Complex visual processing in older adults

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Abstract

Declines in performance on complex visual tasks have been shown to predict declines in functional independence and mobility in older adults, but the specific perceptual processing mechanisms that decline with age and lead to functional declines are not well understood. Two measures of perception shown to predict functional outcomes (e.g. safe driving) in older adults are measures of the Functional Field of View (FFOV) and of global coherent motion. Age-related change in capacity for the deployment of visual attention and sensitivity of the sub-cortical magnocellular (M) pathway were hypothesised to explain the FFOV and motion processing in older adults. The thesis therefore had four aims: 1) to investigate differences in the capacity of older and younger adults to use bottom-up and top-down attention in the performance of a FFOV task; 2) to investigate the association between FFOV performance and the sensitivity of the M pathway, particularly in older adults; 3) to investigate differences in the capacity of older and younger adults to use top-down attention to facilitate the perception of coherent motion; 4) to investigate the association between motion coherence thresholds and the sensitivity of the M pathway, particularly in older adults.

Study 1 (Chapter 4) aimed to explore how manipulating attentional demands impacted the error rates for a FFOV task in older adults, and how the effect of age on the FFOV varied under different attentional conditions. A specially designed FFOV task with differing levels of bottom-up and top-down attentional demands was conducted using a sample of 42 younger (*M* = 27.38 years, *SD* = 5.41 years, 21 women) and 42 older (*M* = 72.11 years, *SD* = 5.92 years, 23 women) adults. Older adults had higher error rates in all conditions and the effect of age did not vary across conditions indicating similar capacity to attend to and ignore salient peripheral stimuli in older and younger adults. The performance cost of dividing attention between central and peripheral vision in the older group indicated older adults narrowed the focus of attention for an attentionally demanding central task, at the expense of accuracy on the peripheral task. The results indicate that the need to compensate for reduced sensory processing by manipulating the focus of attention contributes to reduced FFOV efficiency in older adults.

Study 2 (Chapter 5) investigated the degree to which FFOV performance (from Study 1) could be explained by the sensitivity of the M pathway. FFOV error rates and contrast sensitivity thresholds were measured for 44 younger (*M* = 27.18 years, *SD* = 5.40 years, 22 women) and 44 older (*M* = 72.18 years, *SD* = 5.82 years, 23 women) adults. Contrast sensitivity was measured using the steady and pulsed pedestal task (Pokorny & Smith, 1997). Older adults performed more poorly on all measures. In older adults, M pathway contrast sensitivity explained a significant proportion of variance in FFOV error rates. These findings support the hypothesis that rapid bottom-up visual attention is reliant on M pathway input, at least in older adults.

Study 3 (Chapter 6) investigated differences in coherent motion thresholds between older and younger men and women, in the presence and absence of a top-down attentional cue. In addition, the extent to which motion coherence thresholds could be explained by sensitivity of the M pathway was explored. Motion coherence thresholds were measured for 40 younger (*M* = 26.05 years of age, *SD* = 5.47 years, 20 men, 20 women) and 35 older (*M* = 72.11 years of age, *SD* = 5.92 years, 17 men, 18 women) adults using a dot motion task in which half the dots were white and half were black. In conditions with no attention cue, motion coherence thresholds were higher in older than younger adults and higher in women than in men. Addition of a cue alerting participants to which dots (black or white) contained the coherent motion signals, improved coherence thresholds for younger women and older men, but not for younger men and older women. The cue helped younger women form a coherent percept of motion but was redundant for younger men. The absence of improvement in older women may reflect resource limitations. Perception of coherent motion is more demanding for women and may require increased top-down attention, which will impact older women because older adults have limited top-down attentional resources. Differences in motion coherence thresholds within the older group, and between younger and older adults, were associated with increased contrast discrimination thresholds in the M and P pathways suggesting that with the tasks used in the current study, reduced coherent motion perception in older adults, is not simply attributable to a reduction in sensory sensitivity specific to the M pathway.

The results indicate that the FFOV and motion coherence tasks assess different perceptual processes that change with age and are impacted in different ways by changes in visual attention and the sensitivity of the M pathway. These findings are important given the increasing proportion of older adults in modern society who rely on functional vision for mobility and independence.

Statement of Originality

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Garry Power

May 2017

STATEMENT OF ETHICAL PROTOCOL

I confirm that ethical clearance was granted by the Griffith University Human Research Ethics Committee (GU Ref No: PSY/C2/08/HREC). I confirm that the research was conducted in accordance with the approved protocols.

Garry Power

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Acknowledgement of Published Papers Included in this Thesis

Included in this thesis is a paper in Chapter 4, which is co-authored with another researcher. This publications is in accordance with Section 9.1 of the Griffith University Code for the Responsible Conduct of Research ("Criteria for Authorship"), Section 5 of the Australian Code for the Responsible Conduct of Research, and Section 9.3 of the Griffith University Code ("Responsibilities of Researchers"). An acknowledgement of my contribution to each co-authored paper is outlined at the front of the relevant chapter with the publication status and bibliographic details (where relevant). Appropriate acknowledgements of those who contributed to the research but did not qualify as authors are included in each paper.

Included in this thesis is a paper in *Chapter 4* which is co-authored with other researchers. My contribution to the co-authored paper is outlined at the front of the relevant chapter. The bibliographic details for this paper including all authors, are:

Power, G. F., & Conlon, E. G. (2017). Perceptual processing deficits underlying reduced FFOV efficiency in older adults. *Journal of Vision, 17*, 4-4. doi:10.1167/17.1.4

18th May, 2017

Garry Power

(Countersigned) ____________________________ (Date)______________

Principal Supervisor: Elizabeth Conlon

Chapter 1: General introduction

1.1 The importance of functional vision for older adults

Individuals in late adulthood (over 65 years of age) make up an increasing proportion of the population in many countries around the world (Gerland et al., 2014; Healey, 1999; World Health Organisation, 2011). For example, the Australian population aged over 65 years is projected to rise from 3.2 million (14% of the population) in 2012 to approximately 10 million (24% of the population) in 2061 (Australian Bureau of Statistics, 2013). This is a worldwide phenomenon confronting most developed and developing nations (United Nations, Department of Economic and Social Affairs, Population Division, 2015) with the proportion of the world's population aged over 65 projected to almost double between 2010 and 2050, and the proportion aged over 85 projected to grow by 350% over the same period (World Health Organisation, 2011). In developed countries, life expectancy has increased in a linear trend since 1840 at a rate of approximately 3 months per year (2.5 years per decade), and there is no indication of an end to this trend in the latest data (Christensen, Doblhammer, Rau, & Vaupel, 2009). Initially this was driven by a reduction in infant mortality, but is now driven by older adults living longer (Christensen et al., 2009). As evidence, the probability that someone who reaches age 80 will live on and reach 90 years of age more than doubled between 1950 and 2002 in developed countries: the probability increased from 12% to 25% for men, and from 16% to 38% for women (Rau, Soroko, Jasilionis, & Vaupel, 2008).

Given that increasing numbers of individuals are surviving into their 70's, 80's and 90's, research into factors impacting the quality of life for these older adults is becoming increasingly important. Functions such as mobility and confidence affecting control over one's physical environment are major determinants of both physical and psychological well-being among older adults (Knight, Davison, McCabe, & Mellor, 2011; Montpetit & Tiberio, 2016; Webber, Porter, & Menec, 2010). An important contributor to both mobility and the capacity to interact effectively with one's environment is the ability to use the visual system to monitor objects and orient oneself while undertaking different tasks (Leat & Lovie-Kitchin, 2008). Even very basic and well-practised tasks in daily life require effective visual monitoring of the environment (Land, Mennie, & Rusted, 1999). It is therefore not surprising that, while aging is often associated with a range of physical and cognitive declines, changes in vision are also associated with functional decline in older adults (Laforge, Spector, & Sternberg, 1992; Sloan, Ostermann, Brown, & Lee, 2005). Specific visual functions such as acuity and contrast sensitivity are associated with independently, efficiently, and easily performing activities of normal daily living such as shopping, preparing meals, and self-care (Haymes, Johnston, & Heyes, 2002; Rubin, Roche, Prasada-Rao, & Fried, 1994). Falls and hip fractures, which can have profound impacts on the lifestyle of older adults, are more common in those with impaired vision (Ivers et al., 2003; Lord & Dayhew, 2001; Reed-Jones et al., 2013). One of the strongest associations that has been found is between measures of visual processing and the capacity of older adults to continue safely driving a motor vehicle (Agramunt et al., 2016; Ball et al., 2006; Owsley et al., 1998).

The influence of age-related change in visual processing for safe driving in older adults has been selected as the focal point for this thesis. Driving is not only important to older adults as a means of maintaining their independence (Marottoli et al., 2000; Ragland, Satariano, & MacLeod, 2005); in many ways, the capacity to continue to safely drive serves as a proxy for general functional independence and quality of life. The ability to drive safely requires physical mobility, cognitive capacity including reasoning skills, and adequate visual and auditory perception, (Anstey, Wood, Lord, & Walker, 2005). If the capacity to safely drive is compromised, an older person may well require major adjustments to living arrangements and substantially increased support from family and society (Marottoli et al., 2000; Wahl, Iwarsson, & Oswald, 2012). A failure to identify the need to restrict or stop driving may come at a high price both to the older person and to others if an accident is the result, particularly as older drivers have higher risks of serious injury and fatality as a result of accidents due to their increased frailty (Koppel, Bohensky, Langford, & Taranto, 2011; G. Li, Braver, & Chen, 2003; Wang & Abdel-Aty, 2008). Accidents are also a rich source of data for the analysis of possible functional consequences of reduced visual processing as the details of accidents are often objectively and meticulously recorded by official bodies such as police and transport authorities (Oxley, Fildes, Corben, & Langford, 2006).

A considerable body of research has identified key predictors of driving difficulties in older adults (Anstey et al., 2005; Dickerson, Meuel, Ridenour, & Cooper, 2014). Among the many tasks investigated, measures of the Functional Field of View (FFOV) have frequently been found to be among the best predictors of driving performance (Anstey et al., 2005; Clay et al., 2005; Wood & Owsley, 2014). The FFOV (also referred to as the Useful Field of View, UFOV) is defined as the visual field within which two tasks can be completed simultaneously without the aid of head or eye movements (Mackworth, 1965; Sanders, 1970). It is typically assessed by presenting a central identification task with a simultaneous peripheral localisation task, often with the addition of peripheral distractors. In older adults, poor performance on a test of the FFOV has been shown to be associated with more frequent motor vehicle accidents (Ball, Owsley, Sloane, Roenker, & Bruni, 1993; Ball et al., 2006; Cross et al., 2009; De Raedt & Ponjaert-Kristoffersen, 2000; Owsley, Ball, Sloane, Roenker, & Bruni, 1991; Rubin et al., 2007), more errors in driving assessment tasks both on the road (Anstey & Wood, 2011; Classen, Wang, Crizzle, Winter, & Lanford, 2013; De Raedt & Ponjaert-Kristoffersen, 2000; Wood, 2002) and in simulated driving tests (Eramudugolla, Price, Chopra, Li, & Anstey, 2016), and with poor performance on a driving hazard detection task (Anstey, Horswill, Wood, & Hatherly, 2012).

Prominent among other measures associated with driving difficulties in older adults are contrast sensitivity and motion perception. Reduced capacity for motion perception in older drivers, often measured by tests of the capacity to detect coherent motion in a dot motion display, has been shown to predict on-road driving performance (De Raedt & Ponjaert-Kristoffersen, 2000; Wood, 2002), simulated driving performance (Eramudugolla et al., 2016), self-reported driving difficulties (Conlon & Herkes, 2008), and hazard perception (Lacherez, Au, & Wood, 2014). Reduced contrast sensitivity has also been found to predict increased risk of motor vehicle crashes (Agramunt et al., 2016; Ball et al., 1993; McGwin, Owsley, & Ball, 1998), driving test performance (Baldock, Mathias, McLean, & Berndt, 2007; Henderson, Gagnon, Collin, Tabone, & Stinchcombe, 2013; Wood, 2002), and in particular, self-restriction of driving in older adults (J. Davis, Conlon, Ownsworth, & Morrissey, 2016; Freeman, Munoz, Turano, & West, 2006; Keay et al., 2009).

To date, much of the research on visual measures that relate to driving difficulties for older drivers have been motivated by the need to identify the subset of older adults who are at sufficiently increased risk to warrant restriction or removal of their licence to drive. However, while the literature reviewed indicates that these measures can identify increases in crash risk, reviews of the current evidence suggest they cannot be used as a pass/fail indication of fitness to drive: too many drivers would unnecessarily be prohibited from driving (Bédard, Weaver, Dārzin, & Porter, 2008; Jim Langford, 2008). An alternative, but equally important, focus in this area of research is to explore the components of visual processing mechanisms that may contribute to age-related change in these measures, and how these may be linked to the visual processing requirements for safe driving, and other functional outcomes in the lives of older adults. This is the focus of the current thesis.

Much of the literature on the FFOV uses the commercially available “UFOV Test” developed by Ball and colleagues (Ball & Owsley, 1993). The UFOV Test includes the standard central identification task and peripheral localisation task as well as optional presentations allowing for the addition of peripheral distractors and increasing the complexity of the central task. For all variations of the task, performance is measured by the minimum stimulus duration required for an observer to achieve 75% accuracy on the peripheral localisation task on trials for which the central identification task is also performed correctly. As a result, poor performance on this task is frequently described as a reduction in an individual's speed of processing (Owsley, 2013). There has been little research undertaken to establish the reasons for the reduced efficiency of the FFOV in older adults.

However, the FFOV as originally conceived is a measure of the allocation of visual attention (Mackworth, 1965; Sanders, 1970). It involves the requirement to attend centrally to the identification of an object, and simultaneously attend peripherally to detect the location of a peripheral target. The fact that some observers require a longer stimulus duration to successfully perform the task does not necessarily indicate that they are distinguishable from others simply by having a reduced processing speed. Longer stimulus durations required by older adults may reflect other changes in the mechanisms used to reach a perceptual decision, not merely a slowing in these processes. For example, the pre-attentive processing of stimulus features, which would ideally operate in parallel across the FFOV and provide efficient guidance of bottom-up attention to the peripheral target (Wolfe, 1994, 2014), may be less efficient in older adults for a number of reasons, such as reduced sensory sensitivity, or more internal neural noise. These or other age-related changes could lead to compensatory changes in attentional strategies such as greater reliance on top-down control (Whiting, Sample, & Hagan, 2014). Each of these alternative explanations could account for the need for a longer exposure to the stimulus before a perceptual decision threshold is reached. There is evidence in support of such changes in the neural system of older adults. Older adults have been shown to rely more heavily on top-down control of attention, and to recruit additional neural resources to compensate for less efficient sensory processing and bottom-up guidance of visual attention (S. W. Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; L. Li & Zhao, 2015; Madden, Spaniol, Bucur, & Whiting, 2007; Madden, Whiting, Cabeza, & Huettel, 2004; Madden, Whiting, Provenzale, & Huettel, 2004; Whiting et al., 2014). When sensory-driven mechanisms fail to provide bottom-up attentional capture, leading to the need for increased top-down guidance of visual search to locate a target, search efficiency is reduced (Wolfe, 2014). Older adults are also known to have increased internal neural noise in visual processing areas of the brain (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Yang, Liang, Li, Wang, & Zhou, 2009), and reduced signal-to-noise ratios can contribute to the need for more time to make perceptual decisions (Eckstein, 1998).

In addition, changes in capacity for visual attention and/or increased internal neural noise could also explain why older adults perform more poorly on motion perception tasks used to link motion perception to driving performance. Motion perception is typically measured in such studies by the signal-to-noise threshold required to identify a coherently moving set of signal dots presented among randomly moving noise dots (Conlon & Herkes, 2008; Eramudugolla et al., 2016; Lacherez et al., 2014; Wood, 2002). Both internal neural noise and changes in the allocation of visual attention have been argued to impact motion coherence thresholds in such dot motion tasks (Bennett, Sekuler, & Sekuler, 2007; Conlon, Brown, Power, & Bradbury, 2015; Conlon, Lilleskaret, Wright, & Power, 2012; Yang, Zhang, et al., 2009). Identifying the mechanisms that contribute to age-related change on measures of the FFOV and coherent motion perception may shed light on the mechanisms which also contribute to older adults having reduced capacity for safe driving (and other functional declines associated with these visual processes).

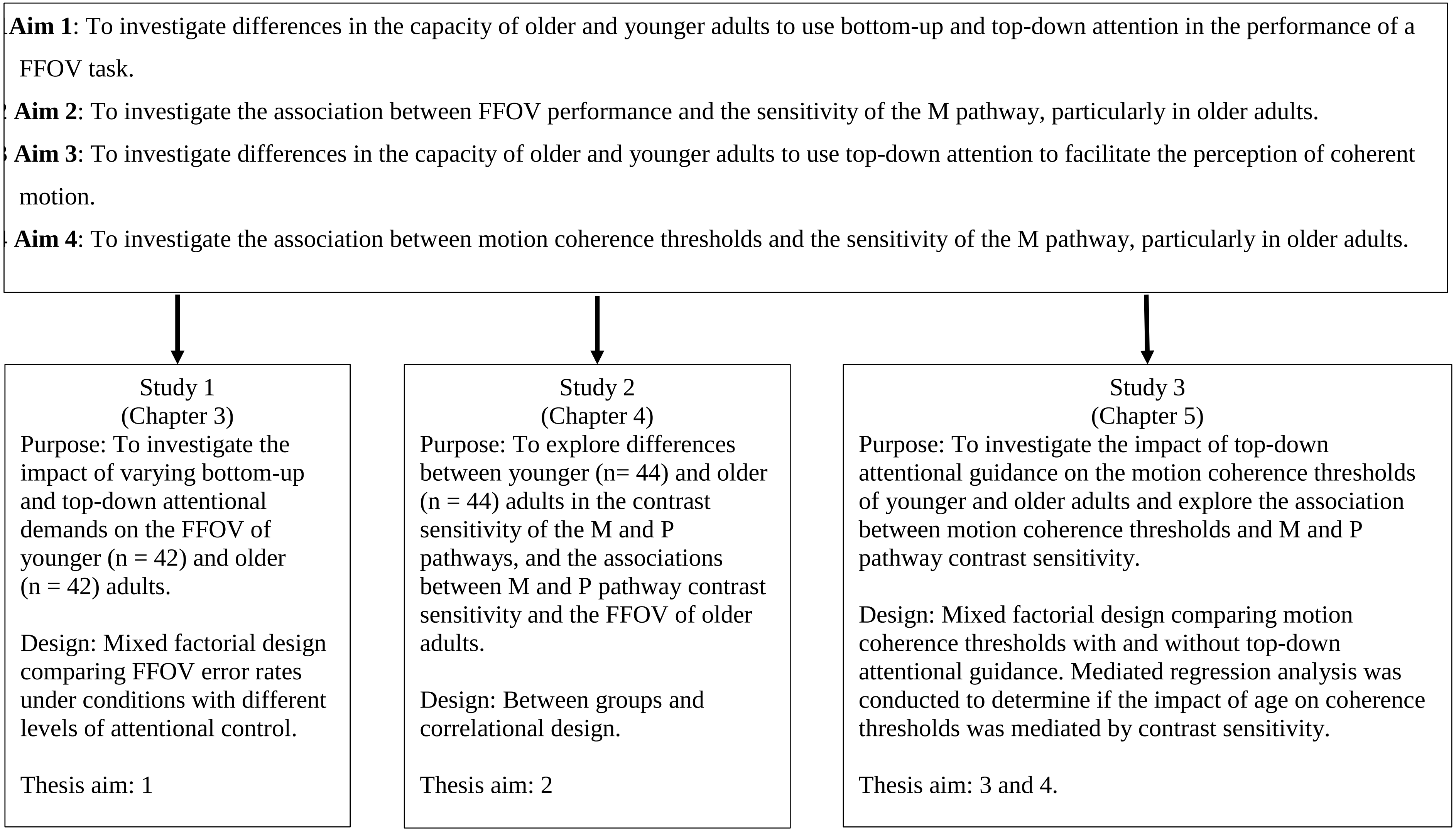
Contrast sensitivity, the other predictor of driving performance highlighted above, may also be related to mechanisms that explain FFOV performance and coherent motion perception in older adults. Older adults are well known to have reduced contrast sensitivity compared to younger adults, and this is understood, in part, to reflect age-related changes in the neural processing of vision (D. Elliott, Whitaker, & MacVeigh, 1990; Owsley, Sekuler, & Siemsen, 1983; Owsley & Sloane, 1987). Contrast sensitivity is a feature of neurons throughout the visual system, and is a key distinguishing characteristic of the sub-cortical Magnocellular (M) and Parvocellular (P) pathways that, along with the Koniocellular (K) pathway, link the retina to the primary visual cortex of the brain. The M pathway is maximally sensitive to low levels of contrast, and its response saturates at higher levels of contrast, whereas the P pathway responds poorly to low contrast, but remains responsive at high contrast (Kaplan & Shapley, 1986). More importantly, the M pathway is thought to provide important, though not exclusive input to the dorsal visual processing stream which carries and processes visual information from V1 in the occipital cortex to the posterior parietal cortex (Nassi & Callaway, 2009). The dorsal stream is understood to rely heavily on rapid transmission of input along the M pathway to process both visual motion (Braddick et al., 2001; Livingstone & Hubel, 1988; Merigan & Maunsell, 2009) and to guide the rapid deployment of sensory driven, bottom-up attention (Bullier, 2001; Vidyasagar, 1999). Indeed, the dorsal stream is understood to be responsible for the processing of vision for action in general: a process that equips individuals to interact dynamically with the surrounding environment (Milner & Goodale, 1995). However, there have been few attempts to gain empirical evidence in support of the association between M pathway processing and dorsal stream functions such as rapid allocation of visual attention and motion processing (Goodbourn et al., 2012).

This thesis, therefore, has four aims (see Figure 1.1). First, to investigate the differences in the capacity of older and younger adults to deploy bottom-up and top-down attention when performing a FFOV task. Second, to investigate the association between

FFOV performance and the sensitivity of the M pathway, particularly in older adults. Third, to determine whether there are differences in the capacity of older and younger men and women when using top-down attention to facilitate the perception of coherent motion. Finally, this thesis aimed to assess the association between motion coherence thresholds and the sensitivity of the M pathway, particularly in older adults. These aims and the ways in which they are linked across the three experimental studies reported in this thesis, are shown in Figure 1.1.

1.2 Summary of thesis chapters:

Chapters 2 and 3 present a general literature review in order to provide a theoretical context for the empirical studies reported in chapters 4, 5, and 6 of the thesis. Chapter 2 reviews current understanding of the post-retinal human visual system. In particular, it focusses on current evidence for parallel processing along the sub-cortical pathways from the retina to V1, and on the structure and functions of the dorsal visual processing stream. It also reviews current evidence for the reliance of the dorsal visual processing stream on input from the Magnocellular (M) sub-cortical pathway, and reviews evidence for age-related change in these processes. The associations between age-related changes in visual processing and functional decline in older adults are also reviewed. Chapter 3 reviews current understanding of the processes involved in the allocation of visual attention. This includes the role of the M pathway in providing primary input into attentional processes. Evidence for age-related change in the operation of visual attention, and the functional consequences of these changes, are also reviewed.



Aim 1: To investigate differences in the capacity of older and younger adults to use bottom-up and top-down attention in the performance of a FFOV task.

Aim 2: To investigate the association between FFOV performance and the sensitivity of the M pathway, particularly in older adults.

Aim 3: To investigate differences in the capacity of older and younger adults to use top-down attention to facilitate the perception of coherent motion.

Aim 4: To investigate the association between motion coherence thresholds and the sensitivity of the M pathway, particularly in older adults.

Study 1
(Chapter 3)

Purpose: To investigate the impact of varying bottom-up and top-down attentional demands on the FFOV of younger (n = 42) and older (n = 42) adults.

Design: Mixed factorial design comparing FFOV error rates under conditions with different levels of attentional control.

Thesis aim: 1

Study 2
(Chapter 4)

Purpose: To explore differences between younger (n= 44) and older (n = 44) adults in the contrast sensitivity of the M and P pathways, and the associations between M and P pathway contrast sensitivity and the FFOV of older adults.

Design: Between groups and correlational design.

Thesis aim: 2

Study 3
(Chapter 5)

Purpose: To investigate the impact of top-down attentional guidance on the motion coherence thresholds of younger and older adults and explore the association between motion coherence thresholds and M and P pathway contrast sensitivity.

Design: Mixed factorial design comparing motion coherence thresholds with and without top-down attentional guidance. Mediated regression analysis was conducted to determine if the impact of age on coherence thresholds was mediated by contrast sensitivity.

Thesis aim: 3 and 4.

Figure 1.1. Outline of thesis aims and corresponding empirical studies.

Chapter 4 reports the first empirical study of the thesis in which a FFOV task was performed by groups of older and younger adults. This is the first study to compare the impact of varying attentional requirements of a FFOV task on younger and older adults. It demonstrates that the effect of age is not easily classifiable as a reduction in either bottom-up or top-down attentional capacities. It is interpreted as showing that older adults rely more heavily on top-down control of attention in performing a FFOV at the expense of reduced benefit from bottom-up attentional capture by the peripheral target.

Chapter 5 reports the results of the steady and pulsed pedestal task performed by older and younger adults and uses the results to examine the association between FFOV performance and the contrast sensitivity of both the M and P pathways. It provides important empirical support for the role of the M pathway in the allocation of visual attention, at least in the older group. In particular it provides the first empirical evidence that the FFOV performance of older adults is associated with the sensitivity of the M pathway.

Chapter 6 reports an experiment in which motion coherence thresholds were obtained from younger and older men and women, both with and without an attentional cue to assist performance. The results replicate the largely unexplained effect of sex found in some previous studies and which remains controversial in the literature. It also shows for the first time that younger women and older men could take advantage of an attentional cue to assist performance, but older women could not. This is interpreted as indicating that women find complex motion processing particularly effortful and that older women could lack sufficient spare resources to use top-down control of attention to improve performance.

Chapter 7 draws together the results of the empirical studies and considers their implications for daily functioning in older adults. The theoretical implications of the results are interpreted in the context of known functional limitations of older adults, specifically an increased risk of motor vehicle accidents, especially at intersections. As such the thesis provides insights into age-related changes in visual processes that are likely to have important functional consequences for the increasing numbers of older adults making up today's society.

Chapter 2: Structure and function of the visual system.

2.1 Introduction

In humans and other primates, visual information is processed along interconnected parallel hierarchies (Ungerleider & Mishkin, 1982). At the bottom of this hierarchy, simple visual information (e.g. contrast, colour, spatial frequency, and temporal frequency) is conveyed from the retina to the primary visual cortex in V1 along three parallel sub-cortical pathways: the Magnocellular (M), Parvocellular (P), and Koniocellular (K) pathways (Kaplan, 2004). From V1, processing continues to advance through the encoding of progressively more complex representations of visual information along somewhat independent parallel processing streams: the dorsal and ventral streams (Livingstone & Hubel, 1987). These two streams are identifiable not only anatomically through tracing axonal connections, but also by the perceptual functions undertaken along each stream (Van Essen & Maunsell, 1983). While processing proceeds hierarchically from simple to more complex representations in both streams, the flow of information is almost always in both directions with both feedforward and feedback connections between levels in the hierarchies allowing substantial recursive processing of signals (Bullier, 2001; Felleman & Van Essen, 1991).

Although the two streams are now recognised to be less independent and more interconnected than once thought, and the degree of independence remains contested (Kaplan, 2014), the two-streams model still usefully describes the major connections and functional hierarchies among the areas responsible for visual processing (Galletti & Fattori, in press; C. J. Perry & Fallah, 2014). The dorsal stream, which proceeds from the primary visual cortex (V1) to the posterior parietal cortex, is known to specialise in the perception of motion (Ungerleider & Mishkin, 1982) and to provide information such as the perception of spatial localisation necessary for interaction with the physical environment: e.g. reaching, and grasping objects (Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003). The ventral stream, which proceeds from V1 to the inferior temporal cortex, is known to process more temporally stable characteristics of the visual scene such as shape and colour, and thereby provide vision for functions such as object identification (Maunsell & Newsome, 1987). As a consequence of these specialisations, the dorsal stream has been described as providing "vision for action", whereas the ventral stream has been described as providing "vision for perception" (Milner & Goodale, 2008). It is a fundamental hypothesis of the current study that the difficulties experienced by older adults interacting with their environment (such as falls and motor vehicle accidents) may be due to decreased capacity for the "vision for action" provided by the dorsal stream (Conlon & Herkes, 2008; Trick & Silverman, 1991). The structure and functions of the parallel processing hierarchies will be reviewed in order to provide context for the following experiments, with particular emphasis on the dorsal stream and the sub-cortical pathways on which the processing streams rely for input.

2.2 Sub-cortical pathways from retina to visual cortex.

Neural processing of visual information proceeds from the retina to the visual cortex primarily along three functionally and structurally distinct pathways: the magnocellular (M), parvocellular (P), and koniocellular (K) pathways (Felleman, 2001). The neurons within these three pathways differ in terms of the visual characteristics to which they respond (see Table 2.1). The M and P pathways in particular have response characteristics that suggest they are specialised for processing distinct kinds of visual input. The K pathway is less well understood, but appears to be less distinct in its response characteristics compared to the M and P pathways (Kaplan, 2004, 2014). As a result, the current study focuses on the sub-cortical M and P pathways in exploring the neural basis of functional vision in older adults.

