*-values.

Table 5.6

Parameter estimates of the fixed effects with their standard errors and t-values for the model representing compensation for eye movements with vertical motion.

	Estimate	Std. error	*t* value [a]
α	-0.047	0.077	-0.616
$AgeGroup\,2$	-0.033	0.14	-0.237
$AgeGroup\,3$	0.0039	0.13	0.0302
$AgeGroup\,4$	-0.044	0.16	-0.273
$\beta_1\, Eye_{ijk}$	0.09	0.05	1.78
$\beta_2\, Background_{ijk}$	0.047	0.045	1.03
$AgeGroup\,2:\beta_1\, Eye_{ijk}$	0.034	0.088	0.39
$AgeGroup\,3:\beta_1\, Eye_{ijk}$	-0.2	0.091	-2.19
$AgeGroup\,4:\beta_1\, Eye_{ijk}$	-0.24	0.13	-1.83
$AgeGroup\,2:\beta_2\, Background_{ijk}$	0.074	0.08	0.919
$AgeGroup\,3:\beta_2\, Background_{ijk}$	0.089	0.075	1.18
$AgeGroup\,4:\beta_2\, Background_{ijk}$	-0.049	0.093	-0.53
$\beta_3\, Eye_{ijk} \times Background_{ijk}$	-0.15	0.046	-3.21
$AgeGroup\,2:\beta_3\, Eye_{ijk} \times Background_{ijk}$	-0.11	0.081	-1.32
$AgeGroup\,3:\beta_3\, Eye_{ijk} \times Background_{ijk}$	-0.079	0.08	-0.982
$AgeGroup\,4:\beta_3\, Eye_{ijk} \times Background_{ijk}$	0.2	0.1	1.92

Note. Number of observations: 2251, groups: Participant, 30. Parameter estimates are for square root transformed response and predictors.

[a] Due to uncertainty over the degrees of freedom (Baayen, 2008; Faraway, 2009), p-values are not presented. Instead, significance values for fixed effects are given by the likelihood ratio tests in text.

Repetition. The four way interaction of age group, repetition, background velocity and pursuit velocity were not significant, $\chi^2(3) = 2.60$, p = 0.46, AIC = 4611.5. The interaction between eye and background velocity did not change with repetition, $\chi^2(1) = 0.08$, p = 0.77, AIC = 4608.1. Repetition also did not interact with age group and eye velocity, $\chi^2(3) = 2.58$, p = 0.46, AIC = 4606.2, or eye velocity alone, $\chi^2(1) = 1.79$, $p = 0.18$, AIC = 4602.8. Nor did it interact with age group and background velocity, $\chi^2(3) = 4.37$, $p = 0.22$, AIC = 4602.6, or background velocity alone, $\chi^2(1) = 0.0025$, $p = 0.96$, AIC = 4601.0. The interaction between repetition and age group significantly improved the model, $\chi^2(3) = 14.03$, $p = 0.003$, AIC = 4599.0. The square root of the response velocity decreased with repetition for age groups two ($AgeGroup\ 2 : \beta_3 Repetition_{ij} = -0.11$) and three ($AgeGroup\ 3 : \beta_3 Repetition_{ij} = -0.09$) compared to age groups one ($\beta_3 Repetition_{ij} = 0.009$) and four ($AgeGroup\ 4 : \beta_3 Repetition_{ij} = 0.08$).

Age group. The interaction of age group, eye and background velocities significantly improved the fit of the model, $\chi^2(3) = 8.27$, $p = 0.041$, AIC = 4609.7. However, parametric bootstrapping gave a similar but non-significant p-value (0.065). Even as a nearly significant trend, the three-way interaction was important to answering the hypothesis and so it was retained in the final model. The slope of the square root of response against the square root of eye velocity decreased as the background speed increased for age groups one, two and three ($\beta_3 Eye_{ijk} \times Background_{ijk} = -0.15$; $AgeGroup\ 2 : \beta_3 Eye_{ijk} \times Background_{ijk} = -0.11$, $AgeGroup\ 3 : \beta_3 Eye_{ijk} \times Background_{ijk} = -0.079$). For age group four the slope increased by 0.05 as background speed increased ($AgeGroup\ 4 : \beta_3 Eye_{ijk} \times Background_{ijk} = 0.2$). Without the three-way interaction term, age group also significantly interacted with eye velocity in determining response velocity, $\chi^2(3) = 18.75$, $p < 0.001$, AIC = 4617.4. The slope of the square root of response velocity against the square root of eye velocity decreased with age from 0.09 for age group one ($\beta_3 Eye_{ijk} = 0.09$) to -0.15 for age group four ($AgeGroup\ 4 : \beta_3 Eye_{ijk} = -0.24$).

Age group did not interact with background velocity in determining response velocity, $\chi^2(3) = 0.92$, $p = 0.82$, AIC = 4609.7.

This model was used to calculate the predicted square root of response velocity from the square root of the background and eye velocities. Values of response and predictor variables were then back-transformed by squaring (retaining their signs) and can be seen in Figure 5.6. The back-transformed predicted and actual mean response velocities can be seen in Figure 5.7 for each age group.

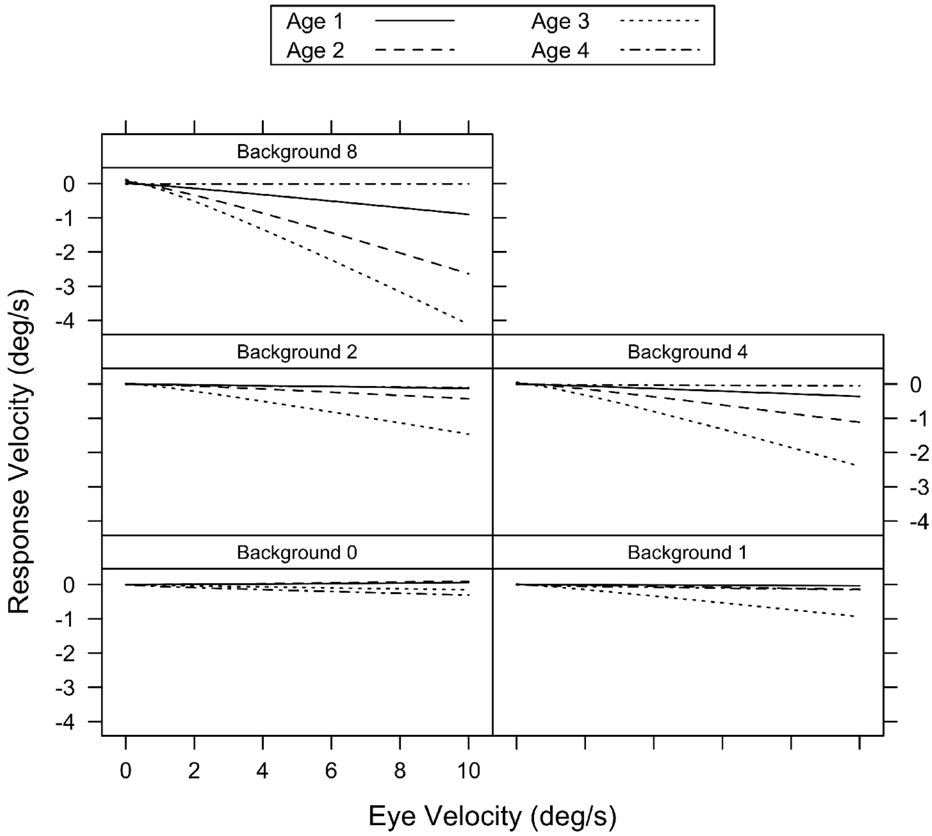

Figure 5.6. Predicted response velocity against eye velocity for each age group from the model representing compensation for eye movements with vertical background motion. Negative values indicate response velocity in the opposite direction to the eye movement.

The predicted extent of the Filehne illusion can be seen in Figure 5.6. in the bottom left segment representing a stationary background. While age groups three and four demonstrated a Filehne illusion which increased with eye speed, groups one and two show no sign of a Filehne illusion. As background and eye speeds increased, the first three age groups demonstrated an increase in the speed of the response velocity in the opposite direction to the eye. Due to the three way interaction of age group, eye and background velocities in the model, an increase in background speed resulted in the slope of response against eye velocity becoming zero for age group four (suggesting perfect compensation for eye movements at higher background speeds). For all segments, a slope of response against eye velocity of zero indicates perfect compensation for eye movements while a negative slope implies under-compensation for eye movements.

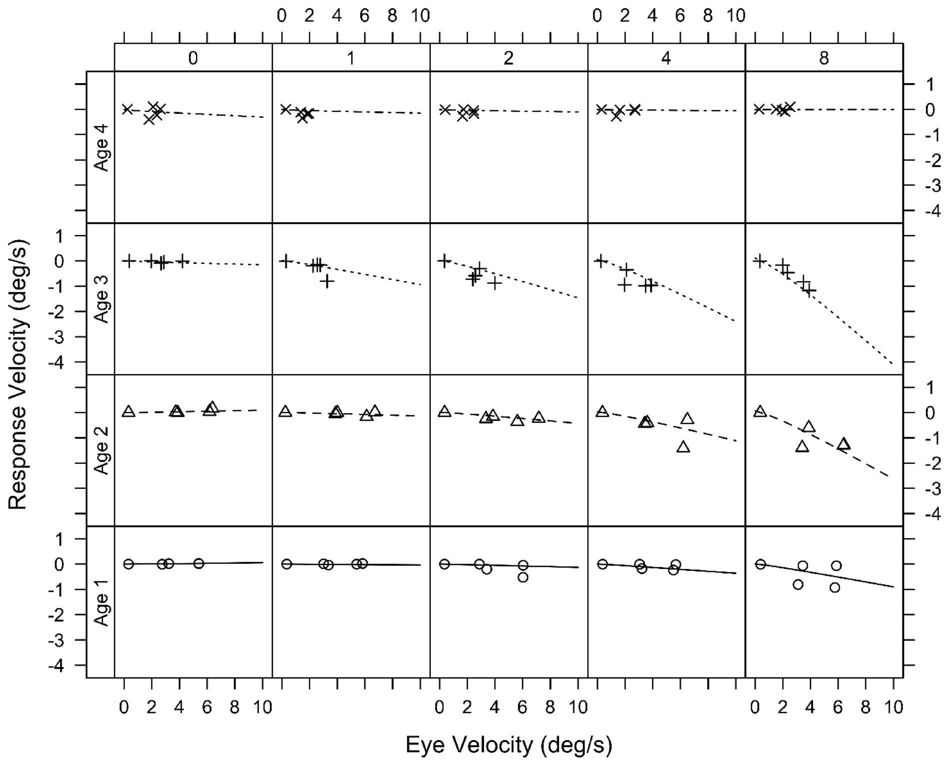

Figure 5.7. Actual and predicted response velocities against eye velocity for each age group and vertical background velocity. Symbols represent the actual mean response velocities for each age group at the mean eye velocity for each target velocity. Lines constitute model predictions. Columns correspond to background velocities and rows to age groups. Negative values indicate response velocity in the opposite direction to the eye movement.

In Figure 5.7. the actual mean response velocities depicted are those at each background velocity against the mean eye velocity for each target velocity. As with the analysis on compensation for eye movements with horizontal motion, age group four shows the smallest range of eye velocities. The restricted range of eye speeds for the oldest age group may have affected the model fit.

Model Residuals and Random Effects

Variance and standard deviation of the random effects can be seen in Table 5.7. Residual error showed slight skew (0.32) and excess kurtosis of 2.07 compared to a normal distribution (Shapiro-Wilk = 0.97, $p < 0.001$; Appendix R). The slope of response against eye velocity for participant (Appendix S) demonstrated slight skew (0.65) and could not be assumed to be normally distributed (Shapiro-Wilk = 0.92, $p = 0.02$). The residuals demonstrated mild heteroscedasticity (Appendix T).

