

Psychophysical correlates of age-related visual decline

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Abstract

Much of what we know about the physical world is afforded to us by vision. With age, our ability to perceive visual information can become compromised, affecting our autonomy and quality of life. Given the rapid aging of populations worldwide, it is imperative to develop a comprehensive understanding of the effects of age on visual function. Therefore, the aim of this thesis was to use psychophysical methods to examine the effects of 'healthy' aging on visual perception, with a particular emphasis on furthering our knowledge of age-related reductions in the perception of motion. In a series of experiments, observers ranging from 18-82 years of age were tested and compared on psychophysical tasks which measured orientation and direction sensitivity, first- and second-order global motion perception, contrast sensitivity, and visual attention as measured by the Useful Field of View. Four key findings are presented within this thesis: (1) older observers demonstrate reductions in orientation and direction sensitivity that can be attributed to increased internal noise in the aged motion pathway, (2) age-related impairments in global motion perception are mediated by reductions in spatial integration, (3) older female populations may be particularly susceptible to age-related impairments in motion perception, and (4) there may be a selective impairment in the processing of second-order radial motion in the aged. The results of these experiments indicate that whilst some aspects of motion processing remain preserved with age, older observers demonstrate marked impairments on a number of motion tasks.

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List of Abbreviations

ACh	Acetylcholine
AChE	Acetylcholinesterase
AMPA	α -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid
ANOVA	Analysis of variance
CRF	Contrast response function
CSF	Contrast sensitivity function
CT	Computer tomography
Dmax	Maximum displacement
Dmin	Minimum displacement
EEG	Electroencephalography
EFT	Embedded figures test
FF	Fano factor
fMRI	functional magnetic resonance imaging
FrACT	Freiberg visual acuity test
FST	Fundus of the superior temporal area
GABA	γ -aminobutyric acid
GABA-IR	GABA-immunoreactive
GABA-T	GABA alphas-ketoglutaric transaminase
GAD	glutamic acid decarboxylase
Glu-IR	Glutamic acid immunoreactive
ISI	Inter-stimulus-interval
LAM	Linear amplifier model

LGN	Lateral geniculate nucleus
M-pathway	Magnocellular pathway
MEG	Magnetoencephalography
MMSE	Mini Mental State Exam
MRI	Magnetic resonance imaging
MST	Medial superior temporal area
MT/V5	Middle temporal visual area
NMDA	N-methyl-D-aspartate
OB	Orientation bias
OKN	Optokinetic nystagmus
P-pathway	Parvocellular pathway
pSTS	Posterior superior temporal sulcus
RDK	Random dot kinematogram
RPE	Retinal pigmented epithelium
SC	Superior colliculus
SDAT	Senile dementia Alzheimer's type
TMS	Transcranial magnetic stimulation
UFOV	Useful field of view
V1	Primary visual cortex/striate cortex
VEP	Visually evoked potential
VIP	Ventral intraparietal area

Chapter 1

General Introduction and Literature Review

1.1. Introduction

Over the last 60 years, population demographics worldwide have been changing drastically. Thanks to advances in healthcare people are living longer than ever before. In many parts of the world, particularly in developed countries, this increase in life expectancy has been accompanied by a simultaneous decrease in fertility rates, creating a shift in population demographics to a more 'aged' population. Older individuals (i.e. 60 years +) now represent a larger proportion of the population than ever before and this shift is only expected to increase in years to come. According to estimates by the United Nations (2011), a 3-fold increase in older populations is expected by 2050, bringing the number of people 60 years of age and over close to 2 billion worldwide. This will mark the first time in the history of humanity that the population of adults 60 years of age and older will surpass that of children aged 0-14 years (United Nations, 2011). Therefore, issues concerning the health and wellbeing of older individuals along with the economic costs of an aging population have now emerged at the forefront of social, political and medical agendas worldwide.

Amongst the health issues afflicting older populations is visual dysfunction. Much of what we know about the physical world is afforded to us by vision; for example, our ability to perceive colour, texture and motion is dependent on the visual system's capacity to accurately encode and process various elements of a visual scene. As such, age-associated changes within the visual system, which could render it less effective or unable to carry out these perceptual tasks, can have wide-reaching consequences for functional vision. Visual problems can affect an individual's quality of life and autonomy, making daily tasks such as reading or driving difficult, and in extreme cases, impossible. Moreover, evidence suggests that poor vision is one of the leading causes of fall-related injury and injury-related death in the elderly (Harwood, 2001).

Age-related changes affecting the ability to integrate and encode motion information can be particularly problematic for older populations. Whilst it may not be initially obvious, motion perception plays a pivotal role in almost every aspect of our daily lives. For example, motion perception is important for spatial awareness and enables us to navigate effectively through space. Similarly, our ability to maintain balance, be it whilst sitting or walking, is dependent on the integration of information from vestibular, proprioceptive and motion systems. Motion perception also breaks camouflage, allowing for objects to be discriminated from their background (e.g. Harrison & Gillan, 2005; Vuong, Friedman, & Plante, 2009). Therefore, impairments in our ability to perceive motion can have drastic effects on our daily lives. Indeed, individuals who suffer from akinetopsia (motion imperception) are often rendered unable to carry out simple tasks such as pouring a cup of tea (Zihl, Von Carmon, & Mai, 1983). Thus,

age-related deficits in motion processing can greatly hinder the lives of older adults. Given the importance of this visual process in everyday life, the primary goal of the experiments carried out in this thesis was to develop a more comprehensive understanding of how our ability to perceive motion is altered by aging.

The sections that follow will provide a brief overview of the visual system, and outline the anatomical and physiological changes that develop as a result of the 'normal' (i.e. disease free) aging process. Behavioural studies that have examined how age affects visual sensitivity, particularly for spatial vision and motion perception, will also be reviewed.

1.2. An overview of the visual system and motion-processing pathway

Visual perception begins when a photon of light is absorbed by retinal photoreceptors, initiating a cascade of neural events that culminate in our conscious perception of a visual image. Prior to this, light must pass through a number of ocular structures that work together to maximise the amount of light transmitted to the retina. Thus, the visual system can be described as consisting of an optical and a neural component. The key ocular structures and neural pathways responsible for visual perception, specifically the perception of motion in a visual scene, will be outlined below.

1.2.1. The eye

The principal structures of the eye include the cornea, iris, lens and retina. These structures are separated by three fluid-filled chambers; namely, the anterior, posterior and vitreous chambers. The anterior chamber separates the cornea and the iris and is filled with a plasma-derived fluid known as aqueous humour. The posterior chamber, also filled with aqueous humour, separates the iris and the lens. The third and largest chamber of the eye, the vitreous chamber, is filled with vitreous humour, a gel-like fluid that separates the lens and the retina. In addition to maintaining the shape of the eye, both aqueous and vitreous humours absorb UV radiation below 300nm in order to reduce the amount of radiation that reaches the retina.

The cornea is the transparent outer coating at the front of the eye. It is the first point of contact for incoming light rays and with a refractive power between 40-45D, it is the principal refractive element of the eye. Light that passes through the cornea's network of dense collagen fibres enters into the first fluid-filled chamber of the eye (the anterior chamber) and is next met by the iris and the pupil.

The iris is a multi-layered structure that provides us with our characteristic eye colour. At its centre is the pupil, a pinhole-like aperture that regulates the amount of light transmitted to the retina. With the help of the circular muscles of the iris, pupil diameter varies as a function of illumination level. When light is readily available (i.e. in photopic conditions), the circular muscles of the iris contract to decrease pupil diameter and improve the quality of the image produced on the retina. A small pupil diameter also increases the depth of field and reduces spherical and chromatic aberrations that produce retinal blurring. When illumination levels are low (i.e. in scotopic conditions), the circular muscles of the iris relax to increase pupil diameter and maximise the amount of light available for transmission.

The lens functions in conjunction with the cornea to refract light onto the retina. Due to its elasticity, the shape of the lens can be altered to adjust its refractive power in order to focus an image on the retina. For example, when viewing a nearby object the ciliary muscles associated with the lens contract, leading to an increase in the curvature and thickness of the lens. This enhances the lens' ability to bend incoming light waves (i.e. increasing its refractive power) and allows these nearby objects to be brought into focus. Conversely, relaxation of these ciliary

muscles leads to a more flattened lens that can readily focus distant images. This process is referred to as accommodation.

The most posterior structure of the eye, and arguably the most important, is the retina. The retina is responsible for the transduction of light energy into a neural signal which then propagates throughout the visual system. Therefore, the neural correlates of visual perception originate at the retina.