Table 2.1.

Properties of the P, M, and K pathways (adapted from Kaplan, 2004)

Property	Stream		
	P	M	K
Spectral (colour) opponency/selectivity	Yes	No	Some (Blue-on)
Luminance contrast gain	Low	High	High
Receptive field size	Small	Large	Large
Acuity of cell group	High	Low	?
Retinal source	Midget retinal ganglion cells (RGCs)	Parasol RGCs	Unknown (some bistratified RGCs)
LGN Projection	Parvocellular	Magnocellular	Koniocellular (Intercalated)
Conduction velocity	Low	High	Varied
Response to light steps	Tonic (sustained)	Phasic (transient)	Phasic, some sluggish
Contrast sensitivity at scotopic luminance	Poor	Good	?
Fraction of LGN population	~80%	~10%	~10%

The M pathway begins from relatively large retinal ganglion cells and projects to the magnocellular layers in the dorsal lateral geniculate nucleus (LGN) of the thalamus (V. H. Perry, Oehler, & Cowey, 1984). The magnocellular layer of the LGN then projects to layer 4Cα in V1 (see Figure 2.1), which in turn projects to layer 4B in V1 (Fitzpatrick, Lund, & Blasdel, 1985; Schwartz, 1999). The retinal ganglion cells and the neurons in the magnocellular layer of the LGN lack colour sensitivity, are highly sensitive to low contrast and relatively less sensitive to high contrast, provide fast conductance speeds, and are distributed peripherally in the retina (Felleman, 2001). The M pathway is more sensitive to high temporal frequencies, particularly for low spatial frequency stimuli (Merigan & Eskin, 1986). The phasic or transient response and faster conduction speed of the M pathway make it ideal for processing rapidly changing stimuli, and providing input for visual processing of motion (Livingstone & Hubel, 1987).

The P pathway begins from retinal ganglion cells that are, compared to those in the magnocellular pathway, small and distributed more foveally in the retina (V. H. Perry et al., 1984). Compared to neurons in the M pathway, both the retinal and LGN parvocellular neurons are characterised by responses to stimuli that are sustained over longer time frames, have slow transmission speeds, provide weak response to changes in contrast, are most sensitive to higher spatial frequencies, and many P-pathway neurons have centre-surround colour opponency structures (Felleman, 2001; Leventhal, Rodieck, & Dreher, 1981; Schwartz, 1999). These features make the parvocellular pathway ideally suited to distinguishing fine detail and the more lasting features of stimuli such as form or shape. The parvocellular layers of the LGN project to areas 4A and 4Cβ of the primary visual cortex, V1 (Fitzpatrick et al., 1985; Schwartz, 1999). The smaller parvocellular neurons outnumber the larger magnocellular neurons approximately ten to one in the LGN. While conductance speeds are slower in the P compared to the M pathway, it has been argued that higher convergence rates of the more numerous parvocellular neurons onto V1 neurons may negate the advantage of the high conductance speed in the M pathway (Kaplan, 2014; Maunsell et al., 1999).

2.3 Two streams for visual processing

The M and P pathways terminate at V1. Neurons at V1 are arranged in layers composed of neurons with small receptive fields which are responsive to relatively simple visual features such as spatial frequency, temporal frequency, direction of motion, speed of motion, colour, and orientation (Fitzpatrick et al., 1985; Hubel & Wiesel, 1968; Muckli et al., 2015; Priebe, Lisberger, & Movshon, 2006). These simple features provide the input for the dorsal and ventral streams which are organised hierarchically with neurons sensitive to more complex features and larger receptive fields found in higher areas.

It was initially thought that the separation of the M and P pathways continued through V1 with the dorsal stream forming an extension to the M pathway via motion sensitive layer 4B in V1, and the ventral stream forming an extension to the P pathway beginning in colour sensitive blobs and form sensitive interblobs of layer 2/3 of V1 (Livingstone & Hubel, 1988; Ungerleider & Mishkin, 1982). This simple model of two separate sub-cortical pathways continuing beyond V1 to form two parallel and independent cortical streams has since been substantially revised (Kaplan, 2014; Merigan & Maunsell, 1993; Nassi & Callaway, 2009). Current understanding of processing within V1 (see Figure 1.1) is that the different cell types within the layers of V1 allow for different degrees of segregation and intermixing of signals from the sub-cortical pathways (Sincich & Horton, 2005). For example, pyramid cells within layer 4B (a layer once thought to only receive M pathway input) have apical dendrites that extend to layer 2/3 where they can receive P pathway input provided by projections from the P pathway dominated layer 4Cβ. There is evidence that these pyramidal cells in layer 4B receive a mix of M and P inputs, whereas the stellate cells in layer 4B receive only M pathway input (Yabuta, Sawatari, & Callaway, 2001). Layer 2/3, which projects to the ventral stream, has been found to receive input from both layer 4Cα (the M pathway terminus) and layer 4Cβ (the P pathway terminus), thus providing intermixed M and P pathway inputs to the ventral stream (Lachica, Beck, & Casagrande, 1992; Yabuta & Callaway, 1998). This layer also has outputs that potentially form a recursive loop passing to layer 6, which then projects back to both layers 4Cα and 4Cβ (Nassi & Callaway, 2009; Sincich & Horton, 2005).

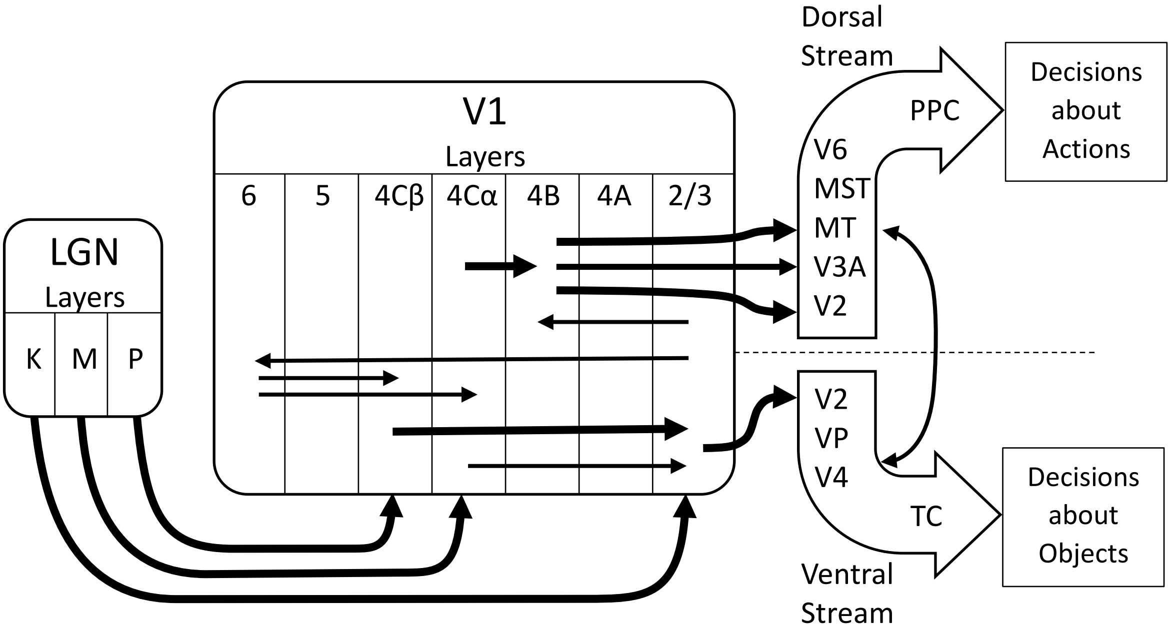


Figure 2.1. A simplified representation of the parallel visual processing system. PPC, Posterior Parietal Cortex; TC, Temporal cortex. See text for details. Bold arrows indicate more dominant connections.

It is therefore clear that M and P pathways often converge in V1, although there is also evidence that at least some cells maintain exclusive links to one sub-cortical pathway (such as the stellate cells in layer 4B described above). As a result, the dorsal and ventral streams are now best understood as receiving a mix of M and P (and K) pathway inputs (Kaplan, 2014; Nassi & Callaway, 2009; Sincich & Horton, 2005). This is consistent with lesion studies which have shown motion perception (a dorsal stream task) to be possible in spite of M pathway lesions (Merigan, Byrne, & Maunsell, 1991).

2.3.1 The dorsal stream: Vision for action

The dorsal stream is composed of areas primarily concerned with processing visual motion and monitoring the location of objects relative to the observer, and together these functions provide the vision necessary for action within a dynamic real world environment (Milner & Goodale, 2008). The research literature shows broad consensus on the main areas included in the dorsal stream, even though there is some disagreement on the dorsal stream's exact structure, and the relative independence of the dorsal and ventral streams (Cloutman, 2012; Galletti & Fattori, in press; Merigan & Maunsell, 1993). The main areas included in the dorsal stream are the thick stripes of V2, areas V3a, MT, MST, V6, and a number of areas in the posterior parietal cortex (see Figure 2.1). While the dorsal stream is hierarchical with more complex processes carried out at higher levels, most if not all areas are linked by both feedforward and feedback connections (Felleman & Van Essen, 1991).

The first area encountered on the dorsal stream beyond V1 is the second visual area (V2). Like area V1, V2 has a complex structure including layers which appear as thick and thin stripes separated by pale stripes. The thick stripes receive projections from layer 4B of V1 and are sensitive to motion (H. D. Lu, Chen, Tanigawa, & Roe, 2010). The thick stripes of V2 also appear to contribute to encoding of depth based on visual disparity, necessary for judging location of objects relative to the observer, (G. Chen, Lu, & Roe, 2008; Thomas, Cumming, & Parker, 2002). V3a receives input from both V1 and V2 and is also motion sensitive in humans (Bartels, Zeki, & Logothetis, 2008; Helfrich, Becker, & Haarmeier, 2013; Sunaert, Van Hecke, Marchal, & Orban, 1999). V3a appears to be more sensitive to coherent motion and less sensitive to random noise motion (Helfrich et al., 2013), and appears to specifically respond to real motion (actual movement in the visual field), and not simply to apparent motion produced on the retina by eye movements (Galletti, Battaglini, & Fattori, 1990).

The area of the dorsal stream that has been studied most is the middle temporal area (MT) also known as V5 (Born & Bradley, 2005). The main function of MT is the processing of visual motion (Zeki, 2015). MT receives projections directly from V1 as well as from both V2 and V3a. The projections travelling directly from layer 4B of V1 to MT originate predominantly in stellate cells which are driven by M pathway input, whereas the indirect input via thick stripes of V2 and V3a appears to derive largely from the pyramidal cells in 4B of V1 that receive a mix of M and P pathway input (Nassi & Callaway, 2006). However, MT also receives a small proportion of its input directly from the LGN, including inputs from the parvocellular (Nassi, Lyon, & Callaway, 2006) and koniocellular (Sincich, Park, Wohlgemuth, & Horton, 2004) layers. MT encodes only two-dimensional representations of motion, including direction and speed (Mikami, Newsome, & Wurtz, 1986; Zeki, 1974). Unlike at V1, neurons sensitive to motion in a particular direction in MT also inhibit responses in neurons sensitive to motion in the opposite direction (Mikami et al., 1986; Snowden, Treue, Erickson, & Andersen, 1991). This allows MT to detect the average motion in a display, or the direction of motion most prevalent in a display containing random motion noise, such as in a random dot kinematogram (Braddick et al., 2001). The larger receptive field sizes of MT neurons also contribute to enhanced capacity to detect coherent motion at MT compared to V1 (Mikami et al., 1986). The neurons in MT sensitive to motion are also sensitive to visual disparity, making MT important in judging visual depth (Smolyanskaya, Ruff, & Born, 2013).

Beyond MT, the dorsal stream continues into the posterior parietal cortex through area MST. This area takes motion processing a step further by processing three-dimensional motion such as optic flow (Cardin, Hemsworth, & Smith, 2012; Smith, Wall, Williams, & Singh, 2006; Uesaki & Ashida, 2015). Optic flow is essential for the perception of self-motion and MST seems to be important for this function because it allows the observer to determine the direction in which he/she is moving (Kovács, Raabe, & Greenlee, 2008). Another area of the dorsal stream which also responds well to optic flow is area V6. which appears to encode optic flow in a way that determines the direction of motion of other objects, such as whether an object will collide with the observer (Cardin et al., 2012). The dorsal stream then projects to various areas in the posterior parietal cortex, thus supplying visual perception for action to those parts of the brain which plan and execute action (Chafee, Averbeck, & Crowe, 2007; Ferraina, Battaglia-Mayer, Genovesio, Archambault, & Caminiti, 2009; Galletti et al., 2003; Milner & Goodale, 2008; Nassi & Callaway, 2009).

The distinction between the role of MST and V6 is consistent with a number of recent studies which argue that the dorsal stream is composed of at least two parallel sub-streams: a dorsal-dorsal stream and a ventral-dorsal stream (Binkofski & Buxbaum, 2013; Rizzolatti & Matelli, 2003). In this model, the dorsal-dorsal stream is centred on V6 with input from V3A and output to the superior parietal lobule, and is concerned with rapidly updating the observer’s knowledge of object locations and guiding ongoing actions: it provides vision for online action. The ventral-dorsal stream includes MT and MST as described above, and projects to the inferior parietal lobule and is described as subserving action understanding, particularly the actions of others (Binkofski & Buxbaum, 2013). While there is evidence for a more complex view of the dorsal stream (Galletti & Fattori, in press), it is clearly the chief source of vision by which humans interact with the outside world, especially when the environment or the objects within it are in motion.

2.3.2 The ventral stream: Vision for understanding

The ventral stream contains areas that begin with the processing of orientation, colours, and shapes, and build towards more complex representations of objects (Livingstone & Hubel, 1987). It has therefore been described as providing “vision for understanding”

(Milner & Goodale, 2008). Anatomically, the ventral stream progresses from V1, through the pale and thin strips of V2 to V4, and then projects primarily to the inferotemporal cortex (H. Rao, Zhou, Zhuo, Fan, & Chen, 2003; Schwartz, 1999; Van Essen & Drury, 1997). At early levels of the ventral stream (V1 and V2), neurons are sensitive to individual stimulus attributes, including orientation, luminance, and spatial frequency and are limited to small receptive fields (Badcock, Clifford, & Khuu, 2005; Wilson & Wilkinson, 1998). Area V2 takes signals encoding orientation, colour, and simple shape from V1 and allows processing of more complex shapes such as contours, and the identification of shape boundaries, which is a preliminary step necessary to the identification of objects (Hegdé & Van Essen, 2000; Zhaoping, 2005a). At V4 these signals from earlier processing areas begin to be pooled to form more complex representations of global form (Badcock et al., 2005; Gallant, Shoup, & Mazer, 2000; Wilson & Wilkinson, 1998). V4 then projects into the inferotemporal cortex, allowing more specific representations, and finally recognition, of objects and faces (Farah, 2000; Schwartz, 1999).

A focus on understanding the contents of the visual field in the ventral stream, rather than its dynamic properties, is also apparent from the different way in which the ventral stream encodes visual disparity, a feature also encoded in the dorsal stream. The neurons at V4 provide encoding of relative disparity (how much further away one feature is than another), whereas the dorsal stream encodes absolute disparity (how far features are from the observer). In addition, the ventral stream encodes fine details of disparity whereas the dorsal stream produces a coarser representation of disparity (Neri, 2005; Neri, Bridge, & Heeger, 2004; Roe, Parker, Born, & DeAngelis, 2007). Fine details of disparity are likely to be important for identification of three-dimensional objects, whereas vision for action can succeed using coarse representations provided they are updated during actions, as provided by the dorsal stream.

Understanding of the ventral stream has remained relatively stable and uncontested in the literature (Milner & Goodale, 2008; Nassi & Callaway, 2009; Ungerleider & Mishkin, 1982; Van Essen & Maunsell, 1983). However, evidence of information shared between the ventral and dorsal streams (C. J. Perry & Fallah, 2014), made possible by the interconnections between various areas in different (Felleman & Van Essen, 1991) streams confirms that the two streams do not function independently of one another (Merigan & Maunsell, 1993). In particular, the recent exploration of two separate sub-streams within the dorsal stream suggest that the ventral-dorsal stream shares connection with the ventral stream, such as those previously identified between MT and V4 (Felleman & Van Essen, 1991), whereas the dorsal-dorsal stream is largely, perhaps entirely, independent of the ventral stream (Galletti & Fattori, in press). The degree of shared information between the streams and how this contributes to the functioning of each stream remains a point of contention in the research literature (Kaplan, 2014; Nassi & Callaway, 2009)

2.4 The effect of age on visual processing

Even healthy aging is associated with change in some aspects of vision, and both optical and neural factors are likely to contribute (Andersen, 2012; Owsley, 2016). At an optical level, gradual changes that begin in early adulthood have noticeable effects on the quality of vision typically by the fourth or fifth decade of life (Schwartz, 1999). These include changes in the crystalline lens that result in decreased accommodation (ability to change focus) and transparency of the lens, reduction in retinal illumination due to reduced pupil diameter (senile miosis), and an increase in the degree to which light scatters as it passes through the lens (Michael & Bron, 2011; Owsley, 2016; Weale, 1986). However, changes at a neural level are also important for functional vision (Andersen, 2012; Haegerstrom-Portnoy, Schneck, & Brabyn, 1999; Owsley, 2011; Spear, 1993). The following review focusses on two major changes likely to result in functional difficulties for older adults, and therefore most relevant to the current project: age-related decline in contrast sensitivity and age-related decline in processing visual motion.

2.4.1 Contrast sensitivity and early processing decline

One of the most prominent effects of age on vision is a reduction in contrast sensitivity across the adult lifespan (Owsley, 2016; Owsley et al., 1983). Some studies have concluded that a decline in neural processing explains at least some of the reduction in contrast sensitivity in older adults (D. Elliott et al., 1990; Pardhan, 2004; Schefrin, Tregear, Harvey, & Werner, 1999; R. Sekuler & Hutman, 1980; Sloane, Owsley, & Alvarez, 1988). For example, Elliott and colleagues simulated the effect of senile miosis and decreased lenticular transparency in younger adults, and found their contrast sensitivity did not decline as a result, but remained superior to that of the older adults. However, other studies suggest optical factors are as, if not more, important than changes at a neural level (Kline, Schieber, Abusamra, & Coyne, 1983; Owsley, 2016; Owsley et al., 1983).

Most studies have found the decline in contrast sensitivity in older adults is more pronounced for high and moderate spatial frequencies with little or no decline in contrast sensitivity in older adults for low spatial frequencies (Andersen, 2012; Kline et al., 1983; Owsley et al., 1983; Spear, 1993). A larger effect of age on contrast sensitivity for higher compared to lower spatial frequencies may suggests a neural source for the decline. When stationary stimuli are presented, some comparisons of contrast sensitivity in younger and older adults have found a greater reduction in the older group for contrast sensitivity when viewing stimuli targeting the P pathway than for stimuli targeting the M pathway (S. L. Elliott & Werner, 2010; Lenoble, Amieva, & Delord, 2012). These findings were achieved using the Steady and Pulsed Pedestal paradigm developed by Pokorny and Smith (1997).

This task involves presentation of a pedestal of four squares, against a background, and takes advantage of the different contrast gain functions of the two pathways: the M pathway response saturates at relatively low contrast (approximately 10%) whereas the P pathway response increases in a linear fashion from low to high levels of contrast (Kaplan & Shapley, 1986, Pokorny & Smith, 1997). Contrast sensitivity is determined by varying the luminance of one of the four squares (chosen at random) on each trial and determining the minimum change in contrast needed to correctly identify the target square. The task is biased towards the P pathway by only providing adaptation to the background, and presenting both the pedestal and the test square as a sudden onset on each trial The sudden onset of the pedestal and test square saturates the contrast response of the M pathway but not the P pathway, leaving the P pathway better able to detect the test square. By providing a period of adaptation to the pedestal as well as the background, the task can be biased towards the M pathway which is more sensitive to low levels of contrast.

Responses on the pulsed pedestal trials of this task have been shown to reflect the contrast response of cells in the P pathway, while responses to steady pedestal trials reflect the contrast response of the M pathway (Leonova, Pokorny, & Smith, 2003). Another study, using a slightly adapted form of the steady and pulsed pedestal task, found equivalent declines in contrast sensitivity in the M and P pathways (McKendrick, Sampson, Walland, & Badcock, 2007). Under scotopic light levels, there is evidence of a greater decline for low spatial frequencies, suggesting declines in contrast sensitivity with age are also present in the M pathway (Schefrin et al., 1999). There is also evidence that contrast sensitivity continues to decline in the M pathway during late adulthood, whereas contrast sensitivity in the P pathway declines sometime before the age of 60 and thereafter remains stable (Lenoble et al., 2012). The age-related decline in contrast sensitivity has also been shown to be stronger for temporally modulated than for static stimuli (Willis & Anderson, 2000). Older adults have higher contrast thresholds than younger adults for a drifting stimulus but not a stationary stimulus at low spatial frequencies, and this effect of age increases for faster moving (high temporal frequency) stimuli (Owsley et al., 1983). The M pathway has been shown to be particularly important for the detection of moving stimuli at low spatial and high temporal frequencies (Merigan et al., 1991). Taken together, these results suggest that age-related decline in the M pathway is more apparent for moving stimuli than when tested using static stimuli. The temporal response properties of the M pathway, which result from its transient response profile and capacity for rapid conductance, mean that perception of moving stimuli is likely to rely more heavily on the M pathway (C. Chapman, Hoag, & Giaschi, 2004).

The decline in contrast sensitivity in older adults has been found to have important functional consequences. Spatial contrast sensitivity in older drivers has been shown to predict driving performance in an on-road driving task (Wood, 2002; Wood & Carberry, 2006), and frequency of driving accidents in the five years preceding testing (Ball et al., 1993). Reduced contrast sensitivity is also an important factor in predicting which older adults will experience falls (Lord, Clark, & Webster, 1991). Neural responses to other features (e.g. motion) also increase as the contrast of the stimulus is increased, and therefore the reduced response to contrast in early vision may result in a reduced response to other features at higher levels. There is evidence that reduced response to contrast in older compared to younger monkeys may be associated with reduced neural response to motion, and increased neural noise, measured in vivo at MT (Yang et al., 2008). Psychophysical studies in humans have also found a relationship between reduced contrast sensitivity and reduced capacity for motion perception (Allen, Hutchinson, Ledgeway, & Gayle, 2010; Conlon et al., 2015). One study obtained separate measures of M and P pathway contrast sensitivity in a sample of older adults with glaucoma, and found more indication of a relationship between motion coherence thresholds and contrast sensitivity for the M pathway than P pathway (McKendrick, Badcock, & Morgan, 2005). Reduced contrast sensitivity in older adults is also associated with reduced capacity for object identification, including the detection and identification of real world objects such as road signs and faces (Owsley & Sloane, 1987; Seichepine et al., 2012). The association between age-related reductions in contrast sensitivity and reduced capacity for object recognition has been found under photopic light levels (Owsley & Sloane, 1987), but is more pronounced under low light conditions (Seichepine et al., 2012). Given that the M pathway is better suited to providing visual information under low light conditions than the P pathway (Purpura, Kaplan, & Shapley, 1988), it may be that object recognition is reduced most when it relies more heavily on input from the M pathway (Schefrin et al., 1999). This suggests reduced contrast sensitivity has implications for the functional performance of both the dorsal and ventral visual processing streams.

The hypothesis that reduced sensitivity in the sub-cortical pathways is explored in studies 2 (Chapter 5) and 3 (Chapter 6) of the current project. In study 2, the hypothesis that the reduced functional field of view of older adults is associated with reduced sensitivity of the M pathway will be tested. There is an argument that rapid allocation of visual attention is reliant on the rapid conductance of signals from the retina to cortex as provided by the M pathway. Using the pulsed and pedestal paradigm (Pokorny & Smith, 1997), separate measures of the contrast sensitivity of the M and P pathway will be used as predictors of FFOV performance. If FFOV performance is better predicted by contrast thresholds in the M than in the P pathway, this will provide evidence that reduced M pathway sensitivity in older adults may be a source of reduced capacity for functional vision. In study 3 the association between reduced M pathway sensitivity and increased motion coherence thresholds will be investigated.

2.4.2 Motion processing and dorsal stream decline

Another prominent focus in research on age-related changes to vision is the effect of age on the perception of visual motion (Hutchinson, Arena, Allen, & Ledgeway, 2012). Older adults have greater difficulty than younger adults in a range of perceptual tasks involving motion, including determining the direction of motion (Snowden & Kavanagh, 2006; Wood, 2002; Wood & Bullimore, 1995), the speed of motion (Norman, Ross, Hawkes, & Long, 2003), determining the direction of optical flow (Warren, Blackwell, & Morris, 1989), detecting 3-dimensional shape from optic flow (Andersen & Atchley, 1995), and detecting biological motion (Mateus et al., 2013; Pilz, Bennett, & Sekuler, 2010). Several studies have used random dot kinematograms (RDK) to show that older adults have higher thresholds than younger groups for detecting coherent motion presented in random noise motion (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Bennett et al., 2007; Billino, Bremmer, & Gegenfurtner, 2008; Conlon et al., 2015; Conlon & Herkes, 2008; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991; Wojciechowski, Trick, & Steinman, 1995). RDKs contain a percentage of dots moving coherently in a given direction, while the remaining dots in the display move in random directions. Capacity to perceive coherent (or global) motion is measured by the minimum threshold proportion of coherently moving dots required to correctly identify their direction of motion. Perception of coherent motion is an important function of the dorsal stream and this task has been shown to rely heavily on MT, along with V3a, more so than on V1 (Braddick et al., 2001). In primate studies, increased age is associated with reduced directional selectivity of neurons, higher maximum response rates, and increased spontaneous discharge at MT (Liang et al., 2010; Yang, Zhang, et al., 2009). The increased internal noise produced by both increased spontaneous firing and reduced selectivity of neural responses may help explain the increased motion coherence thresholds of older compared to younger adults.

However, not all studies have shown increased motion coherence thresholds in older adults. Studies which provided long (> 2000ms) or unlimited stimulus durations have found no difference between older and younger adults on coherent motion thresholds (Kavcic, Vaughn, & Duffy, 2011; Mapstone, Dickerson, & Duffy, 2008; Mapstone, Steffenella, & Duffy, 2003). This may suggest that older adults can overcome the effect of internal noise given time, or that some component of the visual system processing motion slows down with age. There is also evidence that the increase in motion coherence thresholds with age is either greater in (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Conlon et al., 2015; Conlon & Herkes, 2008), or entirely restricted to older women (Gilmore, Wenk, Naylor, & Stuve, 1992). Some studies have also found that women in general have higher motion coherence thresholds than men (Billino et al., 2008; Conlon et al., 2015; Conlon, Power, Hine, & Rahaley, 2017; Pilz et al., 2010; Snowden & Kavanagh, 2006). No explanation for an increased motion coherence threshold in women generally or older women in particular has as yet been firmly established. One possible explanation comes from a recent study in which younger women had higher motion coherence thresholds than younger men for RDKs with 150 dots, but not for RDKs with 600 dots (Conlon et al., 2017). These results suggest greater quantity of available signals in the RDK may allow women (or younger women at least) more opportunity to form a global percept of motion from the fragmented signals present in an RDK.

The precise mechanism which explains reduced motion processing in older adults has not been identified. It has been theorised that reduced motion processing in older adults may result from reduced sensitivity of the M pathway upon which the dorsal stream is heavily reliant (Gilmore et al., 1992; Henderson, Gagnon, Bélanger, Tabone, & Collin, 2010; Trick & Silverman, 1991). This hypothesis is yet to be tested empirically in healthy older adults. However, the effect of age is not consistent across different forms of motion perception, which argues against a common cause in early processing (Andersen, 2012). For example, compared to younger adults, older adults have a substantially reduced capacity to detect coherent translational motion in a dot display, moderately diminished capacity to detect biological motion, and show little deficit in detecting optical (radial) flow (Billino et al., 2008). Other explanations for decreased sensitivity to visual motion in older adults include reduced GABA mediated centre surround antagonism in motion sensitive neurons (Betts, Taylor, Sekuler, & Bennett, 2005), and increased neural noise (Bennett et al., 2007). Increased internal noise in older compared to younger primates has been directly measured in both motion and orientation selective neurons in V1, and in motion selective neurons at MT (Schmolesky, Wang, Pu, & Leventhal, 2000; Yang, Zhang, et al., 2009) and has been associated with age-related reduction in levels of the neurotransmitter GABA (Leventhal et al., 2003). One study which measured thresholds for detecting both coherent motion and coherent form (a ventral stream task carried out at V4), found older adults were less sensitive than a younger group to coherent motion and not coherent form (Conlon & Herkes, 2008). These findings suggest the effect of age has a strong impact on the dorsal stream, or arises in the M pathway on which the dorsal stream is more heavily reliant than the ventral stream.