Table 5.7.

Random effects variances and standard deviations for the model representing compensation for eye movements with vertical motion.

Groups	Name	Variance	*SD*
Participant	$b_i Eye_{ijk}$	0.0053	0.073
	$b_i Eye_{ijk} \times Background_{ijk}$	0.018	0.13
Residual		0.43	0.65

Note. Number of observations: 2251, groups: Participant, 30.

Discussion

In this study, the oldest age group demonstrated different results whether the background stimulus moved horizontally or vertically. This was likely because of the restricted range of eye speeds demonstrated by this age group which could have influenced the model fits. Due to this uncertainty, the results of the oldest age group will be addressed further on. In contrast, the results of the first three age groups were consistent across background stimulus directions and showed a clear trend. For both horizontal and vertical motion the third age group ranging in age from 45 to 54 years demonstrated a greater effect of eye movement on responding than the younger two age groups. A greater effect of eye movement on responses (i.e. a more negative slope in the relationship between response and eye velocity), is indicative of less compensation. Thus, the hypothesis that older adults should demonstrate greater compensation for eye movements in motion perception than young adults was not supported by the present data. Instead the consistent under-compensation of the third age group compared to young people illustrates the possibility that the ability to compensate for eye movements in motion perception lessens with ageing.

In general, a stationary background appeared to move opposite the eyes for the older age groups (Filehne illusion) and with the eyes for the younger participant groups (inverse Filehne illusion); although the speed of the illusory motion was very small regardless of age (Figure 5.1; Figure 5.6). This is in direct contrast to the results of Wertheim and Bekkering (1992) and Freeman et al. (2002) who, at stimulus durations similar to the present study, generally found that their older adults were more likely to demonstrate an inverse Filehne illusion or a very small Filehne illusion while their young participants exhibited large traditional Filehne illusions.

Freeman et al. (2002) found no effect of age on the Aubert-Fleischl phenomenon; both their old and young participant groups underestimated the speed of a stimulus moving with the eyes compared to viewing the same stimulus with stationary eyes. All age groups in the present study also demonstrated the Aubert-Fleischl phenomenon. In the present study, the differences between age groups in the perceived speed of a stimulus were greater when the background moved opposite the eyes (Figure 5.1). When the background moved in the same direction as the eyes, the gap between age groups narrowed (Figure 5.1). This is similar to the findings of Freeman et al. (2002) of a difference between ages for the Filehne, but not the Aubert-Fleischl, phenomenon.

While Freeman et al (2002) interpret different age effects on the Filehne and Aubert-Fleischl phenomena as being inconsistent, they can be explained in the present study as the result of different slopes and intercepts for the different age groups in the relationship between response and eye velocity (Figure 5.1). The older age groups tended to overestimate the speed of a stimulus when the eyes were stationary and thus their intercepts were at a higher *speed* than that of the younger groups. Compared to the younger age groups the older groups also had a greater negative slope of response against eye velocity. Put together, this had the effect of widening the gap between age groups when the eye and background moved in opposite directions and bringing the regression lines closer together when eye and background moved in the same direction (Figure 5.1).

There are several possible reasons for the discrepancy between the results reported here and those of Freeman et al. (2002) and Wertheim and Bekkering (1992). In their studies, eye movements were measured but were not used as a predictor in the response analysis. Instead the target velocity was used to represent eye velocity. This is in contrast to the present study where eye movements were entered directly as explanatory variables in the models for horizontal and vertical motion. While Wertheim and Bekkering (1992) reported that the ability of their older adults to accurately pursue the target was comparable to that of their younger adults, Freeman et al. (2002) showed reduced pursuit gain for older adults in line with the present study. As Freeman et al. (2002) point out, actual eye movements may have affected their results.

The present study also examined a wider range of background and pursuit speeds than the studies of Wertheim & Bekkering (1992) and Freeman et al. (2002) which concentrated on the Filehne and also in the latter case the Aubert-Fleischl phenomena. It is also possible that different stimuli and methods used to measure perceived speed influenced the results. While Freeman et al. (2002) used the method of adjustment to examine the Filehne illusion but a matching task to measure the Aubert-Fleischl phenomena, the present study used a custom designed tool (based on magnitude estimation) to measure both illusions with the same method. Like the study of Freeman et al. (2002), the present study used a random dot field as the background stimulus rather than the sinusoidal grating used by Wertheim and Bekkering (1992). However the size of the background stimulus used in the present study was larger than that used by Freeman et al. (2002).

The responding of participants in the present study was consistent with that reported in the general literature on compensation for eye movements outside of age effect studies. Based on model predictions, for a horizontal background speed of eight degrees per second, age groups one and two had slopes of response against eye velocity of -0.33 and -0.38 respectively. Age groups three and four demonstrated slopes of -0.44 and -0.46 respectively. Perfect compensation would be exhibited by a slope of zero while no compensation is depicted by a slope of negative one (Freeman, 2001; Souman et al., 2005a). Reciprocally, the amount of eye movement compensated for can be estimated by adding one to the slope (Freeman, 2001; Souman et al., 2005a). Therefore, for this background speed, age groups one and two were able to compensate 67 and 62 percent of their eye movements respectively while age groups three and four compensated 56 and 54% of their eye movements (Figure 5.1).

For vertical background motion at a speed of eight degrees per second, age groups one and two compensated 91 and 73% respectively while age group three compensated 58% and age group four compensated for 100% of their eye movements (Figure 5.6). With a stationary background the degree of compensation for all age groups was much higher, measuring around 99 to 104% (inverse Filehne illusion) for the two youngest age groups and 91 (Filehne illusion) to 99% for the two oldest age groups (Figure 5.1, Figure 5.6). While a degree of compensation around 100% is generally higher than that reported in the literature for similar speed matching tasks involving multiple velocities of pursuit and background motion, the amount of compensation reported here is mostly within the range reported in the literature (39 to 65% Freeman, 2001; 34% to 83% Souman et al., 2006; ~80% Turano & Massof, 2001).

For both horizontal and vertical background motion, eye movements generally introduced a component to motion perception in the opposite direction to pursuit (especially at high background speeds), consistent with studies by Souman et al. (2005a, 2005b, 2006). This study supports their assertion that the compensation mechanism is the same regardless of the direction of retinal motion relative to the eye movement direction (Souman et al., 2005a, 2005b, 2006). For the first three age groups in the present study, the slope of response against eye velocity became more negative as background speed increased for both horizontal and vertical motion. This supports the findings of Souman et al. (2005a) that compensation decreases as stimulus speed increases. The authors suggest that as the relationship between actual and perceived speed is not linear, the gain of the retinal signal should increase as the stimulus gets faster (Souman et al., 2005a). Assuming that the extraretinal signal gain remains constant, this will result in less compensation at faster stimulus speeds as the ratio of the two gains decreases (Souman et al., 2005a). This interpretation is consistent with the present study where reported perceived speed was non-linearly related to actual speed.

Models of compensation for eye movements have used non-linear relationships between estimates of retinal and eye velocity and their respective actual velocities to explain the pattern of responding exhibited for motion depending on its direction relative to the eye (Freeman, 2001; Souman et al., 2006; Turano & Massof, 2001). Non-linear relationships have been able to explain why when eye and background move in the same direction, the slope of response against background velocity flattens out while opposite directions of eye and background motion see an increase in slope (Freeman, 2001; Turano & Massof, 2001). This pattern of responding was found in the data of Turano and Massof (2001) and Freeman (2001) obtained via velocity matching tasks and also in the present study (Figure 5.2). This suggests consistency not only between the results of this study and those of Freeman (2001) and Turano and Massof (2001), but also between the magnitude estimation method employed here and the matching task used by those studies (Freeman, 2001; Turano & Massof, 2001).

It has been suggested that the asymmetry in responding based on the relative direction of eye and background motion could be due to a response strategy based on relative motion between target and background stimulus on the retina (Freeman, 2001). Background and target movement in the same direction would cause less differential motion while background motion in the opposite direction to the target would be exaggerated on the retina. In this study eye velocity was entered into the model as an explanatory variable rather than the target velocity. Although it is possible that the participants were responding based on relative motion of target and background, studies where the target disappeared when the background stimulus appeared (Freeman, Champion, Sumnall & Snowden, 2009; Morvan & Wexler, 2009) suggest that participants still use an extraretinal estimate of their eye movement to help judge motion of the target and background.

Testing the effect of repetition suggested that the differences between age groups did not change with time and so could not be explained as effects of experience (Norman et al., 2003). For both horizontal and vertical motion, the effect of repetition did not interact with age group in determining the slope of response on eye or background velocity. With vertical background motion, age groups two and three demonstrated a decrease in response velocity with repetition while age groups one and four increased their response velocity with repetition. This was regardless of background or eye velocity and so had the effect of shifting the function relating response and eye velocity up or down but not changing it. While no other effects of repetition were significant with vertical background motion, the effect of increasing repetition with horizontal motion was to increase the estimate of the background speed and for a given background speed, make the slope of response on eye velocity more negative. This suggests that on average, participants in the study compensated less for eye movements as they repeated the task more. This could have been due to fatigue as the eyes were also shown to slow with repetition (*Chapter Three*), and suggests that the experimental time should be limited in future research.

It is interesting that the oldest age group in this study demonstrated different results for horizontal and vertical background motion. It must be noted however that although their predicted response velocities were different, the pattern of the means of their actual response velocities with horizontal and vertical motion were similar (Figure 5.3, Figure 5.7). This highlights the uncertainty of the results for this oldest age group. Due to the highly variable responding of two aged females whose data were removed, this age group retained the data of only four participants, less than the other three age groups. The range of eye movement speeds exhibited by the older participants was also limited compared to that of younger participants. The reduced pursuit gain of the oldest participants meant that at the highest target speed, their eyes did not move much faster than they did for the lower target speed. Such a restricted range of eye speeds accompanied by variable responding means that their regression fit for response against eye velocity should be interpreted with caution for the analyses of both horizontal and vertical motion. The study should be repeated with a larger group of older participants, a greater range of target speeds and a method that optimises pursuit accuracy in order to obtain more information for the oldest participants.

In saying this, the third group ranging in age from 45 to 54 years had more data and a larger eye movement range than age group four and still demonstrated decreased compensation ability compared to the younger two age groups for *both* horizontal and vertical motion. The similarity of the relationship between background and response for the first three age groups (Figure 5.2) suggest this effect is not due to a different response strategy for this group but rather could reflect the ability to compensate for eye movements.

Chapter Six
General Discussion

The aims of this study were to explore the effects of age on motion perception, smooth pursuit performance and the combination of the two processes. Smooth pursuit over a textured background will produce retinal stimulation opposing the eyes which has the potential to be perceived falsely as motion in the world rather than eye movement induced retinal stimulation. In order to perceive the actual motion of objects in the world uncontaminated by eye movement, the visual system needs to subtract an estimate of the eye velocity from the retinal motion (Perrone & Krauzlis, 2008; Souman et al., 2005a, 2005b, 2006). Changes in this ability with age were studied by having participants use a specially designed magnitude estimation method to record the perceived speed and direction of a field of moving dots while an eye tracker recorded their eye movements as they pursued a small moving target. It was found that the smooth pursuit of older adults from ~40 years of age was slower than that of their younger counterparts, especially at the higher target speed. When their eyes were practically still, the oldest age group of participants over 60 years demonstrated a tendency to overestimate speed of the background dot pattern compared to younger participants. This tendency decreased as background speed increased. Finally, the ability to compensate for the effects of eye movement on background motion perception was lower for participants aged between 40 and 54 than for younger participants. This also seemed to be the case for participants aged over 60 when viewing horizontal motion but not vertical motion. What could account for this pattern of results?