1.2.2. The retina and beyond

The retina has a complex layered organisation. The outermost structure of the retina is a single layer of cells referred to as the pigmented epithelium and the primary function of this cell layer is to maintain the metabolic activity of the neighbouring photoreceptors. Photons of light are absorbed by these photoreceptor cells and transduced into an electrical signal. These electrical signals (impulses) are then transmitted to retinal ganglion cells via bipolar, horizontal and amacrine cells found within the medial layers of the retina. The innermost layer of the retina is comprised of ganglion cells, the axons of which bundle together to form the optic nerve as they exit the eye via the optic disc.

Upon exiting the eye, the fibres of the optic nerve decussate at the optic chiasm such that ganglion cell axons carrying information about the right visual field project to the left lateral geniculate nucleus (LGN) and those corresponding with the left visual field project to the right LGN. A small proportion of retinal ganglion cell axons (i.e. approximately 20%) project to the superior colliculus (SC). The SC is a rudimentary visual area that is involved in the initiation of target-directed eye

movements (e.g. Sparks, 1978; Horwitz & Newsome, 1999; Reyes-Puerta, Philipp, Lindner, & Hoffman, 2011) and has been shown to have a role in motion processing (e.g. Rodman, Gross, & Albright, 1990). As the primary motion pathway proceeds via the LGN, the focus of this section will be the cortical circuitry of the geniculostriate pathway.

The LGN is comprised of 6 layers and is innervated by two main ganglion cell types, midget and parasol cells. Midget cells project to the upper four layers of the LGN known as the parvocellular layers and parasol cells project to the bottom two layers of the LGN referred to as the magnocellular layers, forming the parvocellular (P) and magnocellular (M) processing pathways, respectively. Generally, the P-pathway is associated with extrastriatal processing in temporal cortical areas and the M-pathway with parietal areas and evidence suggests that these two pathways work to encode different aspects of the visual world. Specifically, the P-pathway has been shown to be responsible for the analysis of form and colour whilst the M-pathway has a prominent role in motion detection and analysis (e.g. Ungerleider & Mishkin, 1982; Mishkin, Ungerleider & Macko, 1983; Merigan, 1989; Schiller, Logothetis & Charles, 1990; Merigan, Byrne, & Maunsell, 1991). Whilst the theory of two parallel processing streams has dominated vision literature, there is evidence to suggest that considerable overlap occurs between these two processing pathways (for a review see Merigan & Maunsell, 1993).

The neural signals of motion-sensitive ganglion cells which project to the magnocellular layers of the LGN are relayed to the primary visual cortex (also

known as the striate cortex or V1). Neurons arriving from the LGN synapse with neurons of layer 4 α , after which they form a series of connections with neurons residing in other striatal layers. A defining property of V1 cells is that they are orientation selective, that is, each cell is tuned to respond vigorously to a stimulus presented at a given orientation. A proportion of these cells are sensitive to motion direction as well (Hubel & Wiesel, 1968). In order for these cells to respond maximally to a stimulus presented within their receptive field two criteria must be met: the stimulus must be in the preferred orientation and must be moving in the preferred direction.

Another property of V1 cells, which has important implications for the processing of motion information, is the size of their receptive fields. Hubel and Wiesel (1974) mapped the receptive fields of V1 neurons and concluded that the average size is often smaller than 1 deg² in the fovea. This limits the processing abilities of these neurons by restricting the proportion of a stimulus that can be detected at a particular moment in time. Consequently, an individual V1 cell can detect only the component motion of a moving stimulus (e.g. Movshon & Newsome, 1996). Specifically, these neurons detect the proportion of motion that is orthogonal to the axis of orientation, resulting in ambiguity regarding the 'true' stimulus direction. This limitation inherent to V1 motion detectors is commonly referred to as "the aperture problem", and there is evidence to suggest this limitation is overcome by integrating these local motion signals in the extrastriate middle temporal visual area, (MT/V5) (see Born & Bradley, 2005 for a review). In MT, cells have receptive fields that are approximately 10 times the diameter of those characteristic of V1 (Albright & Desimone, 1987), thereby allowing them to

integrate V1-derived local motion signals across a larger visual field in order to more accurately calculate the direction of motion and resolve the “aperture problem”.

There is an abundance of evidence which suggests MT has a critical role in motion perception (e.g. Allman & Kaas, 1971; Dubner & Zeki, 1971; Newsome & Paré, 1988; Beckers & Zeki, 1995; Cowey, Campana, Walsh, & Vaina, 2006). Zeki (1974) demonstrated that the vast majority of cells that comprise MT (i.e. 90%) are direction selective. These cells receive inputs from a number of visual areas including V1 layers 4b and 6, V2, V3 and V4. MT also receives input from the superior colliculus via the pulvinar nucleus and has a role in this rudimentary visual pathway. It has been argued however, that V1 layer 4b may be the most important projection to MT given that most direction-selective V1 neurons reside in this layer (see Andersen, 1997; Born & Bradley, 2005). Lesion studies have provided compelling evidence for the role of MT in motion perception. For example, Newsome and Paré (1988) induced lesions to area MT in rhesus monkeys and compared pre- and post- lesion performance on tasks of motion discrimination and contrast sensitivity. Lesions resulted in severe performance impairments in the motion discrimination task only, demonstrating that MT has a critical role in motion perception and is constrained by different mechanisms than contrast encoding. In humans, transcranial magnetic stimulation (TMS) has been used to temporarily lesion area MT, resulting in transient deficits in motion perception (e.g. Beckers & Zeki, 1995; Cowey, Campana, Walsh, & Vaina, 2006). Moreover, other studies have shown that MT cells can still elicit a neural response

and demonstrate direction-selectivity in the absence of a functional V1 (Rodman, Gross, & Albright, 1989; Girard, Salin, & Bullier, 1992).

The motion pathway does not terminate with the integration of local motion signals in MT. Signals for complex motion types are subsequently forwarded to higher visual areas for processing. For example, MT neurons project to the medial superior temporal area (MST) which has been shown to be involved in the analysis of optic flow information generated by self-motion (e.g. Grossberg, Mingolla, & Pack, 1999). Neurons in MST have large receptive fields which can cover most of the visual field and respond to pattern motion such as contractions, expansions and rotations (Duffy & Wurtz, 1991; Tanaka & Saito, 1989). Similar to MST, neurons within the ventral intraparietal area (VIP) of primates have been found to be sensitive to optic flow (e.g. Chen, DeAngelis, & Angelaki, 2011) and both visual areas are involved in coding the direction of heading during self-motion (e.g. Maciokas & Britten, 2010). The fundus of the superior temporal area (FST) also receives projections from MT and evidence suggests it is involved in the coding of motion-defined form (e.g. Mysore, Vogels, Raiguel, Todd, & Orban, 2010).

In addition to the forward transmission of neural signals along the visual hierarchy there are extensive feedback connections throughout the visual pathway. These feedback connections have an important role in regulating cell response and allow for long-range communication between cells within the visual pathway (see Bullier, 2001 for a review). Therefore, the visual system is best described as a complex interconnected network extending from the retina to various areas of the cerebral cortex.

1.3. Anatomical changes within the aged visual pathway

1.3.1. Aging optics

There are a number of optic changes that takes place with age which affect the quality of an image formed on the retina. For example, there is a marked reduction in pupil diameter. This age-related reduction in pupil size, commonly described as senile miosis, limits the extent to which this aperture can regulate the amount of light transmitted to the retina. Although the cause(s) of senile miosis is unclear, a number of studies have shown that maximum pupil diameter begins to decrease after adolescence (Birren, Casperson, & Botwinick, 1950; Kadlecova, Peleska, & Vasko, 1958; Winn, Whitaker, Elliott, & Philips, 1994). These age differences are evident under various levels of illumination. For example, Winn et al. (1994) used a continuous recording technique to measure pupil diameter in observers 17 - 83 years of age at 5 luminance levels within the photopic range (i.e. from 9-4400 cd/m²) and found a linear decrease in pupil diameter with age at each luminance level examined. Under the highest luminance conditions (i.e. 4400 cd/m²) pupil size declined at a rate of 0.015 mm per year. At the lowest luminance level (i.e. 9 cd/m²) these pupillary reductions were exacerbated, with pupil diameter declining at a rate of 0.043 mm per year. Under scotopic conditions (i.e. ≤ 0.01 cd/m²), when pupil diameter is greatest, the findings are similar (e.g. Kornzweig, 1954; Kadlecova et al., 1958; Said & Sawires, 1972) with maximum pupil diameter estimated to decline by 2.5 mm between 10 - 80 years of age (Kadlecova et al., 1958).