A further explanation offered for age-related decline in many areas of neural processing is reduced speed of processing in older adults (Owsley, 2013). There is evidence the latency but not the amplitude of motion signals declines with age, whereas the opposite pattern occurs for static pattern structure (processed in the ventral stream): amplitude of signals diminish with age while their latency remains well preserved (Langrova et al., 2006). Therefore, with advancing age, processing speed may decline more in the dorsal than the ventral stream. This may be related to the dorsal pathways reliance on the fast conducting M pathway for processing temporal characteristics of stimuli. There is evidence to show that the main effect of age on the sub-cortical pathways is not a loss of neurons, but a loss of axons

(Calkins, 2013). If the age-related reduction in contrast sensitivity in the M and P pathways is a result of loss of axonal integrity rather than the random death of neurons, the loss in the M pathway may result in a reduced capacity of the M pathway for fast conductance and representation of high temporal frequencies.

Difficulties perceiving motion have been found to be associated with functional consequences, including driving accidents and falls. Reduced motion perception has been associated with both on-road driving performance (De Raedt & Ponjaert-Kristoffersen, 2000; Wood, 2002) and self-reported driving difficulties. Motion perception is also related to risk of falls in older adults (Lord, Smith, & Menant, 2010). Reduced sensitivity to visual motion is associated with poor balance (Freeman, Broman, Turano, & West, 2008), poor judgement of self-motion (Haibach, Slobounov, & Newell, 2009), and reduced capacity to use motion cues to monitor sway and posture on-line (Sotirakis, Kyvelidou, Mademli, Stergiou, & Hatzitaki, 2016). In a study exploring the role of visual processing in falls among older adults, Freeman and colleagues (2008) found motion detection significantly predicted the odds of failing a balance test, whereas measures of visual acuity, contrast sensitivity and visual field did not. This suggests the dorsal stream's capacity to process visual motion plays a role in guiding and maintaining balance in older adults.

Older adults appear to adapt to the declines in visual processing by adopting compensatory strategies (Greenwood, 2007; Reuter-Lorenz & Cappell, 2008). These have been identified by neuro-imaging studies which show patterns of activation across neural areas in response to a given task differ between younger and older adults. One of the more prominent accounts of this phenomenon is the Posterior-Anterior Shift with Aging (PASA) which proposes that older adults engage anterior (frontal and perhaps parietal) areas of cortex to compensate for reduced processing in posterior (occipital) brain areas (Ansado, Monchi, Ennabil, Faure, & Joanette, 2012; S. W. Davis et al., 2008). Other accounts argue that older adults increase activation in many areas, not simply in a posterior to anterior shift (Reuter-Lorenz & Cappell, 2008). This is an argument for reduced specialisation of neural regions in the brains of older compared to younger adults (J. Chen, Myerson, & Hale, 2002). It has also been shown that older adults exhibit less hemispheric lateralisation in a range of tasks than younger adults, again consistent with compensatory recruitment in older adults of additional neural resources (Cabeza, Daselaar, Dolcos, Budde, & Nyberg, 2004b). Consistent with these findings, older adults have also been found to rely more heavily on the cognitive control of visual processing resources through intentional allocation of visual attention, as opposed to the automatic capture of attention which relies on effective and efficient sensory processing (Whiting, Madden, & Babcock, 2007).

Study 3 (see Chapter 6) of the current project is focussed on motion perception in older and younger men and women. The aim is to explore whether older adults can use top-down attention to a visual cue to improve motion coherence thresholds as effectively as younger adults, or perhaps use top-down attention to overcome the effect of age on motion coherence thresholds. It will also seek to replicate the interaction between the effects of age and sex found in some previous studies, but which remains somewhat controversial: specifically that women have greater difficulty than men detecting coherent motion, and that the effect of age is greater for women than for men. Whether older adults, and older women in particular, can use top-down attention to overcome difficulties in complex motion processing will also be explored in Study 3. The mechanisms through which visual attention is allocated, how this may change with age, and the functional consequences of age-related change in visual attention for older adults will be reviewed in Chapter 3.

Chapter 3: Visual Attention

3.1 Introduction

Information overload was a term coined by Bertrand Gross in the 1960’s to refer to the phenomenon of the incoming information exceeding the resources available for its processing, and which leads to poor and inefficient decision making (Gross, 1962). Visual attention is the means by which humans avoid visual information overload by selecting a subset of available visual input for further cognitive processing at the neglect of the remaining concurrent input. By doing so, the information necessary for appropriate decision making is supplied to conscious awareness, while the irrelevant is ignored. Consider the complex and dynamic visual information a driver must process. The visual field can contain considerably more visual stimuli than the driver can fully process in a given moment: other cars on the road, traffic signs, pedestrians, the car’s instruments and mirrors, and a host of less relevant and constantly changing elements in the surrounding environment. To extract the important visual information for safe driving, a driver must strike a balance between intentionally restricting attention to what is known to be relevant, such as the road ahead, yet maintaining enough peripheral awareness of the surrounding environment for important but unpredictable features, such as road signs or a pedestrian entering the roadway, to be attended as necessary (P. R. Chapman & Underwood, 1998).

The capacity to appropriately filter the available input and process only that which is relevant and necessary is particularly important for older adults who have both more limited capacity for complex cognitive processing in general (Timothy A. Salthouse, 2004) and reduced capacity for visual processing in particular (Andersen, 2012; Owsley, 2016). As evidence for the functional importance of visual attention for older adults, older drivers with a reduced capacity for efficient deployment of visual attention, as measured by tests of the functional field of view (FFOV), are at increased risk of driving accidents compared to other older adults or younger adults (Anstey et al., 2005; Ball et al., 1993; Clay et al., 2005). A major objective of the current project is to investigate how changes to the way in which visual attention is allocated in older compared to younger adults might impact the FFOV in older adults. The current chapter will therefore review relevant aspects of visual attention, discuss the neural mechanisms that underlie visual attention, and consider how visual attention changes in normal ageing.

3.2 The mechanisms of visual attention

At a neural level, attending to a feature or location has been show to enhance processing of that feature or location (Hopfinger & Mangun, 1998; Huk & Heeger, 2000; Kastner & Ungerleider, 2001; Maunsell & Treue, 2006), and this can occur even before any stimulus is presented (Giesbrecht, Weissman, Woldorff, & Manqun, 2006). This has been found throughout the visual system from as early as the LGN (O'Connor, Fukui, Pinsk, & Kastner, 2002), throughout all levels of the ventral (R. P. N. Rao, 2005) and dorsal pathways (R. P. N. Rao, 2005; Wannig, Rodriguez, & Freiwald, 2007), in the posterior parietal cortex, and in the frontal eye fields of the pre-frontal cortex (Buchel et al., 1998). Attention therefore influences the relative salience of a feature such that an attended feature will be responded to as if it were more intense than if it were not attended to. When multiple stimuli are presented in the receptive field of a neuron, not only is the response to the attended stimulus enhanced, but the response to alternative stimuli are reduced through inhibition (Reynolds & Desimone, 2003). There is evidence to suggest this is achieved by increasing the contrast gain of neurons responsive to the attended feature so that the neurons respond as if the feature was presented in higher contrast than it actually is (Cutrone, Heeger, & Carrasco, 2014; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Martinez-Trujillo & Treue, 2005; Reynolds & Chelazzi, 2004; Reynolds & Desimone, 2003). The mechanisms of visual attention are therefore a means by which locations in the visual field compete for the available processing resources (Carrasco, 2011; Kinchla, 1992).

The processes by which a particular item or location is selected for attention involves the interaction of a number of mechanisms (Parks & Madden, 2013). Broadly speaking these mechanisms are classified as bottom-up attention, which is reflexively directed in a stimulus driven fashion, or top-down attention, in which attention is intentionally directed to a particular location or feature expected to be relevant to the current task (B. Hahn, Ross, & Stein, 2006; Jonides, 1981). These processes are integrated by top-down attention introducing bias into the judgement of relative salience, so that both relative salience and current task demands influence the ultimate allocation of attention (Desimone & Duncan, 1995; Itti & Koch, 2001; Wolfe, 1994). While in almost any real-world setting bottom-up and top-down mechanisms operate simultaneously and are highly inter-related, they are theoretically distinct processes and need to be considered separately in order to achieve the current aim of exploring how changes in attentional processes might impact functional vision in older adults.

3.2.1 Bottom-up attention

Bottom-up attention refers to the automatic, reflexive allocation of visual attention to salient locations or objects (Jonides, 1981). The most compelling evidence for reflexive, bottom-up attention comes from visual search studies that have shown that an irrelevant stimulus which is a salient colour or form singleton (Theeuwes, 1989; Theeuwes & Burger, 1998), or has an abrupt onset (Theeuwes, 1991; Yantis & Jonides, 1984), can reduce the efficiency of target detection, even when the observer knows the distractor is not relevant. Studies of free-viewing of natural scenes have also found the relative salience of locations can predict eye movements, indicating bottom-up influence over covert shifts of attention in real-world settings (Carmi & Itti, 2006; Parkhurst & Niebur, 2005; Peters, Iyer, Itti, & Koch, 2005; Zetzsche, 2005). In particular, the locations which are fixated are high in local luminance contrast (within a 1 deg square area) and more varied in their luminance (less correlation among neighbouring pixels) compared with locations selected at random or less often chosen for fixation (Parkhurst & Niebur, 2003).

In the absence of bias from task priorities, bottom-up attention is understood to emerge from feature-based saliency maps (Borji, Sihite, & Itti, 2013; Buschman & Miller, 2007; Itti & Koch, 2000, 2001; Koch & Ullman, 1985; Wolfe, 1994, 2014), which represent the relative intensity of features across the visual field. A number of features, such as colour, motion, contrast, or orientation, are thought to contribute feature maps encoding the relative intensity of feature values across the visual field based on retinal input (Itti & Koch, 2001). These feature maps are then combined into a single saliency map, with attention automatically allocated to - essentially captured by - the location that is most salient on the combined map.

Where this overall saliency map for driving bottom-up attention is encoded neurally is a matter of debate. Some researchers have suggested the saliency map is formed by neurons in parietal cortex (Buschman & Miller, 2007), an area which is important for the bottom-up allocation of spatial attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; De Fockert, Rees, Frith, & Lavie, 2004). Other researchers have suggested the saliency map is produced in early visual processing regions such as the LGN or V1, with feedback from higher cortical areas (Koch & Ullman, 1985; Zhaoping, 2005b). A saliency map encoded in an early visual area such as LGN or V1, would allow for the manipulation of the contrast gain at a particular location in early vision to enhance response to that location at all subsequent levels of processing for that input (Bullier, 2001). Alternatively, the saliency map may not be encoded in a single neural location, but be produced by the interaction of a network of areas distributed throughout the visual system (Treue, 2003).

It has also been suggested that the magnocellular visual pathway (M pathway) plays an important role in the bottom-up allocation of attention (Vidyasagar, 1999). It has been argued that signals passing rapidly along the M pathway from the retina to V1, and then travelling via the dorsal stream to the posterior parietal cortex, dominate the first wave of activation in the visual system, which then guides the allocation of attention in subsequent processing (Bullier, 2001). This argument is based on two key observations: that the M pathway is characterised by faster conductance speeds than the parallel parvocellular (P) pathway, and that the neuroanatomy of the M pathway indicates that it dominates input to the dorsal stream, which in turn projects to the posterior parietal cortex and is important in the control of visual attention. This model has been further developed to suggest the M pathway input provides a feedforward sweep of activation through the dorsal stream and parietal cortex, and then through frontal cortex to allow re-entrant feedback signals to meet and potentially modify input from the P and Koniocellular (K) pathways arriving at V1 and areas in the ventral and/or dorsal streams (Bullier, 2001; Laycock, Crewther, & Crewther, 2008; Laycock, Crewther, Fitzgerald, & Crewther, 2007; Laycock, Crewther, & Crewther, 2007).

Support for the M pathway playing a priority role in the allocation of visual attention comes from studies showing that lower spatial frequencies in a stimulus are more influential in driving the bottom-up allocation of visual attention than higher frequency components (Carretié, Ríos, Periáñez, Kessel, & Alvarez-Linera, 2012; B. A. Steinman, Steinman, & Lehmkuhle, 1997). There is also evidence that low spatial frequency information is used preferentially in establishing an initial impression – the rapid formation of an overall “gist” – when viewing natural scenes (Oliva, 2005). The role of this initial gist in guiding the allocation of attention has recently been highlighted by Jeremy Wolfe (2014), who points out that perceiving the basic nature of natural scenes (e.g. a street scene versus a kitchen) influences how attention is subsequently deployed. This gist of the scene is determined faster than objects in the scene can be processed, and must therefore be based on an overall impression rather than accumulated knowledge of the objects comprising the scene (Wolfe, 2014). One of the aims of the experiments in the current project is to investigate whether attentional influences on perceptual performance in older adults are linked to the sensitivity of the M pathway. If the M pathway is important for allocation of attention, a reduction in the sensitivity of the M pathway in older adults could undermine their capacity for efficient and effective use of visual attention to enhance perception.

3.2.2 Top-down attention

Visual attention is not purely determined by salience in a bottom-up manner. Individuals can also choose to pay attention to particular features or locations relevant to their goals or to the task at hand. This voluntary allocation is termed top-down attention as it begins with intentional decisions to exert cognitive control over the allocation of attention, and arises largely from prefrontal cortex (Buschman & Miller, 2007; Frith, 2005). For example, knowledge of the colour of a target and how it differs from distractors can facilitate search for the target, so long as the colour of the target is sufficiently different to that of any of the distractors (Daoutis, Pilling, & Davies, 2006). The ability to ignore a salient colour target also increases when the colour of both the target and distractor is predictable and known to the observer prior to search, thus allowing top-down influence over response to both target and the salient distractor (Theeuwes & Burger, 1998). The influence of top-down attention to a particular location or feature increases the neural response to that location or feature and therefore introduces bias into the saliency map through which location and features compete to capture visual attention (Corbetta, Miezin, Dobmeyer, Shulman, &

Petersen, 1990; Desimone & Duncan, 1995). As a result, a number of researchers have recommended the term “priority map” rather than “saliency map” to refer to the representation of the visual field which ultimately guides competition for visual attention (Awh, Belopolsky, & Theeuwes, 2012; Bisley & Goldberg, 2010; Molenberghs, Mesulam, Peeters, & Vandenberghe, 2007; Ptak, 2012)

The interaction between bottom-up and top-down attention is achieved by the frontoparietal attention network (FPAN). While the parietal cortex has long been implicated in the orienting of visual attention (Posner, 1980; Posner, Walker, Friedrich, & Rafal, 1984), a heavily interconnected network linking the posterior parietal cortex (in particular the intraparietal sulcus) and the dorsal prefrontal cortex (particularly the frontal eye fields) is understood to play a crucial role in orienting visual attention and, particularly, in integrating the bottom-up and top-down influences on the allocation of attention. Activity in the FPAN is associated with switching attention between both locations and features (Scolari, Seidl-Rathkopf, & Kastner, 2015). Activation has been found to be stronger in frontal regions during top-down guidance of visual search (reflecting conscious or planned direction of attention under the control of areas of frontal cortex), and in parietal areas during tasks reliant on bottom-up capture of attention (Buschman & Miller, 2007; Chambers, Stokes, Janko, & Mattingley, 2006; De Fockert et al., 2004).

The FPAN has been divided into two components: a) the dorsal frontoparietal network (DAN), which includes the intraparietal sulcus, superior parietal lobule, and a dorsal prefrontal area which may be the frontal eye field, and b) the ventral frontoparietal network (VAN), which includes the temporoparietal junction (including the posterior portion of the superior temporal sulcus and gyrus), the ventral portion of the supramarginal gyrus, and the ventral frontal cortex (Corbetta, Patel, & Shulman, 2008). The DAN is understood to be specialised for maintaining selection of relevant inputs and maintaining connections between input and responses, while the VAN is only activated when the network needs to be reset and reorganised to link new input to different responses. While the current task is maintained, the VAN is suppressed by the DAN in order to avoid interruption of the current task, and the DAN maintains the task-oriented biasing of the attentional priority map to ensure task goals are met (Corbetta et al., 2008). The full details of the connections and functions within this complex neural network are still being investigated (Scolari et al., 2015; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010).

3.3 The effect of age on visual attention

Older adults and younger adults have been found to experience similar attentional capture by irrelevant singleton distractors (Kramer, Hahn, Irwin, & Theeuwes, 1999), suggesting automatic bottom-up attentional capture is preserved in older adults. Older adults are also capable of highly efficient bottom-up deployment of visual attention in less demanding tasks. For example, both older and younger adults are able to search efficiently for a target distinguished by a single feature (e.g. a red X among green Xs). Although older adults overall have slightly longer reaction times when performing such tasks (Hommel, Li, & Li, 2004; Humphrey & Kramer, 1997; Plude & Doussard-Roosevelt, 1989), increasing the number of distractors has little effect on time required to detect the target in either age group, suggesting the target exhibits a bottom-up pop-out effect, and that this effect is not influenced by age (Plude & Doussard-Roosevelt, 1989). While this might suggest that reduced processing speed, rather than changes in attentional processes, could explain differences in visual search performance between older and younger adults (Humphrey & Kramer, 1997; Madden & Whiting, 2004), it is also possible that changes in the functioning of attentional mechanisms lead to longer reaction times (Madden, Whiting, Cabeza, et al., 2004). It is therefore important to also consider the evidence for age-related changes in the operation of attentional mechanisms.

A number of studies have found other differences in the processes of visual attention in older adults, in addition to a reduction in processing speed. For example, a study of event-related potentials recorded during a pop-out type search found the N2pc component (which is understood to reflect orienting of attention) is not only delayed but is also attenuated in older compared to younger adults (Lorenzo-López, Amenedo, & Cadaveira, 2008). There is also a shift in the pattern of activation of the FPAN with age during visual search, with older adults showing more activation in frontal areas compared to younger adults, (Ansado, 2012; Li, & Zao, 2015). This shift in activation from more posterior areas (including occipital cortex) towards more frontal areas, and other areas associated with top-down control of attention, is part of a wider pattern of age-related change known as the Posterior Anterior Shift with Aging (PASA). The PASA phenomenon is understood to be a compensatory strategy used by older adults to help limit the consequences of poor sensory input to visual processing (S. W. Davis et al., 2008). The use of more frontal areas in visual search by older compared to younger adults may also reflect another compensatory strategy: a greater reliance on top-down control of attention to compensate for reduced capacity for bottom-up processing (Madden, Spaniol, Whiting, et al., 2007).

As with simple search tasks, more complex search tasks that rely heavily on top-down attention, are performed more slowly by older adults than younger adults (Madden, 2007; Zanto & Gazzaley, 2014). Searching for a target defined by the conjunction of two features (e.g. a red X among red Os and green Xs) is more reliant on top-down control of attention. Because the target is not salient on either feature alone, and shares each of its two feature values with half the items in the display, pre-attentive processing of features will be less likely to provide bottom-up attentional capture by the target (Wolfe, 1994). Instead, top-down attention to the conjunction of target features is required, which reduces the efficiency of visual search and produces set-size effects: longer reaction times are found as the number of distractors increases (Treisman & Gelade, 1980; Wolfe, 1994, 2014). Studies using this type of visual search have shown that older adults are impacted to a significantly greater degree by increasing the number of distractors (i.e. greater set size effects) than younger adults suggesting older adults have more difficulty using top-down attention to ignore distractors than younger adults (Hommel et al., 2004; Humphrey & Kramer, 1997; Plude & Doussard-Roosevelt, 1989).

A number of different studies have provided additional evidence that older adults have more difficulty ignoring an irrelevant stimulus, a process which relies on the top-down control of attention. Kramer and colleagues, for example, found that oculomotor capture by irrelevant distractors is similar in younger and older observers when awareness of the distractors is low (i.e., when targets and distractors are equiluminant), but older observers make more eye movements to the distractors compared to younger observers when the distractors are brighter than targets and therefore awareness of the distractors is high (Kramer, Hahn, Irwin, & Theeuwes, 2000). Pratt and Belomo (1999) found that, compared to younger adults, older adults were more susceptible to attentional capture by irrelevant onset cues, but equally susceptible to capture by irrelevant colour cues. While these studies show older adults are less able to use top-down attention to ignore irrelevant salient distractors, not all studies have found older adults more prone to capture by irrelevant stimuli (Colcombe et al., 2003).

Age-related differences in the capacity to use top-down attention to ignore irrelevant stimuli are more likely to emerge as the complexity of the task is increased (Verhaeghen & Cerella, 2002). For example, in an experiment where trials providing two sources of top-down attention were compared to trials with only one source, younger adults gained an advantage from the second source of top-down guidance whereas older adults did not (Whiting et al., 2007). This may suggest either that older adults are more resource limited when using top-down attentional guidance or that their increased reliance on top-down attention more rapidly exhausts their available cognitive resources (Zanto & Gazzaley, 2014). The PASA phenomenon by which older adults recruit additional neural resources to compensate for reduced processing efficiency has been shown to increase with the cognitive load (number of items to be processed) of the task under investigation (Ansado et al., 2012).

Alternatively, older adults may simply have more difficulty supressing irrelevant items, and the consequences of reduced inhibition may be more apparent in more complex tasks. A number of studies have found evidence for reduced inhibition in older adults both generally (Hasher & Zacks, 1988), and in visual processing in particular (K. M. Butler, Zacks, & Henderson, 1999; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Rowe, Valderrama, Hasher, & Lenartowicz, 2006), which may make the maintenance of top-down attention more effortful for older adults. Changes in the functioning of neurotransmitters have been implicated in a reduction in inhibition in older adults including GABAergic (Leventhal et al., 2003), and cholinergic functioning (Balducci, Nurra, Pietropoli, Samanin, & Carli, 2003; Coull, 2005; Taylor, Hartley, & Taylor, 2006). This suggests that maintaining appropriate bias over relative salience of targets and distractors, a function of the DAN (Corbetta et al., 2008), may be more effortful or less effective for older adults. The reduction in capacity for neural inhibition in older adults has also been linked to increased internal neural noise due to greater spontaneous firing of neurons and reduced capacity to respond selectively to a preferred stimulus (Schmolesky et al., 2000).

An important aspect of visual attention which has been show decline with age is the FFOV (Ball, Beard, Roenker, Miller, & Griggs, 1988; Ball, Bruni, & Roenker, 1990; J. D. Edwards et al., 2006; Scialfa, Kline, & Lyman, 1987). The most commonly used method for measuring of the FFOV is to require observers to identify a centrally presented target and indicate the location of a simultaneously presented peripheral target, often with the inclusion of peripheral distractor items, with only a very brief stimulus duration. The effect of age on the FFOV was initially conceptualised as a restriction of the size of the FFOV (Ball et al., 1990). However, similar effects of age on FFOV tasks have been found at small and large eccentricities and these findings suggest the effect of age on the FFOV is not a reduction in the extent of the FFOV, but rather a reduction in the efficiency of the FFOV (Seiple, Szlyk, Yang, & Holopigian, 1996; A. B. Sekuler, Bennett, & Mamelak, 2000). However, there is also evidence that older adults are slower and have more difficulty than younger adults adjusting the focus of attention in response to task requirements (Greenwood & Parasuraman, 2004; Jefferies et al., 2015), and whether this contributes to reduced efficiency of older adults on FFOV tasks has not been explored. Importantly the reduced efficiency of the FFOV in older adults has been shown to be associated with functional outcomes such as driving accidents (Clay et al., 2005) and falls, and general declines in daily activities (Owsley, 2016).

Little research has been conducted to explain the reduced efficiency of the FFOV in older adults. It is often taken to simply reflect a general reduction in processing speed in older adults (Owsley, 2013) given that older adults can successfully perform the task if allowed longer stimulus durations. Evidence has also been presented to suggest the FFOV performance in older adults reflects difficulty disengaging attention from the central target to locate the peripheral target, although this explanation presumes a serial rather than simultaneous performance of the two tasks (Cosman, Lees, Lee, Rizzo, & Vecera, 2012a). This slow-to-disengage account of the effect of age on the FFOV also suggests it relates to reduced capacity to control attention in a top-down manner. However, it is also possible that the slow disengagement by older adults reflects greater reliance on top-down control stemming from a less effective bottom-up response to the elements in the display. One of the aims of the first experiment in the current project is to explore this possibility.

An alternative explanation is that a reduction in the M pathway, which is understood to provide input to bottom-up and top-down attention (Bullier, 2001; Laycock, Crewther, & Crewther, 2007; Vidyasagar, 1999), may underlie a reduced efficiency in the FFOV of older adults (J. D. Edwards, Walley, & Ball, 2003). It has been argued that cognitive tasks requiring rapid visual processing, and this would apply to standard FFOV tasks, may suffer due to cell loss in the M pathway associated with age (Charles T. Scialfa, 2002). Alternatively, it might be that a loss of axons (Calkins, 2013), or a degradation in the myelination of axons (Pannese, 2011), found in older adults could explain the age-related reduction efficiency in the FFOV. Deterioration in the number or myelination of axons in the M pathway may well have a more substantial impact on visual function than a similar deterioration in the P pathway, since rapid conductance of signals is important to the functions served by the M pathway. Evidence in support of a link between M pathway decline and reduced bottom-up attention in older adults comes from a study in which younger and older adults were shown a line-motion illusion under two conditions designed to be preferentially processed by the M and P pathways. The illusion relied on reflexive bottom-up attention to small changes in the length of a line to induce a perception of motion. Older adults were found to perceive the line to move less than the younger adults, and particularly so in the condition preferentially processed by the M rather than the P pathway (S. B. Steinman, Steinman, Trick, & Lehmkuhle, 1994).

A reduction in the effectiveness of the M pathway when called upon to provide guidance of attention in a rapidly changing scene, could also explain difficulties for older adults directing attention using motion as the guiding feature. Older adults have been shown to have difficulty inhibiting irrelevant moving stimuli. Folk and Lincourt (1996) found older adults gained less benefit from coherent motion among distractors compared to younger adults in a search involving the conjunction of form and motion. Similarly, Watson and Maylor (2002) found that older adults were able to inhibit distractors in a conjunction search using visual marking for static displays, but not for displays involving motion. Visual marking occurs in conjunction search when one set of distractors is presented first, followed after a delay (e.g. 1000 ms) by presentation of the target and the second set of distractors. This allows observers to inhibit the feature of the first set of distractors, and use feature search for the target among the remaining distractors. Watson and Maylor (2002) used this approach to show younger adults could reduce display size effects (i.e., the increase in search time as the number of items in the display is increased) to near zero both when the stimulus contained both static and moving items. For older adults, on the other hand, the display size effects persisted for moving but not for static stimuli (Watson & Maylor, 2002). This suggests older adults had particular difficulty inhibiting moving stimuli, which may in turn indicate reduced capacity to use top-down control to inhibit irrelevant items in the dorsal stream. If motion is poorly encoded in the visual system of older adults as a result of degradation of the M pathway, then applying attention to motion may be more demanding for older adults. Alternatively, the reduction in the inhibitory neurotransmitter GABA found in older adults (Leventhal et al., 2003) has been implicated in reduced motion sensitivity in older adults (Bennett et al., 2007), and may make inhibition of motion more difficult for older than younger adults. While recent evidence shows older adults can use bottom-up attention to facilitate motion perception (Conlon et al., 2015), whether they can use top-down attention to enhance perception of motion has not been evaluated. The capacity of older adults to use top-down attention in the processing of visual motion will be investigated in experiment 3 of the current project.

Chapter 4: Perceptual processing deficits underlying reduced FFOV efficiency in older adults

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Statement on Authorship Contribution: As the co-author of the published paper entitled, “Perceptual processing deficits underlying reduced FFOV efficiency in older adults

”, I confirm that Garry Power has made the following contributions:

a) Formulation of the study hypotheses and critical review of the relevant literature;
b) Development of the FFOV task with direction and feedback from the co-author;
c) Collecting and entering the data into the statistical software package;
d) Analysing and interpreting the data under the direction of the co-authors\;
e) Writing the paper with direction and feedback from co-author.

Furthermore, I agree to the inclusion of the paper in this research thesis for examination.

Garry Power Date: 18th May 2017

Elizabeth Conlon Date: 26th May, 2017

4.1 Abstract

Older adults are known to perform more poorly on measures of the functional field of view (FFOV) than younger adults. Specific contributions by poor bottom-up and/or top-down control of visual attention to the reduced FFOV of older adults were investigated. Error rates of older and younger adults were compared on a FFOV task in which a central identification task, peripheral localisation task, and peripheral distractors were presented in both high and low contrast. Older adults made more errors in all conditions. The effect of age was independent of the contrast of the peripheral target or distractors. The performance cost of including the central task was measured and found to be negligible for younger adults. For older adults performance costs were present in all conditions and greater with distractors than without, and greater for a low than a high contrast central stimulus when the peripheral target was high contrast. These results are consistent with older adults compensating for reduced sensory input or bottom-up capture of attention by relying more heavily on top-down control for which they are resource limited.

4.2 Introduction

Older adults have a less efficient Functional Field of View (FFOV, also referred to as the Useful Field of View) than younger adults: they are slower and less accurate when identifying the location of a peripheral target when required to perform a simultaneous task presented at fixation, and particularly so if peripheral distractors are present (Ball et al., 1990; Fiorentino, 2008; Owsley, 2013; Seiple et al., 1996; A. B. Sekuler et al., 2000). FFOV tasks have been used to successfully identify older adults at greater risk of falls (Owsley & McGwin, 2004) and driving accidents (Ball et al., 2006; Hoffman, McDowd, Atchley, &

Dubinsky, 2005; Wood, 2002). However, the perceptual processes that explain poorer FFOV efficiency in older adults have not been clearly established.