Response Strategy

It could be that the oldest participants were using a different response strategy compared to the younger participants. This could explain their different perceived speed of the background when the eyes were stationary and during smooth pursuit. Perhaps they were using the magnitude estimation method differently to the younger people. Their criteria for responding with a particular speed may have been lower and thus their responses would be higher for the same perceived speed. Participants were trained to respond based on six speeds of motion when the eye was stationary (0 – 16 °/s). The fastest of these speeds was not presented in the experimental sessions and so the highest response value should not have been used if responses were to be true to background speed. In fact, the mean response of the oldest participants did not reach the fastest speed when the eyes were stationary suggesting, like younger participants, they were applying the method properly and not stretching responses to match the scale given (Poulton, 1979). With stationary eyes and horizontal and vertical motion, all three lower age groups produced very similar relationships between background and response speed. The oldest age group also demonstrated similar relationships between response and background speed with horizontal and vertical retinal motion. This suggests consistency between participants in the use of the method and reliability of the measurement tool.

Relative Motion

During smooth pursuit, responding to background motion may have been based on the relative motion between target and background on the retina (Freeman, 2001; Freeman et al., 2009; Morvan & Wexler, 2009). The contribution of the retinal slip of the target to perceived speed of the background was confounded with the eye velocity; an increase in eye speed decreased the retinal slip. Older age groups pursued more slowly and thus had more retinal slip of the target. This means that differences between age groups in retinal slip of the target and/or extraretinal estimate of eye velocity could have contributed to the results reported. The decrease in compensation ability found for the participants aged between 40 and 54 years would suggest that their responses are closer to retinal motion of the background than the younger age groups. This is because with no compensation, motion perception is purely retinal (Haarmeier et al., 1997). Other studies of sensorimotor integration have suggested that vestibular and somatosensory signals break down with age making older adults more reliant on vision for controlling posture and locomotion (Anderson et al., 1998; Bugnariu & Fung, 2007; Cavanaugh, 2002). Greater reliance on vision rather than extraretinal estimates of eye movements in the present task should promote a retina based strategy of responding based on the relative retinal motion between the target and background stimulus (Freeman, 2001; Freeman et al., 2009; Morvan & Wexler, 2009). However, with such a strategy it would be expected that when background and target are moving with the same speed and direction and both are followed by the eyes, the response would be zero because there is no retinal motion. In these cases, the response of older adults, like the younger adults was not zero suggesting that they were using at least some extraretinal signal. In addition, compared to the younger observers the reduced pursuit gain of the older adults would cause more retinal slip of the target but it would also cause less retinal motion of the background stimulus. The relative motion of target and background should therefore be the same for young and older adults.

O'Connor, Freeman and Margrain (2008) have suggested that the extraretinal signal may be relatively preserved with age. This is supported by the narrowing of differences between age groups in the perceived speed of the background when it moves with the eye as found by the present study and that of Freeman et al. (2002). When the eyes are following the background stimulus, there is no retinal motion and so only an extraretinal signal can provide an estimate of background velocity. Since age differences are smaller in this case, this suggests little change in the extraretinal signal with age. Wertheim & Bekkering (1992) suggested that the over-compensation of older adults compared to younger adults in their study of the Filehne illusion could be due to older adults needing more time to build up a veridical retinal signal. In comparison, the results of the present study could be attributed to the over-estimation of the retinal signal of older adults compared to younger adults at the short duration. While this interpretation is consistent with the results of the retinal analysis for the oldest age group, it does not especially seem to be the case for the participants in the third age group. The third age group demonstrated reduced compensation ability compared to the younger two age groups but their relationship between background and response speed when the eyes were stationary was very similar to the younger participants.

Low Level Visual Function

Ageing is associated with functional loss at all levels of the visual pathway from the optical characteristics of the eye and the receptive capabilities of the retina through to the processing integrity of the cortex (Spear, 1993). These changes impact on low-level visual functions such as visual acuity and contrast sensitivity (Spear, 1993). These functions could in turn impact on motion perception and smooth pursuit. Generally older adults have difficulty viewing fine detail compared to younger adults (Spear, 1993). The minimum contrast required to perceive a stimulus of high spatial frequency (i.e. fine detail) is elevated in older observers (Snowden & Kavanagh, 2006). As such, objects containing high spatial frequencies, such as bars and dots will appear blurred to an older adult. Older observers also show elevated contrast thresholds for high temporal frequency stimuli suggesting a deficit in detecting rapid motion (Snowden & Kavanagh, 2006). Cataracts will also impact upon visual acuity and contrast sensitivity (Quillen, 1999) causing the blurring of a stimulus.

It could be that the results of the oldest age group were mediated by the reduced ability to see the stimulus associated with the mild cataracts of two of the observers. Indeed, the data of two other observers with cataracts was removed from the response analysis because they showed little relationship between the background motion and their responding. This was not the case with the remaining two observers who performed the task reliably suggesting their vision was not substantially impaired. However, the effect of cataracts can not be ruled out when interpreting the results of this group. This is a limitation of the present study and further research should be conducted to identify their influence. It is unlikely however that cataracts can explain the results of the second oldest age group.

Studies on motion perception have found deficits with age which could not be accounted for by reduced retinal illuminance, visual acuity or contrast sensitivity (Andersen & Enriquez, 2006; Atchley & Andersen, 1998; Betts et al., 2005; Bidwell et al., 2006; Gilmore et al., 1992; Habak & Faubert, 2000; Norman et al., 2003; Raghuram et al., 2005; Snowden & Kavanagh, 2006; Wojciechowski et al., 1995). Others have found age related differences despite both younger and older observers showing normal functional visual acuity (Bennett et al., 2007; Billino et al., 2008). Similarly, reduction in smooth pursuit ability with age has been found despite both younger and older participants having visual acuity

(Knox et al., 2005; Moschner & Baloh, 1994; Paige, 1994; Sharpe & Sylvester, 1978) and contrast sensitivity within the normal range (Kolarik et al., 2010)

These studies suggest that differences with age in motion perception and smooth pursuit stem more from changes related specifically to these functions than to more general low-level visual functions (Andersen & Enriquez, 2006; Atchley & Andersen, 1998; Betts et al., 2005; Billino et al., 2008; Gilmore et al., 1992; Habak & Faubert, 2000; Knox et al., 2005; Moschner & Baloh, 1994; Norman et al., 2003; Snowden & Kavanagh, 2006).

Neural Changes and Reduced Inhibition

While it is interesting to speculate on how neural changes with age may have contributed to the present results, the relationship between activity in cortical motion processing areas and the perception of motion speed and direction is still uncertain and is neither simple nor direct (Perrone, 2004; Perrone & Krauzlis, 2008). The following is therefore a discussion of whether the present results could be consistent with findings of age effects on neural processing reported in the literature. It is not intended to be anything more than speculation.

One of the main neural changes hypothesised to occur with age and impact upon motion perception is reduced inhibition and centre-surround suppression in motion processing cortical areas including area MT (Betts et al., 2005; Yang, Zhang et al., 2009). In the study of Betts and colleagues (2005), an increase in the size of a high contrast motion stimulus led to an increase in the direction discrimination threshold of young adults. This indicated to the authors that the motion processing neurons of young adults were being suppressed at high contrast as the size of the stimulus increased (Betts et al., 2005). At low contrast, direction discrimination thresholds decreased with size indicating spatial summation (Betts et al., 2005). For older adults thresholds decreased with size at low contrast but did not change with size at high contrast (Betts et al., 2005). This suggested weakened surround suppression for older adults (Betts et al., 2005). In the present study, the stimulus was a large pattern of random dots with a Weber contrast of 12.3 which can be considered high. Assuming that the findings of Betts et al. (2005) for direction discrimination ability could have an analogous effect on speed discrimination, the speed discrimination ability of older adults with a large high contrast stimulus might be expected to be better than that of young adults. This was indicated in the present study by a higher slope of response on background velocity for older observers at slower background speeds.

Yang, Zhang and colleagues (2009) suggested that ageing and the effects of lowering the contrast of a stimulus on the neural responding and perception of young monkeys may share their processes. They likened the broadening of speed tuning curves and the reduction in preferred speed of MT neurons in senescent monkeys to the effects of lowering the contrast of a stimulus on the speed tuning of young monkey MT neurons (Pack, Hunter & Born, 2005; Krekelberg, van Wezel & Albright, 2006). Yang, Zhang et al. (2009) suggested that both contrast and age effects may be mediated by lowered surround suppression. Pack et al (2005) found that neurons in young monkey MT which preferred high speeds at high contrast reduced their preferred speed at low contrast and increased the bandwidth of their tuning curve. These neurons also seemed to be more strongly surround suppressed than others as indicated by correlation between preferred speed and neural change in responding with increasing size and contrast; "neurons with strong surround suppression decrease their responses to large stimuli as contrast is increased" (Pack et al., 2005, p.1812). Krekelberg et al. (2006) also found that the preferred speed in area MT is decreased at low contrast.

Due to these response changes, Pack et al (2005) and Krekelberg et al (2006) predicted that, based on the pattern of responding for a population of MT neurons, speed should be overestimated for low contrast as compared to high contrast stimuli. In the present study, participants aged over 60 years overestimated speed compared to the younger age groups; an effect which lessened as stimulus speed increased. These results could be consistent with the suggestion of Yang, Zhang et al. (2009) that lowering the contrast of a stimulus and ageing affect the responding of MT and speed perception in similar ways. However, most psychophysical studies report that the speed of a stimulus appears to decrease as contrast is lowered (Thompson, 1982; Krekelberg et al., 2006).

This prediction is also not consistent with the results of the third age group whose relationship between perceived and actual speed was much the same as the younger two age groups. This suggests that centre-surround suppression might not be affected in this group. Yang, Zhang et al. (2009) were able to predict the speed discrimination thresholds of old and young monkeys based on the response properties of their MT neurons. As they point out, the thresholds they found were similar to those reported in the study of Snowden and Kavanagh (2006) with human subjects. In both studies, thresholds increased with age (Snowden & Kavanagh, 2006; Yang, Zhang et al., 2009). However, demonstrated and predicted discrimination thresholds for both young and old subjects were less than one degree per second (Snowden & Kavanagh, 2006; Yang, Zhang et al., 2009). Since this was the smallest difference in speed used for stimuli in the present study, the third age group may have demonstrated deficits consistent with reduced inhibition that were not large enough to be detected by the method used.

Centre surround antagonism may also be involved in the ability to compensate for eye movements. As Tadin and Blake (2005) point out, reduced surround suppression may impact negatively on the ability to " "ignore" background motion" when making eye or head movements (p.326). It is possible that this could account for the greater Filehne illusion exhibited by older age groups in the present study. Pack et al. (2001) have developed a model of pursuit compensation using the centre surround relationships of MT and MST neurons. Like MT, neurons in MST can be classified on the basis of their responding to large and small motion fields (Pack et al., 2001). The dorsal part of MST is well suited to the motion of large patterns such as a background stimulus while the ventral neurons of MST prefer small objects like a moving target (Pack et al., 2001). In the model of Pack et al. (2001), the MT neurons project to the MST neurons with similar spatial relationships. Ventral MST neurons preferring motion in the same direction as the pursuit target are connected to dorsal MST neurons which respond to large field motion opposite the pursuit target direction (Pack et al., 2001). This is because large field motion opposite the pursuit target is consistent with pursuit in the direction preferred by the ventral MST neuron (Pack et al., 2001). Two such partnerships between ventral and dorsal neuron populations preferring pursuit in opposite directions compete for control of smooth pursuit eye movements and motion perception through inhibitory connections (Pack et al., 2001).