Irrespective of its underlying aetiology, senile miosis leads to a reduction in the amount of light that can reach the retina. Although decreases in retinal illumination may exacerbate age-related visual deficits under levels of low illumination such as in dim lighting, in some instances, senile miosis may prove advantageous. Smaller pupils diminish the effects of spherical aberrations, increase depth-of-focus, and reduce retinal blur. Guirao et al. (1999) measured optical performance by determining the modulation transfer functions (MTF) of subjects 20 - 70 years of age at three artificial pupil diameters (3, 4, and 6mm). The results of this study indicated that MTFs decrease with age, a finding that may be expected given the optical changes that are known to occur. However, when natural differences in pupil size amongst observers of different age groups were accounted for, age-related differences in MTF were minimised, especially at low luminances. These findings may be indicative of an adaptive advantage to senile miosis in the aged. These advantages however are limited in extent, as diffraction becomes a greater issue at very small pupil diameters.

Age-related changes in the lens are responsible for some of the most common optical problems experienced by older individuals. For example, as the lens loses its pliability with age, the amplitude of accommodation (i.e. the dioptric difference between the farthest and nearest viewing distances in which an object can remain in focus) is reduced, leading to a loss in the ability to focus near objects (presbyopia). The onset of presbyopia typically occurs around 45 years of age and is characterised by the blurring of near objects on the retina (see Weale, 1989 for a review). Whilst the exact cause of this reduction in accommodative ability is not known, lenticular changes (e.g. Fisher, 1977; Glasser & Campbell, 1998) and/or

changes in extralenticular regions (e.g. changes in ciliary muscle activity) have been implicated (see Atchison, 1995).

In addition to the loss in accommodative amplitude with age, the lens also undergoes a number of structural changes, these include: increases in cell density, yellowing of the lens and increases in the molecular mass of lens proteins. Together, changes in lens density and colour lead to a decline in transparency and a shift in the absorption spectrum of the lens such that short wavelengths within the visible light spectrum are more readily absorbed (e.g. Said & Weale, 1959; Coren & Girgus, 1972; Weale, 1985; Mellerio, 1987; Kessel, Lundeman, Herbst, Andersen, & Larsen, 2010; Artigas, Felipe, Navea, Fandiño, & Artigas, 2012). For example, Gaillard, Zheng, Merriam, and Dillon (2000), demonstrated a shift in the primate and human lens absorption characteristics, with maximum absorption occurring at 320nm in aged lenses in comparison to 360nm in young. In more extreme cases, age-related lenticular changes can lead to the development of a cataract. Although all aging lenses develop some degree of opacity, when the opacity becomes severe and begins to interfere with vision it is generally diagnosed as a cataract and requires medical intervention. In these instances, the cataractous lens can be surgically removed and replaced with an artificial implant.

Collectively, the age-related changes in the structure and function of the pupil and the lens have two major effects on retinal image formation. Firstly, these alterations lead to a reduction in retinal illumination. Weale (1963) established that between 20 and 60 years of age retinal illumination is decreased by approximately one third. Secondly, there is an increase in intraocular light scatter

(Wolf & Gardiner, 1965), which can create a veiling luminance in front of the retina such that the contrast of any retinal image is reduced. Changes in the molecular mass of lens proteins are also associated with increased retinal light scatter (Spector, 1983). Therefore, age-related optic changes can have important implications in low levels of illumination and/or at low contrasts. In spite of these structural changes, degraded optics cannot account for many of the age differences obtained for psychophysical measures of visual performance, thereby suggesting a neural underpinning to these performance differences (e.g. Allen & Vos, 1967; Elliott, Whitaker, & MacVeigh, 1990; Whitaker & Elliott, 1992).

1.3.2. Changes in the number and structure of aged neurons

Retinal cells, like neurons in the brain, are permanently lost and not replaced when damaged. Therefore, if the normal aging process leads to cell death at any point along the visual pathway (i.e. from the retina extending to extrastriatal visual areas), severe consequences may ensue. A number of studies have investigated the effects of age on the size and morphological characteristics of cell populations within the visual pathway (e.g. Brody, 1955; 1970; Gao & Hollyfield, 1992; Curcio, Millican, Allen, & Kalina, 1993; Pakkenberg & Gundersen, 1997; Eliasieb, Liets, & Chalupa, 2007; Giannaris & Rosen, 2012). The findings of these studies are outlined below.

Age-related declines in retinal photoreceptor populations have been shown to be dependent upon photoreceptor type and retinal location. For example, Gao and Hollyfield (1992) investigated cell loss in the retinae of postmortem humans ranging from 10 - 89 years of age and demonstrated that rod photoreceptors were

more susceptible to the effects of age than cones. In a similar study of postmortem human retinæ, Curcio et al. (1993) found that cone populations (foveal retina) remained relatively stable across the lifespan, whilst rod photoreceptors declined by approximately 30% between 27 and 90 years of age. However, in the far periphery (i.e. 13mm temporal to the fovea), rod populations remained stable with age.

In a recent study examining the effects of age on retinal pigmented epithelial (RPE) cell populations, Harman, Fleming, Moore and Hoskins (1997) demonstrated that whilst RPE cell numbers are preserved with age, there is an increase in cell density in the macular region. This led the authors to propose that the retinal sheet is drawn together with age in order to maintain the integrity of the fovea. In order to test this hypothesis Harman, Abrahams, Moore and Hoskins (2000) sampled the entire ganglion cell layer in the retinæ of postmortem donors 17-77 years of age. In agreement with previous findings (e.g. Gao & Hollyfield, 1992; Curcio & Drucker, 1993), age-related reductions in ganglion cell number were evident, with an estimated mean reduction of 0.53% per year. In macular regions this decline was less pronounced, with cell loss estimated to progress at a rate of 0.29% per year. These findings support their hypothesis that the retinal sheet is “drawn together” to preserve neuron number in macular regions.

The hypothesis proposed by Harman et al. (2000) sheds light on a recurring observation in aging literature; the visual system demonstrates a high degree of plasticity to compensate for age-related cell loss. For example, Curcio et al. (1993) found that declines in rod photoreceptor populations were minimised by an

increase in the size of the inner segments of remaining rods, leading to similar rod coverage across the lifespan and diminishing the possibility for any gaps in the rod mosaic. In a similar vein, Eliasieb et al. (2007) demonstrated how neural reorganization takes place with age in order to maintain the integrity of the retina. Rods, On-cone bipolar cells (bipolar cells which are activated by the presence of a light source) and horizontal cells, normally confined to the outer plexiform layer of the retina, were found to extend into the outer nuclear layer in the retinae of older postmortem human donors. Rods and On-cone bipolar cells were also shown to be present in higher density (Eliasieb et al., 2007). Thus whilst cell loss is a result of the aging process it appears that, at least at the retinal level, there are a number of compensatory mechanisms at work to maintain retinal activity.

Early work by Brody (1955; 1970) and others (e.g. Henderson, Tomlinson, & Gibson, 1980; Shefer, 1973; Devaney & Johnson, 1980) suggested that a significant proportion of cerebral neurons are lost with age. However, more recent investigations of neuron populations have challenged this finding, citing a number of methodological issues which could have led to overestimations of cell loss in these studies (for a review see Coleman & Flood, 1987). At present, the general consensus is that neuron number remains relatively stable across the lifespan (e.g. Haug, 1985; Terry, Deteresa, & Hansen, 1987; Pakkenberg & Gundersen, 1997). A cross-sectional study carried out by Pakkenberg & Gundersen (1997) assessed neocortical properties in postmortem adults ranging from 18 to 93 years of age. Their results indicate neuron populations are changed minimally throughout adulthood with approximately a 10% reduction in neuron number with age. Studies that have focused on age-related changes in the striate cortex have

reported minimal cell loss in humans (Leuba & Kraftsik, 1994) and in primates (Kim, Pier, & Spear, 1997; Peters, Nigro, & McNally, 1997; Giannaris & Rosen, 2012). Furthermore, in aged primates, cell loss in the LGN has also been found to be minimal (Ahmad & Spear, 1993).

A recurring issue when investigating age-related changes in the visual system, regardless of which brain region or species is being evaluated, is the high degree of interindividual variability in cell numbers (Curcio & Drucker, 1993; Gao & Holyfield, 1992; Hendersen et al., 1980; Pakkenberg & Gundersen, 1997). Pakkenberg and Gundersen (1997) noted that interindividual variability in cell numbers was as high as 19%. Gender differences were also prevalent, with men having 16% more neurons than women. Furthermore, regardless of gender, the left cerebral hemisphere was also shown to have greater cell numbers than the right hemisphere (Pakkenberg & Gundersen, 1997). In the visual cortex, large variability in surface area and volume (Peters et al., 1997), as well as 3D shape (Leuba & Kraftsik, 1994), have been documented. This variability limits the accuracy with which age-related cortical changes can be described.