The FFOV is an index of an individual's capacity to efficiently deploy visual attention in that it requires dividing attention between central and peripheral vision, and when distractors are added to the task, the capacity to selectively attend to a target and ignore distractors (Owsley, 2013). However, the deployment of visual attention relies on a complex process broadly understood as comprising two distinct but interacting mechanisms: bottom-up attention which involves automatically attending to the most salient input, and top-down control of attention in which the observer intentionally deploys attention to the most relevant feature or location (Buschman & Miller, 2007; Pinto, van der Leij, Sligte, Lamme, & Scholte, 2013).

Both bottom-up and top-down attention are likely to play a role in the efficient performance of FFOV tasks. The FFOV is typically assessed by measuring accuracy or speed of processing when observers are simultaneously given an object identification task presented centrally, and an object localisation task presented peripherally, either with or without peripheral distractors. Both dividing attention between central and peripheral vision, and selectively attending to targets amid distractors, require top-down control of attention. At the same time, the peripheral target will be detected most efficiently if it is able to capture attention automatically in a sensory-driven, bottom-up manner (Itti & Koch, 2000; Wolfe & Horowitz, 2004).

Increasing the attentional demands of the FFOV task increases the differences between older and younger groups. Relative to younger groups, older groups are less accurate in locating the peripheral target when no distractors are present, and the difference between age-groups is increased when distractors are added (Ball et al., 1988; Seiple et al., 1996; R. Sekuler & Ball, 1986). However, whether the reduced efficiency of the FFOV of older adults reflects poor top-down control or reduced capacity for bottom-up attention, or is independent of these mechanisms and attributable to some other factor such as general cognitive slowing (Timothy A Salthouse, 1996; Yamani, McCarley, & Kramer, 2015), has not been fully determined. The current study therefore used a modified version of the standard FFOV paradigm to investigate the impact of varying the attentional demands of the task (increasing or decreasing the salience of the central and peripheral stimuli, and removing the central task) on FFOV performance in younger and older adults. The aim was to identify whether reduced FFOV efficiency in older adults could be attributed to a reduced capacity for either bottom-up or top-down attentional processes.

Normal aging is associated with a decline in the efficient deployment of visual attention, but the decline is not consistent across all aspects of visual attention (Madden, 2007; McAvinue et al., 2012). Whether top-down control or bottom-up capture of attention is more prone to age-related decline is unclear (Zanto & Gazzaley, 2014). Older adults have been shown to exercise top-down attention just as effectively as younger adults when attending to a predictable target feature (Madden, Whiting, Cabeza, et al., 2004), and when using a cue to avoid bottom-up capture by irrelevant distractors (Muller-Oehring, Schulte, Rohlfing, Pfefferbaum, & Sullivan, 2013; Whiting et al., 2007). It has been argued that older adults have a reduced capacity for bottom-up attention due to poorer sensory input or increased internal neural noise, and compensate by relying more heavily on top-down attentional mechanisms (Madden et al., 2002; Whiting et al., 2014). However, bottom-up capture of attention has been shown to be equivalent in older and younger adults when searching for a target defined by a single feature (Muller-Oehring et al., 2013; Plude & Doussard-Roosevelt, 1989), or when irrelevant salient distractors disrupt visual search (Kramer et al., 1999).

More reliable differences between older and younger adults have been found when performing more complex visual search tasks. Searching for a target defined by the conjunction of two features among distractors that share one of the target-defining features, is a more complex task than search for a target defined by a single feature. Searching for a conjunction of two features produces longer search durations as the number of items to be searched increases, known as a set size effect. These effects are greater in older adults than in younger adults, suggesting that older adults have more difficulty with the increased attentional demands of the conjunction search. However set size effects are likely to reflect both top-down serial deployment of attention, and bottom-up response to pre-attentive processing of signal in noise (Eckstein, 2011; Liesefeld, Moran, Usher, Müller, & Zehetleitner, 2016; Wolfe, 2003). Creating conditions that manipulate the extent to which performance is determined by bottom-up and top-down processes is one way to determine how the different forms of attention contribute to age differences in perception.

Older adults may also be more resource limited in their capacity for top-down control of attention. This group is able to ignore inconspicuous distractors (equiluminant with targets) which exert relatively little bottom-up capture, but are less effective than younger adults at using top-down control of attention to overcome bottom-up attentional capture by highly conspicuous (higher luminance) distractors (Kramer et al., 2000). Older adults are also less able to take advantage of additional sources of top-down guidance. Whiting, Madden and colleagues varied multiple sources of top-down guidance: a consistent versus an inconsistent cue feature, and knowledge of whether the cue would be informative or not (Whiting et al., 2007). They found younger adults could gain additional advantage in search reaction times from combining both sources of top-down guidance relative to gains from one source, whereas older adults improved with one source of guidance but gained no further advantage from a second source. This may be a result of older adults having more limited resources for top-down attention, or their need to use greater top-down control to compensate for a poorer bottom-up response leaving insufficient additional resources to take advantage of a second source of top-down control (Whiting et al., 2007; Zanto & Gazzaley, 2014).

The specific contributions of reduced capacity for top-down or bottom-up attentional mechanisms to the reduced efficiency of the FFOV of older adults have not yet been systematically investigated. There is evidence that the FFOV of older adults deteriorates more than that of younger adults when the attentional demands of the central task are increased (Coeckelbergh, Cornelissen, Brouwer, & Kooijman, 2004). It has also been argued that those older adults who are poorer at a demanding FFOV task also have more difficulty disengaging attention from one location (i.e. the central task) in order to attend another (Cosman et al., 2012a). Both of these findings suggest the poor FFOV of older adults is linked to reduced capacity to control top-down attention. However, they are also consistent with older adults having an increased reliance on top-down attention to compensate for reduced bottom-up response to the stimuli as suggested by Whiting, Madden and colleagues (2007). This would lead to a greater impact on already stretched top-down control when the central task is made more demanding, and to more effortful re-orientation of attention if it is being directed by top-down rather than bottom-up mechanisms.

The goal of the current study was to investigate whether the reduced FFOV in older adults was due to poor bottom-up attentional capture by the peripheral target, or poor top-down control when dividing attention between the central and peripheral stimulus. We manipulated the bottom-up attentional component of the FFOV by varying the contrast of the peripheral target and distractors across trials. High contrast elements should capture bottom-up attention more effectively than low contrast elements (Wolfe & Horowitz, 2004). Bottom-up attention should therefore improve performance when the peripheral target is high contrast and the distractors low contrast, and impair performance when the target is low contrast and the distractors high contrast. If older adults have a reduced capacity to deploy bottom-up attention, the advantage of a high contrast peripheral target among low contrast distractors should be diminished for older compared to younger adults, as should the difficulty presented by a low contrast peripheral target among high contrast distractors. Top-down control of attention will be required to ignore high contrast distractors and attend to low contrast peripheral targets. Any deficit in top-down control in the older group will result in a greater difference in error rates between the younger and older groups in this condition compared to conditions requiring less top-down control.

The need to divide attention is the major top-down control required in the FFOV task. Investigation of performance costs of the inclusion of the central task by comparing error rates when both the peripheral and central tasks are presented simultaneously to error rates on the peripheral localisation task presented alone, allows the impact of dividing attention on the FFOV to be evaluated. Previous research has demonstrated that the cost of adding the central task is greater for older than for younger adults (A. B. Sekuler et al., 2000). In the current study, the interaction of top-down and bottom-up attentional mechanisms can be investigated by comparing performance costs in conditions with different bottom-up characteristics provided by different combinations of high and low contrast central and peripheral stimuli. The inclusion of a low contrast central stimulus will require more effortful top-down allocation of attention to central vision than the inclusion of a high contrast central stimulus, particularly for older adults if they use top-down control of attention to compensate for reduced sensory input or bottom-up attention. This will result in increased performance costs of the central task for older adults whose top-down attentional resources are thought to be more limited (Whiting et al., 2007).

4.3 Method

4.3.1 Participants

Participants were 42 younger (*M* = 27.38 years of age, *SD* = 5.41 years, 21 men, 21 women) and 42 older (*M* = 72.11 years of age, *SD* = 5.92 years, 19 men, 23 women) adults who reported they were free from ocular pathologies such as cataracts, glaucoma or macular degeneration. All participants were screened for visual acuity and contrast sensitivity. Participants wore their preferred corrective lenses for screening and all testing. No participant had poorer than 6/9 (20/40) corrected visual acuity, or contrast sensitivity as measured by the Pelli-Robson chart poorer than 1.65 Db. The younger group were first year Psychology students who received course credit for participation, and the older group were volunteers recruited from the local community. To meet the requirements of a larger project, all participants were currently licensed drivers with a minimum of three years driving experience. This study had University Human Research Ethics Committee approval with all volunteers providing written informed consent.

4.3.2 Stimuli

Screening of participants was conducted using the Pelli-Robson Contrast Sensitivity (Pelli, Robson, & Wilkins, 1988) and Snellen Visual Acuity charts. The Pelli-Robson chart presents triplets of letters at decreasing contrast with contrast sensitivity determined by the lowest contrast at which 2 out of 3 letters can be correctly identified. The chart was presented at a luminance of 100 cd/m^2, and viewed at a distance of 1 metre. Stimuli for the FFOV were produced using Macromedia Director and displayed by a NEC NP 500WS data projector controlled by a Dell computer. Viewing distance was 110cm and this was monitored by the experimenter. All elements were presented in either high (90 cd/m^2) or low

(6 cd/m^2) luminance (and therefore contrast) against a dark (2 cd/m^2) background in a room where the display was the only light source. FFOV performance was measured as the proportion of errors made on the peripheral task when the central task (if present) received a correct response. On trials where both the peripheral target and central task were included, only responses in which the centre target was correctly identified were considered valid trials. Invalid trials were excluded from the data analysis.

The display consisted of varying combinations of three stimuli: a central stimulus, a peripheral target, and distractors (noise elements). The central stimulus was a solid 3° by 5° car shape (see Figure 1) presented at fixation which was present or absent, with the stimulus present in 50% of randomly chosen trials. The peripheral target stimulus was a solid 3° by 5° car or truck shape placed at one of eight evenly spaced radial points around an imaginary circle with a radius of 30° centred on the central fixation point at a viewing distance of 110cm. Participants were required to report the location of the peripheral target by choosing the appropriate number on a subsequent response screen, with possible target locations numbered 1 through 8. Distractors were 3° by 5° triangles placed in 11 positions randomly chosen from the 23 available locations at 10, 20, or 30 degrees from fixation on the same eight evenly spaced radians as the peripheral target. In conditions with no distractors, based on Wood (2002), the stimulus duration was 90ms. The stimulus duration for conditions in which distractors were present was 240ms due to high numbers of older adults performing no better than chance level in pilot testing with 90ms stimulus durations.

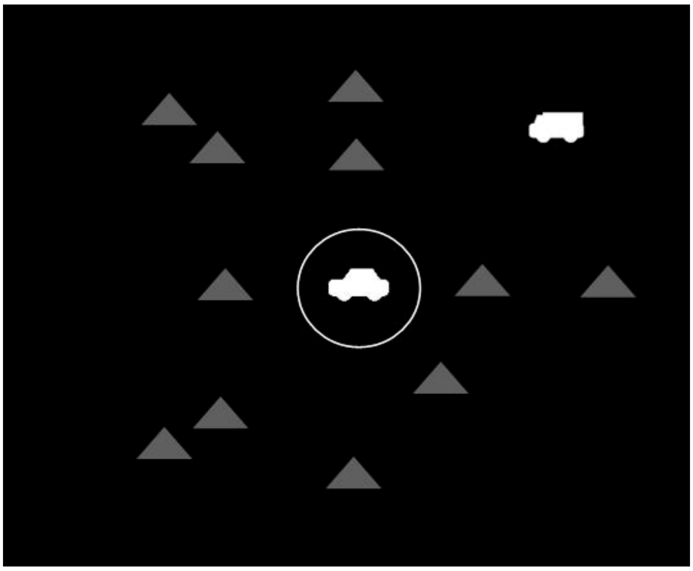

Figure 4.1. FFOV stimulus showing all elements present with central stimulus and peripheral target in high contrast and peripheral distractors in low contrast.

4.3.3 Procedure

Participants were first screened for age appropriate contrast sensitivity and visual acuity using the Pelli-Robson and Snellen charts. This was followed by two sessions of FFOV testing, one session included the central task in all blocks, the other included blocks without the central task. The session including the central task was arranged in three blocks of trials. The first block presented the central task alone, the second block included the centre task and peripheral target without distractors, and the third block added distractors to the stimulus from the second block. The session without the central task in the stimulus comprised two blocks: the first presented only the peripheral target, and the second presented the peripheral target with distractors. The order of sessions was counterbalanced across participants and the two sessions were separated by at least a 10 minute break. Testing was conducted in a darkened room after participants dark adapted for 10 minutes. Each block began with 10 practise trials in which stimulus duration was 3000ms for the first trial and was halved on successive trials until reaching the test duration.

Each trial began with presentation of a fixation cross for 750ms in the centre of the display. A white circle 12° in diameter at the centre of the display surrounded the fixation cross and remained on the screen for the full duration of the trial. Following presentation of the FFOV stimulus a mask containing a cross hatch pattern covering all possible target and distractor locations was presented with the same duration as the FFOV stimulus. This was replaced by a response screen with options to indicate whether the central stimulus was present or absent, and numbers 1 to 8 at each of the possible peripheral target locations. Participants stated their response to the experimenter who then entered responses into the computer. No feedback was provided about response accuracy.

When both the central task and peripheral target were included, a trial was only considered valid if the central task was performed correctly. Replacement trials were added to the end of each block to ensure 6 valid trials were recorded for each combination. Each block terminated after 6 valid trials for each possible combination of high and low contrast presentations of the included element/s (central stimulus, peripheral target, and distractors). Therefore, there were 12 valid trials required to complete a block for a single element (either central stimulus or peripheral target presented alone), 24 valid trials per block for the combination of two elements (either central stimulus and peripheral target without distractors, or peripheral target and distractors without the central task), and 48 valid trials required for the block combining of all three elements. Within each block the order of presentation for the possible combinations of high and low contrast elements was random. An additional short break was provided at the mid-point of the longest block to ensure participants did not become fatigued.

4.3.4 Design

For the current experiment the FFOV task was performed with, and then without, inclusion of the central task. Two dependent variables were analysed. First error rates (arcsine transformed) were considered for the peripheral target on trials when the central task was included. In a second analysis the performance cost of adding the central task was investigated. For this analysis the dependent variable was the difference in arcsine transformed error rates between trials (matched for peripheral target and distractor contrast) in which the central target was or was not included. In both analyses, two independent variables were investigated through mixed factorial ANOVA. Age-group (younger or older) was a between groups factor, and presentation condition was a within-subjects factor. Presentation condition had eight levels formed through the manipulation of the contrast of the central task, peripheral target, and peripheral distractors in the FFOV task (see Table 4.1).

Table 4.1.

FFOV task presentation conditions when the central task was included.

Presentation condition	Central task contrast	Peripheral target contrast	Peripheral distractor contrast
1	High	High	High
2	High	High	Low
3	High	Low	High
4	High	Low	Low
5	Low	High	High
6	Low	High	Low
7	Low	Low	High
8	Low	Low	Low

4.4 Results

Prior to analysis, the FFOV data was arcsine transformed to reduce the impact of floor effects commonly found in such data (A. B. Sekuler et al., 2000). Floor effects in the younger group were further controlled by combining data for the high and low contrast centre stimulus conditions for analyses comparing younger and older groups, and eliminating the no distractor condition from the analysis. No floor or ceiling effects were found in the older group for any condition. All other assumptions of the analyses were met. Error rates were also examined for detection of the central stimulus alone to ensure the centre stimulus could be detected. Few errors were made across trials in either the younger (2.4% errors 1/42) or older, 9.5% errors: 4/42) groups. No further analyses were conducted on these data.

4.4.1 Age group differences in FFOV performance

The first analysis evaluated age group differences in FFOV performance across presentation conditions when the centre and peripheral tasks were presented simultaneously together with peripheral distractors. The distractors and peripheral targets were of either high or low contrast (see Figure 4.2). The dependant variable was the arcsine transformed proportion of errors made across 12 trials per condition, with a score of 1.2 reflecting chance performance.

Results of a mixed factorial ANOVA showed that regardless of condition significantly more errors were made by the older than the younger group, $F_{(1,82)} = 195.53$, $MSE = .10$, $p < .001$, $\eta_p^2 = .71$, confirming previous findings that older adults have a less efficient FFOV than younger adults. There were no significant interactions with age group, all F’s (1, 82) < 2.39, all p’s > .126, indicating the effect of target and distractor contrast,

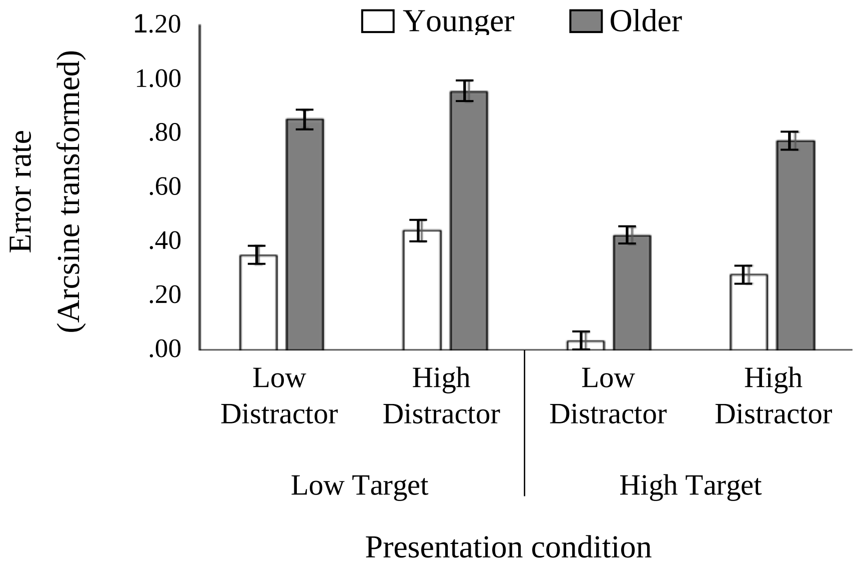

Figure 4.2. FFOV performance (errors as proportion of valid trials arcsine transformed: (0 = 0%, 1.57 = 100% error) showing each combination of peripheral target contrast and peripheral distractor contrast. Error bars represent ± 1 SE.

and their interaction, were similar for younger and older groups. For both age groups significantly fewer errors were made when the peripheral target was presented in high compared to low contrast, $F_{(1,82)} = 142.76$, $MSE = .04$, $p < .001$, $\eta_p^2 = .64$, and when distractors were low relative to high contrast, $F_{(1,82)} = 105.13$, $MSE = .03$, $p < .001$, $\eta_p^2 = .56$. There was a significant interaction between peripheral target contrast and distractor contrast, $F_{(1,82)} = 24.99$, $MSE = 0.03$, $p < .001$, $\eta_p^2 = .23$. The difference between high and low contrast peripheral targets was greater when presented among low contrast distractors, $F_{(1,82)} = 161.58$, $p < .001$, $\eta_p^2 = .66$, than among high contrast distractors, $F_{(1,82)} = 30.03$, $p < .001$, $\eta_p^2 = .27$. Also, as can be seen in Figure 4.2, regardless of age group the difference in error rates between the high and low contrast distractor conditions was greater when the peripheral target was high contrast, $F_{(1,82)} = 113.84$, $p < .001$, $\eta_p^2 = .58$, than when the peripheral target was low contrast, $F_{(1,82)} = 12.10$, $p = .001$, $\eta_p^2 = .13$. Figure 4.2 shows that presentation of a high contrast peripheral target among low contrast distractors resulted in fewer errors compared to all other conditions. This reflects the bottom-up capture of attention by a high contrast target among low contrast distractors. In the other conditions, the peripheral target was either the same or of lower contrast than the distractors, resulting in less bottom-up attentional capture. This pattern of results also demonstrates that high contrast distractors are harder to ignore than low contrast distractors, requiring greater top-down control of attention. The consistency of the effect of age group across conditions, indicated by the lack of any interaction between age group and any other variable, shows that the proportion of errors made in the older group is a simple linear function of the proportion of errors made by the younger group (see Figure 4.3).

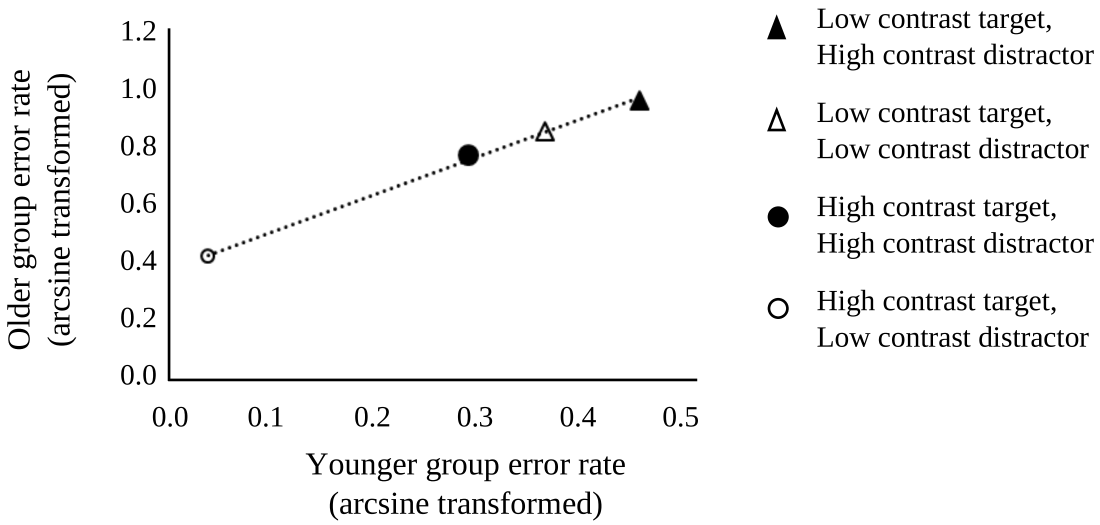

Figure 4.3. Relationship between the mean proportion of errors made by the younger and older groups across conditions. Triangles and circles represent low and high contrast peripheral targets respectively, filled and unfilled symbols represent high and low contrast distractors respectively.

4.4.2 The effect of dividing attention on older adults

The effect of dividing attention was examined by comparing error rates for the peripheral localisation task with and without simultaneous presentation of the central identification task. The performance cost of including the central task was calculated by subtracting error rates when only the peripheral target localisation task was included from error rates for the dual task FFOV (central and peripheral task presented simultaneously). Performance costs were calculated separately for each unique combination of high and low contrast centre task stimulus, high and low contrast peripheral target and peripheral distractor condition (none, low contrast, and high contrast). For the younger group performance costs were negligible in all conditions although significantly different from zero in two conditions: the high ($M = 0.15$, $SD = 0.34$, $t_{(41)} = 2.84$, $p < .007$) and low ($M = 0.04$, $SD = 0.12$, $t_{(41)} = 2.07$, $p = .044$) contrast distractor conditions when both the central stimulus and peripheral target were high contrast. This indicates that the requirement to divide attention between central and peripheral vision had almost no impact on the ability of the younger group to locate the peripheral target. Consequently, the performance cost of the central task for the younger adults was not further analysed. For the older group all conditions with distractors present had costs significantly different from zero (all t’s > 2.57, all p’s < .014), indicating the requirement to divide attention did reduce their ability to locate the peripheral target, especially when distractors were present (see Figure 4.4). The impact of varying the contrast of the components of the stimulus on performance cost of including the central task was examined by comparing costs across experimental conditions.

The performance cost of the central task for the older group was analysed using a fully repeated measures ANOVA with performance costs as the dependent variable, and centre stimulus contrast (low and high), peripheral target contrast (low and high) and distractor condition (none, low, and high contrast) as the independent variables. All assumptions of the analysis were met. The only significant main effect was for distractor condition, $F(2, 82) = 5.23$, $MSE = 0.17$, $p = .007$, $\eta_p^2 = .11$. Pairwise comparisons revealed that, compared to the no distractor condition, the performance cost of adding the central

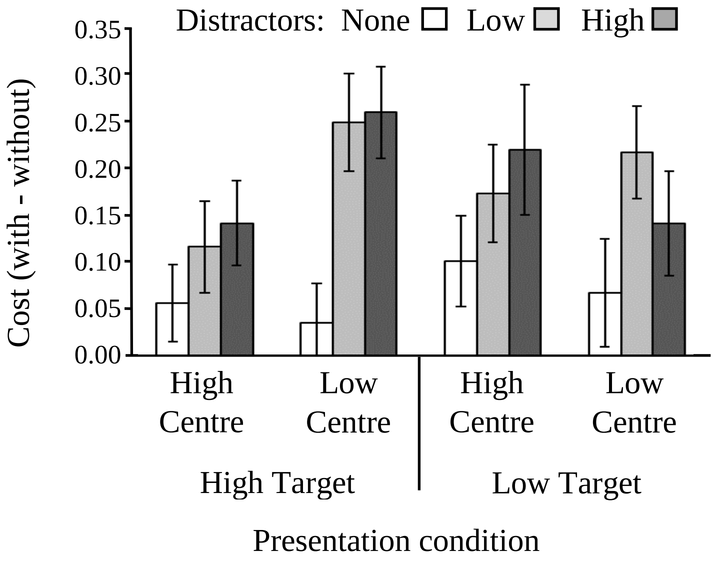

Figure 4.4. Cost of dividing attention for the older adult group across conditions formed by combining distractor (none, low contrast, high contrast), peripheral target contrast, and centre stimulus contrast conditions. Cost calculated by subtracting FFOV error rates (arcsine transformed) made without the centre task included from those made with the centre task included. Error bars represent ±1 SE.

task was greater when distractors were present at both high, *p* = .014, and low, *p* = .008 contrast. There was no significant difference to the cost of including the central task between high and low contrast distractor conditions, *p* = .967, indicating the performance cost of adding the central task was independent of the contrast of the distractors (see Figure 4.4).

The only significant interaction was between centre stimulus contrast and peripheral target contrast, *F*(1, 41) = 5.29, *MSE* = 2.45, *p* = .027, η_p^2 = .11. It was expected that a low contrast central stimulus would result in greater performance costs of the central task for older adults. Simple effects analysis indicated that when a high contrast peripheral target was used, the performance cost of adding a high contrast central stimulus was less than the performance cost of adding a low contrast central stimulus, *F* = 8.03, *p* = .007, η_p^2 = .16. When the peripheral target was low contrast, the contrast of the central stimulus (high or low) had no effect on the performance cost of adding the central task, *F* = 0.42, *p* = .521, η_p^2 = .01.

In sum, for the older adults, when the peripheral target was low contrast, the contrast of the added central task made no difference to its performance cost. However, when the peripheral target was high contrast, the performance cost of including the central stimulus was influenced by the contrast of the central stimulus: the central task had a lower performance cost when it was high contrast and a greater performance cost when a low contrast central stimulus was used.

4.5 Discussion

The main aim of the current study was to determine whether the reduced efficiency in the FFOV of older adults reflected a reduction specific to the capacity for either top-down or bottom-up allocation of visual attention. We hypothesised that a high contrast peripheral target presented among low contrast distractors would reduce difficulties older adults experience in deploying bottom-up attention, while attending to a low contrast peripheral target among high contrast distractors would exacerbate difficulties in the allocation of top-down attention. We also hypothesised that older adults would have greater reliance on top-down rather than bottom-up control of attention. As a result, we anticipated that the performance cost of dividing attention between the central and peripheral tasks would be greater for the older adults when a low contrast central stimulus was used, because this condition would require more top-down focus of attention to central vision. In the following sections each of these hypotheses will be addressed and the theoretical implications discussed.

4.5.1 The effect of age on FFOV errors

As expected older adults made more errors in all conditions on the FFOV task than younger adults, replicating previous research (Ball et al., 1988; Coeckelbergh et al., 2004;

Scialfa, Kline, et al., 1987; Seiple et al., 1996; A. B. Sekuler et al., 2000). However, as expected older and younger groups made fewer errors when a high contrast peripheral target was presented amongst low contrast distractors, demonstrating both groups were able to use bottom-up capture by a salient target to improve accuracy. Both age-groups also found high contrast distractors more difficult to ignore than low contrast distractors. The difference in the proportion of errors made between high and low contrast distractors was less for the low contrast peripheral targets than for the high contrast peripheral targets. For low contrast peripheral targets, top-down attention is required to attend to the target for both high and low contrast distractors because in neither condition is the target salient. Low contrast distractors were presented at the same contrast as the low contrast target, increasing target-distractor similarity, which limits bottom-up capture by the peripheral target and requires top-down attention to ignore the distractors. With a low contrast peripheral target, high contrast distractors were particularly difficult to ignore because they and not the target exert bottom-up capture of attention which must be overcome by top-down control. For high contrast peripheral targets, low contrast distractors were much easier to ignore than high contrast distractors. The low contrast distractors were less salient than the high contrast peripheral target allowing bottom-up attentional capture by the target and a reduced need for top-down control. When the peripheral target and the distractors were both of high contrast, the target and distractor were more similar and therefore less bottom-up attentional capture was exerted by the target resulting in increased error rates in both age groups.