The Filehne illusion is explained by Pack et al. (2001) as being due to the firing of ventral MST neurons to the motion of the background stimulus on the retina. Perceived speed is proportional to the neuronal activity (Pack et al., 2001). Most of the responding is inhibited by the ventral cells responding to the pursuit direction as these cells are bolstered by MST dorsal neurons responding to the background and an efference copy of the eye movement (Pack et al., 2001). The marginal firing of the ventral neuron which is not inhibited is seen as the background motion of the Filehne illusion (Pack et al., 2001). If older observers have reduced inhibition, then it is not surprising that these relationships could be altered with age. Weakened inhibition and surround suppression should have the effect of increasing firing of these MSTv neurons relative to younger adults. This would have the effect of increasing the response of ventral MST neurons to the large background stimulus. This increased response in the opposite channel to pursuit movement should be seen as a greater Filehne illusion, as found in the present experiment for the older age groups. While participants aged between 40 and 54 demonstrated reduced compensation ability than younger adults for all speeds of vertical and horizontal background motion, those participants aged over 60 demonstrated less compensation for horizontal motion but more compensation for vertical motion. As mentioned previously, the results of this oldest group need to be interpreted with caution as their range of eye movement speeds was not very large and the effect of cataracts on motion perception can not be ruled out.

The model of Pack et al. (2001) is also relevant to pursuit gain when following a target over a background stimulus. The same activity in the MSTv neurons in the opposite channel to pursuit direction which is perceived as the Filehne illusion should provide competition for those MSTv neurons in the same direction as pursuit and slow down the eye movement (Pack et al., 2001). However, the MSTv cells driving pursuit inhibit this command in the opposing direction in order to maintain the eye movement (Pack et al., 2001). If older adults have less inhibitory capacity, the competing MSTv activity should not only be higher but should not be suppressed as much and pursuit gain should decrease. This agrees with the suggestion of Kolarik et al (2010) that there may be differences with age in the ability to suppress the reflex to follow background motion with the eyes when pursuing a target. While older adults in this study demonstrated reduced pursuit gain, there were no significant differences between age groups in the effect of the background on pursuit. The failure to analyse pursuit gain before and after the background exposure meant that differing effects of background on eye movements for the age groups can not be ruled out. Further research should be conducted to assess any such differences. Since in the model of Pack et al. (2001) the perceived speed of the target is bolstered by the efference copy and MSTd cells encoding background motion reflective of accurate pursuit, it could also be interesting to explore age-related changes in not only the pursuit speed across different backgrounds but the perceived speed of the target.

Attention and Processing Speed

It is also possible that differences in attentional functioning with age could have affected the results. It becomes more difficult with age to divide attention between two concurrent sources of information in general (Woodruf-Pak, 1997) and in motion processing tasks (Tsotsos, Sekuler & Bennett, 2009). In the present task, participants would have had to divide attention between pursuing the target and noticing the speed and direction of background motion. This suggests that the results of the present study could have been influenced by differences in divided attention with age. Dividing attention has been shown to impair smooth pursuit maintenance (Hutton & Tegally, 2005). The lowered pursuit gain of the older adults may thus have been due to less effective attentional allocation. The possible influence of differential cortical motion processing with age discussed previously, may in fact be mediated by differences in attentional ability. There is evidence that attention can modulate activity in human areas MT and MST (Beauchamp, Cox & deYoe, 1997; Corbetta, Miezin, Dobmeyer, Shulman & Petersen, 1991; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997) and alter the centre-surround relationships of MT neurons (Anton-Erxleben, Stephan & Treue, 2009).

Effects of attention are generally considered to be mediated by the frontal cortex via 'top-down' control of sensory processing (Greenwood, 2000). The frontal lobe has been suggested to be an area of the brain particularly affected by ageing (Greenwood, 2000). However, Greenwood (2000) suggests that rather than this hypothesis of localised degradation, ageing effects can be better explained as reductions in the efficiency of relationships between cortical areas due to wear and tear of connections between neurons. Myelin around the axons carrying messages between neurons increases the speed and efficiency of neural communication (Peters, Moss, & Sethares, 2000). It has been suggested that a breakdown in myelin with age is linked to general slowing of information processing and cognitive decline with age (Peters et al., 2000; Salthouse & Madden, 2008) and prolonged reaction time to motion onset (Porciatti et al., 1999). It has also been linked to prolonged transfer of information within and between cortical areas in monkey visual cortex (Peters et al., 2000; Wang et al., 2005). Wang et al (2005) suggest that functions provided by higher order cortical areas should not only be disrupted from delays but that the delays imposed on inputs coming from different cortical areas should be desynchronised with age. Prolonged excitation or inhibition of neurons could be induced by this desynchronisation (Peters et al., 2000).

Greenwood (2000) suggests that because functions involving more than one lobe of the brain would likely require long myelinated connections between lobes, these are the functions likely to be more affected by ageing. This is consistent with the hypothesis of Habak and Faubert (2000) that tasks requiring extended and complex cortical processing are those which show greater impairment with age. The compensation for eye movements is one such function. Integrating retinal and extraretinal information is hypothesised to use an efference copy of the eye movement command to subtract eye movement induced retinal stimulation from that occurring in the world (Perrone & Krauzlis, 2008; Souman et al., 2005a, 2005b, 2006). Along with the brainstem where smooth pursuit eye movements are generated, a proposed origin of the efference copy is the frontal eye fields in the frontal cortex which “may reflect a more cognitive “memory” of target velocity” (Pack et al., 2001, p.113).

If connections between brain areas begin to degrade with ageing this could explain the reduction in compensation for eye movements found for the adults aged between 40 and 54 at the very brief stimulus duration used. Wertheim and Bekkering (1992) and Freeman and colleagues (2002) found that the perception of the Filehne illusion for older adults was more similar to that of younger adults at a longer duration. Like these studies, the present study also found difference between age groups at a brief duration. This suggests that if participants are tested at a longer duration the gap between younger and older participants should narrow.

Links to Schizophrenia and Alzheimer's Disease

Support for the impact of reduced inhibition and attention on the effective motion processing of higher cortical areas may come from studies on schizophrenia and Alzheimer's disease. Both these conditions have been linked to impairments in motion processing and eye movements (Gilmore et al., 1994; Hong et al., 2009). Weakened surround suppression and degradation of GABA systems have been linked not only to ageing but to schizophrenia (Tadin et al., 2006). As with older adults, schizophrenic patients demonstrate less change in direction discrimination thresholds for a high contrast stimulus as size increases when compared to healthy young adults (Tadin et al., 2006). Schizophrenia has been associated with low pursuit gain (Ross et al., 1999), abnormal motion perception (Bidwell et al., 2006) and decreased ability to reconcile extraretinal eye and retinal motion signals (Hong et al., 2009; Lindner et al., 2005). Bidwell et al. (2006) suggested that schizophrenia and ageing share neural changes in GABA such that adults with schizophrenia do not show deterioration of velocity discrimination with age as their inhibitory ability is already affected.

Reduced inhibition, attention and processing speed have been linked to optic flow processing impairments demonstrated by older adults with Alzheimer's Disease (Kavcic & Duffy, 2003; Mapstone et al., 2008; Thiyagesh et al., 2009). Thiyagesh and colleagues (2009) found reduced activation of higher motion processing cortical areas in patients with Alzheimer's disease when viewing radial flow and suggest that this “could be explained by impaired 'top-down' attentional modulation” (p.115). In a study by Mapstone et al. (2008) heading discrimination thresholds were increased in older adult controls and persons with Alzheimer's Disease as compared to younger adult controls when the radial flow stimulus was surrounded by coherent motion moving away from the direction of heading (i.e. if heading was to the left of the centre of the screen then surrounding motion was rightwards). The authors suggest that these older adults demonstrated a greater illusionary shift in heading direction (which mediated the increase in thresholds) due to weakened centre-surround antagonism in MT or MST (Mapstone et al., 2008). They go on to propose that in normal older adults this centre-surround deficit is related to the reduction in inhibitory feedback from the frontal cortex

(Mapstone et al., 2008). With this reduction comes damage to these motion processing areas via hyperactivity that may be involved in the development of Alzheimer's Disease (Mapstone et al., 2008), a condition associated with parieto-occipital cortical pathology, decreased motion processing ability and visuospatial disorientation (Gilmore et al., 1994; Kavcic, Fernandez, Logan & Duffy, 2006; Kavcic, Ni, Zhu, Zhong & Duffy, 2008; Mapstone et al., 2008; Tetewsky & Duffy, 1999). Alzheimer's disease is associated with reduced ability to process optic flow important for heading, navigation and spatial orientation (Mapstone et al., 2003; O'Brien et al., 2001). Such global pattern motion processing shares area MST with the compensation for eye movements (Andersen et al., 1997; Bradley et al., 1996). This shared neural loci and the deficits of patients with AD in motion perception and tracking eye movements (Gilmore et al., 1994) suggests that their ability to compensate for eye movements is likely to be impaired. This could be an interesting topic for future study.

The commonalities between ageing, schizophrenia and Alzheimer's disease highlight the importance of disentangling the normal effects of age on perception to those linked more closely to neural pathology. With refinement to reduce testing time and improve tracking ability, the method used in the present study could become a valuable clinical tool for assessing motion processing, tracking eye movements and the compensation for eye movements which share higher-level cortical processing.

Limitations

Although links have been made between the present study and the literature regarding age effects on motion perception, centre-surround antagonism, inhibition and the perceptual consequences of schizophrenia and Alzheimer's disease, the limitations of the present study must be borne in mind making any such connections equivocal. This is especially the case for the oldest age group of which the results regarding compensation for eye movements were uncertain.

Limitations of the present study include the small and unequal sample sizes for each age group and the failure to randomly select participants from the population. The generalisability of cross-sectional studies such as the present one to the effects of ageing are limited (Kerber et al., 2006). Although differences may be found between age groups, it is not necessarily the case that these differences will be found between ages for the same people. The generalisability of the present results are not only limited by the cross-sectional design and convenience sampling used but also by the model fitting. The number of parameters in each model may reduce their generalisability to other samples (Pitt & Myung, 2002). While model parameters were chosen based on theory, it is possible that the final models chosen are specific to the data set at hand, especially since the amount of data for each age group was relatively small. Model diagnostics suggested that assumptions regarding normality and homoscedasticity of the residuals and random effects were also violated in several cases. While random effects are likely to be biased in these cases, inference based on the fixed effects in linear mixed models has been demonstrated to be robust to such violations (Jacqmin- Gadda, Sibillot, Proust, Molina & Thiébaut, 2007; Verbeke & Lesaffre, 1997; Zhang & Davidian, 2001). It would perhaps be prudent in future modelling to use an alternative to the normal distribution for the assumptions regarding the residual error and random effects. Estimates of the slopes for each age group are sensitive to the differences in variances between age groups, however, the estimate of the difference between the slopes based on age group is robust (Jacqmin-Gadda et al., 2007). Similarly, multicollinearity between variables such as linear effects and their quadratic polynomials is likely to bias estimates of the fixed effects and inflate their standard errors (Bonate, 1999; Shieh & Fouladi, 2003). This would have the effect of rendering one or more of the covariates non-significant (Bonate, 1999; Shieh & Fouladi, 2003). This is unlikely to have influenced age effects in the present study as the change in log-likelihood associated with the age effects reported was always significant. While age effects were found in the present study, extrapolation and prediction based on the reported models to other ages and background or eye velocities is not recommended. The study should be repeated with a larger and more representative sample of adults of all ages to help verify the results.

Despite these limitations the analyses suggest that further study of the patterns of age effects highlighted is both justified and needed as understanding of age effects on motion perception has practical consequences.