Despite the stability of neuron number with age, there is evidence that suggests the normal aging process leads to a number of changes in the morphological characteristics of cortical neurons (e.g. Brunso-Bechtold, Linville, & Sonntag, 2000; Duan et al., 2003; Pakkenberg & Gundersen, 1997; Leuba & Kraftsik, 1994). Whilst dendritic morphology has been shown to remain relatively stable in primates (Gazzaley, Siegel, Kordower, Mufson, & Morrison, 1996) some age-related regression has been observed in the apical dendrite (Duan et al., 2003). In aged

rats, decreases in synaptic density and inhibitory synaptic vesicles in the sensorimotor cortex have been identified (Brunso-Bechtold et al., 2000). In the human brain, Leuba and Kraftsik (1994) identified an age-related decrease in brain weight, surface area and caudorostral length. Pakkenberg and Gundersen (1997) corroborated these findings, reporting decreases in brain weight and surface area, in addition to reduced brain volume and white matter in old adults. In the rhesus monkey, Peters et al. (1997) failed to find age differences in brain surface area and volume but did recognize a high degree of variability in these parameters across primates.

In summary, the existing literature suggests that, contrary to initial opinions, aging does not lead to a generalised loss in cortical cell number but rather cell numbers are relatively well preserved with age. However, it is worth noting that the high degree of interindividual variability in cell numbers makes quantifying age-related losses difficult. Despite the preservation of cell number with age, there is evidence to suggest that changes in neuron structure occur with age. These changes may influence the synaptic interactions between individual neurons however, at present, the repercussions of these changes are not well understood.

1.4. Neurophysiological consequences of aging

Our current understanding of the human visual system has been greatly enriched by *in-vivo* neurophysiological investigations in lower species, particularly in non-human primates. In recent years, single-cell electrophysiological recording techniques have highlighted a number of key age-associated differences in the response properties of neurons within striate and extrastriate visual cortical areas. These findings have led to the 'γ-aminobutyric acid (GABA) hypothesis of aging' in which it is proposed that age-related changes in neuron sensitivity are due to the degradation of intracortical inhibition within the visual system (e.g. Schmolesky, Wang, Pu, & Leventhal, 2000; Yu, Wang, Li, Zhou, & Leventhal, 2006; Liang et al., 2010). The sections below will outline the evidence that suggests neuron properties change with age and discuss why these changes have been linked to reductions in GABAergic inhibition. Given the extent of cortical similarity between humans and these primates, particularly with respect to motion-sensitive neurons (Lynn & Curran, 2010), these findings may extend to neuron populations in the human visual system as well.

1.4.1. Changes in neuron sensitivity

In the primary visual cortex of the rhesus monkey, spatial and temporal frequency sensitivity decline with age. Zhang et al. (2008) compared measures of optimal spatial and temporal frequencies, spatial resolution (i.e. the maximum spatial frequency for which neurons were responsive) and high temporal frequency cut off values obtained from cells in young and aged rhesus. Aged V1 cells consistently demonstrated lower optimal frequencies (both spatial and temporal), along with

lower spatial resolution and high temporal frequency cut-offs. Similar findings have been demonstrated in the feline visual system; Hua, Shi, Zhou, Peng and Hua (2011) found neurons in area 17 (striate cortex) of old cats had lower optimal spatial frequencies and lower high spatial frequency cut offs than area 17 neurons in younger animals. Interestingly, it has previously been shown that, at least in primates, neurons in the LGN remain relatively well preserved during aging with little change in spatial and temporal frequency preferences (Spear, Moore, Kim, Xue & Tumosa, 1994). These differential findings may implicate V1 as the first site at which age-related changes in cortical activity occur.

There is evidence that aged neurons are also less adept at encoding contrast. For example, Yang, Liang, Li, Wang, and Leventhal (2008) constructed CRFs for V1 and MT neurons in the rhesus monkey and found that aged neurons saturated at higher contrasts. The slopes of the CRFs of aged neurons were also less steep than those derived for young neurons, suggesting these neurons may be less sensitive to local changes in contrast (Sclar, Maunsell, & Lennie, 1990). Whilst age-related changes in sensitivity were apparent in cells from both visual areas, reductions in contrast sensitivity were more pronounced in aged MT neurons. The findings of this study highlight regional variations in the effects of aging and suggest that the observed deficits in the extrastriate are not merely inherited from their V1 inputs, rather may reflect further degradation at higher levels of visual processing as well.

The orientation and direction selectivity of a motion-sensitive neuron can be quantified in terms of bias. Now a widely used measure, cell bias was first computed by Leventhal, Thompson, Liu, Zhou, and Ault (1995), and is based on the

maximum to minimum ratio of a neuron's responses to preferred and non-preferred orientations and directions. In recent years this method has been used to demonstrate an age-related reduction in orientation and direction selectivity in both the primary visual cortex (Schmolesky et al., 2000; Fu et al., 2010) and extrastriate visual areas (Yu et al., 2006; Liang et al., 2010). Schmolesky et al. (2000) found that in comparison to neurons in young macaques, the proportion of aged V1 cells demonstrating strong ($OB \geq 0.2$) and/or significant orientation bias ($OB \geq 0.1$) was reduced. This was also found to be the case when direction selectivity was assessed (Schmolesky et al., 2000). In agreement with the findings in primates, cells located within the striate of the aged cat exhibited similar reductions in orientation and direction selectivity (Hua et al., 2006). However, in the feline visual system, a more pronounced loss in strongly biased cells was observed (Hua et al., 2006).

In extrastriate visual areas the findings are similar. Yu et al. (2006) showed that biases for orientation and direction were reduced in V2 cells of aged rhesus monkeys. In these neurons, orientation sensitivity was more adversely affected than direction sensitivity; this differs from the findings in V1 where orientation and direction sensitivity were similarly affected by age (e.g. Yu et al., 2006), and suggests that the effects of age may be more pronounced in higher visual areas. In support of this finding, directional bias has been shown to be more severely reduced in aged MT cells, relative to V1 cells in the same animal (Liang et al., 2010). This same study revealed a broadening of the tuning bandwidths which characterized aged MT cells (bandwidths provide a measure of the range of directions over which a neuron will respond and are dependent upon the shape of

the tuning curve around its peak; more narrow bandwidths indicate stronger selectivity), as well as a reduction in the proportion of neurons which were responsive to pattern motion (Liang et al., 2010). Together the results of these investigations provide compelling evidence to support an age-related decline in sensitivity to orientation and direction that generally tends to increase in severity at higher processing levels.

Yang et al. (2009b) have shown that the speed preferences in primates are also affected by aging. Random dot kinematograms (RDKs) ranging in speed from 0.5 – 64°/s were used to assess the effects of age on speed tuning in macaque area MT. Whilst there was considerable overlap in the range of preferred speeds between animals, aged neurons differed notably from young neurons in two ways; firstly, MT neurons demonstrated significantly lower preferred speeds and secondly, the proportion of neurons selective for high speeds was reduced in these primates. Based on the obtained responses, modulation and discrimination indices were also calculated for all recorded neurons. These indices can be used to assess the sensitivity of individual neurons to minute changes in a stimulus. Specifically, a modulation index provides a measure of a neuron's ability to alter or 'adjust' their activity, relative to their maximal response, in response to variations in a given stimulus. Thus, in the context of speed selectivity, a larger modulation index is indicative of stronger speed tuning. Similarly, a discrimination index provides a measure of how adequately a neuron can discriminate between subtle stimulus changes and internal levels of variability or noise. Values for both indices were found to be lower in aged neurons. Therefore, in addition to age-related changes in speed preferences, aged neurons appear to be less efficient at encoding stimulus

changes and modulating their activity in response. Similar reductions in speed preferences have been reported in areas 17 and 18 of the aged rat (Mendelson & Wells, 2002).