The differences among these conditions therefore reflect the interaction of bottom-up and top-down attention. Neither facilitation by bottom-up attention to a peripheral target of higher contrast than the distractors, nor increased need for top-down attention to ignore distractors of equal or higher contrast than the peripheral target, produced a change in the effect of age: the difference between the age groups remained constant across all conditions in which both the central task and distractors were included. This surprising result suggests the effect of age on the FFOV is not a simple result of poorer bottom-up or top-down control of attention when locating the peripheral target.

When interpreted from the perspective of signal detection theory, the localisation of the peripheral target among distractors is a signal in noise task. A high contrast target presented among low contrast distractors will produce a high signal to noise ratio which attracts bottom-up attention. A low contrast target presented among high contrast distractors produces a low signal to noise ratio and requires top-down attention to either reduce response to noise or enhance response to the signal (Z.-L. Lu & Dosher, 1999). The difference between the age groups did not change across conditions even though the relative strength of the signal and noise components varied. The effect of age is therefore independent of the signal to noise ratio inherent in the stimulus. Older adults have been found to have higher levels of internal neural noise, which diminishes their capacity on signal in noise tasks (Bower & Andersen, 2012; Conlon et al., 2015). Increased internal neural noise can impair perception by reducing the signal to noise ratio independent of the external stimulus characteristics, depending on whether the internal noise is additive or multiplicative (Z.-L. Lu & Dosher, 1999). Therefore, increased internal neural noise in older adults may explain the consistent effect of age found across conditions.

4.5.2 Performance costs of dividing attention in the older group

For the older adults, the cost of a more demanding (low contrast) central task was greater than that for a less demanding central task (high contrast) when the peripheral target was more easily detected (high contrast). This was not the case when the peripheral target was low contrast. This suggests that when greater top-down control of attention was required to focus centrally and detect a low contrast central stimulus, the capacity for a salient peripheral target to pop-out due to bottom-up attentional capture was reduced.

Previously two explanations have been offered as to why older adults perform more poorly on the FFOV: generalised slowing (Owsley, 2013) and reduced efficiency when shifting attention from central to peripheral targets (Cosman et al., 2012a). While these accounts can explain the cost of the central task being greater when it is more perceptually demanding (i.e. low contrast), they would not anticipate the difference being present only for high contrast peripheral targets. The current results are best explained by a narrowing of attentional focus effectively inhibiting processing of the peripheral stimulus in order to allow processing of a perceptually demanding central task. This is consistent with a FFOV study which allowed eye movements, and found older adults had a narrower FFOV and employed more eye movements than younger adults when the eccentricity at which the peripheral target was presented increased (Coeckelbergh et al., 2004).

This explanation of the reduced FFOV in older adults is consistent with the finding that older adults exert more top-down control of attention in order to compensate for reduced sensory input or a poor bottom-up attentional response (Madden, 2007), something that would be exacerbated by a low contrast central stimulus. The cost of including the central task was also greater when distractors were present than when no distractors were present, but the performance cost did not vary between high and low contrast distractor conditions. This suggests the cost of using top-down control to divide attention between central and peripheral vision was increased by the need to also use top-down attentional control to ignore distractors. This is consistent with older adults being more resource-limited in terms of their capacity for using multiple sources of top-down attentional control simultaneously (Whiting et al., 2007).

Part of the evidence for greater reliance on top-down control in older adults comes from studies of the neural areas engaged during visual search by younger and older adults. Relative to younger adults, older adults performing visual search tasks recruit more frontal areas, associated with cognitive and therefore top-down control, and show less activity in occipital and parietal areas from which bottom-up attention arises (Buschman & Miller, 2007; Cabeza, Daselaar, Dolcos, Budde, & Nyberg, 2004a; Lorenzo-López et al., 2008). It is understood that this pattern, known as PASA (Posterior-Anterior Shift in Aging) allows older adults to recruit frontal regions to compensate for declines in posterior neural processing (S. W. Davis et al., 2008), and that this phenomenon is stronger when older adults perform more complex tasks (Ansado et al., 2012). In attentionally demanding visual search tasks older adults increase top-down control both intentionally and reflexively through greater activation of the dorsal component of the frontoparietal attention network (the dorsal attention network or DAN) and related areas which reduce bottom-up capture by salient peripheral signals arising from the ventral component of the frontoparietal attention network (Geerligs, Saliasi, Maurits, Renken, & Lorist, 2014). When focused attention is required, the DAN can block the capacity of the ventral attention network to draw attention to salient stimuli outside the current focus of attention (Corbetta et al., 2008; Corbetta & Shulman, 2002). This phenomenon would account for the pattern of results seen in the current study if older adults use top-down attention to narrow the focus of attention around a low contrast central target more than a high contrast central stimulus, and in doing so block some of the capacity of the high contrast peripheral target to capture bottom-up attention more effectively than a low contrast peripheral target.

4.5.3 Conclusion

The current results indicate that when selectively attending to the peripheral target among peripheral distractors, older adults can use bottom-up and top-down control of attention as effectively as younger adults. While older adults make more errors, varying the bottom-up and top-down requirements of the peripheral task had no impact on the age-group difference. We explored how older adults cope with the requirement to divide attention in the FFOV task by investigating the performance cost of including the central task. The results suggested older adults use top-down attention to focus available resources centrally, at the expense of reduced processing capacity for peripheral vision. The cost of narrowing the focus to central vision was found to be greater when the central stimulus was perceptually more difficult (low contrast) and the peripheral target was more salient. This suggests focussing centrally reduces the ability of salient peripheral objects to exert bottom-up attentional capture. This appears to be a compensatory strategy due to some more fundamental processing deficit exacerbated by a low contrast central stimulus. The current study cannot determine what this more fundamental deficit is. Previous research has suggested poor sensory input (Madden, 2007), increased internal neural noise (Whiting et al., 2014), or general cognitive slowing (Yamani et al., 2015) as possible general deficits for which older adults could use top-down attention to compensate. However, the use of a narrowed focus of attention to compensate for a general decline in perception may have implications for everyday tasks. For example, older drivers have been found to engage in a more active or serial search strategy, shown by a greater number of eye movements than younger drivers, when identifying other vehicles on the road, (Maltz & Shinar, 1999). Older drivers also have more accidents involving other vehicles approaching from outside their current focus of attention at uncontrolled intersections (J. Langford & Koppel, 2006). More research is needed to identify the underlying deficit that requires older adults to adjust their attentional priorities towards central vision in complex visual environments.

Chapter 5: Magnocellular not Parvocellular sensitivity predicts the Functional Field of View in older adults

5.1 Abstract

Poorer accuracy on Functional Field of View (FFOV) tasks is associated with increased motor vehicle accident rates and falls in older adults. The study explored associations between FFOV error rates and contrast discrimination thresholds mediated via the Magnocellular (M) and Parvocellular (P) sub-cortical pathways using the steady and pulsed pedestal paradigms of Pokorny and Smith (1997) in 44 younger (*M* = 27.18, *SD* = 5.40 years) and 44 older (*M* = 72.18, *SD* = 5.82 years) adults. Older adults made more FFOV errors, and had higher thresholds in both the steady and pulsed pedestal paradigms, than younger adults. FFOV errors in the younger group were not related to contrast thresholds. In the older group FFOV errors were strongly predicted by contrast discrimination thresholds mediated via the M pathway, but not the P pathway. The results suggest declines in the FFOV of older adults may be related to reduced M pathway contrast sensitivity.

5.2 Introduction

The Functional Field of View (FFOV) is defined as the visual field across which observers can perform two simultaneous tasks without the use of head or eye movements. It is typically assessed by the brief simultaneous presentation of two perceptual tasks, one presented to the central visual field and one presented peripherally. The capacity to perform the two tasks simultaneously is reduced when the eccentricity of the peripheral task, or the perceptual demands of the central task, are increased, and when noise or distractors are added peripherally (Mackworth, 1965; Sanders, 1970). As such, the FFOV is, in part, a measure of an individual’s capacity to divide visual attention between central and peripheral vision and selectively attend to the peripheral target when peripheral distractors are present. Because the Magnocellular (M) sub-cortical pathway is thought to provide primary input to areas of the parietal lobe that contribute to the control of visual attention (Vidyasagar, 1999), it has been proposed that the FFOV reflects the sensitivity of the M pathway (J. D. Edwards et al., 2003). To date, this hypothesis has not been tested empirically.

Compared to younger adults, the performance of older adults on FFOV tasks is slower and less accurate (Ball et al., 1990; Fiorentino, 2008; Owsley, 2013; R. Sekuler & Ball, 1986). In older adults, decline in the FFOV predicts increased risks of falls (Owsley & McGwin, 2004) and motor vehicle accidents (Ball et al., 1993; Ball et al., 2006; Hoffman et al., 2005; Wood, 2002). The effect of age on the FFOV is currently understood to reflect a reduction in the efficiency of the FFOV rather than in its extent (Owsley, 2013; A. B. Sekuler et al., 2000). In older adults this reduced efficiency has been attributed to generalised slowing (Owsley, 2013), or to increased difficulty redirecting attention from one location to another (Cosman et al., 2012a).

In visual search tasks, older adults rely more heavily on the less efficient top-down, cognitive control of visual attention rather than the more efficient stimulus-driven, automatic, bottom-up allocation of visual attention (Madden, 2007; Madden, Whiting, Provenzale, et al., 2004). In a partner study to this one, we have presented findings that suggest the shift to greater reliance on top-down attention contributes to the reduced FFOV efficiency in older adults (Power & Conlon, 2017, see Chapter 4). There is also evidence that the shift toward reliance on top-down attention in older adults is an attempt to compensate for reduced responses in early processing of visual input (Ansado et al., 2012; S. W. Davis et al., 2008), which relies on input carried from the retina to the primary visual cortex primarily by the Magnocellular (M), Parvocellular (P), and Koniocellular (K) pathways (Kaplan, 2004; Livingstone & Hubel, 1987). Compared to younger adults, older adults have been shown to have reduced contrast discrimination thresholds in both the M pathway and P pathways (S. L. Elliott & Werner, 2010; Lenoble et al., 2012; McKendrick et al., 2007). The current study compared younger and older adults on FFOV error rates and contrast discrimination thresholds for the inferred M and P pathways, and explored the association between FFOV performance and the contrast discrimination thresholds of the M and P pathways in the older group.

The role of the M pathway in the FFOV has been hypothesised on the basis that the posterior parietal cortex is involved in directing attention to unpredictable peripheral targets (Bisley & Goldberg, 2010; Buschman & Miller, 2007; Constantinidis & Steinmetz, 2005), and the posterior parietal cortex (PPC) is in turn primarily reliant on the M pathway for input (Ungerleider & Mishkin, 1982; Vidyasagar, 1999). A role for the M pathway in allocating visual attention has also been proposed based on the faster conductance speeds in the M than in the P pathway (Laycock, Crewther, Fitzgerald, et al., 2007). The faster signal conductance along the M pathway, could make it ideally suited to providing rapid input to higher cortical areas (such as the PPC and frontoparietal attention network) which then provide feedback to earlier visual processing areas (e.g. V1, V5, V4, or LGN) so as to modulate processing of subsequent input (Bar, 2003; Bullier, 2001; C.-M. Chen et al., 2007). In support of this hypothesis a stronger line-motion illusion (an illusion which relies on the automatic bottom-up allocation of visual attention), and more efficient guidance of top-down visual search has been found for stimuli processed predominantly by the M pathway, compared to stimuli processed predominantly by the P pathway (Cheng, Eysel, & Vidyasagar, 2004; B. A. Steinman et al., 1997).

However, other studies have shown stimulus characteristics to which the M pathway is relatively insensitive, such as isoluminant colour, are able to attract visual attention, indicating the P pathway can also drive the bottom-up capture of visual attention (Ries &

Hopfinger, 2011; Snowden, 2002; Zhang & Luck, 2009). Longer stimulus durations are required to capture attention using isoluminant colour, than to capture attention using features to which the M pathway is more sensitive (Braithwaite, Hulleman, Watson, & Humphreys, 2006; Shena, 2006). This may be due to the slower conductance speeds found in the colour sensitive P pathway relative to the M pathway (Maunsell et al., 1999). Laycock, Crewther, and Crewther (2007) reconcile these findings by suggesting that the M pathway should not be regarded as the only source of input for the allocation of bottom-up attention, but as the most efficient source. This suggests that age-related reduction in M pathway sensitivity might contribute to the reduced efficiency of the FFOV in older adults.

While designing stimuli to suit either pathway exclusively is problematic (Kaplan, 2014), the steady and pulsed pedestal paradigm (Pokorny & Smith, 1997) has been shown to provide psychophysical estimation of the sensitivities of the M and P pathways. It does so by taking advantage of the fact that the M pathway saturates at low contrast while the P pathway maintains a linear increase in contrast response from low to high contrasts (Pokorny, 2011). Using this paradigm, older adults have been shown to have reduced contrast sensitivity in both pathways (McKendrick et al., 2007), with some studies showing a greater reduction in contrast gain in the P than the M pathway (S. L. Elliott & Werner, 2010; Lenoble et al., 2012).

In the current study, the steady and pulsed paradigm was used to measure contrast discrimination thresholds for the inferred M and P pathways in groups of younger and older adults. Associations were then explored between thresholds from the steady and pulsed task, and error rates for a FFOV task requiring the simultaneous detection of a central target (present or absent), and localization of a peripheral target among distractors. Older adults were expected to make more errors on the FFOV task, and to have higher contrast discrimination thresholds on both the steady and pulsed pedestal tasks. We expected that overall FFOV performance would be more strongly associated with M pathway contrast discrimination thresholds because of its priority role in providing input to attentional processes. The FFOV task used included different combinations of high and low contrast elements (central stimulus, peripheral target and peripheral distractors). This allowed investigation of whether any association found between FFOV performance and contrast thresholds in the M or P pathways was dependent on the attentional demands of the FFOV task: a high contrast target among low contrast distractors would benefit from highly efficient bottom-up attention while a low contrast peripheral target among high contrast distractors would require effective top-down control to ignore the distractors and attend to the target. It was hypothesized that the association between contrast thresholds for the M pathway and FFOV error rates would be greater in conditions relying on the efficiency of bottom-up attention and less in conditions reliant on top-down control of attention. Because some studies have found differences between men and women, especially in older groups, on motion coherence tasks which also rely on the M pathway (Atchley & Andersen, 1998; Conlon et al., 2017; Snowden & Kavanagh, 2006), sex differences on the FFOV task were also explored, although previous research has failed to find differences between men and women on the FFOV (J. D. Edwards et al., 2006).

5.3 Method

5.3.1 Participants

There were 44 individuals aged between 20 and 39 years (*M* = 27.18 years of age, *SD* = 5.40 years, 22 men, 22 women) in the younger group, and 44 individuals aged between 61 and 89 years (*M* = 72.18 years of age, *SD* = 5.82 years, 19 men, 25 women) in the older group. The current project was part of a larger study for which all participants were required to be licenced drivers with at least 3 years driving experience. Best corrected Snellen visual acuity was 6/9 or better for all participants. Participants wore their preferred corrective lenses for all testing. The younger group were University students who received course credit for participation, and the older group were healthy volunteers recruited from the local community. This study had University Human Research Ethics Committee approval with all volunteers providing written informed consent.

5.3.2 Stimuli and procedure

5.3.2.1 Steady and Pulsed Pedestal Task

All stimuli were generated using a Cambridge Research Systems visual stimulus generator running in an IBM compatible computer with a Pentium 4 processor and were displayed on a calibrated 17 inch CRT monitor operating at a frame rate of 120 Hz in order to minimise artefacts from the monitor refresh on the detection mechanisms (Zele & Vingrys, 2007). The stimuli for the pedestal paradigms are shown in in Figure 5.1. The pedestal consisted of an array of four squares, each 1 deg^2 in size at a viewing distance of 57cm with each square separated from both its neighbouring squares by a gap of .05 deg. A small (2 x 2 pixels) square black fixation point was displayed continuously at the centre of the screen. The pedestal luminance of 45cd/m^2, was set against the 30cd/m^2 adapting background. The luminance settings were chosen in order to target points at which the contrast detection functions of the M and P pathways predict a large separation between the two thresholds (Pokorny, 2011).

The two pedestal conditions were identical except for the opportunity to adapt to the pedestal in the steady pedestal condition. For the steady pedestal condition the 4-square array was present continuously during an additional one minute of adaptation prior to the first trial, and continuously during the testing period (in order to maintain adaptation). For the pulsed-pedestal condition, the 4-square array was only present during the 30 ms test trials when one square chosen at random was decremented in luminance relative to the remaining three squares, and participants were required to identify the decremented square (four alternative forced choice).

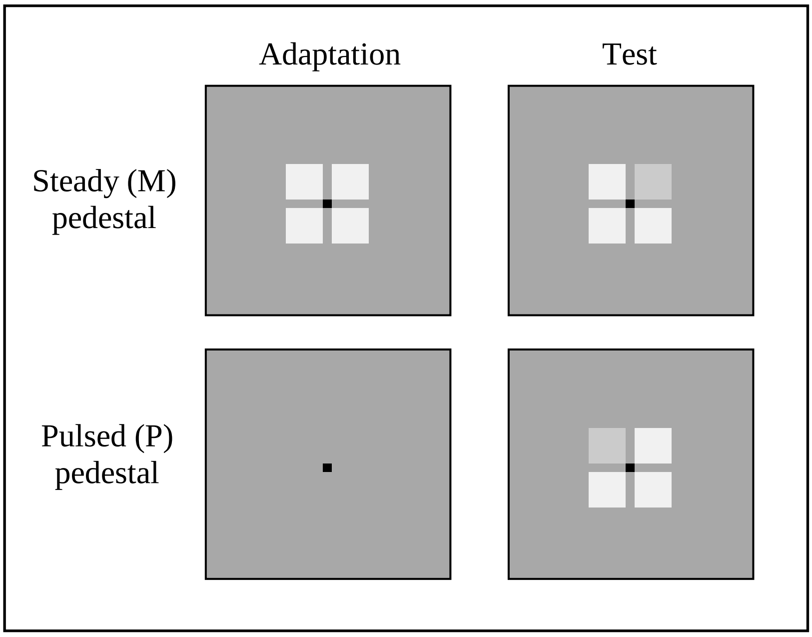

Figure 5.1. Steady (above) and pulsed (below) pedestal stimuli with adapting stimuli on left and test stimuli on right (based on Pokorny and Smith, 1997).

The steady and pulsed presentations allow inferred mediation of contrast sensitivity by the M and P pathways respectively. The validity of this inference has been supported by results from studies using the steady and pulsed pedestal presentations reflecting the response characteristics of the individual cells of the M and P pathways respectively (Pokorny, 2011; Pokorny & Smith, 1997; Zele, Wood, & Girgenti, 2010).

All testing was conducted in a darkened room with 10 minutes dark adaptation before initiating the test protocol. For both steady and pulsed presentations, the protocol began with 2 minutes of adaptation to the uniform surround (30cd/m^2). In the steady presentation, participants had a further 1 minute adaptation to the surround plus the pedestal prior to the first trial. On each trial participants identified which of the four possible locations contained the target square by pressing the left or right button up or down on a response box. Threshold contrast at which participants could discriminate the target square from the pedestal was determined using a three-up one-down (three yes, one no) staircase procedure. The luminance of the test square was 37 cd/m^2 for the first trial, making the target easily distinguishable. The initial step size was large (.048 log units for the steady presentation and .024 log units for the pulsed presentation) with step sizes progressively halved until a step size of .0015 log units was achieved. Blocks ended after 10 reversals with contrast discrimination threshold calculated as the mean luminance of the last 8 reversals. Two blocks of trials for each presentation condition were conducted, with presentation order counter-balanced across participants, and thresholds were averaged across blocks prior to analysis.

5.3.2.2 FFOV Task

Stimuli for the FFOV were produced using Macromedia Director and displayed by a NEC NP 500WS data projector controlled by a Dell computer. The display consisted of three stimuli: a central stimulus, a peripheral target, and distractors (see Figure 5.2). The central stimulus was a solid 3 deg by 5 deg car shape presented in the centre of a circular fixation frame. This stimulus was present in 50% of trials chosen at random. The peripheral target stimulus was a solid 3 deg by 5 deg car or truck shape placed at one of eight evenly spaced radial points (separated by 45 deg) at an eccentricity of 30 deg from the centre of the display. The distractors were 3 deg by 5 deg triangles placed in 11 positions randomly chosen from the 23 available locations at 10 deg, 20 deg, or 30 deg from fixation on the same eight evenly spaced radians as for the peripheral targets. The centre stimulus, peripheral target, and distractors were presented either in high (60 cd/m^2) or low (5 cd/m^2) luminance against the dim background (3 cd/m^2) which provided Michelson contrasts of 90% (high contrast) and

25% (low contrast). The stimulus duration was 240 ms. Participants were asked to indicate whether the centre stimulus was present or absent, then report the location of the peripheral target by choosing the appropriate number on a subsequent response screen, with possible target locations numbered 1 through 8. Performance was measured as the proportion of errors made on the peripheral task when the central task was correct (valid trials). If the response to the central task was incorrect, the trial was re-presented at the end of the block of trials. Viewing distance was 110 cm.

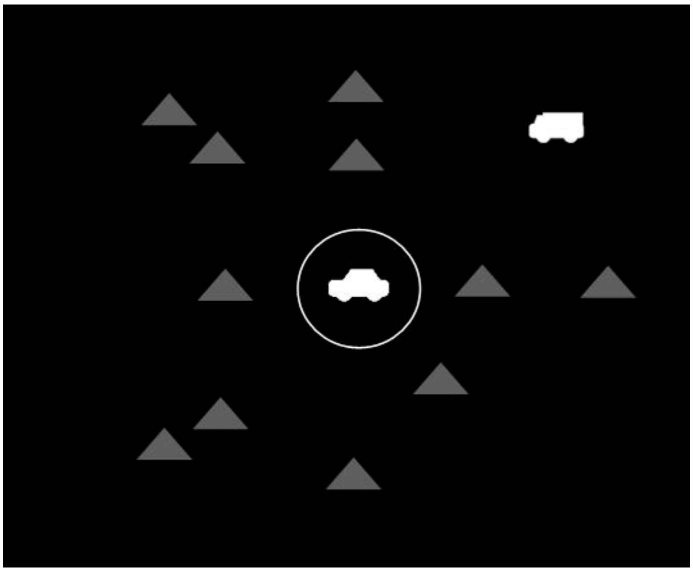

Figure 5.2. FFOV stimulus showing all elements present with central stimulus and peripheral target in high contrast and peripheral distractors in low contrast.

The FFOV task began with 10 practise trials in which the stimulus duration was 3000 ms for the first trial and was halved on successive trials until reaching the test duration of 240 ms. Each trial began with presentation of a fixation cross for 750 ms in the centre of the display. A white circle 12 deg in diameter at the centre of the display surrounded the fixation cross and remained on the screen for the full duration of the trial. Following presentation of the FFOV stimulus a mask containing a cross hatch pattern covering the entire screen was presented for the same duration as the FFOV stimulus. This was replaced by a response screen with options to indicate whether the central stimulus was present or absent, and the numbers 1 to 8 indicating the eight possible positions of peripheral target. Participants stated their response to the experimenter who then entered responses into the computer. No feedback was provided about response accuracy. All possible combinations of high and low contrast central stimulus, high and low contrast peripheral target and high and low contrast distractors were presented, requiring 8 different combinations. A minimum of 48 presentations were required to provide 6 valid trials each for the eight possible combinations high and low contrast elements. The order of presentation for the possible combinations was randomised across participants within each block of trials. A short break was provided at the mid-point of the block of trials to counteract participant fatigue.

5.3.3 Design

The study was a cross-sectional design with age-group (younger and older) as a between subjects factor, and pedestal presentation (steady and pulsed) as a within subjects factor, and log transformed contrast discrimination threshold as the dependent variable. Associations between FFOV error rates and steady and pulsed pedestal thresholds were also examined, through analysis of bivariate correlation, followed by multiple regressions using steady and pulsed contrast discrimination thresholds as predictors and FFOV error rates as the dependent variable. FFOV error rates were collapsed across central task contrast conditions which reduced the number of FFOV conditions to four: all possible combinations of the peripheral target contrast (high and low) and peripheral distractor contrast (high and low). As a result, five multiple regressions were conducted: one for each presentation condition and one for the total errors across all presentations combined. Multiple regression allowed examination of whether steady and pulsed contrast discrimination thresholds explain unique or shared variance in FFOV error rates.

5.4 Results

A preliminary analysis established there was no significant difference between men and women, and no interaction between sex and any other variables for the contrast discrimination thresholds, so all analyses were conducted with male and female groups combined to simplify reporting. To investigate age differences in the steady and pulsed pedestal task, a 2 (age group: younger and older) × 2 (presentation: steady and pulsed pedestal) mixed factorial ANOVA was conducted with log contrast discrimination thresholds (i.e. the difference between the pedestal and target luminance) as the dependent variable. The older group had significantly higher discrimination thresholds than the younger group, $F(1,86) = 13.30$, $p < .001$, $\eta_p^2 = .13$, indicating the older group required a larger difference in luminance to detect the target. Significantly higher thresholds were found for the pulsed than the steady condition, $F(1,86) = 2585.70$, $p < .001$, $\eta_p^2 = .97$. As shown in Figure 5.3, the difference between age-groups was slightly stronger for the pulsed presentation than for the steady presentation, however the interaction between age-group and presentation was not significant, $F(1,86) = 0.86$, $p = .356$, $\eta_p^2 = .10$.

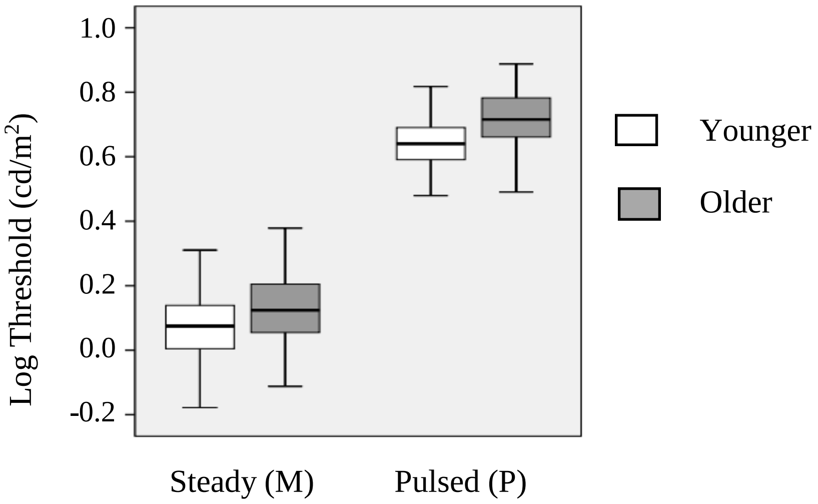

Figure 5.3. Boxplots showing median and range of log luminance thresholds for younger and older groups on steady and pulsed pedestal tasks (N = 44 for both groups).

The data for the FFOV error rates within each presentation condition were arcsine transformed to normalise the distributions. A FFOV total error rate was also produced to represent arcsine transformed total errors combined across all conditions. A preliminary ANOVA found there were no differences between men and women and no significant interactions between sex and either age-group or presentation condition (all *F's* < 1.78, all *p's* > .185), so the data for men and women were combined for all analyses. In order to simplify results and increase statistical power, data for high and low contrast centre stimulus conditions were combined. The results reported below did not meaningfully differ across these two conditions. As a result, four presentation conditions were analysed representing each possible combination of a high and low contrast peripheral target and high and low contrast distractors (see Table 5.1 for descriptive statistics). A 2 (age group) × 4 (presentation condition) mixed factorial ANOVA was conducted which replicated the long established finding that older adults make more errors on a FFOV task than younger adults, $F(1, 86) = 201.59$, $p < .001$, $\eta_p^2 = .70$. Following a Greenhouse-Geisser correction due to lack of sphericity, a non-significant interaction between presentation and age-group confirmed the effect of age-group was independent of presentation condition, $F(3, 233) = 2.07$, $p = .105$, $\eta_p^2 = .02$. There was a significant main effect of presentation condition, $F(3, 233) = 102.96$, $p < .001$, $\eta_p^2 = .55$ and all pairwise comparisons between presentation conditions were significant: all t's > 3.12, all p's < .002 (see Table 5.1). Both age groups made fewest errors with presentation of a high contrast peripheral target with low contrast distractors.

Table 5.1.

FFOV error rates across presentation conditions (arcsine transformed: chance performance = 1.20) for younger (n = 44) and older (n = 44) age groups.

Age Group	Presentation Condition								Total	
	High TC, High DC		High TC, Low DC		Low TC, High DC		Low TC, Low DC			
	M	*(SD)*	*M*	*(SD)*	*M*	*(SD)*	*M*	*(SD)*	*M*	*(SD)*
Younger	0.29	(0.23)	0.03	(0.09)	0.44	(0.27)	0.35	(0.25)	0.34	(0.16)
Older	0.75	(0.19)	0.42	(0.28)	0.95	(0.18)	0.84	(0.23)	0.75	(0.13)

Note: TC = Target contrast, DC = Distractor contrast.