Practical Implications and Future Research

Altered speed perception, slowed smooth pursuit and the possibility that there is a reduced ability to compensate for eye movements with age are likely to have implications for the everyday tasks of older adults. Similarly the results of the oldest age group highlight the possible influence of cataracts on motion perception. Although the present study was conducted with a very short background stimulus duration, this may be typical of real life perception during self motion where many eye movements are made alternating between saccades which jump between interesting objects to the tracking motion of the eyes following salient stimuli (Grigo & Lappe, 1999). Grigo and Lappe (1999) suggest that the “normal sampling of the optic flow field consists of only 300-550 ms” (p.2090) between saccades. Impaired compensation ability for older adults at a short duration may be expected to impact on self-motion perception; following a moving object with the eyes while navigating would impair the ability to detect the direction of heading by introducing spurious background motion (Banks et al., 1996; Royden et al., 1992; Royden et al., 1994; Stone & Perrone, 1997; van den Berg, 1993; Warren & Hannon, 1988). Since the ability to perceive motion has been linked to motor vehicle accident risk (Raghuram & Lakshminarayanan, 2006) and difficulty with driving (Conlon & Herkes, 2008; Raghuram & Lakshminarayanan, 2006) in the elderly, reduced compensation ability could further impact upon driver safety in this population. Similarly, the role of motion perception in postural stability means that its alteration with age could impact upon falls in the elderly (Cavanaugh, 2002).

The possible perception of motion with eye movements would likely contribute to feelings of dizziness (Haarmeier et al., 1997) which is itself a considerable source of complaint for elderly New Zealanders (Matheson, Darlington & Smith, 1999b). Fortunately, training may improve motion perception of older adults (Ball & Sekuler, 1986) while visual speed of processing and attentional training of older adults has shown lasting results that can carry over into enhanced daily living including driving performance (Ball, Edwards & Ross, 2007). This highlights the potential for eye movement compensation ability to be improved with practice.

The findings of the present study have highlighted interesting and important avenues for further research.

- Firstly, the ability to compensate for eye movements in observers over the age of 60 years needs to be clarified. This could be achieved by increasing the range of motion of eye movements for this age group by improving the pursuit task. The acceleration of the pursuit target could be ramped to improve acquisition while the speed of the target could be extended to increase the maximum speed of the eyes.
- The contributions of eye velocity as compared to target velocity in the compensation for eye movements could be disentangled by having the target disappear during the background exposure (Freeman et al., 2009; Morvan & Wexler, 2009).
- Further research could determine whether age differences are better explained in terms of speed or distance judgements (Snowden & Kavanagh, 2006) by varying the duration of background exposure between trials.
- Studies on ageing and motion perception have demonstrated gender effects where older females perform worse than males (Atchley & Andersen, 1998; Billino et al., 2008; Gilmore et al., 1992; Norman et al., 2003; Raghuram et al., 2005; Snowden & Kavanagh, 2006). This study was not designed to test gender effects and so their possible influence is unknown. This could be a subject of future research.
- The role of processing speed in changes with age could be examined by assessing whether age differences transfer to longer durations.
- The possible contribution of centre-surround relationships of motion processing neurons to age effects could be considered by varying the contrast and size of the background stimulus (Betts et al., 2005; Betts et al., 2009) and assessing the perceived speed of the pursued target (Pack et al., 2001).
- The method used in the present study could be developed for use with clinical populations. A first study might assess a potential reduction in the ability of persons with Alzheimer's disease to compensate for eye movements.

Conclusion

The importance of motion perception for guiding self-motion necessitates an understanding of its changes with normal ageing. Ageing could affect the processing of the retinal image and the comparison of retinal and eye movement signals by the visual system at higher cortical motion processing areas. An understanding of relative contributions to impaired motion perception in the older adult could lead to interventions for improving mobility and independence. It could also improve knowledge on the underlying neuropathology and genetic risk for schizophrenia and Alzheimer's disease. The findings of this thesis provide a step towards improving such an understanding.

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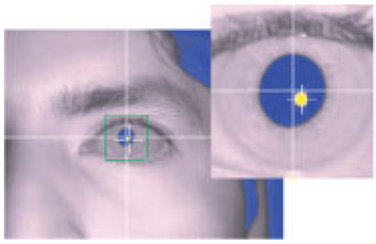
Appendix A. Advertisement

Participants Needed

Eye Movement Compensation Over Age

People **aged from 17 to 80+** are needed to take part in a study measuring how motion is seen while moving the eyes.



- This is a graduate research study. It involves using a computer mouse to judge the direction and speed of background dots presented while a target dot is followed by the eyes. Participants' eye movements will be monitored by an eye tracker.

Participation is expected to take **between 30 and 50 minutes**.

Reimbursement - Participants will receive either a $10 book voucher or, if first year Psychology students, can receive 1% course credit.

All data will be confidential with access limited to the researcher and supervisor.

Please contact me with any questions.

Kirstyn Rawley (kmr31@waikato.ac.nz), Room J.1.23

Supervisor: Assoc Prof. John Perrone, (x8292)
jpnz@waikato.ac.nz

Appendix B. Questionnaire

Questionnaire **Participant:**

Thank you for your time. Please complete this questionnaire. Do not answer any questions that make you feel uncomfortable.

Gender: (Please circle) M F

Age: Please tick the box corresponding to your age.

17 – 19		40 – 44		65 – 69	
20 – 24		45 – 49		70 – 74	
25 – 29		50 – 54		75 – 79	
30 – 34		55 – 59		80 +	
35 – 39		60 – 64			

Ocular and General Health

Do you have any problems with your eyes or any other health problems that affect your vision or eye movements? Please tick the boxes or make a note in the 'Other' section (this could include conditions such as Schizophrenia or medication such as sedatives):

Ocular		**General**	
Cataracts		Diabetes	
Macular degeneration		Dizziness (on more than one occasion over the past month)	
Glaucoma			
Other			

Appendix C. Standardised instructions.

Thank you for agreeing to take part in this experiment. You are free to leave at any time without explanation.

Training Condition – Part one: Demonstration

You will see a bright blank screen flashed. A cross will then appear in the centre of a dark screen. This cross will change to a large dot, please keep your eyes on this dot and try not to blink. A background pattern of dots will appear very briefly. All of the dots in this pattern will be moving together to the right. After the dot pattern disappears a screen will appear with a series of circle outlines out from the centre. The circles are meant to be used as a type of ruler for speed. You will see the computer move a cross to the circle which best represents the motion of the dots seen. The cursor is placed to the right because the dot pattern is moving towards the right. The cross is at the centre of the screen when the dot pattern is not moving at all. You will see the computer demonstrate where the cursor should be for each speed of dot motion starting with no motion and getting faster. This will be repeated twice. You will then see the same procedure but with any speed presented on each trial i.e. random order. This will be repeated twice.

Training Condition - Part two: Practice with Feedback

Now that you have seen the computer demonstrate the method please have a go at it yourself. Any speed of dot motion could be presented on each trial. Please keep in mind the speeds of the dots you saw earlier and the circle to which they corresponded. Because the circles are meant to be used as a ruler for speed you may click between the circles if you think the motion did not correspond exactly to what you saw earlier. If you are not sure, please just guess. Move the cursor to where you think is best and click the left mouse button once to record your response. The computer will then show you the correct response with a hand-shaped cursor and the next trial will begin. Please keep your eyes on the large dot and try not to blink while the background dot pattern is being presented. You may move your eyes while making your response.

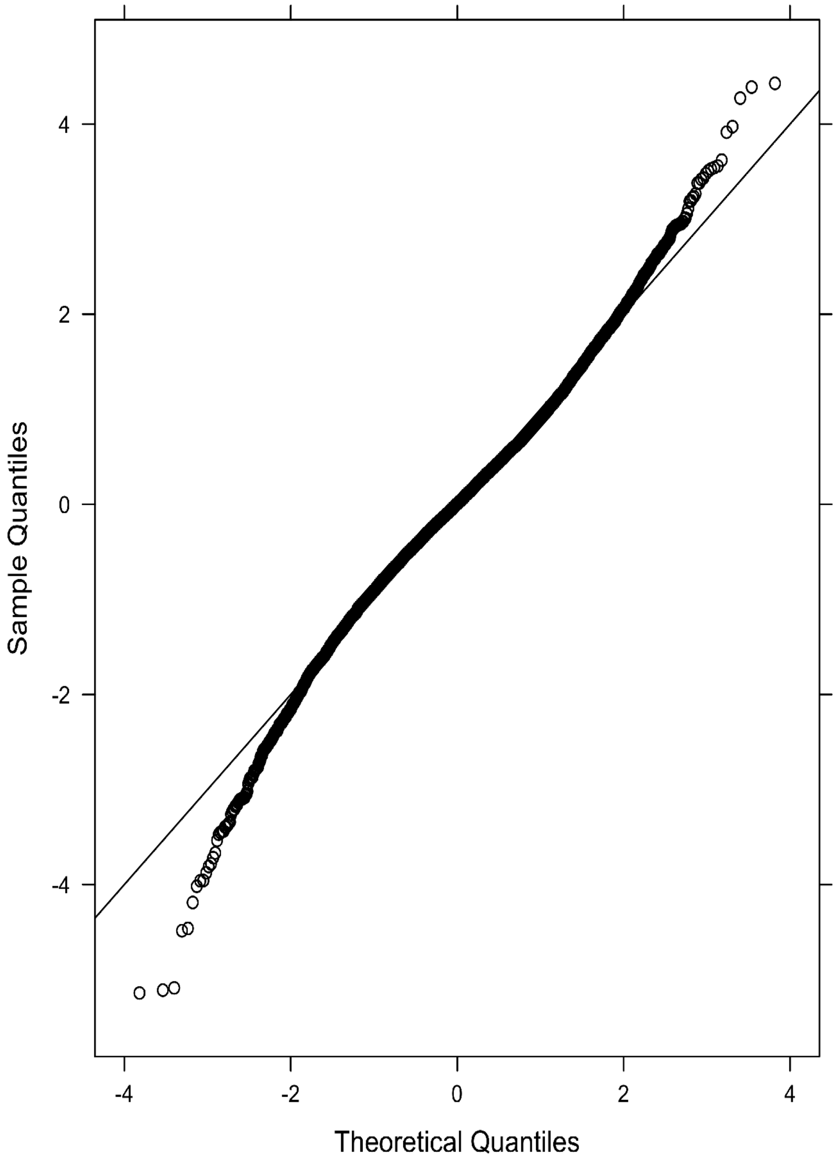
Training Condition - Part three: Practice without Feedback

Now we will do the same as before but the computer will not show you the correct response after each trial. Please remember that you may click between the circles and if you are unsure just to guess.