A recurring finding in these single-cell studies is that age has a more pronounced effect on neurons in higher visual areas. For example, in comparison to visual cortex neurons, reductions in sensitivity to contrast (e.g. Yang et al., 2008), orientation (e.g. Yu et al., 2006), and direction (e.g. Liang et al., 2010) were all greater in extrastriate visual areas. Most recently, Liang et al. (2012) proposed the “hierarchical-aggravation hypothesis” which states that the effects of aging are more severe at higher levels of visual processing because of an accumulation of age-related changes inherited from earlier processing stages. In order to test this hypothesis, the authors compared the orientation and direction selectivities of simple and complex V1 cells in young and old rhesus monkeys. The results of these comparisons revealed an interaction between age and cell type; only complex cells demonstrated age-associated reductions in orientation and direction biases. Simple cells demonstrated similar tuning profiles in young and old. Whilst this is the first study to demonstrate a selective effect of aging between two cell types within a specific visual area, the “hierarchical-aggravation hypothesis” bears a striking resemblance to the “processing complexity hypothesis of aging” proposed by Faubert (2002). This hypothesis suggests that the effects of age are more pronounced on perceptual tasks that have complex processing requirements, and is supported by evidence from studies in motion perception (e.g. Habak & Faubert, 2000) and visual working memory (e.g. Sara & Faubert, 2000; Faubert & Bellefeuille, 2002) which have shown that age differences can be exacerbated by

increasing the processing demands of the task. For example, Sara and Faubert (2000) assessed observers' ability to make size discriminations between stimuli presented either simultaneously or sequentially and found performance was impaired in older observers only in the simultaneous presentation condition. Whilst the two theorems arise from different lines of evidence, it is interesting to note that both suggest the effects of age are greater for complex/higher-order visual processes.

1.4.2. Changes in response latency

Visually-evoked responses of young and old neurons also differ in a number of their more general properties. For example, Wang, Zhou, Ma and Leventhal (2005) examined the response latencies of primate V1 and V2 neurons in response to flashing visual stimuli and provided the first line of evidence for age-related signal degradation. The results indicated that V1 layer 4 neurons receiving direct input from the LGN did not differ in response latency with age, however outside of layer 4, aged V1 cells demonstrated longer latencies. This difference was even more pronounced in V2. In addition, there was greater variability in the response latencies of V1 and V2 cells in the aged primates (Wang et al., 2005). In agreement, aged rat visual cortex neurons have demonstrated prolonged onset latencies in response to a flashing stimulus relative to cells in young rats (Wang, Xie, Li, Chen, & Zhou, 2006). Furthermore, studies of cell adaptation and synaptic plasticity have indicated that aged neurons demonstrate greater adaptation (Wang et al., 2006; Yang et al., 2008) and decreased plasticity (Wang et al., 2006). Together, these results suggest an age-related slowing in signal transmission and increased vulnerability to fatigue in older neurons.

1.4.3. Lower signal-to-noise ratios in the aged

Along with the aforementioned changes in neuron sensitivity, a particularly robust finding across these neurophysiological studies is that of increased neural activity exhibited by aged neurons. Schmolesky et al. (2000) were the first to note that V1 neurons in aged rhesus monkeys demonstrate an increase in neural responsiveness to both optimal and non-optimal visual stimuli in comparison to neurons in younger animals. Thereafter, a number of studies have shown that in V1 and extrastriatal areas such as V2 and MT, aged neurons demonstrate significantly higher peak responses, as well as a reduction in selectivity and an increase in baseline (or spontaneous) activity (e.g. Schmolesky et al., 2000; Wang et al., 2005; Yu et al., 2006; Liang et al., 2010; Yang et al., 2008; Zhang et al., 2008).

In the feline visual system the findings are similar. Hua et al. (2006) assessed orientation sensitivity in area 17 neurons in young and old cats and demonstrated that across all orientations aged neurons had higher average responses in comparison to those elicited by young neurons. Similarly, in response to optimal stimuli (i.e. stimuli determined to be of optimal size, spatial and temporal frequencies, orientation and drifting direction) the average response was also shown to be higher in these aged cells (Hua et al., 2006). Therefore, aged neurons in the feline visual cortex can also be characterised by an increase in responsiveness to both preferred and non-preferred visual stimuli.

The variability of a neuron's response to a given stimulus also increases with age (Yang, Liang, Li, Wang, & Zhou, 2009a; Yang et al., 2009b). Yang et al. (2009b) examined the effects of age on the speed tuning properties of MT neurons and

noted that responses were more variable in aged neurons. Specifically, when neuronal spike rates were compared between young and old primates, average variance/mean ratios were higher in old cells. Yang et al. (2009a) sought to quantify age-related differences in response variability for neurons in areas V1 and MT in the macaque monkey. In this study, isolated neurons were presented with luminance-defined gratings at optimal stimulus parameters, and their responses to these stimuli were recorded across a number of presentations (stimuli were presented 6-12 times per neuron). Response variability was measured using a calculation referred to as the Fano factor (FF), which describes the ratio of a cell's variance/mean spike count (Kara, Reinagel, & Reid, 2000). In V1 and MT the findings were similar, aged cells had higher FFs. For each age group measures of variability were similar between visual areas (Yang et al., 2009a), suggesting that early visual processes such as photoreceptor response for example, may govern patterns of response variability and may underlie the observed age-related changes.

Perhaps the most striking age-related change in neuronal responsiveness is the increase in baseline (spontaneous) activity recorded from aged cells. In the absence of visual stimulation, neurons in aged primates, cats and rodents all demonstrate a marked increase in spontaneous discharge rates (Schmolesky et al., 2000; Wang et al., 2005; Hua et al., 2006; Wang et al., 2006; Yu et al., 2006; Liang et al., 2010; Yang et al., 2008; Zhang et al., 2008). With the exception of the findings in the rat visual cortex (i.e. Wang et al., 2006), age-related increases in spontaneous activity have been coupled with increases in peak response (e.g. Schmolesky et al., 2000; Hua et al., 2006; Liang et al., 2010). However, it is the spontaneous firing

rates of neurons that are most drastically changed in the aged. In primates, for example, estimates range from a 242% increase in spontaneous activity in V1 (Zhang et al., 2008), to 200% in V2 (Yu et al., 2006) and a 151-200% increase in MT (Liang et al., 2010; Yang et al., 2008). In cat striate cortex the increase in the spontaneous activity of aged cells is estimated to be 464% (Hua et al., 2006).

Due to the increases in neural responsiveness, response variability and spontaneous activity, a number of studies have reported lower signal-to-noise ratios (SNRs) with age (e.g. Hua et al., 2006; Yu et al., 2006; Yang et al., 2009a). SNRs refer to the ability of a cell to extract information regarding a visual signal from background neural “noise”. Generally defined as the peak-to-baseline response (Schmolesky et al., 2000), higher SNRs indicate stronger cell selectivity whereas lower SNRs are indicative of reduced selectivity and increased responsiveness to non-optimal stimuli. As will be described below, the leading explanation for this increase in neural responsiveness and consequent reduction in SNRs is a breakdown in intracortical inhibition within the visual system (e.g. Schmolesky et al., 2000; Yu et al., 2006; Liang et al., 2010; Yang et al., 2008).

1.4.4. The role of GABA

GABA is the primary inhibitory neurotransmitter of the cerebral cortex and has been shown to have a key role in maintaining the orientation and direction selectivity of visual cortex neurons (e.g. Rose & Blakemore, 1974; Sillito, 1975; Tsumoto, Eckart & Creutzfeldt, 1979; Li et al., 2008; Jirrmann & Pernberg, 2009; Katzner, Busse & Carandini, 2011). Recently, Katzner et al. (2011) used the GABA_A antagonist gabazine to confirm the role of GABAergic inhibition in maintaining the

orientation and direction selectivity of neurons in the feline visual cortex, and demonstrated that the tuning of inhibition matched that of excitation, suggesting that inhibition is closely mapped to the excitatory drive. As such, it has been proposed that age-related changes in neuron response properties may reflect a breakdown in GABAergic intracortical inhibitory mechanisms (e.g. Schmolesky et al., 2000; Wang et al., 2006; Liang et al., 2010; Fu et al., 2010). A number of findings have lent support to the 'GABA hypothesis'. For instance, Leventhal, Wang, Pu, Zhou and Ma (2003) showed that the electrophoretic application of GABA and/or the GABA_A agonist muscimol could restore the orientation and direction selectivities of aged V1 neurons; aged neurons were more narrowly tuned, had lower peak responses and less spontaneous activity. Conversely, the application of the GABA_A antagonist bicuculline could severely diminish the selectivity of young V1 neurons, temporarily inducing an 'aged-like' state in these cells.