Correlations between age, steady and pulsed thresholds, and total error rate for the FFOV are presented in Table 5.2. Total error rate was examined in order to maximise the number of observations underlying the estimates and simplify reporting. Correlations between steady and pulsed contrast thresholds and FFOV errors for each condition show that neither age nor FFOV errors were correlated with steady or pulsed presentation thresholds for the younger group (see Table 5.2). The associations among the variables are not further analysed for this group. In the older group, FFOV performance was positively associated with thresholds in both pathways indicating FFOV error rates increased as thresholds increased (see Table 5.2 and Figure 5.4). In the older group a significant association was found between age and Steady presentation threshold, whereas no significant association with age was found with Pulsed presentation threshold. These results indicate that, among the older adults, older age is associated with an increase in contrast discrimination thresholds on the M but not the P pathway.

Table 5.2.

Correlations between Age, total FFOV error rate and discrimination thresholds for the steady and pulsed pedestal presentations for older (shown above diagonal, n = 44) and younger (shown below diagonal, n = 44) groups.

Variable	Age	Steady (M)	Pulsed (P)	FFOV total
Age	-	.32*	.03	.27
Steady (M)	-.08	-	.49**	.66***
Pulsed (P)	.02	.46***	-	.37**
FFOV	.24	-.16	.01	-

* *p* < .05, ** *p* < .01, *** *p* < .001.

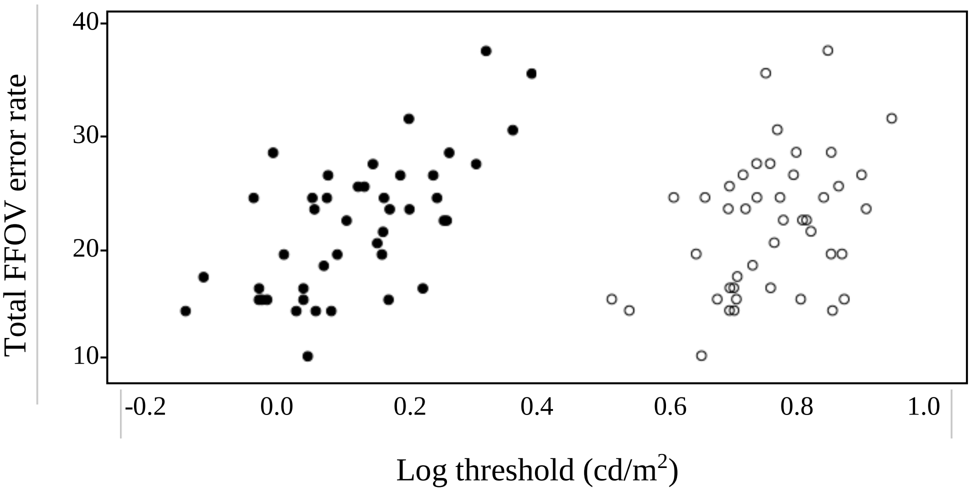

Figure 5.4. Association between FFOV error rates (total errors across conditions) and steady (filled circles) and pulsed (empty circles) pedestal thresholds in the older group (n = 44).

Table 5.3.

Results of multiple regression analyses predicting FFOV error rate from steady (M pathway) and pulsed (P pathway) discrimination thresholds (log cd/m^2*) for the older group (N = 44).*

FFOV Presentation		R^2 (%)	Predictor	β	sr^2 (%)	*B*	95% CI for *B*		Bivariate correlation
Target	Distractor						Lower	Upper	
High	Low	31.3**	Steady (M)	.60**	26.83	11.89	5.89	17.88	.56***
			Pulsed (P)	-.08	0.01	-2.21	-10.09	5.68	.21
Low	Low	21.6**	Steady (M)	.43**	14.21	7.97	2.07	13.87	.46**
			Pulsed (P)	.06	0.02	1.37	-6.40	9.13	.27
High	High	19.0*	Steady (M)	.34*	8.58	6.52	.20	12.84	.41**
			Pulsed (P)	.16	1.82	3.95	-4.36	12.26	.32*
Low	High	14.8*	Steady (M)	.31	7.40	6.48	-0.46	13.41	.37*
			Pulsed (P)	.12	1.06	3.22	-5.91	12.34	.27
FFOV Total		50.6***	Steady (M)	.68***	34.11	40.89	22.56	59.23	.66***
			Pulsed (P)	.07	0.34	4.95	-17.27	27.17	.39**

Note: * p < .05, ** p < .01, *** p < .001, M refers to Magnocellular pathway, P to Parvocellular pathway

For the older group multiple regression analyses were conducted with the steady (M pathway) and pulsed presentations (P pathway) contrast detection thresholds as IVs and proportion of FFOV errors (arcsine transformed) across the four conditions analysed as dependent variables (see Table 5.3). All assumptions of the analyses were met and no individual observations were unduly influential on the results.

The combination of steady and pulsed thresholds explained significant variance in FFOV error rates in all presentation conditions, with between 15.7% and 28.8% of variance accounted for across specific conditions (all *F*’s > 3.83, all *p*’s < .030), and 44.1% of variance explained in mean FFOV error rate for total errors combined across all conditions. The steady threshold explained significant unique variance in FFOV performance in all but the condition with a low contrast peripheral target and high contrast distractors, independently contributing between half and three quarters of the explained variance (as shown by comparing sr^2 to R^2 values in Table 5.3) across conditions. The pulsed presentation thresholds did not contribute unique variance in any condition. The unique contribution of the two thresholds was compared using t-tests (Cohen, Cohen, West, & Aiken, 2003) comparing the standardised regression coefficients for the two independent variables within each condition. While the steady threshold appears to make a greater unique contribution than the pulsed presentation across all conditions, the coefficient for the steady presentation was significantly greater than the coefficient for the pulsed presentation only in one condition: when the peripheral target was high contrast and the distractors low contrast, $t(41) = 2.22$, $p = .032$.

5.5 Discussion

The aim of the current study was to investigate whether the reduced efficiency of the FFOV in older adults was associated with higher discrimination thresholds of the sub-cortical M pathway. As expected, the older group had reduced contrast thresholds on both the steady pedestal (M) and pulsed pedestal (P) tasks. Previous findings that the older adults performed more poorly on the FFOV task were also replicated (Ball et al., 1990; A. B. Sekuler et al., 2000), and similar to previous results (J. D. Edwards et al., 2006) no effect of sex was found for the FFOV error rates. In the older group, as hypothesised, FFOV errors were significantly associated with contrast thresholds in the steady pedestal task to a much greater degree than the pulsed pedestal task, after controlling for variance in FFOV errors explained jointly by both pathways. The moderate positive correlation between the steady and pulsed pedestal thresholds suggest there are factors which influence contrast discrimination in both presentations, perhaps reflecting factors which influence both the M and P pathways. The multiple regression results allow these factors to be controlled and contributions unique to either pathway to be evaluated. Comparison of sr^2 and R^2 in Table 5.3 shows the unique contribution of the steady thresholds made up between half and two-thirds of the total variance explained by both pathways in combination. Therefore while factors contributing to both thresholds do explain variance in FFOV error rates, these results are consistent with the hypothesis that FFOV performance is associated predominantly with the sensitivity of the M pathway, at least in older adults.

The pattern of age-group differences for the steady and pulsed contrast discrimination thresholds also replicated those seen in previous studies (S. L. Elliott & Werner, 2010; Lenoble et al., 2012). Specifically, the older group had higher thresholds for both the steady and pulsed pedestal tasks than the younger group. There was a slightly greater effect of age for the pulsed than for the steady pedestal, although the difference in effects was not statistically significant. Previous research has produced mixed results for the interaction between age-group and presentation condition on the steady and pulsed pedestal task. McKendrick and colleagues (2007) found similar impacts of age on both pulsed and steady presentations, while Elliott and Werner (2010) found a greater effect of age for the pulsed pedestal presentation. Elliot and Werner (2010) gathered data for multiple pedestal contrasts and compared contrast gain between the two groups, whereas in the current study and that of McKendrick and colleagues (2007) only a measure of contrast discrimination at one pedestal contrast was produced. The use of contrast gain as the dependant variable may be necessary to fully capture the different effects of age on contrast thresholds for the pulsed and steady presentations. Consistent with previous findings, within the older group, higher thresholds were associated with older age for the steady but not the pulsed presentation (Lenoble et al., 2012). These finding indicate that contrast sensitivity in the M pathway continues to decline with advancing age in older adults, while contrast gain in the P pathway declines somewhere between early and late adulthood but does not decline further with advancing age in older adults.

The degree to which steady pedestal contrast discrimination thresholds explained FFOV error rates varied across the four FFOV conditions. The association between FFOV error rates and steady presentation thresholds was strongest when the target was high contrast and distractors low contrast, and was weakest when the peripheral target was low contrast and distractors high contrast. A high contrast peripheral target among low contrast distractors allows sensory driven bottom-up attention to be captured by the peripheral target (Itti & Koch, 2000). This enables greater efficiency in the FFOV as shown by lower error rates in this condition relative to other conditions for both younger and older groups. When the peripheral target is low contrast and distractors high contrast, bottom-up attentional capture by the distractors must be overcome in order to direct attention to the target. This reduces the efficiency of the FFOV as shown by increased error rates for both age-groups in this condition. The results therefore suggest that FFOV performance is more closely related to the sensitivity of the M pathway when the peripheral target is more salient (higher contrast) and bottom-up attention facilitates performance, and less so when bottom-up attention must be overcome by top-down control. This is consistent with the M pathway playing a central role in the rapid allocation of attention driven by sensory input (Bullier, 2001; Laycock, Crewther, & Crewther, 2007; B. A. Steinman et al., 1997; Vidyasagar, 1999)

There was no significant association between error rates on the FFOV and performance on either presentation of the steady and pulsed pedestal task in the younger group. It seems unlikely that reliance on the M pathways for performing the FFOV task only develops in later life. The lack of association between FFOV errors and steady and pulsed thresholds found in the younger group is more likely to be due to a lack of variation in the FFOV performance in the younger group in the current study. Reduced variability in either the younger or older groups is a common difficulty in studies of the FFOV (Fiorentino, 2008; A. B. Sekuler et al., 2000). The arcsine transformation employed normalises the data sufficiently to allow statistical comparison across groups, but cannot produce differences amongst individuals if the measure fails to discriminate between them. In the current study the older group was of most interest and parameters of the FFOV task were set to maximise sensitivity to individual differences within the older group. The use of FFOV tasks which are more sensitive to individual differences in younger adults should be explored in future studies to properly determine whether FFOV performance is related to M or P pathway sensitivity in this group.

The current study was motivated by the need to identify possible underlying causes of a reduced FFOV in older adults because a reduced FFOV is associated with increased risk of falls and driving accidents. The evidence supports the hypothesis that reduced sensitivity of the M pathway, which is understood to provide input to visual attention, may contribute to a reduced FFOV in older adults (J. D. Edwards et al., 2003; Vidyasagar, 1999). While the current study failed to fully confirm previous findings that the sensitivity of the P pathway declines more than the M pathway with age (S. L. Elliott & Werner, 2010), it does suggest that the decline in the M pathway might have more important functional consequences for dynamic tasks such as driving. The results also support the contention that the M pathway continues to decline in late adulthood, whereas P pathway sensitivity declines prior to 60 and then appears to be maintained beyond that (Lenoble et al., 2012). It is important to note that the association between M pathway sensitivity and FFOV error rate was stronger than that between age and FFOV error rate in the older adults. As such it reinforces the argument to rely less on chronological age (DeCarlo, Tuokko, Williams, Dixon, & MacDonald, 2014) as an indicator of functional competence and suggests changes in early visual processing in the M pathway may be a factor in the functional decline of some older adults.

Chapter 6: Motion perception in older adults

6.1 Introduction

An age-related decline in motion perception has been found to predict driving performance and falls in older adults, suggesting the capacity for motion perception may have implications for the ongoing independence and mobility of these individuals (Anstey et al., 2005; De Raedt & Ponjaert-Kristoffersen, 2000; Lord et al., 2010; Wood, 2002). Compared to young groups, older adults have higher thresholds for motion on tasks including minimum motion (Snowden & Kavanagh, 2006; Wood & Bullimore, 1995), relative speed of motion (Norman et al., 2003; Snowden & Kavanagh, 2006), detection of global coherent motion (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Ball & Sekuler, 1986; Bennett et al., 2007; Billino et al., 2008; Conlon & Herkes, 2008; Hutchinson et al., 2012; Snowden & Kavanagh, 2006; Trick & Silverman, 1991), biological motion (Pilz et al., 2010), the direction of optic flow (Atchley & Andersen, 1998; Warren et al., 1989), and perception of 3-dimensional shape from motion (Andersen & Atchley, 1995; Mateus et al., 2013). However, some studies have found other patterns of results: either no evidence of age-related differences on motion tasks (Brown & Bowman, 1987; Kavcic, Martin, & Zalar, 2013; Mapstone et al., 2003; Pilz, Miller, & Agnew, 2017), that the effect of age is greater in women for two dimensional but not three dimensional motion (Andersen & Atchley, 1995; Atchley & Andersen, 1998) that the effect of age is restricted to women (Gilmore et al., 1992), or even that in certain circumstances older adults are more sensitive to visual motion than younger adults (Hutchinson, Ledgeway, & Allen, 2014). These results can partially be explained by the stimulus parameters used in different tasks.

6.1.1 Effects of stimulus parameters on motion discrimination tasks

Random dot kinematograms (RDK) are commonly used in motion discrimination tasks, such as detecting differences in the speed of motion or the direction of global coherent motion. In tasks that use a RDK two processes are required: individual motion signals (including direction or speed of the target dots) are extracted from among randomly moving noise dots, then integrated across space and time to form a coherent motion percept (Newsome & Paré, 1988). Capacity to correctly perceive the motion parameter is based on the proportion of dots required to achieve a required criterion such as percentage correct performance. For coherent motion tasks this is referred to as the motion coherence threshold. When RDK's are used to investigate age-related differences in motion discrimination, age group differences are more likely to be found if shorter stimulus durations, or fewer perceptual signals are presented in the stimulus (Conlon et al., 2017). For example, older adults are significantly less accurate than younger adults when discriminating speed when the stimulus duration is 400 ms, but no age group differences are found when the stimulus duration is 600 ms (Mateus et al., 2013). When detecting the direction of global motion, studies using stimulus durations of between 500 and 2000 ms, and an RDK with 300 or fewer dots, have found older individuals have higher coherence thresholds than younger individuals (Conlon et al., 2015; Conlon et al., 2017; Tran et al., 1998; Trick & Silverman, 1991). However, in studies using stimulus durations greater than 2000 ms and more than 500 dots in the RDK no significant age group differences are found (Kavcic et al., 2011; Mapstone et al., 2008; Mapstone et al., 2003). Older adults have been shown to recruit additional neural resources to compensate for reduced perceptual capacity in a range of tasks (S. W. Davis et al., 2008; Park & Reuter-Lorenz, 2009). Presentation of longer stimulus durations could allow older adults to reduce motion coherence thresholds by drawing on additional but less efficient neural resources for perceptual decision making.

6.1.2 Sex differences on motion discrimination tasks

In some studies that use an RDK as the stimulus to detect the direction of global motion, the age group differences have also been shown to depend on the sex of the participant. In most of these studies older women have higher coherence thresholds than older men (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Conlon et al., 2015; Conlon & Herkes, 2008). While initially explained by a greater rate of degenerative loss in older women at a neuronal level in the dorsal stream responsible for motion processing, or in the M pathway upon which it is heavily reliant for input (Gilmore et al., 1992), this explanation was weakened by findings that older men and women do not have different sensitivities on measures of temporal processing speed, optic flow (Atchley & Andersen, 1998; Conlon & Herkes, 2008; Fischer & Hartnegg, 2002; Charles T. Scialfa, 2002; Snowden & Kavanagh, 2006) or when there are no noise dots included in the RDK (Norman et al., 2003; Pilz et al., 2010). In addition, if the stimulus duration is less than 500ms, women of all ages perform more poorly than men on motion coherence and biological motion tasks (Billino et al., 2008; Conlon et al., 2015; Conlon et al., 2017; Pilz et al., 2010; Snowden & Kavanagh, 2006). In one recent study, the number of dots presented in the RDK was manipulated (Conlon et al., 2017). Younger women had higher thresholds than younger men for an RDK containing 150 dots, but not when 600 dots were presented. This finding was interpreted as evidence that younger women sampled the signal dots less efficiently than younger men, and this was ameliorated by increasing the number of signal dots available. In contrast, younger men had already reached maximum sensitivity to global motion with presentation of 150 dots, so increasing the number of dots did not provide further benefit. Older men and women did not gain benefit from an increase in the number of dots, with older women demonstrating consistently higher thresholds than older men regardless of the number of dots presented (Conlon et al., 2017). It was suggested that the short dot lifetimes (which increase the neural noise response to the RDK), as well as the increased internal neural noise in the older visual system explain the failure of older adults to take advantage of the increased number of dots in the RDK. Increased spontaneous firing of neurons (which creates additive internal noise) and reduced direction selectivity at MT has been found in older primates (Schmolesky et al., 2000; Yang, Liang, et al., 2009) and implicated in age-related decline in motion processing in humans (Bennett et al., 2007; Betts, Sekuler, & Bennett, 2007). However, top-down attention can enhance signal processing, and decrease the impact of internal noise on perception (Z.-L. Lu & Dosher, 1998). Older adults have recently been found to use top-down control of attention to reduce the impact of visual noise elements in a display (Whiting et al., 2014). The ability of older adults to do so in a motion coherence task has not previously been assessed.

6.1.3 Does attention influence global motion thresholds?

There has been little research on the ability of older adults to use visual attention to enhance the perception of global coherent motion. Bottom-up attention to signal and away from noise in a global motion task has been shown to reduce global motion thresholds in older and younger individuals, but does not eliminate the effect of age (Conlon et al., 2015). Similarly, in a visual search task, both motion onset and offset of a target has been shown to capture attention in a comparable way for older and younger individuals (Christ, Castel, & Abrams, 2008), but again older adults performed the task more poorly than younger adults in all conditions. Older adults have been shown to rely more heavily on top-down attention than younger adults in visual search tasks in order to compensate for reduced efficiency in sensory processing (Whiting et al., 2014). However, older adults more easily exhaust their capacity for top-down attention either because they are more resource limited than younger adults, or because of their over-reliance on top-down control of attention (Whiting et al., 2007; Zanto & Gazzaley, 2014).

Mixed results have been obtained in the studies that have examined the capacity for older adults to use top-down attention to enhance motion perception. Compared to younger adults, in a visual marking task older adults were found to be equally able to ignore previewed static elements in visual search, but unable to ignore previewed moving elements (Watson & Maylor, 2002). These results were interpreted as indicating that older adults have specific difficulty applying top-down attention to ignore irrelevant moving stimuli. However, other studies suggest older adults can use top-down attention to motion as effectively as younger adults. Older and younger groups gain similar benefits when the direction of motion is in an expected versus an unexpected direction in a dot motion display, although this form of top-down attention did not overcome the age-group differences (Zanto, Sekuler, Dube, & Gazzaley, 2013). Older adults typically perform less efficiently on conjunction search tasks than younger adults, and similar differences between the age groups have been found for displays using static and moving elements (Folk & Lincourt, 1996; Kramer, Martin-Emerson, Larish, & Andersen, 1996), suggesting attending to moving elements is no more difficult for the older adults than attending to static elements. A study which compared performance on a functional field of view task to thresholds for coherent optical flow presented within an annulus defined by lateral motion found a strong association between the two measures in healthy older adults (Mapstone et al., 2008). These results suggest the same attentional processes are at work in older adults regardless of whether the stimulus is static (as in the functional field of view task) or involves motion. Taken together, these conflicting findings suggest the issue of whether older adults can use top-down attention to enhance motion perception warrants further examination.

6.1.4 The current study

A global coherent motion task was presented with half the dots presented in high luminance against a grey background (white dots) and half the dots presented in low luminance against the grey background (black dots). In any one condition, the signal dots were present in either the white or black dots only. Thresholds were obtained in two conditions for older and younger men and women: one condition with a cue directing attention to the dots containing coherent motion signals, black or white, and one condition with no cue. Consistent with previous findings, in the uncued condition, older men and women were expected to have higher motion coherence thresholds than the younger group. The parameters for the task were designed to allow replication of previous studies showing women to have higher coherence thresholds than men given a short stimulus duration and limited number of dots in the RDK. The cue condition allowed participants the opportunity to direct attention in a top-down manner to the dots containing the coherent motion. If participants are able to use the cue to ignore the half of the dots containing only noise dots, they will substantially improve the signal to noise ratio. If older adults are able to use top-down attention to compensate for increased difficulties ignoring visual noise, as reported in visual search tasks (Whiting et al., 2007), the availability of a cue may reduce the effect of age. However, the allocation of visual attention to a cue in a motion coherence task is effectively a second source of top-down attention given attention is already directed to the target lateral motion, and away from other directions of motion which distinguish the noise dots. Therefore older adults may struggle to take advantage of the cue as they have been found to be more resource limited than younger adults for top-down control of attention in previous studies (Madden, Spaniol, Bucur, et al., 2007). While younger men have demonstrated they need no help ignoring noise dots in such tasks and may gain no benefit from a cue, the younger women are expected to show reduced motion coherence thresholds in the cued compared to the uncued condition as the top-down cue will facilitate sampling efficiency in the same way bottom-up attention to signal has previously been show to do (Conlon et al., 2017).

The second aim of the study was to examine whether the increased global motion thresholds in older adults reflect a deficit in early, sub-cortical visual processing. It has been suggested that decreased sensitivity in the M pathway may underlie the difficulties experienced by older adults in perceiving global motion because motion sensitive areas in V1 and MT rely heavily on the M pathway for input (Gilmore et al., 1992; Henderson et al., 2010; Trick & Silverman, 1991). However, the effect of age on coherent motion tasks may be mainly influenced by difficulties in the dorsal stream, rather than in the sub-cortical M pathway (Conlon & Herkes, 2008). Global perception of motion requires both the extraction of local motion signals, which are first detected at V1, and their integration to form a global percept, which occurs at MT/V5 (Braddick, 1997; Maunsell & Van Essen, 1983; Snowden et al., 1991). Age-related decline in either of these areas, rather than in the sub-cortical M pathway, may be the source of age-related decline in global motion perception (Yang, Zhang, et al., 2009). In addition, MT/V5 in the dorsal stream has been found to receive projections from the P pathway indicating dorsal stream functions, such as perception of motion, may also make use of P pathway input. Weak to moderate associations have been found between sensory sensitivity of early vision (as indicated by contrast sensitivity) and global motion thresholds (Conlon et al., 2015). There is some evidence for an association between motion coherence and contrast sensitivity in the M but not the P pathway in glaucomatous older adults (McKendrick et al., 2005), however associations between global motion coherence thresholds and contrast sensitivity in the M and P pathways have not previously been explored in healthy normal older adults.

The current study will explore whether thresholds for the sub-cortical M or P pathways, as measured by the steady and pulsed paradigm of Pokorny and Smith (reported in Study 2 – see Chapter 5), explain global motion thresholds in older adults. This issue will be addressed in two ways. First, the association between coherent motion thresholds and contrast discrimination thresholds for the steady and pulsed tasks within the younger and older groups will be assessed. This first analysis will address the hypothesis that a reduction in the sensitivity of the M pathway may contribute to decreased functional vision (i.e. perception of complex motion), especially among older adults. A second question is whether the difference between younger and older adults is explained by an age-related decline in the sensitivity of the M pathway. This would suggest that the sensitivity of the M pathway mediates the association between age and motion processing. Therefore a separate mediation analysis will be performed to test this question using the contrast discrimination thresholds of both the M and P pathways as mediators of the effect of age on motion coherence thresholds.

6.2 Method

6.2.1 Participants

Participants were 40 younger (*M* = 26.05 years of age, *SD* = 5.47 years, 20 men, 20 women) and 35 older (*M* = 72.11 years of age, *SD* = 5.92 years, 17 men, 18 women) adults. The younger group were University students who received course credit for participation and the older group were volunteers recruited from the community. All participants reported no ocular pathology and were screened using the Pelli-Robson contrast sensitivity chart (Pelli et al., 1988) and Snellen visual Acuity chart. All participants provided written informed consent and the study received approval from the University Ethics Committee.

6.2.2 Stimuli & Apparatus

The stimuli for the steady and pulsed pedestal task were the same as those described previously (see chapter 5). The stimuli for the motion coherence task were programmed in C++ and generated using the Cambridge Research System running Visual Stimulus Generator 6 installed in a Dell Optiplex GX1 computer. They were displayed on a Hitachi HM-4721-D monitor running at 120 Hz and viewed at a distance of 57cm maintained by a chin rest. The global dot motion task (see Figure 6.1) consisted of 300 dots, 150 dots presented at 0.54 cd/m^2 (black dots) and 150 dots presented at 24 cd/m^2 (white dots), against a grey background (9 cd/m^2). The dots were presented within a circular area 10° in diameter in the centre of the computer screen. The velocity of the coherent dots was 12 deg/s. Signal dots had a dot lifetime of 50 ms (three 16.66 ms animation frames) following which they were regenerated at a random location within the display. A standard wrap-around technique was used for the signal dots that reached the edge of the display. Noise dots were randomly relocated in each animation frame. Stimulus duration was 700ms. On each trial a variable percentage of dots were chosen to be signal dots and these dots moved coherently either left or right. On any one trial signal dots were drawn either exclusively from the white dots or exclusively from the black dots. All remaining dots were noise dots. To reduce glare, the computer screen was masked by a black cover with the stimulus viewed through a circular aperture 12 degrees in diameter.

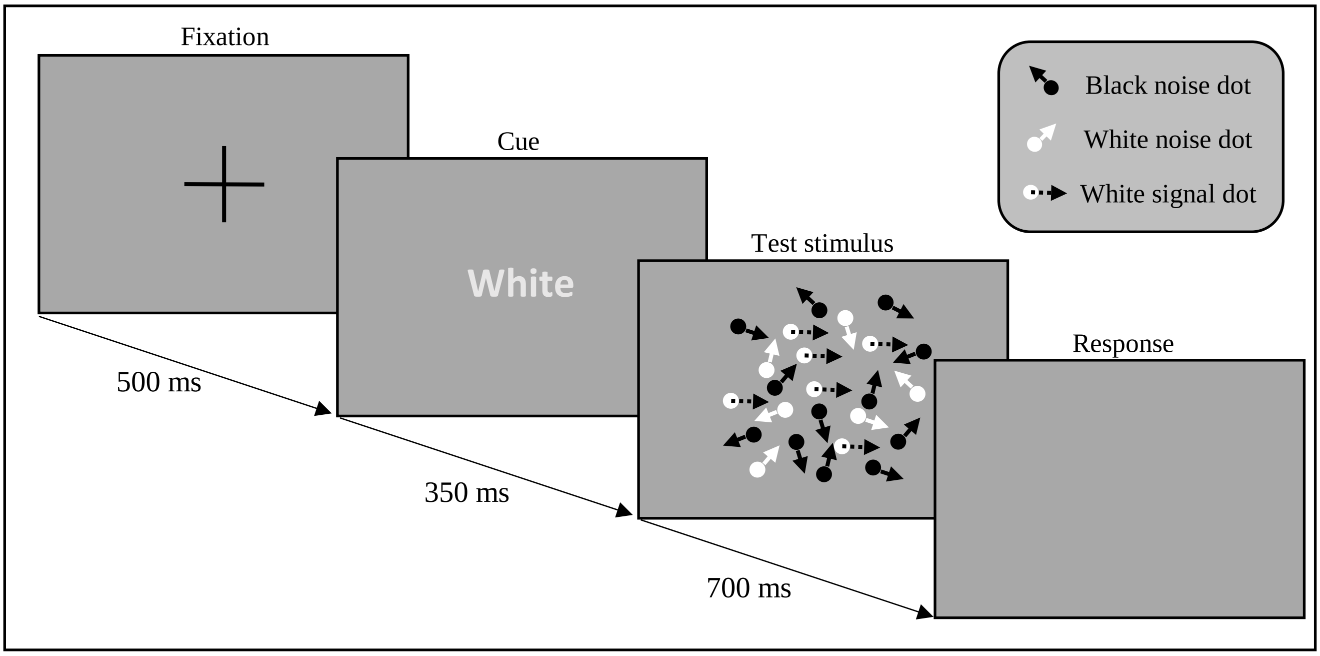

Figure 6.1. Representation of the global motion task. Arrows used to indicate motion were not part of the stimulus. On uncued trials the Cue screen was not presented.

6.2.3 Procedure

The procedure for the steady and pulsed task was the same as that described in chapter 5. Capacity to detect coherent global motion was determined using a two-alternative forced-choice task. The task was performed in a darkened room following 10 minutes of dark adaptation. On each trial participants were asked to indicate whether the coherent motion was to the left or to the right and entered their response by pressing the corresponding (left or right) button of a response box. No feedback was provided.