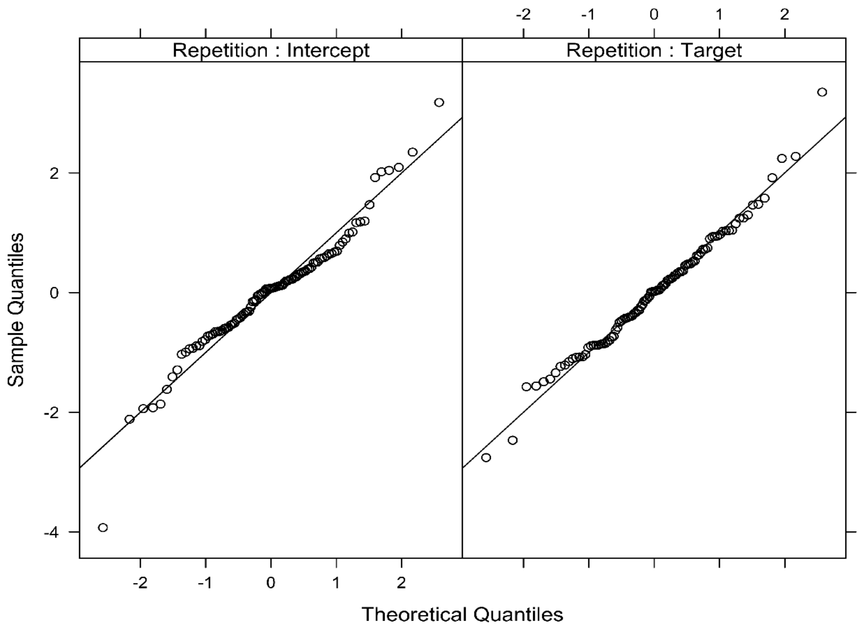
Experimental Condition

Now that you are familiar with the method we will move on to the experiment. In this part the large dot will either remain stationary in the centre of the screen or it will disappear and reappear to the left or the right of the centre of the screen. It will then move either towards the right or the left. Please keep your eyes on this large dot at all times and follow it with your eyes when it moves. While your eyes are on this larger dot, the pattern of smaller background dots will appear. You will need to judge the motion of the pattern of smaller background dots as you did earlier using the circles as a ruler. Remember you can click on or between the circles depending on how fast you think the dots are going. You will also need to judge the direction you see them moving in. To judge the direction you click either on or between the circles at an angle out from the centre. For example, if you saw the dots move to the right click to the right of the centre or if you saw them move upwards click up from the centre. You may move your eyes while making your response. Please blink only while responding or if you need to, when the cross is in the centre of the screen or the blank white screen is on. Please do not blink when the large dot is on. Please do not judge the speed and direction of the dot you are following with your eye, only judge the background dot pattern.

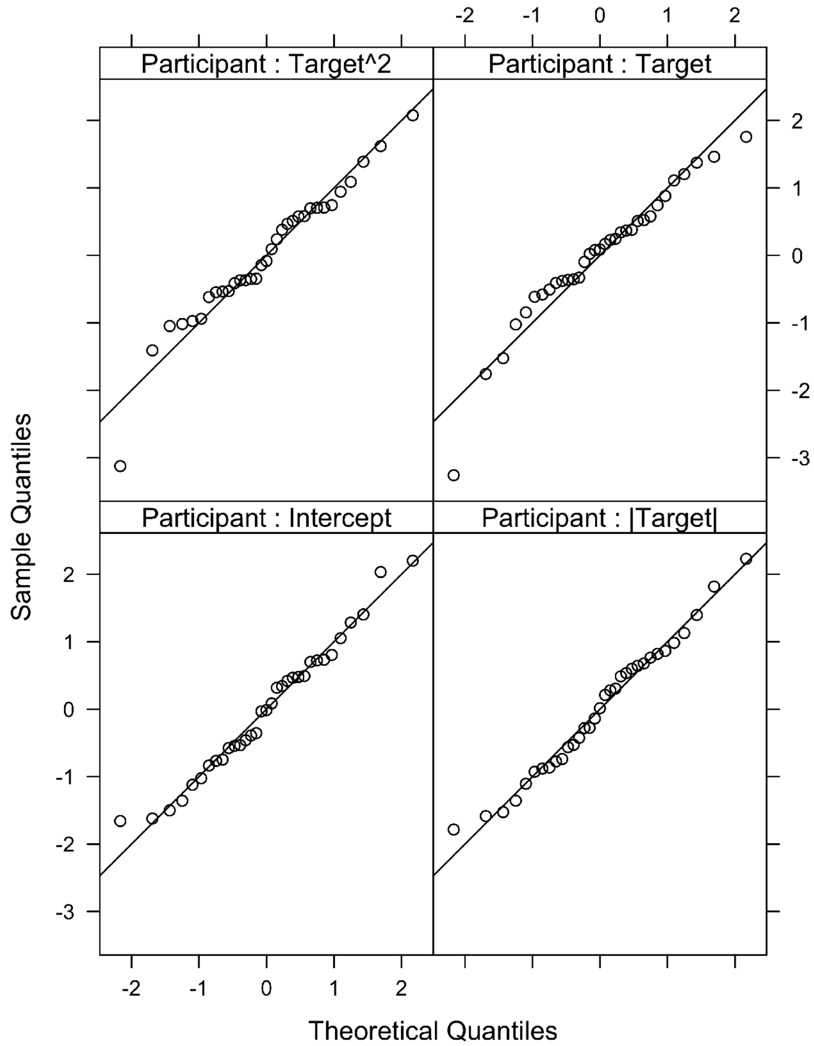
Appendix D. QQ-plot of the normalised residuals for the final model representing pursuit gain.



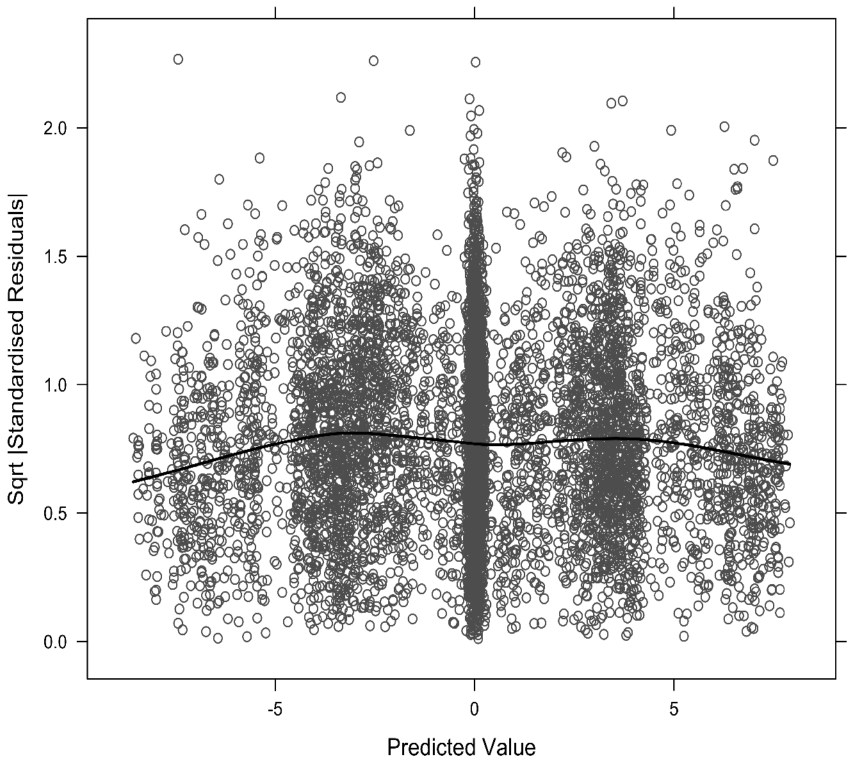
Appendix E. QQ-plots of the random effects for repetition within participant in the model representing pursuit gain. 'Target' is the slope of eye velocity on target velocity.



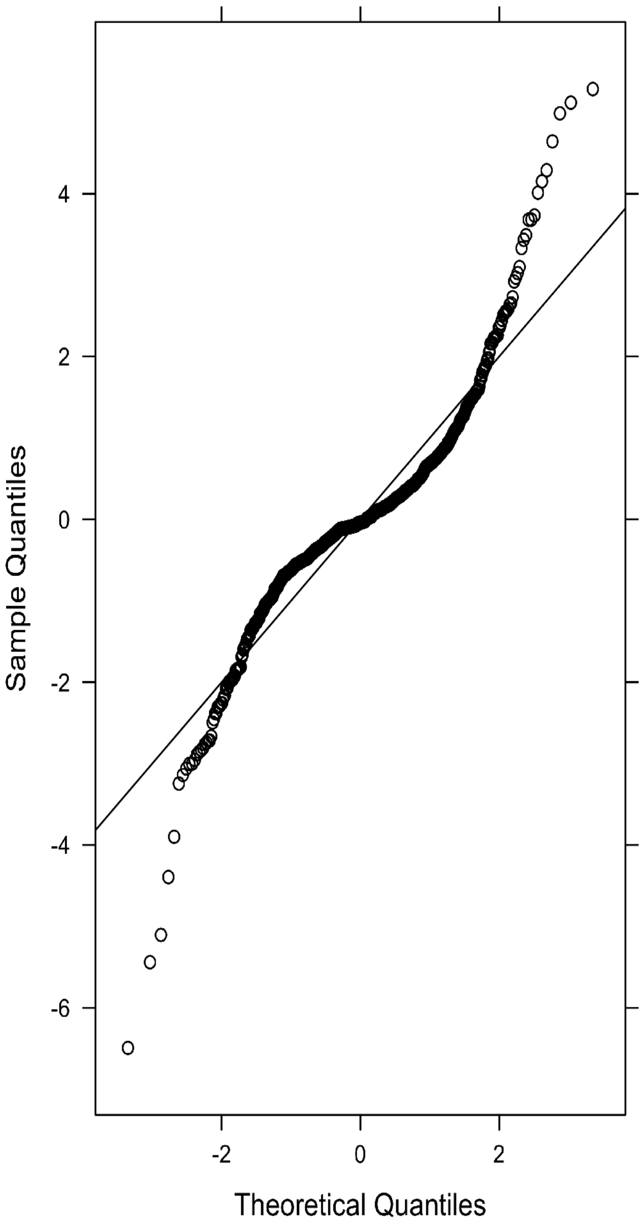
Appendix F. QQ-plots of the random effects for participant in the model representing pursuit gain. 'Target' is the slope of eye velocity on target velocity, '|Target|' is the slope of eye velocity on the absolute value of target velocity and 'Target^2' is the slope of eye velocity on the signed value of target velocity squared.



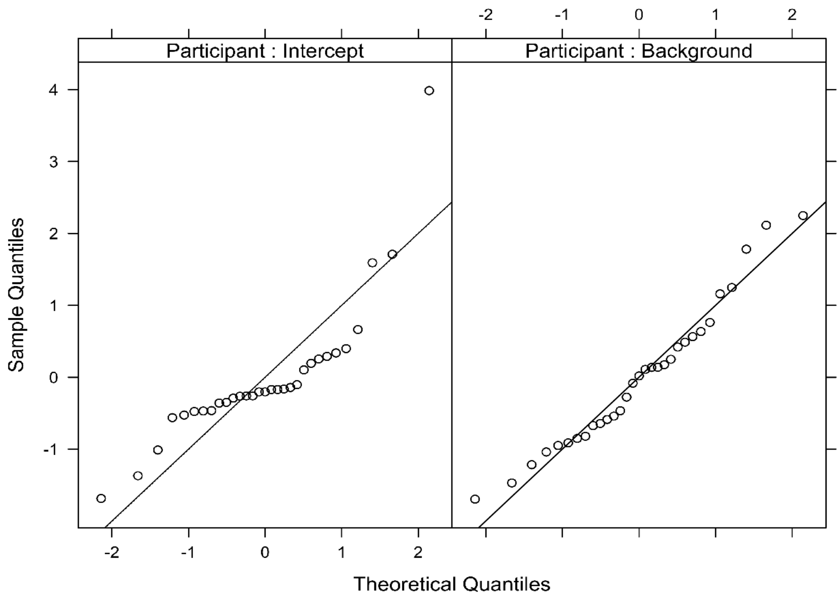
Appendix G. Plot depicting variance of the residuals for the model representing pursuit gain. Shows the square root of the absolute value of the standardised residuals against the predicted values of the model. The 'flatness' of the line is used to indicate homogeneity of variance.