There is also direct evidence to suggest GABA concentration is reduced in the aged brain. Hua, Kao, Sun, Li and Zhou (2008), studied age differences in the concentration of GABA neurons in the cat striate cortex. Using immunohistochemical techniques, GABA-immunoreactive (GABA-IR) neurons within each striatal layer were quantified. In spite of the findings that total neuron density did not change with age, in each striatal layer there was a marked reduction in GABA-IR neurons. Therefore, in the aged cat, the ratio of GABA-IR to total neurons is reduced in the striate cortex. In support of these findings, Diao, Xu, Li, Tang, & Hua (2009) have also found an age-related decrease in GABA-IR neurons in the feline visual cortex. Furthermore, two different enzymes involved in the synthesis of GABA, glutamic acid decarboxylase (GAD) and GABA alpha-

ketoglutaric transaminase (GABA-T), have been shown to decrease in the aged brain (Fonda, Acree, & Auerbach, 1973; McGeer & McGeer, 1976; 1978).

In summary, aged neurons in primates, cats and rodents all demonstrate key changes at the cortical level. There is an increased responsiveness of aged neurons to both optimal and non-optimal stimuli and this is accompanied by an increase in spontaneous activity. Together these changes lead to a reduction in the signal-to-noise ratios in aged cells, making it more difficult for the visual system as a whole to extract signal information. At present the leading explanation for these changes is an age-related degradation of GABAergic inhibition.

1.5. Psychophysical investigations of spatial vision in the aged

1.5.1. Age-related changes in contrast sensitivity

The contrast sensitivity function (CSF) is a psychophysically-obtained measure of the visual system's sensitivity to a broad range of spatial frequencies. Given the evidence that the visual system behaves as a Fourier analyser and is spatially-tuned (e.g. Campbell & Robson, 1968; Blakemore & Campbell, 1969; Blakemore & Sutton, 1969; Sachs, Nachmias, & Robson, 1971) the CSF has become an invaluable tool to further our understanding of the mechanisms underlying spatial vision (Owsley, Sekuler, & Siemsen, 1983). In order to construct a CSF, detection thresholds (i.e. the minimum contrast required to just detect the grating) are determined for sinusoidal gratings presented at various spatial frequencies. For each spatial frequency examined, contrast sensitivity is defined as the reciprocal of the threshold contrast; therefore, low contrast thresholds are indicative of high contrast sensitivity and high contrast thresholds indicate low contrast sensitivity. The resulting CSF defines an observer's window of visibility. A CSF reflects both the efficiency with which the sine waves are transmitted through optical media and the neural mechanisms which encode this information and thus is a measure of the overall performance of the system (Owsley, 2003).

Studies that have assessed contrast sensitivity throughout adulthood have demonstrated a marked loss in sensitivity with age (e.g. Owsley et al., 1983; Ross, Clarke, & Bron, 1985; Sloane, Owsley, & Alvarez, 1988; Elliott, Whitaker, & MacVeigh, 1990; Norton, McBain, & Chen, 2009). The magnitude of this sensitivity

decline has been shown to vary with spatial frequency and luminance level. Under photopic levels of illumination (i.e. $> 3\text{cd/m}^2$), sensitivity to low spatial frequencies appears to be relatively well preserved in the elderly (e.g. Owsley et al., 1983; Ross et al., 1985; Tulunay-Keesey, Ver Hoeve, & Terkla-McGrane, 1988; Elliott et al., 1990). At spatial frequencies ≥ 2 c/deg, age-related declines in contrast sensitivity are apparent (e.g. Derefeltdt, Lennerstrand, & Lundh, 1979; Kline, Schieber, Abusamra, & Coyne, 1983), and are most pronounced at high spatial frequencies (Whitaker & Elliott, 1992). These studies are outlined in detail below.

Owsley et al. (1983) examined contrast sensitivity in adults 19 – 87 years of age for static sine gratings ranging in octaves from 0.5-16 c/deg. For each spatial frequency, a measure of contrast sensitivity was obtained by determining monocular contrast thresholds using a detection task. The results demonstrated that at low spatial frequencies (i.e. 0.5 and 1 c/deg) performance did not differ as a function of age. At spatial frequencies ≥ 2 c/deg, losses in sensitivity emerged in individuals 40-50 years of age and became more severe with increasing age. In fact, the results suggest that at 60 years of age there is a pronounced shift in the peak of the contrast sensitivity function from 4 c/deg to 2 c/deg. This spatial frequency dependent loss in contrast sensitivity with age has been established under both monocular and binocular viewing conditions (Derefeltdt et al., 1979; Ross et al., 1985).

Under low levels of illumination, contrast sensitivity losses are exacerbated in the elderly (e.g. Sloane et al., 1988; Jackson & Owsley, 2000). Scheffrin, Tregear,

Harvey, and Werner (1999) measured scotopic contrast sensitivity in observers 20-88 years of age by reducing the mean retinal luminance of all observers to -0.85 log Trolands using neutral density filters. Participants completed a maximum-likelihood, 2-alternative temporal forced choice detection task for horizontal sine gratings presented within 2D Gaussian envelopes and ranging in spatial frequency from 0.2-3 c/deg. For all observers the CSFs obtained were low-pass. Age-related sensitivity loss was evident at all spatial frequencies examined and, unlike in photopic conditions, was pronounced for spatial frequencies ≤ 1.2 c/deg. Also of note was the leftward shift in high spatial frequency cut off apparent on the CSFs of older individuals, indicating that the range of perceptible spatial frequencies is reduced with age. Thus under low levels of illumination, age-related differences in contrast sensitivity become more pronounced with differences apparent at low, as well as intermediate and high, spatial frequencies.

1.5.1.1. Age and contrast sensitivity for temporally modulated gratings

Contrast sensitivity, particularly to low spatial frequencies, can be facilitated by temporal modulation (Kelly, 1974). With age, this facilitatory effect is diminished (Owsley et al., 1983; Sekuler, Hutman, & Owsley, 1980) and in some cases temporal modulation can exacerbate age differences, leading to greater reductions in contrast sensitivity in older populations (e.g. Clark, Hardy, Volbrecht, & Werner, 2010; Whitaker & Elliott, 1992). Owsley et al. (1983) examined the role of temporal modulation on contrast sensitivity in young and older observers and found older observers benefit less from the addition of a temporal component. Temporal enhancement (defined as the ratio of contrast sensitivity to moving stimuli to that of stationary gratings) was measured for a 1 c/deg grating drifting

at either 1.1 or 4.3 °/s. In both age cohorts, contrast sensitivity increased with temporal modulation, however at the highest drift speed age differences emerged; older adults demonstrated reduced temporal enhancement relative to their younger counterparts.

The addition of temporal modulation does not always lead to enhancements in contrast sensitivity, rather the effects of temporal modulation are heavily dependent on temporal frequency. Sekuler et al. (1980) identified an interaction between age and drift rate when measuring contrast sensitivity to drifting gratings. In this study, a 1 c/deg grating was presented to young (mean age = 20.2 ± 3.1 years) and older (mean age = 75.0 ± 4.8 years) observers at drift rates of 0.5 and 10 Hz. Older observers demonstrated reduced sensitivity to the gratings than younger observers which were particularly pronounced at 10Hz. Recently, Clark et al. (2010) have shown that increasing temporal frequency led to a shift in the high spatial frequency fall off in old observers. Indeed, evidence suggests that age-related deficits in contrast sensitivity are exacerbated at high spatiotemporal frequencies (Tulunay-Keesey et al., 1988; Elliott et al., 1990; Whitaker & Elliott, 1992; Clark et al., 2010) particularly at low luminance levels (Sloane, Owsley & Jackson, 1988; Sloane, Owsley & Alvarez, 1988). Therefore, in older populations, the addition of a temporal component often leads to greater reductions in contrast sensitivity, especially at high temporal frequencies.

1.5.1.2. Optical and neural contributions to the age-related loss in contrast sensitivity

Declines in contrast sensitivity that are associated with aging could be attributed to degraded optics, neural breakdown further in the visual pathway, or a combination of these two factors. To assess the relative contributions of each of these components, age-related optic changes are often simulated in young observers. In general, if the performance of young observers in these simulated conditions resembles that demonstrated by older observers under “normal” viewing conditions then age differences can largely be attributed to optical degradation. However, if simulation of the aged optical system cannot explain the results obtained by the older sample then it is reasonable to assume a neural origin for these performance reductions.

Studies of spatial vision in older populations have most frequently simulated the reduction in retinal illumination that develops as a result of the aging process. This reduction is primarily due to senile miosis and increased light absorption by the aged lens. Weale (1963) estimated that a 20 year old eye transmits approximately three times more light than that of a 60 year old, which is equivalent to a 0.5 log difference in illumination. In order to simulate this reduction, Owsley et al. (1983) assessed contrast sensitivity in young observers in the presence of a 0.5 neutral density filter to reduce display luminance by a factor of 3. Detection thresholds were measured for static sine gratings ranging from 0.5-8 c/deg in young and old observers under “normal” viewing conditions and again in young observers under these simulated conditions. The findings indicated that at high spatial frequencies (i.e. ≥ 4 c/deg) reduced retinal illumination could adequately explain the age-related differences in sensitivity observed under normal viewing conditions.