Two blocks of trials were performed with a cue (either the word “White” or the word “Black” presented in the luminance of the white and black dots respectively) appearing at fixation preceding each trial indicating whether the white or black dots would include the signal dots. In the cued condition the staircases for white and black dots were performed consecutively with a staircase for one colour of signal dots (e.g. white) completed first, followed by the other staircase (e.g. black signal dots). The order of presentation of the staircases for the black and white dots was chosen randomly by the software for each block of trials. Instructions appeared on screen at the start of each staircase to indicate which colour dots participants should attend to on the subsequent set of trials. A further two blocks of trials were performed with no cue provided. On each trial either the black or the white dots were randomly chosen as the signal dots. Separate interleaved staircases were conducted simultaneously to determine threshold motion coherence for black and white dots in the uncued condition. A minimum of five catch trials at 75% coherence were included in each block of trials to monitor response bias, and no participant was observed to respond in a biased manner on these trials.

Threshold global motion detection was determined using a three-down, one-up, staircase procedure. Following three correct responses coherence was increased 1.5 db, and following an incorrect response coherence was decreased by 0.5 db. Coherence thresholds were calculated from the number of coherent dots in the stimulus on each reversal, expressed as a percentage of all dots in the display. The staircase was terminated after eight reversals with thresholds calculated from the geometric mean of thresholds calculated at all eight reversals. This procedure provides an estimate of the coherence required for 79% correct performance. Prior to each block of test trials, a block of 20 practise trials was conducted.

6.2.4 Design

The main variables for the current study were the within-subjects factor of cue condition (cued and uncued), and the between groups factors of age-group (younger and older), and sex (male and female). These effects and their interactions were examined using a mixed factorial ANOVA with motion coherence threshold as the dependent variable. A further investigation used steady and pulsed contrast discrimination thresholds to predict motion coherence thresholds using a multiple regression technique. To investigate the nature of the contribution of steady and pulsed contrast discrimination thresholds to the effect of age on motion coherence thresholds, a mediation model was tested with both contrast discrimination thresholds entered as mediators of the association between age-group and motion coherence thresholds.

6.3 Results

6.3.1 Effects of age and sex on motion coherence thresholds

Motion coherence thresholds were analysed using a mixed factorial ANOVA with cue (cued and uncued) and dot colour (high luminance white and low luminance black) as within subjects factors, and sex (men and women) and age group (older and younger) as between groups factors. Colour had no effect and interacted with no other variable, therefore a simplified analysis was conducted and is reported below with colour excluded as a variable. The data was log transformed and a small number of outliers (1 younger woman, and 1 younger and 1 older man) were removed to normalise the distributions, following which the data met the assumptions of the analysis. The pattern of results is shown in Figure 6.2.

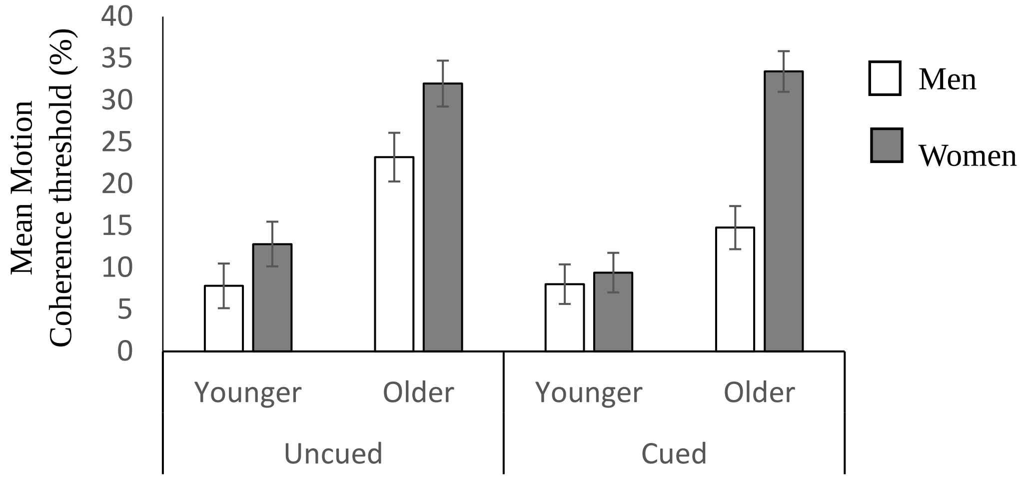

Figure 6.2. Mean coherent motion thresholds for older and younger men and women across cue conditions. Error bars represent ± 1 standard error.

The analysis revealed significant main effects of age group, *F*(1, 68) = 76.19, $p < .001$ $\eta_p^2 = .53$, sex, *F*(1, 68) = 15.79, $p < .001$, $\eta_p^2 = .19$, and cue condition, *F*(1, 68) = 9.08, $p = .004$, $\eta_p^2 = .12$, although these were impacted by a significant interaction between sex, age group, and cue condition, *F*(1, 68) = 11.30, $p = .001$, $\eta_p^2 = .14$. No other significant interactions were found. The significant interaction between sex, age group, and cue condition was investigated using interaction contrasts with the interaction between sex and age group examined separately in cued and uncued conditions first, followed by examination of the interaction between age and cue condition within each age group to determine if the effect of the cue was particularly beneficial for the men and women.

An age group by sex ANOVA for the uncued condition revealed significant main effects of age group, *F*(1, 68) = 58.22, $p < .001$ $\eta_p^2 = .46$, and sex, *F*(1, 68) = 11.10, $p = .001$ $\eta_p^2 = .14$, with no significant interaction between them, , *F*(1, 68) = 0.01, $p = .919$ $\eta_p^2 < .01$. The results in the uncued condition (see Figure 6.2) replicate the pattern found in previous studies with increased thresholds in older compared to younger adults, and in women compared to men.

In the cued condition significant main effects were found for age group, *F*(1, 68) = 71.76, $p < .001$ $\eta_p^2 = .51$, and sex, *F*(1, 68) = 16.15, $p < .001$ $\eta_p^2 = .19$, which were modified by a significant, interaction between them, *F*(1, 68) = 7.51, $p = .008$ $\eta_p^2 = .10$. Simple effects analysis confirmed the pattern seen in Figure 6.2, that in the cued condition there was no longer a difference between the thresholds of the younger men and women, $p = .355$, but the older women have higher thresholds than the older men, $p < .001$, and that the older group had higher thresholds than the younger group for both men and women in the cued condition, $p < .001$, just as they did in the uncued condition.

To investigate whether the cue was as effective for the older and younger adults, two cue by age group ANOVAs were conducted separately for the men and the women. The interaction between age group and cue condition was significant for both the men, *F*(1, 33) = 4.48, *p* = .042, η_p^2 = .12, and the women, *F*(1, 35) = 7.94 *p* = .008, η_p^2 = .19. However the pattern produced in each interaction was very different. For the men significant differences in thresholds between cued and uncued conditions were found for the older, *F*(1, 33) = 7.67, *p* = .009 η_p^2 = .19, but not the younger men, *F*(1, 33) = 0.01, *p* = .611 η_p^2 < .01, with lower thresholds for the older men in the cued condition than in the uncued condition (see Figure 6.2). In the women the opposite pattern was found. Thresholds for the younger women were significantly lower in the cued compared to the uncued condition, *F*(1, 35) = 14.13, *p* = .001 η_p^2 = .29, while for older women there was no significant change across cue conditions, *F*(1, 35) = 0.75, *p* = .786 η_p^2 < .01. This indicates that coherence thresholds in younger women improved following the provision of a cue, but older women received no benefit from a cue. In contrast, for men the older adults improved motion coherence discrimination following the presentation of a cue, while the younger men did not gain any benefit from a cue.

6.3.2 Associations between motion coherence and contrast discrimination thresholds

There was missing data for the steady and pulsed pedestal task for two younger women and two older men. Contrast discrimination thresholds for the steady and pulsed pedestal task were calculated as the log transformed difference in luminance between the pedestal and the target square (see Chapter 5 for further details). As reported previously (see Chapter 5), the steady pedestal thresholds for the older adults (*M* = .13, *SD* = .10) were higher, *t*(66) = 2.29, *p* = .025, than for the younger adults (*M* = .07, *SD* = .13). The pulsed pedestal thresholds were also higher, *t*(66) = 3.50, *p* = .001, for the older (*M* = .72, *SD* = .08) than the younger (*M* = .64, *SD* = .10) adults.

Bivariate correlations were examined to determine whether motion coherence thresholds (log transformed) could be explained by changes in the M pathway (see Table 6.1). In the older group, but not in the younger group, moderate positive associations were found between coherent motion thresholds for the uncued condition and both the steady and pulsed contrast discrimination thresholds. No significant associations were found between motion coherence and contrast discrimination thresholds in either age-group for the cued condition.

Table 6.1

Correlations between contrast discrimination and motion coherence thresholds. Older adults (n = 32) shown above the diagonal, and younger adults (n = 36) shown below the diagonal.

Variable		*1*	*2*	*3*	*4*
1	Steady (M)		.57**	.42**	.32
2	Pulsed (P)	.53**		.37*	.34
3	Uncued	.25	.20		.66***
4	Cued	.12	.19	.76***	

*p < .05, ** p < .01, *** *p* < .001

To assess whether motion coherence thresholds in the older group were better predicted by contrast discrimination thresholds on the steady pedestal task than on the pulsed pedestal task (reflecting the M and P pathways respectively), a multiple regression was conducted with the steady and pulsed thresholds as predictors of motion coherence in the uncued condition. The uncued condition is most comparable to the motion tasks used in previous studies, and the cued condition showed no association with either steady or pulsed pedestal thresholds (see Table 6.1). While the combination of the two contrast discrimination thresholds explained 20.5% of the variance in uncued motion coherence thresholds, $F(2, 29) = 3.73$, $p = .036$, neither the steady ($\beta = .31$, $p = .14$), nor pulsed ($\beta = .20$, $p = .33$) were found to independently explain motion coherence thresholds (see table 6.2).

Table 6.2

Multiple regression predicting uncued motion coherence thresholds from steady and contrast discrimination thresholds (N = 32)

Predictor	β	*B*	*SE (B)*	95% CI for *B*		sr^2%
				Lower	Upper	
Steady (M)	.31	0.81	0.53	-0.27	1.88	6.45
Pulsed (P)	.20	0.62	0.62	-0.64	1.88	2.76

The results above indicate that motion coherence thresholds in older adults can be explained by contrast sensitivity in general, but not by a decline specific to the M or P pathway. As shown in Table 6.1, there is a moderate correlation between the two contrast discrimination thresholds. This is likely to reflect shared contributions to contrast discrimination in both the M and P pathways such as any optical factors effecting contrast discrimination across a broad range of spatial frequencies, or perhaps a neural factor common to both pathways. The shared variance resulting from such factors explains why the thresholds of the two pathways fail to explain any unique variance in motion coherence thresholds. The focus of the current study is to determine if thresholds in the M pathway in particular, rather than shared factors common to both pathways, predict motion coherence thresholds in older adults. The current results do not support a decline in the M pathway explaining motion coherence thresholds in older adults.

However, it has also been suggested that the difference between older and younger adults in motion coherence thresholds could be due to an age-related reduction in the sensitivity of the sub-cortical pathways, in particular of the M pathway. This would suggest the sensitivity of the M pathway mediates the effect of age-group on motion coherence. Models including the steady and pulsed pedestal thresholds as mediators of the effect of age-group on motion coherence thresholds were tested using a bias corrected bootstrapping technique (Hayes, 2013). Results are reported for the uncued condition which is most comparable to results reported in other literature. When tested individually, significant mediation effects were found for both steady thresholds, β = .07, bootstrapped CI_{95} .01 to .16, and pulsed thresholds, β = .09, bootstrapped CI_{95} .02 to .20. When entered together as concurrent mediators, the combined indirect effect, β = .10, bootstrapped CI_{95} .01 to .21, is little more than that seen in the separate indirect models, and neither steady, *p* = .097, nor pulsed, *p* = .284, pedestal thresholds contribute unique variance to the motion coherence thresholds after controlling for age-group. It should also be noted that the independent direct effect of age-group on motion coherence thresholds was much stronger than the independent effect of either the steady or pulsed pedestal thresholds (see Figure 6.3). This suggests that

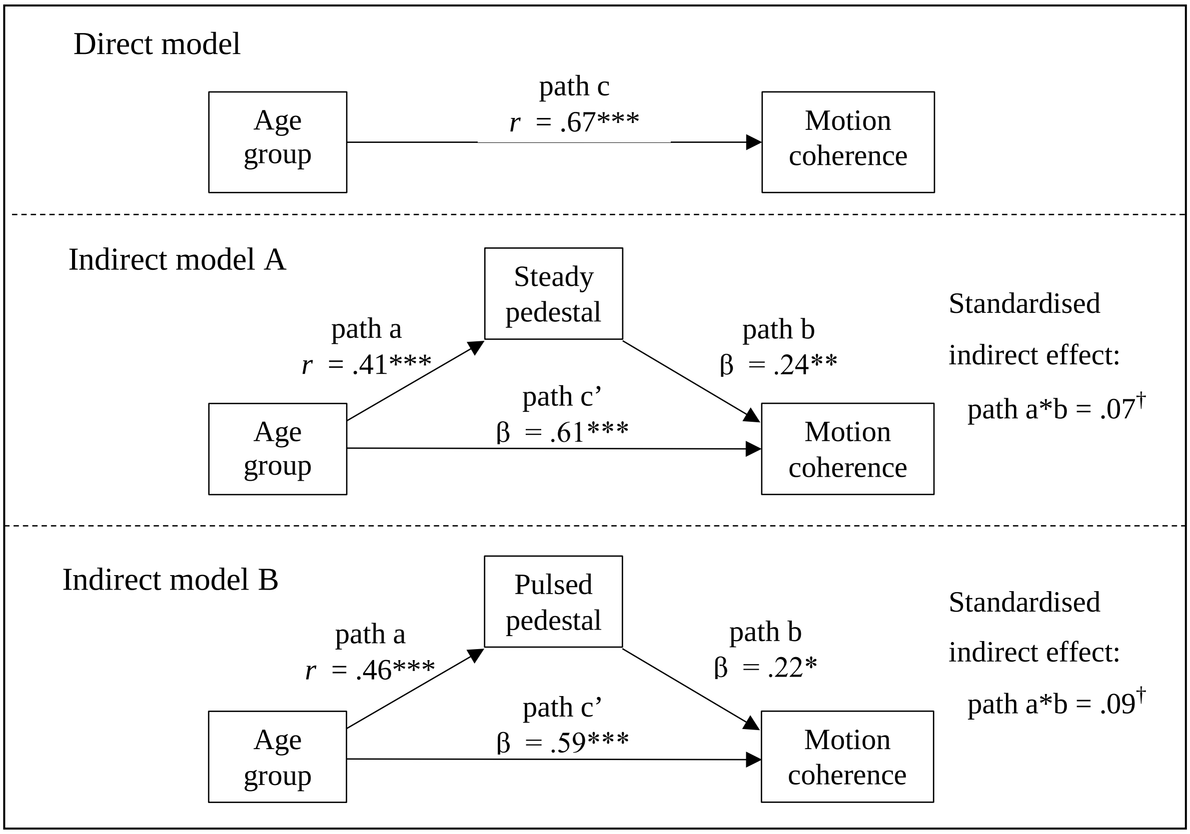

Figure 6.3. Model of the association between age and motion coherence mediated by contrast thresholds on the steady (Model A) and pulsed (Model B) pedestal task. β's from regression of motion coherence thresholds on age-group, and either steady or pulsed pedestal contrast thresholds.
* $p < .05$, ** $p < .01$, *** $p < .001$, † Bootstrapped $p < .05$.

some of the age-related increase in motion coherence thresholds is explained by an increase in contrast discrimination thresholds in general, whether measured by stimuli targeting the M or P pathways.

6.4 Discussion

The current study confirms the findings of previous studies that older adults have higher global motion thresholds than younger adults on a motion coherence task (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Bennett et al., 2007; Billino et al., 2008; Conlon et al., 2015). The effect of adding a cue indicating which set of dots (black or white) contained the relevant motion signals depended on the age and sex of the participants. Older men and younger women had reduced motion coherence thresholds when a cue directed attention to the dots containing the coherent motion relative to an uncued condition. Neither older women nor younger men received any benefit from the cue. The implications of these results will be discussed for older and younger adults separately. The current study also demonstrated that the effect of age on motion coherence thresholds is partly indirect and mediated by contrast sensitivity, although this is not attributable to reduced contrast sensitivity in either the magnocellular or parvocellular sub-cortical pathways in particular. Implications of these results will be discussed following consideration of the effects of sex and age on motion coherence thresholds. The younger group is considered first so they can then be used as a reference group to consider the effect of age on motion coherence thresholds in older men and women.

6.4.1 Younger adults

Consistent with a general effect of sex reported previously in similar studies using an RDK containing 300 dots or fewer, younger women had higher motion coherence thresholds than younger men in the uncued condition (Conlon et al., 2017; Gilmore et al., 1992). The addition of a cue reduced the motion coherence thresholds in younger women, but not in younger men, producing equivalent thresholds for both groups. This suggests that the processing advantages provided by top-down attention enabled younger women to become as sensitive as younger men in the processing of coherent motion. It is likely that the younger men failed to receive any benefit from the cue due to already low coherence thresholds in the uncued condition. This suggests younger men could attend to signal and exclude noise very effectively without the aid of a cue, making the cue redundant (Conlon et al., 2017).

Previous studies have shown younger men and women benefit equally from bottom-up attention to signal dots in motion coherence tasks (Conlon et al., 2015), and that younger women but not younger men reduce motion coherence thresholds when the number of dots in the display is increased (Conlon et al., 2017). These studies suggest younger women differ from younger men in their capacity to make full use of the available motion signals to form a coherent motion percept. The current study suggests younger women did gain additional help from top-down attentional guidance when extracting signal dots. Top-down attention enhances perception by both inhibiting processing of noise, and enhancing relevant signal by enhancing responses of neurons sensitive to the attended feature (Giesbrecht et al., 2006; O'Connor et al., 2002). It may be that attending to the luminance feature (white or black dots) indicated by the cue enabled younger women to increase the neural response to the signal dots and thereby increase their capacity to form the relevant signals into a coherent percept of global motion. This may be equivalent to the increase in ability to perceive coherent motion when the number of dots is increased for younger women (Conlon et al., 2017). When the overall number of dots is increased, coherence thresholds will decrease if correct perception depends on the number of signal dots (quantity of signal present) rather than the proportion of signal relative to the noise. This occurs because coherence thresholds are expressed as the percentage of the total number of dots needed to correctly perceive the motion. The results of Conlon et al. (2017 were taken to indicate that, once the signal was extracted from the noise, younger women used the available signal less effectively than younger men, and this was overcome when a higher number of overall dots provided a greater quantity of signal once noise was excluded. The equivalent effect in the current study to that of Conlon et al. (2017) suggests that for younger women, applying top-down attention is similar to increasing the available quantity of signal available for processing at a neural level. This suggests top-down attention to signal elements by younger women improves their perception of coherent motion through enhancing neural response to signal, rather than by inhibiting neural response to noise (Lu & Dosher, 1998). Compared to the younger men therefore, younger women were not as effective in processing motion coherence, a deficit which could be overcome by enhancing the neural response to the signal dots through top-down attention.

The younger men did not gain assistance from the cue, perhaps because their bottom-up processes, by which correlated motion signals are extracted from random motion noise, are sufficiently effective to produce minimum thresholds without the aid of top-down attention. However, Conlon et al (2015) found that bottom-up attention did improve motion coherence thresholds for younger men when signals were high contrast and noise dots low contrast, compared to a condition in which signal and noise dots were of equal contrast. In the current study a stimulus duration of 700ms was used, whereas Conlon et al. used 400ms. It is possible that this longer stimulus duration allowed younger men to achieve thresholds in the uncued condition that could not be improved through attention to the dots containing the signal motion in the cued condition of the current study.

The current study adds further weight to the conclusion that men and women differ in motion processing, and supports calls for more research into the source of sex differences found (Vanston & Strother, 2017). Sex differences in cognitive abilities are a contentious issue in the research literature (Levine, Foley, Lourenco, Ehrlich, & Ratliff, 2016). Differences in sex hormones have been suggested as one possible explanation for differences in motion processing in men and women (Conlon et al., 2017; Hutchinson et al., 2012). Pre- and post-natal hormonal differences have been used to explain neurological differences underlying sex differences in spatial reasoning of children (N. Hahn, Jansen, & Heil, 2009), and testosterone and estradiol levels are associated with patterns of brain activation in spatial cognition in adults (Moffat & Hampson, 1996; Schöning et al., 2007). The most widely endorsed sex difference in spatial cognition is an advantage for men in mental rotation (Miller & Halpern, 2014). This difference can be reduced by activities such as playing action video games (Feng, Spence, & Pratt, 2007), suggesting social/environmental factors rather than biological differences may underlie the observed differences.

6.4.2 Older Adults

Consistent with previous studies, older men had lower motion coherence thresholds than older women (Conlon et al., 2017; Gilmore et al., 1992), and this was found to be independent of additional top-down attention to signal dots in the cued condition. However, the addition of the cue had different effects for men and women. The older men improved with the addition of a cue that guided attention to the dots containing the coherent motion. While older men were still poorer than the younger men in the cued condition, the effect of age on motion coherence was reduced by the addition of the cue for the men. This is consistent with previous studies finding older adults can use top-down attention to compensate for reduced sensory processing (Madden, Spaniol, Bucur, et al., 2007; Madden, Whiting, Cabeza, et al., 2004), although this does not entirely eliminate the difference in motion coherence thresholds seen between younger and older men. These results are also consistent with Conlon et al (2015) who found older men were able to improve motion coherence thresholds when bottom-up attention was attracted to signal dots by increasing their salience. Therefore, while directing attention to signal dots facilitates motion coherence processing in older men, they still have higher thresholds than younger men, perhaps suggesting their difficulty is in integrating motion signals to form the global percept as well as extracting signal.

Older women not only had higher motion coherence thresholds than older men, but also gained no benefit from the presence of a cue directing attention to the dots containing the coherent motion. Therefore top-down attention fails to improve motion coherence thresholds for older women whereas it enabled younger women to become as sensitive to coherent motion as younger men. Previous studies showing that older adults benefit from top-down attention in visual search tasks have not investigated any differences in attentional capacity between older men and women. However, older adults have been found to be more resource limited in their capacity for top-down attention. Older adults can use a single top-down attentional cue to facilitate visual search as efficiently as younger adults, but gain no advantage from a second source of top-down attention, whereas younger adults can use a second source of guidance to improve search compared to a single source of top-down attention (Whiting et al., 2007). This indicates older adults can use top-down attention as effectively as younger adults, but are more resource limited in doing so. It has also been suggested that the greater reliance on top-down attention by older adults, which is a compensatory response to reduced sensory processing, may lead them to exhaust cognitive resources for top-down attention sooner than younger adults (Zanto & Gazzaley, 2014).

The act of extracting signal dots from a RDK requires attention to motion as a feature, and maximum sensitivity will be attained by attending to motion known to be relevant in a top-down fashion: e.g. attending to lateral motion and ignoring all other directions (Maunsell

& Treue, 2006; Saproo & Serences, 2014). It might be that for women, who are less sensitive to coherent motion (as shown in the younger group), the motion coherence task may be more attentionally demanding. In support of this explanation women have been found to take more of a cognitively controlled or top-down approach to mental rotation tasks, compared to men who take a more bottom-up approach (T. Butler et al., 2006). If women also take a more effortful, top-down approach to extracting signal from noise in a RDK task, then older women might find they are resource limited in also using top-down attention to simultaneously direct attention based on a cue, as was the case in the current study. As a result, for the older women in the current study, attending to both the relevant motion feature and dot colour simultaneously might have been beyond the limit of their available cognitive resources.

This account would explain why Conlon et al. (2015) found older women reduced their motion coherence thresholds when bottom-up attention to signal dots was enhanced by increasing the salience of the signal dots. This bottom-up attention would not compete in the same way for cognitive resources as the top-down cue used in the current study. Indeed top-down attention applied to motion when signal and noise differ in contrast as in Conlon et al, would amplify the effect of increased salience rather than compete with it for attentional resources. Further support for this interpretation comes from a study in which young adult women show more activation at the Lateral Geniculate Nucleus (LGN) than young adult men when viewing point-light displays of biological motion, which has been interpreted as an effect of greater top-down control of attention in women (Anderson et al., 2013). There is also evidence that reduced estradiol following menopause leads to reduced capacity for top-down attentional control due to interactions with the cholinergic neurotransmitter system (Newhouse & Dumas, 2015). Further research is needed to explore sex differences in attentional control strategies when viewing motion. For example, do women (and older women in particular) engage more frontal brain areas, indicating more effortful top-down control of attention, than men when performing motion coherence tasks, as shown in mental rotation tasks (T. Butler et al., 2006)?

6.4.3 Can contrast sensitivity in sub-cortical pathways explain motion coherence thresholds?

A second aim of the current study was to examine the association between global motion coherence thresholds and sensitivity of the M sub-cortical pathway. The steady and pulsed paradigm of Pokorny and Smith was used to assess the contrast sensitivity of the M and P pathways. In the older group, associations were found between motion coherence thresholds for the uncued condition and contrast discrimination in both the M and P pathways. When combined as predictors, contrast discrimination in neither the M nor the P pathway independently predicted motion coherence thresholds in the uncued condition. This is contrary to the expectation that increased motion coherence thresholds in older adults would be explained by reduced contrast sensitivity in the M pathway (Conlon & Herkes, 2008; Gilmore et al., 1992; Henderson et al., 2010; Trick & Silverman, 1991).

A separate question was whether an age-related reduction in contrast sensitivity could explain the difference between older and younger adult’s motion coherence thresholds. Contrast sensitivity in general was found to partially mediate the association between age and motion coherence thresholds. However, this mediating role was found for the effect of age on both the M and the P pathways (as reflected by the steady and the pulsed pedestal thresholds respectively), suggesting that it is a general age-related decline in contrast sensitivity that contributes to reduced motion coherence in older adults. Therefore, contrary to predictions, neither differences among older adults in motion coherence thresholds, nor the effect of age on motion coherence thresholds, are attributable specifically to a decline in the sensitivity of the M pathway. These findings could be explained by the fact that both the M and P pathway show reduced contrast sensitivity in older adults, and both pathways make a contribution to motion processing in the dorsal stream (Maunsell, Nealey, & DePriest, 1990). It may be the case that a reduction in both sub-cortical pathways contribute to increased motion coherence thresholds (Snowden & Kavanagh, 2006). However, it should be noted that the stimulus used in the steady and pulsed pedestal task is static, and this task may fail to capture age-related declines in the temporal processing characteristics of the M pathway, which are likely to be important in motion perception.

The indirect effect of age on motion coherence mediated by contrast discrimination explained only a small proportion of the overall effect of age on motion coherence thresholds, indicating other factors contribute substantially to the effect of age on motion perception. Age-related changes at a cortical level, such as in the dorsal visual processing stream, are likely to contribute to increased motion coherence thresholds in older adults (Kavcic et al., 2013). Studies in Macaque and Rhesus monkeys have shown degradation of speed tuning, greater spontaneous discharge, and increased response variability in neurons in MT, a crucial area for motion perception in the dorsal stream (Yang et al., 2008; Yang, Zhang, et al., 2009), and a greater reduction in contrast sensitivity at MT than for motion selective neurons at V1 (Yang, Liang, et al., 2009).

6.4.4 Conclusions

Motion processing is an important capacity in the visual system required for successful mobility. Reduced motion processing in older adults has been associated with difficulties with functional tasks such as driving (Conlon & Herkes, 2008; Wood, 2002). The current results confirm earlier reports that women in general and older women in particular are less sensitive to global motion than younger men. The current results extend previous findings by showing that top-down attention, by which older adults are known to compensate for reduced sensory input, is ineffective for older women when applied to moving stimuli, at least for the parameters tested here. This is of particular concern in modern societies in which older adults are making up an increasing proportion of the population, and continued mobility is important for maintaining quality of life (Christensen et al., 2009; Montpetit & Tiberio, 2016). The current study is the first to show motion coherence thresholds in older adults are associated with contrast sensitivity in general (and not primarily in the M pathway), and that a decline in contrast sensitivity partially mediates the association between age and motion coherence thresholds. However, the current experiment is limited in that the steady and pulsed pedestal measure of contrast sensitivity does not capture temporal contrast sensitivity. Temporal contrast sensitivity declines in older adults have been reported (D. Elliott et al., 1990) and may be more relevant to motion perception, particularly in the M pathway, and therefore should be the focus of future research. Further research is required to identify other the specific mechanisms involved in the effect of age on motion perception, and why these are particularly problematic for older women.

Chapter 7: General Discussion

The purpose of this thesis was to investigate whether the performance of older adults on visual tasks known to predict functional decline, could be explained by age-related change in specific perceptual processes. Specifically, the aim was to explore whether the capacity to deploy visual attention, or the sensitivity of the Magnocellular (M) visual pathway, could explain error rates for the localisation of a peripheral target in the functional field of view (FFOV) and motion coherence thresholds in older adults. Declines in both the FFOV and the capacity to detect coherent motion have functional consequences for older adults, such as a reduction in the range of activities of daily living in which these individuals participate (Owsley, Sloane, McGwin, & Ball, 2002), an increased risk of motor vehicle accidents (Clay et al., 2005), and an increased incidence of falls (Owsley & McGwin, 2004). The associations found between functional decline in older adults and both FFOV performance and motion coherence thresholds, suggest these tasks tap into perceptual processes that are critical for older adults maintaining mobility and independence. It is therefore important to identify which perceptual processes are influenced by age-related change that leads to a reduction in FFOV performance and higher motion coherence thresholds. In the following sections, the findings of the thesis regarding the contribution of visual attention and the M pathway to sensitivity to age-related change in performance on the FFOV and coherent motion tasks will be discussed and compared with alternative explanations, followed by consideration of the limitations of the reported studies, and recommendations for future directions of research in this area.