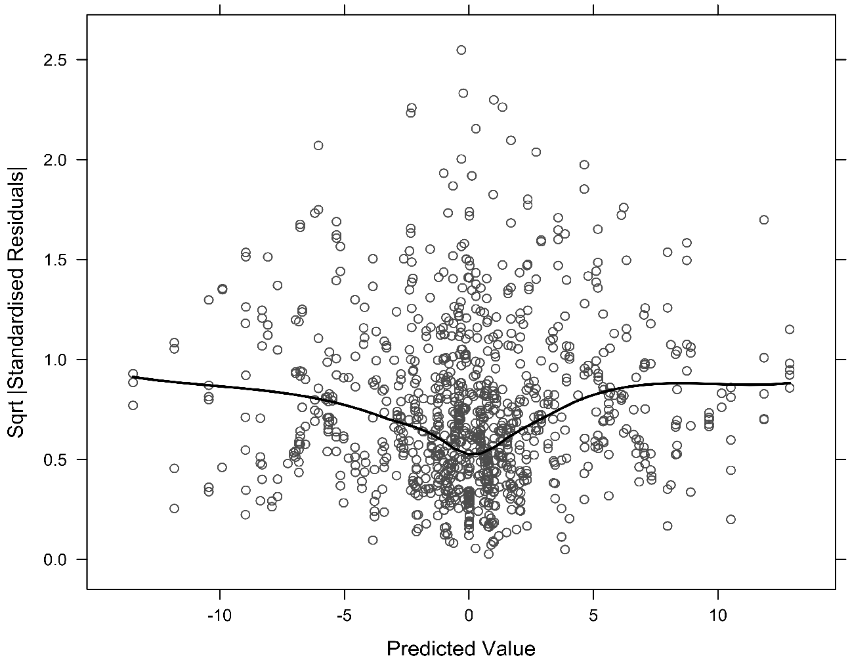
Appendix H. QQ-plot of the normalised residuals for the final model representing horizontal retinal motion perception.



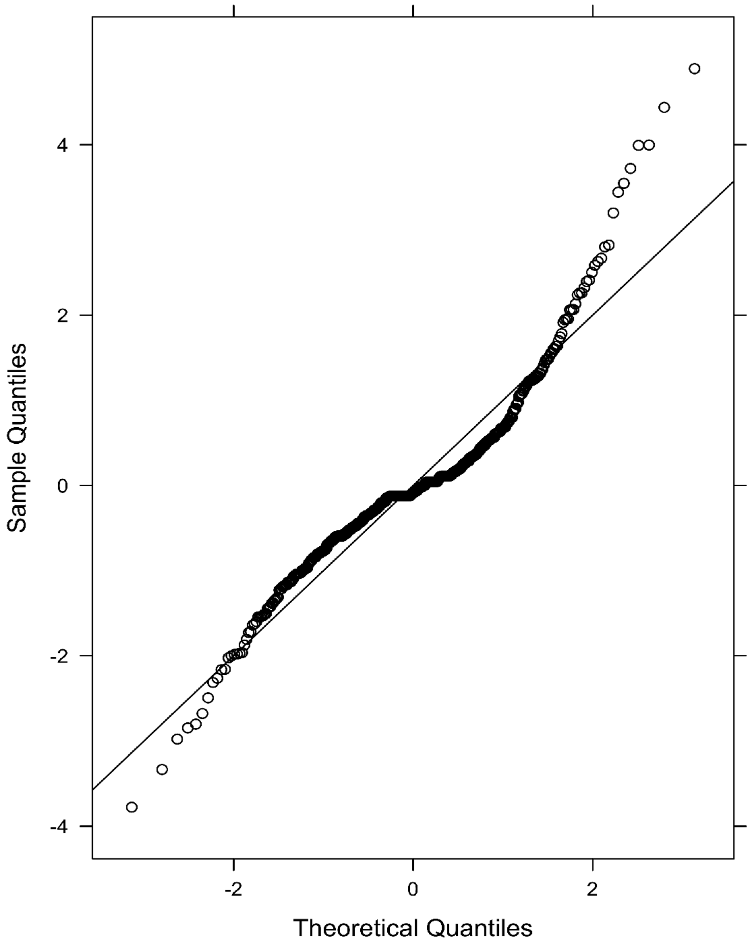
Appendix I. QQ-plots of the random effects for participant in the model representing horizontal retinal motion perception. 'Background' is the slope of response velocity on background velocity.



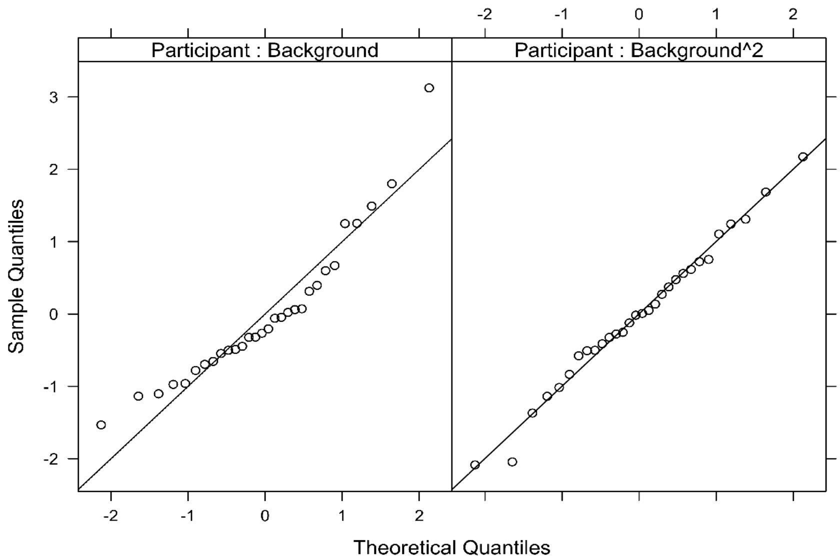
Appendix J. Plot depicting variance of the residuals for the model representing horizontal retinal motion perception. Shows the square root of the absolute value of the standardised residuals against the predicted values of the model. The 'flatness' of the line is used to indicate homogeneity of variance.



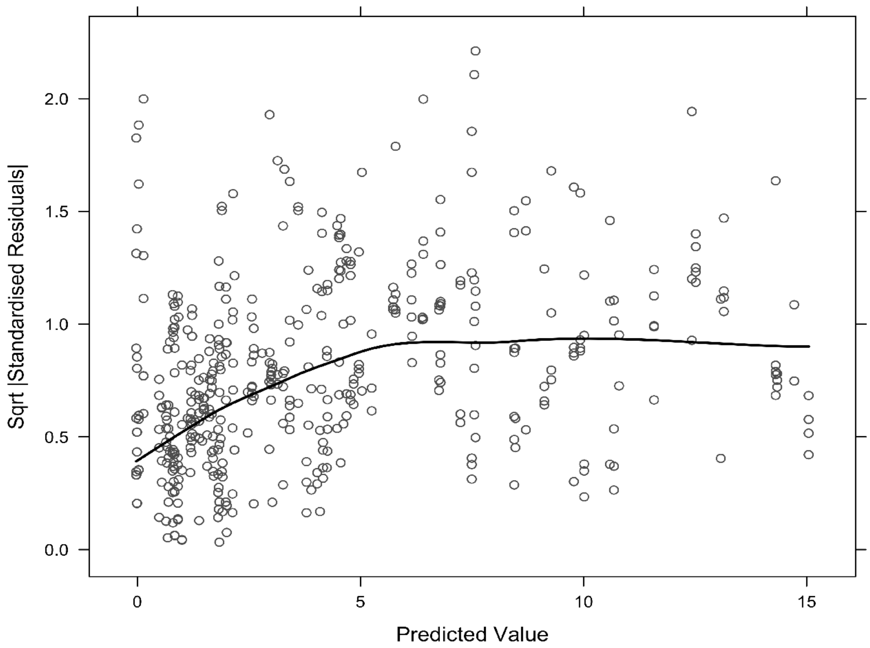
Appendix K. QQ-plot of the normalised residuals for the final model representing vertical retinal motion perception.



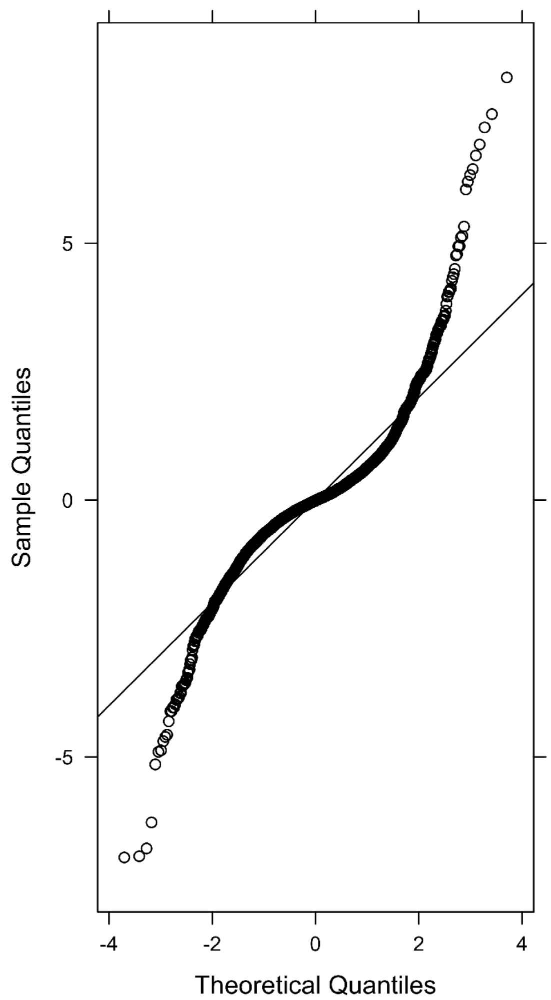
Appendix L. QQ-plots of the random effects for participant in the model representing vertical retinal motion perception. 'Background' is the slope of response velocity on background velocity while 'Background^2' is the quadratic term for background velocity.



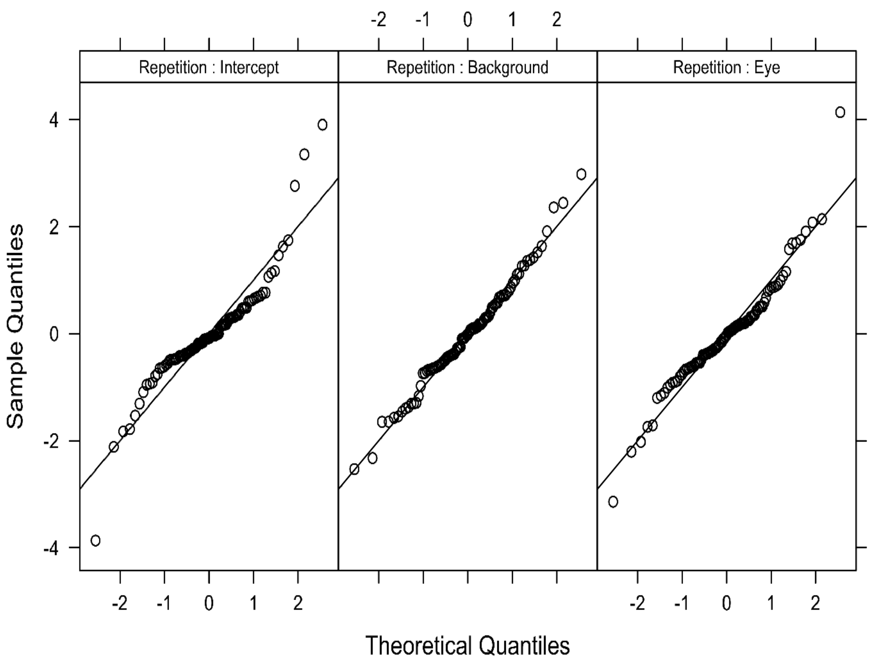
Appendix M. Plot depicting variance of the residuals for the model representing vertical retinal motion perception. Shows the square root of the absolute value of the standardised residuals against the predicted values of the model. The 'flatness' of the line is used to indicate homogeneity of variance.