Contrast sensitivity was subsequently measured for sine gratings of the same spatial frequency however in this instance gratings drifted at two speeds: 1.1 and 4.3 °/s. With the addition of this temporal component, performance could no longer be attributed to reductions in retinal illumination. Thus the findings of this study demonstrate that degraded optics may influence the perception of static gratings but do not appear to contribute to the age-related loss in contrast sensitivity when gratings are drifting, thereby suggesting that these results may be mediated by a neural deficit in the motion pathway.

Unlike Owsley et al. (1983), the results of other studies that have investigated the role of degraded optics in the age-related decline in contrast sensitivity suggest that deficits have a neural origin. Specifically, studies which have simulated *both* senile miosis and increased light absorption have failed to find any evidence to suggest these optic changes are responsible for the contrast sensitivity loss demonstrated by older populations at any spatial frequency (Elliott et al., 1990; Whitaker & Elliott, 1992). This discrepancy may be due to the additional consideration of senile miosis in the studies carried out after Owsley et al. (1983). Both Elliott et al. (1990) and Whitaker and Elliott (1992) used 0.125% Thymoxamine to temporarily reduce pupil size in young observers in addition to reducing the luminance of the display, providing a more complete simulation of aged optics. It has also been suggested that there may be some advantages to the development of senile miosis with age, specifically smaller pupil diameters can reduce optical aberrations and increase depth-of-focus. Indeed, Sloane et al. (1988) have shown that under a range of luminance levels (0.107 -107cd/m²) both

young and old adults achieve their best performance on a contrast detection task when pupils are at their natural size.

In addition to reduced retinal illumination, the effect of increased light scatter on contrast sensitivity has also been examined. Lenticular density increases with age leading to an increase in the amount of forward light scatter, this creates a veiling luminance on the retina consequently reducing image contrast. Research that has examined the effects of the aging lens on contrast sensitivity has failed to show a causal relationship between increases in light scatter and decreases in sensitivity (e.g. Allen & Vos, 1967; Oswley, Gardner, Sekuler, & Lieberman, 1985; Whitaker & Elliott, 1992). Moreover, when reductions in retinal illumination and increased light scatter are simulated simultaneously, optical degradation still fails to account for age-related losses in contrast sensitivity (Whitaker & Elliott, 1992).

Laser interferometry has provided another line of evidence to suggest that neural mechanisms are the main determinants of contrast sensitivity (Campbell & Green, 1965; Morrison & McGrath, 1985). Morrison and McGrath (1985) used a laser interferometer to bypass the optical system, this involved focusing two separate laser beams of light by a microscopic objective which then projects the light onto a plane that passes through the posterior nodal point located in front of the retina. With the addition of this technique they were able to assess contrast sensitivity using conventional methods and laser interferometry to obtain detection thresholds with contributions from the optical system and without, respectively. The findings of this study revealed that neural transmission set the limit to visual resolution and is the main determinant of contrast sensitivity.

In summary, the results of studies that have simulated age-related optic changes largely suggest that age-related losses in contrast sensitivity cannot be sufficiently explained by degraded optics alone. When these optic changes are simulated in young observers, performance remains relatively unaffected by these manipulations, rendering them unable to adequately describe the performance differences observed between age cohorts. Therefore, age-related reductions in contrast sensitivity most likely reflect changes within the visual pathway beyond the optic system.

1.5.2. Age-related changes in orientation sensitivity

Very few studies have examined the effects of age on the processing of orientation information, and the results of those that have suggest that declines in orientation sensitivity are not all encompassing. For example, masking paradigms have been used to demonstrate that, despite the findings for orientation selectivity at the neuronal level (e.g. Schmolesky et al., 2000; Yu et al., 2006; Fu et al., 2010; Liang et al., 2010), perceptual orientation tuning curves do not change with age (Delahunt, Hardy, & Werner, 2008; Govenlock, Taylor, Sekuler, & Bennett, 2009).

The effects of age on the ability to discriminate stimulus orientation are less clear. For example, Habak and Faubert (2000) failed to find age differences in orientation discrimination for static sine gratings presented at 1c/deg. Conversely, age-related reductions in orientation discrimination have been demonstrated for stimuli presented at 2 c/deg (Tang & Zhou, 2009). Delahunt et al. (2008) measured discrimination thresholds for Gabor patterns presented at 1 and 4 c/deg and found

that older observers performed worse at both spatial frequencies however, performance differences on this task could be explained by age-related losses in contrast sensitivity and thus did not reflect changes in orientation discrimination *per se*.

In the presence of additive noise, age-related changes in orientation discrimination have also been shown. Betts, Sekuler and Bennett (2007) embedded Gabor patterns of similar orientations in varying levels of external noise (see Chapter 3 for more on the external noise technique) and required young and old observers to detect which of two alternatives was the horizontal Gabor. The results of this study demonstrate that older observers were less able to accurately identify the horizontal Gabor at low levels of external noise only. Further investigation revealed this performance difference could not be explained solely by age-related reductions in retinal illumination therefore the authors proposed changes in orientation discrimination were of neural origin (Betts et al., 2007).

1.6. Psychophysical evidence for age-related changes in motion perception

1.6.1. Changes in sensitivity to translational motion

1.6.1.1. Changes in direction discrimination

Ball and Sekuler (1986) were among the first to identify an age-related decline in direction sensitivity. In their study, young (18-28 years) and old (62-72 years) observers were required to compare the direction of two sequentially presented spatially-fixed dot patterns that translated either in the same direction or were offset by 2, 4, 6, or 8° clockwise or anticlockwise. Observers were required to judge whether the two dot patterns were the same or different. Older observers were found to be less sensitive to differences in dot direction than younger observers at small to intermediate spatial offsets (i.e. 2 & 4°). Furthermore, whilst training on this motion task improved the performance of older observers, age differences persisted post-training (Ball & Sekuler, 1986). O'Connor, Margrain and Freeman (2010) employed similar spatially-fixed dot patterns to assess direction discrimination in young and old observers under two viewing conditions, fixation and pursuit and demonstrated a speed-dependent effect of age on performance. Specifically, direction discrimination thresholds were elevated in older participants when dot patterns were presented at a speed of 2 °/s but not at 8 °/s and this was true under both viewing conditions. These findings suggest slow stimulus speeds may exacerbate the effects of age on direction discrimination.

1.6.1.2. Changes in sensitivity to global motion

The vast majority of research investigating motion perception across the lifespan has focused on the perception of translational motion and has used random dot kinematograms (RDKs) to measure sensitivity to coherent global motion (e.g. Trick & Silverman, 1991; Wojciechowski, Trick & Steinman, 1995; Snowden & Kavanagh, 2006). An RDK is a motion stimulus made up of a collection of moving local dots, the individual trajectories of which come together to create a larger global stimulus. Although individual elements move along different local trajectories, their combined (global) direction appears to move coherently in a given direction. Human observers, and also non-human primates, are adept at encoding the direction of global motion. They typically only require a small percentage of local elements, often less than 5%, to move in a given direction to be able to accurately determine the global direction of motion (e.g. Newsome & Paré, 1988).

A number of studies have demonstrated that sensitivity to coherent global motion declines with age (e.g. Trick & Silverman, 1991, Andersen & Atchley, 1995; Wojciechowski et al., 1995; Atchley & Andersen, 1998; Tran, Silverman, Zimmerman, & Feldon, 1998; Billino, Bremmer, & Gegenfurtner, 2008). For example, Trick and Silverman (1991) measured sensitivity to global motion in adults 25 to 80 years of age as well as in older adults diagnosed with senile dementia Alzheimer's type (SDAT). In this study, motion coherence thresholds (defined as the percentage of signal dots required to discern motion direction with 75% accuracy) were obtained using a direction-discrimination task in which observers were required to indicate whether dot patterns were moving up, down,

left, or right whilst signal dot coherence ranged from 0 to 50%. The results of this study indicate that SDAT patients had reduced motion sensitivity relative to their healthy aged counterparts. Moreover, healthy observers also demonstrated reduced sensitivity to global motion with age; motion coherence thresholds increased (i.e. sensitivity was reduced) by approximately 1.36% per decade. Subsequent investigations of global motion sensitivity throughout adulthood have produced estimates of a 0.4% (Tran et al., 1998), 1.1% (Wojciechowski et al., 1995) and a 2.7% (Billino et al., 2008) per decade increase in motion coherence threshold with age.