7.1 Contributions of visual attention and M pathway sensitivity to the FFOV in older adults

The results of Study 1 (Chapter 4) showed that the effect of age on FFOV error rates was not simply attributable to a general decline in either bottom-up or top-down attention. The FFOV task required simultaneous identification of a central target and localisation of a peripheral target among distractors. Both older and younger adults took advantage of bottom-up attentional capture by high contrast peripheral targets, and had equal difficulty using top-down attention to ignore high contrast, (i.e. more salient) peripheral distractors. However, when the cost of including the central task was assessed, compromises between top-down and bottom-up attention were found to impact the performance of the older group. Increased difficulty was found in this group when the perceptual demands of the central task were high (i.e., when it was presented in a low contrast). In this condition, older adults gained less benefit from a high contrast (i.e. salient) peripheral target. This suggests that when it is more difficult to reach a perceptual decision on the central task through pre-attentive or bottom-up sensory processing, older adults use more top-down attention to focus available resources on the central task. The results suggest this reduced their capacity to use bottom-up attentional capture in peripheral vision, resulting in increased performance costs in the periphery from the addition of a low compared to a high contrast central target.

In Study 2 a strong association was found between contrast discrimination thresholds for the M pathway and error rates on the FFOV task in the older group. This supports the theory that the M pathway contributes to sensory driven bottom-up allocation of visual attention (Bullier, 2001; Laycock, Crewther, & Crewther, 2007; Vidyasagar, 1999). This association was not found in the younger group because of limitations in the design of the study, making it insensitive to individual differences within this group.

Taken together, the results of studies 1 and 2 suggest that a decline in the functioning of the M pathway could reduce the capacity for some older adults to use rapid pre-attentive processing of the stimulus to simultaneously perform the central and peripheral components of the FFOV task, especially when the central task requires a more difficult perceptual decision. This is consistent with the argument that older adults use top-down attention to overcome difficulties in sensory processing, and the bottom-up attention driven by that sensory processing (Whiting et al., 2007; Whiting et al., 2014). The results in Study 2 showed that, for older adults, the association between FFOV errors and the contrast thresholds of the M pathway were strongest in those conditions in which the peripheral target in the FFOV was a higher contrast than the distractors, and therefore capable of capturing attention in a bottom-up manner. This suggests that, at least for older adults, the FFOV task is most reliant on the M pathway when bottom-up attentional capture by the peripheral target most contributes to performance. In other words, the FFOV is at its most efficient when the M pathway can guide attention to the peripheral target in a bottom-up manner. The results also suggest that older adults with a less sensitive M pathway have particular difficulties using bottom-up attention to detect salient peripheral objects in a visually complex setting.

The use of top-down attention by older adults to compensate for declines at a sensory level, or for reductions in the sensitivity of the M pathway, can also explain the results of previous research into the effect of age on the FFOV. Using the UFOV Test (Ball & Owsley, 1993) which provides simultaneous presentation of a central task requiring identification of a single object (a car or a truck), and a peripheral localisation task similar to the one used in studies 1 and 2 together with peripheral distractors, older adults require stimulus durations of approximately 330 ms to achieve 75% accuracy on the peripheral task (J. D. Edwards et al., 2006). By comparison, younger adults achieve 75% accuracy with brief stimulus durations of approximately 90 ms on average (Fiorentino, 2008; McManus, Cox, Vance, & Stavrinos, 2015). The brief stimulus durations required by younger adults suggests that this group can perform the central and peripheral tasks in parallel. The stimulus durations of less than 100 ms are consistent with the time required to use covert attention to select the destination for a saccadic eye movement (Belopolsky & Theeuwes, 2009; Caspi, Beutter, & Eckstein, 2004). In the older adults the mean stimulus durations required on the UFOV Test, and the variability of these durations, are consistent with findings that many older adults need sufficient time (approximately 260 ms) to vary the focus of attention in order to complete the central and peripheral tasks in a serial fashion (Jefferies et al., 2015). When the central task is made more complex by providing two objects and requiring participants to judge if they are the same or different (as opposed to simply identifying whether a car or truck was presented), older adults only achieve 75% accuracy on the peripheral task when stimulus durations are increased to approximately 420 ms {Edwards, 2006 #398}. Restricting the focus of attention in response to task demands has been shown to increase the time required to search for multiple targets (Belopolsky & Theeuwes, 2010). Therefore greater need to shift attention in order to respond to a more difficult central task could also explain the findings of Edwards et al. (2006). This is consistent with the finding in Study 1 that the older adults appeared to restrict attention in order to process a low contrast central task. The results of Study 1 therefore argue that the interpretation of stimulus durations required in the UFOV Test as simply reflecting slower processing are overly simplistic. The older adults are not just taking longer to perform the same functions as younger adults: they are performing the tasks using different, more serial, less efficient attentional mechanisms – especially when the processing demands for the central task are increased.

To argue that the reduced processing speed account is not a sufficient description of the effect of age on FFOV performance is not to say that reduced processing speed makes no contribution. The strong association between contrast discrimination thresholds in the M pathway and FFOV error rates in Study 2 supports the hypothesis that rapid conductance of signals is important in maximising the efficient and effective allocation of visual attention. While it was initially thought that cell loss in the M pathway might be responsible for functional impairments in older adults (Conlon & Herkes, 2008; Gilmore et al., 1992; Charles T. Scialfa, 2002), there is now evidence that a loss of axons (Calkins, 2013) and reduction in white matter integrity including degraded myelination (S. W. Davis et al., 2009) in older adults are more important than reduced numbers of neurons. If these changes are at work in the M pathway, then the efficient conduction of signals in the pathway may be undermined in older adults. Further research into the loss of axons and white-matter in the M pathway is therefore required. Future research should also focus more on the temporal characteristics of the signals in the M pathway than was the case in Study 2 of the current project.

The increased reliance by older adults on top-down attention to vary the focus of attention in FFOV tasks also argues against the hypothesis that older adults with an inefficient FFOV have more difficulty disengaging attention from the central task (Cosman et al., 2012a; Cosman, Lees, Lee, Rizzo, & Vecera, 2012b). This hypothesis is based on comparing visual search performance of older adults who required long stimulus durations to meet the 75% correct criterion on the UFOV Test with that of older adults who performed the same task more efficiently. They found those with a less efficient FFOV also showed a greater increase in reaction times from an invalid spatial cue for a single target (Cosman et al., 2012a), and a greater increase in visual search response times in a classic conjunction-type visual search (Cosman et al., 2012b). The results of Study 1 suggest a different interpretation of these results. In Study 1, when a low contrast central target was added to the display, performance costs for the older adults were greater for a high contrast peripheral target than for a low contrast peripheral target. If older adults have difficulty disengaging from the central task to attend to the peripheral target, this difficulty should be reduced, and performance costs lowered, by a high contrast peripheral target that would draw attention to the periphery thus facilitating disengagement. Instead, the results of Study 1 suggest the results of the Cosman studies could reflect more reliance on less efficient top-down attention in visual search tasks by older adults with an inefficient FFOV, rather than difficulty disengaging from the central target.

7.2 Contributions of visual attention and M pathway sensitivity to increased motion coherence thresholds in older adults

Consistent with previous studies (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Bennett et al., 2007; Conlon & Herkes, 2008; Conlon et al., 2017; Snowden & Kavanagh, 2006), regardless of cue condition, older adults had higher motion coherence thresholds than younger adults. In Study 3 it was found that motion coherence thresholds were significantly associated with contrast discrimination thresholds only in the older group, and only for the uncued condition. This suggests that, at least for the older adults, early sensory processing (i.e. contrast discrimination) is less important when top-down attention is used to guide attention to signal dots in a motion coherence task. This is consistent with the results of Study 2 where stronger associations were found between FFOV error rates and contrast discrimination thresholds in conditions where bottom attention to high contrast peripheral targets was facilitating performance. However, unlike in Study 2, in Study 3 this association was not specifically attributable to the thresholds reflecting either the M or P pathways. Similarly, the association between age and coherent motion thresholds was partially mediated by contrast discrimination as measured in both the M and P (Parvocellular) sub-cortical pathways, but neither pathway was an independent mediator of the effect of age on motion coherence thresholds.

These results are contrary to the expectation that increased motion coherence thresholds in older adults would be primarily explained by a reduction in the sensitivity of the M pathway with age (Conlon & Herkes, 2008; Gilmore et al., 1992; Charles T. Scialfa, 2002). However, it is consistent with reports that the P pathway also provides input into MT, the area considered most responsible for coherent motion processing (Braddick et al., 2001; Nassi et al., 2006), and that motion processing is not entirely and M pathway task (Merigan et al., 1991). While increases in motion coherence thresholds in the older compared to the younger group were partly mediated by reductions in contrast sensitivity in the M and P pathways, the difference between the groups was largely independent of these measures of early visual processing. This suggests that, while an age-related decline in contrast sensitivity in the early visual system contributes to the effect of age on motion coherence, the major effect of age is likely to be on processing higher in the dorsal stream. An age-related increase in internal neural noise and reduction in the selectivity of motion sensitive neurons has been found in the dorsal stream at V1 and MT (Liang et al., 2010; Yang, Liang, et al., 2009). Both V1 and MT contribute to coherent motion processing with MT constructing a global coherent percept based on local motion signals generated at V1 (Braddick, 1997; Helfrich et al., 2013; Perrone & Thiele, 2002). It has been argued that reduced sensitivity to motion in older adults is due to reduced centre-surround antagonism in direction selective neurons, and this is most likely to occur at MT, although further research is required to determine whether declines in other areas in the dorsal stream (such as V1 or V3A) also contribute (Betts et al., 2005).

In the uncued condition, which was equivalent to a standard motion coherence task, women had higher motion coherence thresholds than men independent of age-group, which also replicates previous findings (Billino et al., 2008; Conlon et al., 2015; Conlon et al., 2017; Pilz et al., 2010; Snowden & Kavanagh, 2006). In the cued condition, sex differences were abolished in the younger group, but increased in the older group. In the younger group, motion coherence thresholds were improved for women, but not men when the cue was added. It was concluded that the younger men gained no advantage from a cue because they exhibited very low thresholds in the uncued condition and could gain no further improvement. For the younger group, this pattern of results is similar to a previous study in which higher thresholds were found for women than for men when the RDK contained 150 dots, but no sex difference was found when the RDK contained 600 dots (Conlon et al., 2017). It was concluded that top-down attention to the cue had a similar effect to increasing the number of available dots, and enabled younger women to more effectively form a coherent percept of motion, and thereby achieve thresholds equivalent to that of younger men.

In the older group, men but not women were able to take advantage of the cue to improve motion coherence thresholds. These results differ from the findings of Study 2 for a FFOV task in which a single peripheral target had to be localised among distractors. The different combinations of high and low contrast presented in the distractors and peripheral targets manipulated the amount of bottom-up and top-down attention required to perform each task. It was found that, regardless of presentation condition, FFOV error rates did not differ between men and women in either age-group, and the differences between presentation conditions were equivalent in men and women. This is consistent with previous research showing no differences between older men and women on a FFOV task (J. D. Edwards et al., 2006). Previous studies that have investigated effect of age on visual attention have not reported differences between men and women (Madden, 2007). However, older adults have been shown to have more difficulty using two sources of top-down attention in combination: they appear only to have sufficient resources to use one source of top-down attention (Whiting et al., 2007). If women in general use more top-down attentional resources in spatial cognition (T. Butler et al., 2006), then older women may face resource limitation when attempting to use a second source of attentional guidance such as the cue used in Study 3. If men in general rely more on bottom-up, sensory driven attention to extract and process motion signals in an RDK, then older men may retain greater capacity to use top-down attention in response to a cue. While reduced capacity for top-down attention in older women should be explored in future research, it was concluded that the failure of older women to gain an advantage from the attentional cue was due to resource limitations in older adults combined with greater reliance on top-down attention by women in general when performing the motion coherence task. Previous research has also found that sex differences are more evident in motion coherence tasks, especially in older groups, than for perceptually simpler tasks (Conlon & Herkes, 2008). The increased processing requirements of the motion coherence task may also have exhausted the resources of the older women, leaving little capacity for top-down attention based on the available cue.

Importantly, the pattern of results found when examining the contributions of attention and M pathway sensitivity to motion coherence are quite different to the pattern of results found for the FFOV. After controlling for variance shared by both pathways, the unique associations with M pathway contrast discrimination are much weaker for motion coherence than for the FFOV. Similarly, where the contrast sensitivity of the P pathway contributes to motion coherence in older adults in a way comparable with the M pathway, FFOV performance for this group is strongly related to the M pathway with very little association between FFOV errors and P pathway sensitivity after controlling for variance shared by both pathways. On the motion coherence task, in the uncued condition women had higher thresholds than men, whereas there was no effect of sex for either age-group in the FFOV results. The varying attentional requirements of the different FFOV conditions also had the same impact on men and women, whereas older women were unable to gain any benefit from top-down attention in the motion coherence task.

The effect of age on motion coherence thresholds was largely independent of contrast sensitivity. This may be because the effect of age is on processing at higher cortical levels where more complex processing is required to perceive coherent motion, perhaps due to the impact of increased neural noise and decreased direction selectivity at MT in the dorsal stream of older adults (Liang et al., 2010; Yang, Liang, et al., 2009; Yang, Zhang, et al., 2009). On the FFOV task, the main difference between older and younger adults was an increased reliance on top-down attention when a central target was difficult to perceive (low contrast), suggesting top-down attention was used by older adults to compensate for reduced early level sensory input. Taken together, these findings suggest motion coherence and FFOV tasks rely on different perceptual processes, and that the effect of age on the FFOV requires a different explanation than the effect of age on motion coherence. This is consistent with evidence that argues against a simple common underlying cause for all age-related changes in perception (Andersen, 2012; Zanto & Gazzaley, 2014).

7.3 Functional consequences of age-related changes in perception

The combination of changes in the FFOV and motion processing could contribute to the explanation of the accident patterns in older drivers: collisions with vehicles approaching from outside the focus of attention at intersections. Older drivers are over-represented in accidents at intersections involving the older driver’s car turning across the path of another vehicle (Ichikawa, Nakahara, & Taniguchi, 2015; OECD - Organisation for Economic Co-operation and Development, 2001). An Australian study found older drivers (aged 65+ years) were twice as likely as middle-aged drivers (aged 40 to 55 years) to be involved in an accident where the older driver turned into the path of an approaching vehicle where the other vehicle had right-of-way, twice as likely to be involved in an accident at a right angled intersection, and five times more likely to have an accident where the older driver turned across the path of a vehicle approaching from head on, and intending to continue straight through the intersection (J. Langford & Koppel, 2006). This pattern suggests older drivers might focus attention too narrowly on their intended path of travel, and fail to notice vehicles approaching from outside that narrow focus of attention, especially in complex and perceptually demanding situations. The side impacts of such accidents, together with the frailty of older adults, are also thought to contribute to the serious injuries and fatalities that are more likely to result from an accident involving an older driver (J. Langford & Koppel, 2006).

This pattern seems to closely reflect the findings of Study 1 in which older adults reflexively adopted a more narrow focus of attention in demanding situations, and consequently blocked the capacity of the bottom-up attentional system to alert them to the location of a relevant peripheral object. This suggests that the insights gained by exploring the specific perceptual mechanisms contributing to FFOV performance in older adults can identify the perceptual processes which fail older adults in key functional settings such as driving. Consistent with top-down restriction of the FFOV in demanding situations reported in Study 1, the eye movements of older drivers involve more fixations and shorter saccades than are found in younger drivers, suggesting a more top-down directed, serial search of the driving environment (Maltz & Shinar, 1999).

Study 3 demonstrates the effect of age on motion coherence thresholds is likely to involve different perceptual processes to those involved in the effect of age on the FFOV. Older adults also have more injuries in accidents involving poor judgement of the gap between approaching vehicle, which relies on accurate perception of the motion of the approaching vehicles (Classen, Shechtman, Awadzi, Joo, & Lanford, 2010). Older adults are also known to make more errors in judging the speed (Scialfa, Lyman, Kline, & Kosnik, 1987), and time-to-arrival of approaching vehicles, and older women are less accurate than older men (Schiff & Oldak, 1990). Therefore the difficulties experienced by older adults, and older women in particular in processing coherent motion may also contribute to difficulties judging their interaction with other traffic, particularly at intersections. Motion processing of approaching objects has been shown to decline in older compared to younger adults and result in less time available at intersections to safely complete a driving manoeuvre such as crossing the path of oncoming traffic (Poulter & Wann, 2013). Older women, although they drive less than older men, are at higher risk of an accident per kilometre driven than men (OECD - Organisation for Economic Co-operation and Development, 2001), and older women are more likely to be involved in a fatal car accident than older men, especially one involving two vehicles (Williams & Shabanova, 2003). In addition, a higher proportion of the accidents experienced by older women involve misjudgements regarding the speed of an approaching vehicle and of the gap between approaching vehicles (Cicchino & McCartt, 2015).

Taken together these findings could explain why measures of the FFOV and motion processing are among the best predictors of motor vehicle accident risk in older drivers (Anstey et al., 2005). The apparent links between patterns in motor vehicle accidents and changes to perceptual processing in older adults that emerge from the current study also highlight the need for research, which will show the link between specific perceptual processes and driving manoeuvres. Most research on older drivers to date has been focussed on finding tests that can identify those most at risk of accidents. While this is an important research agenda, it should not be treated as the whole story. Once a particular test is shown to predict functionally significant outcomes (Owsley, 2011), it becomes important to explore in detail the perceptual mechanisms to which that particular test is sensitive, and which of those mechanisms are related to the functional consequences the test predicts. Knowing with precision which specific perceptual processes are changing with age and leading to functional problems allows for the exploration of measures to ameliorate or overcome these difficulties. For example, training has been shown to improve both the FFOV (Richards, Bennett, & Sekuler, 2006) and motion perception in older adults (Bower & Andersen, 2012), and motion coherence thresholds in older monkeys have been improved through pharmacological manipulation of the neurotransmitter GABA (Leventhal et al., 2003).

7.4 Limitations of the current research and recommendations for future research

An important contribution from the current project is the finding that reduced contrast sensitivity in the M pathway was associated with increased errors on the FFOV task in older adults. This same result was not obtained in the younger group. However, the FFOV test used was targeted towards capturing individual difference among the older adults, so based on this methodology was not as sensitive to individual differences among younger adults. This limited both the types of analysis that could fully explore potential differences between younger and older groups. Designing a single test that can capture individual differences among both younger and older adults presents a significant challenge for this area of research. Future research should consider different ways of manipulating the difficulty of the FFOV task, or of manipulating the stimulus duration differently for older and younger adults, so that performance in both groups can be discriminating.

While the steady and pulsed pedestal task assesses contrast discrimination thresholds in the M and P pathways, and important insights were gained using this measure, as currently implemented it does not capture temporal aspects of the M pathway. In future studies, temporal contrast sensitivity in the M and P pathways could be explored using an adaptation of the task. For example, McKendrick and colleagues (2007) adapted the steady and pulsed task by using a static sine-wave grating instead of the four-squares of the original pedestal in order to measure contrast sensitivity across a range of spatial frequencies. Their task could be adapted further to provide a sine-wave drifting at a range of temporal frequencies, which would allow contrast sensitivity in the M and P pathways at different temporal frequencies to be assessed. Whether use of temporal contrast sensitivity improves the ability of change in the M pathway to explain change in motion coherence thresholds could then be explored. It may be that while contrast sensitivity to a brief stationary stimulus, such as is used in the standard steady and pulsed task, captures the characteristics of the M pathway that subserve the allocation of bottom-up attention within the FFOV, the temporal characteristics of the M pathway may contribute more to motion perception. Use of different adaptations of the steady and pulsed task may provide insights into the different perceptual mechanisms required for these two different tasks (FFOV and motion coherence), and explain why they each contribute to explaining functional declines in older adults.

The findings regarding the FFOV of older adults in the current project suggest some directions for future research. For example, it was shown in Study 1 that older adults lose some of the benefit of a high contrast peripheral target on a FFOV task because of a reflexive focusing of attention to a difficult (low contrast) central task. This could be further explored through testing the effect of eccentricity of the peripheral target on FFOV errors under different manipulations of the difficulty of the central task. The current findings suggest the eccentricities at which older adults can successfully perform the peripheral task will decrease as the difficulty of the central task is increased, and this will occur to a lesser extent for younger adults. Older adults have been found to be slower to narrow the focus of attention (Jefferies et al., 2015), and to have a less flexible attentional focus (Greenwood & Parasuraman, 2004). Future studies should explore whether older adults with a reduced FFOV are especially slow, or have particular difficulties, when altering the extent of the focus of attention. Whether older adults with a less efficient FFOV have difficulties manipulating the extent of the FFOV, or difficulties disengaging and shifting attention, should also be further investigated (Cosman et al., 2012a).

The current results support the interpretation that older adults use top-down attention to compensate for reduced sensory or bottom-up input in performing the FFOV, and that older men but not older women can use top-down attention in response to a cue to reduce coherent motion thresholds. In tasks requiring the combination of multiple local elements to form a coherent global percept, such as identifying a fragmented object (Kennedy, Rodrigue, Head, Gunning-Dixon, & Raz, 2009), or identifying coherent global motion (Conlon et al., 2017), women require more local signals than men. In motion coherence tasks, differences are not found between younger men and women with longer stimulus durations (Atchley & Andersen, 1998; Conlon & Herkes, 2008) or with presentation of an increased number of dots (Conlon et al., 2017). Study 3 also shows the sex differences in the younger group were eliminated by the addition of a top-down cue which could direct attention to the signal dots. Top-down attention to motion as a feature could facilitate processing of coherent motion for women and reduce their difficulty combining the complex local signals into a coherent percept. The FFOV task does not require the combination of multiple elements to produce a global percept, which may explain why no differences were found between men and women on this task across conditions with differing attentional demands. Similarly the coherent motion task requires more spatial reasoning to selectively ignore random motion in the noise dots and detect the direction of motion in the coherent signal dots, and women engage more top-down attention when performing spatial reasoning tasks (T. Butler et al., 2006). If the motion coherence task requires top-down attention to motion in women more than men, either because of the fragmented nature of the stimulus or because of the spatial reasoning required, older women but not older men may have exhausted their available cognitive resources leaving them unable to make use of the cue provided. The need to use top-down attention to focus attention on a demanding central task in the FFOV task may not have differentially impacted women because it did not require the combination of multiple elements or spatial reasoning, leaving older men and women with equivalent cognitive resources for deploying visual attention. These findings therefore suggest older women in particular may be resource limited in dynamic visual environments requiring complex motion perception, such as those encountered while driving.

Future research could confirm the differences in attentional mechanisms being deployed by older adults, and older women in particular, through VEP and neuro-imaging studies. The fact that older adults experienced greater performance costs for the high contrast peripheral target when a low contrast central target was added to the FFOV display was interpreted as the older adults recruiting the inhibitory functions of the dorsal attention network (DAN) component of the frontoparietal network. Although this would be consistent with findings from previous studies (Geerligs et al., 2014), further research focused on the different neural activations in older and younger men and women performing more or less demanding FFOV tasks will be required to confirm whether this hypothesis is supported. Similarly, the activation of neural areas associated with top-down attention in older and younger men and women could be explored during performance of a motion coherence task. This will confirm whether women engage more top-down attention in motion perception tasks as has been shown in mental rotation tasks (T. Butler et al., 2006).

Similarly further research is required to explore the effect of age on inhibitory and excitatory aspects of the mechanisms of visual attention. Difficulty inhibiting neural activity has been proposed as a general explanation of the effects of age on cognition (Hasher & Zacks 1998). Greater difficulty inhibiting irrelevant stimuli by older compared to younger adults has been found in visual search when distractors were high luminance and therefore salient, but not when distractors were low in salience (Kramer, Hahn, Irwin, & Theeuwes, 2000). Study 1 attempted to identify whether difficulty attending to a high salience target, inhibiting a high salience distractor, or some combination of these processes, contributed to the effect of age on FFOV performance. The results suggest the effect of age cannot be directly attributed to inhibiting irrelevant objects or enhancing response to targets, but is of a more general nature. The findings from Study 1 that older adults tend to inhibit peripheral processing when required to respond to a more demanding (i.e. low contrast) centrally presented stimulus argue against a general reducion in the capacity for inhibition explaining the effect of age on FFOV performance. A more targeted methodolgy such as that used by Lu and Dosher (1999) might enable the effect of age on inhibition of irrelevant external noise versus enhancement of excitatory response to signal to be disambiguated. Similarly, methodologies involving the measurement of neural responses through fMRI or VEPs might shed light on this question, but the current project cannot.

The parallel between the attentional strategy used by older adults reported in Study 1 (focus attention centrally and ignore the periphery) and the pattern of driving accidents found among older drivers, suggests particular driving errors may be explained by a declining FFOV. As such, measures of specific components of the FFOV, such as the performance cost of adding a more demanding central task, should be compared with specific tests of driving performance such as detecting and avoiding vehicles approaching from outside the current focus of attention. Research has previously shown that older drivers make more eye movements while driving, but scan a smaller proportion of the scene, than younger drivers (Maltz & Shinar, 1999). Skilled drivers have been shown to maintain more flexible control of the focus of attention than novice drivers (P. R. Chapman & Underwood, 1998), and failure to maintain flexible attentional focus has been shown to lead to more accidents in a simulated driving task (Most & Astur, 2007). Associations between changes to aspects of the

FFOV and specific driving behaviours that can contribute to accidents should be tested empirically.

Similarly, associations between motion perception, as indicated by motion coherence thresholds, and specific driving behaviours should be examined. As noted earlier, reduced accuracy when judging the approach of vehicles at intersections has been found in older compared to younger drivers (Scialfa, Guzy, Leibowitz, Garvey, & Tyrrell, 1991), and in women compared to men (Schiff & Oldak, 1990), and this may contribute to accidents in critical situations. Of particular interest would be the association between motion coherence thresholds and driving errors in complex intersection in older women. Studies of this type could also be used to determine whether improvements in motion perception through training (Bower & Andersen, 2012) can reduce difficulties for older adults, and older women in particular, in complex driving situations. There is evidence that exposure to complex motion through video games can reduce sex differences in spatial reasoning in younger adults (Feng et al., 2007), that the efficiency of the FFOV benefits from training in older adults (Richards et al., 2006), and that such training transfers to improved capacity for performance of simple but important daily activities such as finding instructions on medicine containers (Jerri D. Edwards, Ruva, O'Brien, Haley, & Lister, 2013).

7.5 Conclusions

The current project showed that older adults use top-down attention to compensate for reduced sensory processing and efficient bottom-up attentional processing when performing a FFOV task. However, it also showed that this strategy is not always available, especially to older women, and is not always effective at overcoming perceptual difficulties. Unlike older men, older women could not take advantage of top-down attention to improve coherent motion detection, possibly because their available attentional resources were already exhausted in trying to attend to the relevant motion signals. While older men gained a benefit from attending to a cue in a motion coherence task, they were still substantially less sensitive in the perception of coherent motion than younger men. Use of top-down attention in a FFOV task to ensure processing of a hard-to-see central target came at the cost of reducing the capacity to detect the location of a high contrast (salient) and relevant peripheral target. These short-comings in the ability of older adults to overcome perceptual difficulties could explain why these particular tasks are effective predictors of older adults at increased risk of functional difficulties.

The current study also determined that reduced sensitivity in the M sub-cortical visual pathway helps explain both the FFOV of older adults, and the effect of age on coherent motion processing. For the FFOV, it was found that error rates in older adults were well predicted by the contrast sensitivity of the M pathway, especially in those conditions most reliant on bottom-up allocation of attention, while the contrast sensitivity of the P pathway made little if any contribution. This supports the hypothesis that the M pathway plays an important role in the rapid deployment of visual bottom-up attention. The contribution of the M pathway to sensitivity on a motion coherence task was found to be similar to, and shared by, the P pathway. Contrast sensitivity across the M and P pathways partially mediated the effect of age on motion coherence thresholds suggesting that some of the effect of age on motion coherence perception is due to age-related reduction in contrast sensitivity which in turn leads to reduced motion coherence perception. This supports previous evidence that motion processing is not a purely M pathway task (Merigan et al., 1991; Nassi et al., 2006), at least for the complex coherent motion tested in the current project. Because much of the effect of age on motion coherence thresholds was independent of contrast sensitivity in the M and P pathways, the results also suggest that the more important impact of age is higher in the visual system: most likely in the dorsal stream beyond V1, possibly at MT, where coherent motion is primarily processed (Braddick et al., 2001; Helfrich et al., 2013).

Future research should further investigate the specific perceptual changes associated with age that could explain age-related change in functional vision. Doing so will identify the particular perceptual mechanisms that decline with age and thereby fail to provide effective functional vision for older adults. In a future where an increasing proportion of the population will seek to remain active, mobile, and independent well into later adulthood, identifying the underlying causes of functional visual decline will become increasingly important.

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