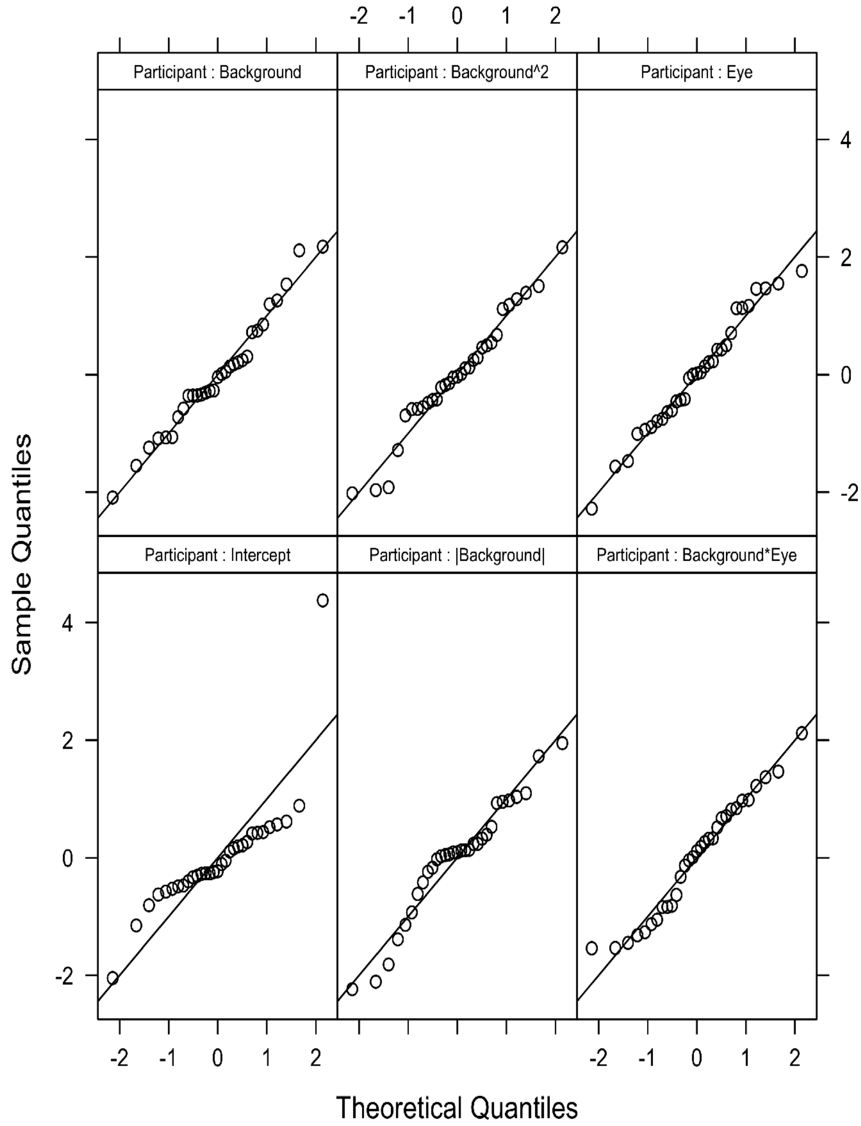
Appendix N. QQ-plot of the normalised residuals for the final model representing compensation for eye movements with horizontal motion.



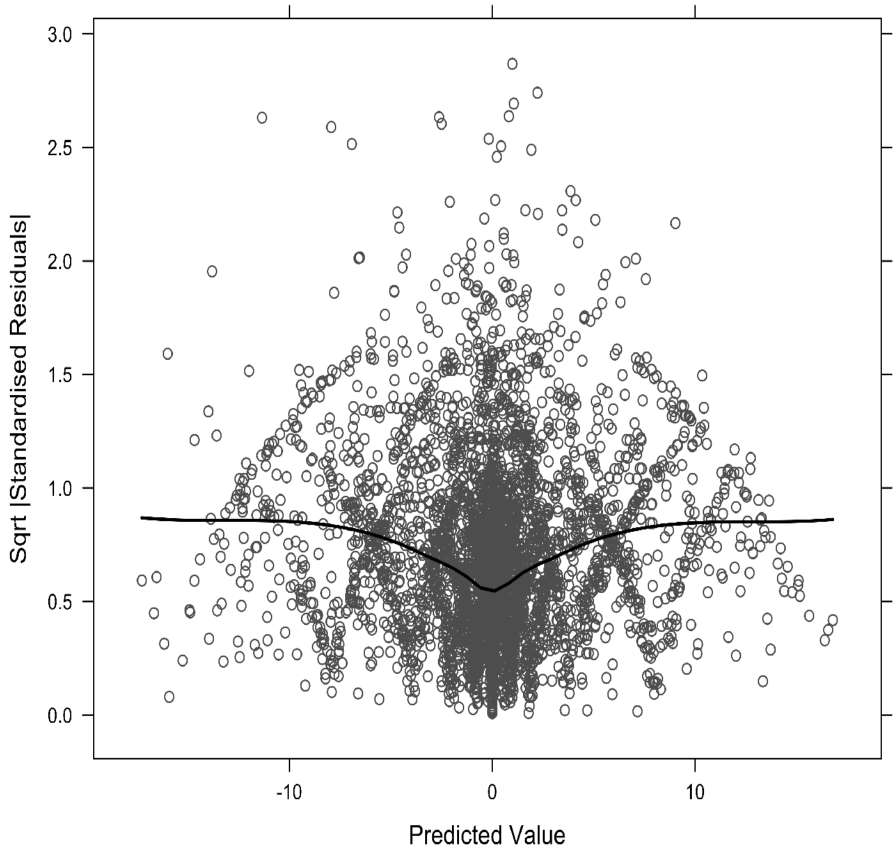
Appendix O. QQ-plots of the random effects for repetition in the model representing compensation for eye movements with horizontal motion. 'Background' is the slope of response on background velocity while 'Eye' is the slope of response on eye velocity.



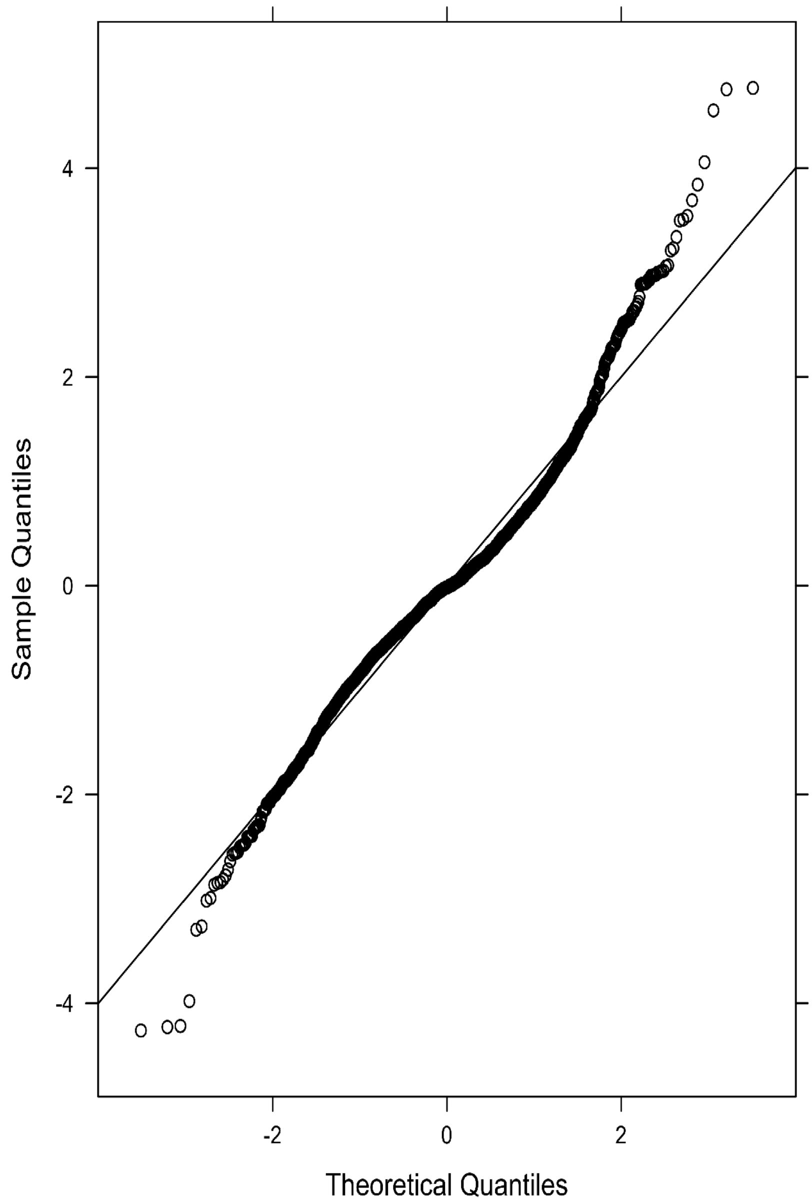
Appendix P. QQ-plots of the random effects for participant in the model representing compensation for eye movements with horizontal motion. 'Background' is the slope of response on background velocity, 'Background^2' the quadratic background term, '|Background|' the absolute value of background velocity and 'Eye' the slope of response on eye velocity.



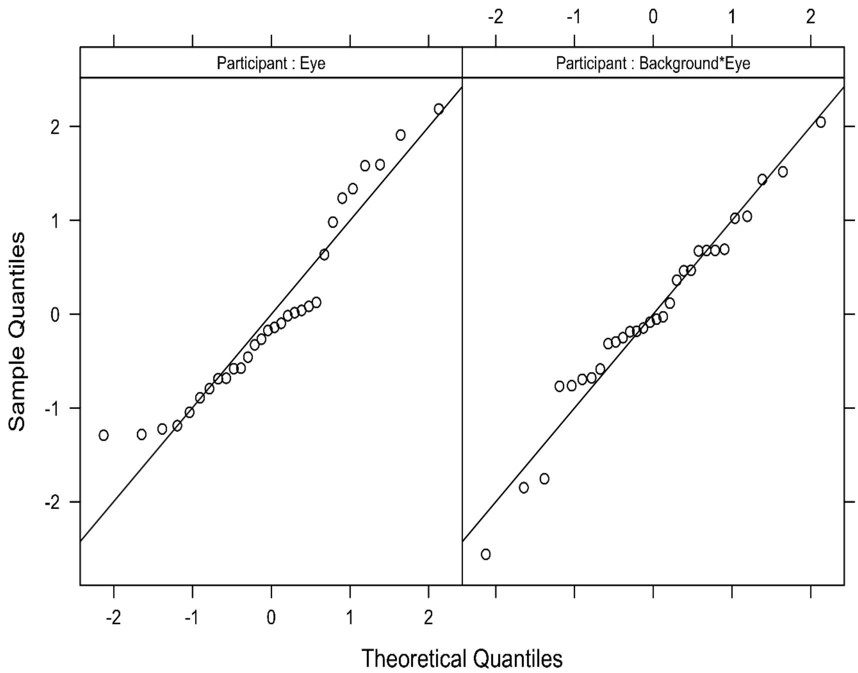
Appendix Q. Plot depicting variance of the residuals for the model representing compensation for eye movements with horizontal motion. Shows the square root of the absolute value of the standardised residuals against the predicted values of the model. The 'flatness' of the line is used to indicate homogeneity of variance.



Appendix R. QQ-plot of the normalised residuals for the final model representing compensation for eye movements with vertical motion.



Appendix S. QQ-plots of the random effects for participant in the model representing compensation for eye movements with vertical motion. 'Eye' is the slope of response on eye velocity while 'Background*Eye' is the interaction between background and eye velocity.



Appendix T. Plot depicting variance of the residuals for the model representing compensation for eye movements with vertical motion. Shows the square root of the absolute value of the standardised residuals against the predicted values of the model. The 'flatness' of the line is used to indicate homogeneity of variance.