There is some evidence to suggest that age-related impairments in motion perception may be more severe in female populations. Gilmore, Wenk, Naylor and Stuve (1992) assessed the effects of age and gender on motion perception by measuring coherence thresholds in young and old observers using a single-interval direction discrimination task. The results of this investigation indicated there were significant age-related performance differences between young and older observers. However, when the effect of gender was taken into account, the findings were suggestive of a gender-specific effect of aging. Specifically, older women had higher motion coherence thresholds in comparison to all other observers. Closer examination revealed that the age differences in global motion sensitivity were driven solely by the performance of older females. Older male observers, on the other hand, demonstrated similar motion sensitivity to the younger group. Andersen & Atchley (1995) replicated this study and once again identified an increased susceptibility to age-related declines in motion perception in elderly women. However, in this study older males did show some degree of

reduced motion sensitivity relative to young observers, albeit to a lesser extent than older female observers.

Further research into the age-associated decline in motion sensitivity suggests that impairments may be mediated by stimulus parameters such as speed and contrast. For example, Snowden & Kavanagh (2006) measured motion coherence thresholds in young and old participants for RDK patterns presented at four speeds in the range of 0.5- 4 °/s and found that performance differences were only apparent at the lowest speeds tested (i.e. at speeds of 0.5 & 1 °/s). At higher speeds (i.e. 2 & 4 °/s) motion coherence thresholds did not differ between young and old observers, suggesting that stimulus speed may contribute to the age-related decline in global motion sensitivity.

Allen, Hutchinson, Ledgeway and Gayle (2010) demonstrated a contrast-dependent effect of aging on global motion sensitivity. Global motion coherence thresholds for translational dot patterns were measured in young (mean age = 21 ± 2.8 years) and old (mean age = 73 ± 3.4 years) observers for RDKs across a range of local element contrasts. Overall, older observers demonstrated reduced sensitivity in comparison to their younger counterparts, however this was largely dependent on dot contrast. Performance differences were greatest at low dot contrasts. At high dot contrasts, there was little effect of age on performance.

Some studies have sought to disentangle the effects of age on motion detection and sensitivity to global motion. For example, Tran et al. (1998) used infrared oculography to detect optokinetic nystagmuses (OKN) whilst 12 young observers

(19-29 years) and 10 old observers (60-92 years) completed a motion coherence task. On each trial, the presence of an OKN, which can be characterized by eye movements alternating between smooth pursuit in one direction and saccadic movement in the other, provided an objective measure of motion detection in addition to the observers' subjective responses to motion direction. This allowed for two measures of motion sensitivity to be included in this study: motion detection and perception. With this approach, the researchers were able to separate the participants' ability to track motion via eye movements and their conscious perception of motion direction. The findings revealed old observers had reduced sensitivity in both measures. Detection thresholds (defined as the dot coherence required to produce an OKN in the corresponding direction 75% of the time) increased by 1.1% per decade and perception thresholds (defined as the coherence required to accurately identify dot direction with 75% accuracy) increased by 0.4% per decade. Thus it appears that whilst motion detection and perception were both reduced in older observers, age had a more pronounced effect on older observers' ability to make eye movements in the direction of the moving dot patterns.

Bennett, Sekuler, and Sekuler (2007) have also assessed motion detection and direction identification in the aged. In this study, participants (23 to 81 years of age) were required to view moving kinematograms. After each stimulus presentation observers were asked to: (1) identify the direction of motion; (2) indicate whether the stimulus was a 'signal' (dots moved in a coherent direction) or 'noise' (dots moved at random); and (3) rate their confidence in their judgment. In comparison with all other age cohorts, older adults (i.e. >70 years of age) were

significantly less sensitive to the presence of motion and less accurate at identifying its direction. Likewise the expressed confidence by older individuals (70+) was judged as much lower than all other age groups for short stimulus durations. These findings suggest changes in motion perception manifest beyond the age of 70 and result in reductions in motion detection and direction discrimination as well as changes in perceived confidence of motion judgments.

Age-related declines in motion processing are not localized to central vision but extend to the peripheral visual field as well. Wojciechowski et al. (1995) used a direction discrimination task to compare young (mean age = 22.9 ± 1.3 years) and older (mean age = 66.6 ± 4.5 years) participants' global motion perception in central vision and 18° in the nasal, temporal, superior and inferior peripheral visual fields for RDKs traveling at a speed of $28^\circ/\text{s}$. Age-related impairments were most marked in central vision however, sensitivity differences between young and old observers were apparent at all visual field locations. As in central vision, age-related declines in motion sensitivity in the peripheral visual field may also be mediated by the speed of the stimulus. For example, Atchley and Andersen (1998) identified an interaction between age, stimulus speed and retinal eccentricity when measuring motion detection thresholds for translationally moving dot patterns presented at four viewing angles ($0, 10, 20$ & 40°). In central vision (i.e. 0°), age differences were pronounced when dot patterns travelled at a speed of $4.8^\circ/\text{s}$ only. However, when stimulus speed was set to $22^\circ/\text{s}$, older observers were found to perform worse at all but the greatest retinal eccentricity (Atchley & Andersen, 1998). Taken together, the findings of these studies suggest that whilst age-associated reductions in motion sensitivity are most marked in central vision,

sensitivity differences extend to the peripheral visual field when stimuli are presented at high speeds.

1.6.2. Speed Perception

A number of studies have demonstrated that speed perception is affected by aging (e.g. Norman, Ross, Hawkes, & Long, 2003, Raghuram, Lakshminarayanan, & Khanna, 2005; Bidwell, Holzman, & Chen, 2006; Snowden & Kavanagh, 2006; Norman, Burton, & Best, 2010; Kavcic, Vaughn, & Duffy, 2011). Norman et al. (2003) assessed how well young and old observers could judge the speed of a motion pattern relative to that of a 'standard' stimulus. The standard speeds were 1.22, 5.48 and 24.34°/s. For each standard speed, older observers had higher discrimination thresholds than young observers. This was true for both high and low-contrast displays. In a subsequent study, Norman et al. (2010) examined the effects of binocular disparity on speed perception in young and old observers and noted that regardless of condition (i.e. crossed vs. uncrossed surround disparity) speed judgments were less precise in older individuals.

Similar results have been obtained using luminance-defined sinusoidal gratings. Raghuram et al. (2005) examined speed discrimination in young and old observers for gratings drifting at 2 and 8 °/s at two presentation durations (500 & 1000ms). The results of this study revealed older observers had higher discrimination thresholds, with age differences particularly pronounced at presentation durations of 500ms. In agreement, Snowden and Kavanagh (2006) assessed speed discrimination for gratings drifting at 0.125, 1, and 8 °/s and observed an age-

related reduction in discrimination at each of these speeds. There is also some evidence to suggest the effects of age on speed perception may be mediated by gender. Specifically, in addition to an overall age-related decline, older females were found to be particularly impaired in speed perception (Norman et al., 2003; Raghuram et al., 2005).

Age-related changes in speed perception have been shown to extend to patterns of optic flow. Kavcic et al. (2011) presented young and old participants, as well as patients with Alzheimer's disease, a radial motion stimulus that had a central focus of expansion divided along the vertical meridian. In this study, the spatio-temporal composition of the stimulus was manipulated by moving elements in the optic flow display. The task required participants to decipher which half of the display they perceived to be moving faster. Older 'healthy' participants performed similarly to patients with Alzheimer's disease, with both groups demonstrating elevated discrimination thresholds. Older participants also showed greater sensitivity to the spatio-temporal composition of the optic flow pattern, relative to young participants, demonstrating the largest impairments at low temporal periodicities.

1.6.3. Changes in sensitivity to more complex motion types

1.6.3.1. Rotational and radial motions

Random dot displays can be used to study other types of global motion. For example, presenting dots along trajectories that are consistent with expansions and contractions can simulate radial motion and patterns consistent with optic flow. Likewise, dot patterns with clockwise/anticlockwise trajectories can be used

to simulate rotational motion. Studies of radial motion or 'optic flow' in the aged have led to conflicting findings. Atchley and Andersen (1998) and Billino et al. (2008), measured sensitivity to radial expansion in young and old observers and found no evidence of reduced performance with increasing age. Conversely, for psychophysical tasks which require observers to discriminate between expanding and contracting dot patterns in noisy displays, older individuals have demonstrated reduced sensitivity relative to young observers (O'Brien, Tetewsky, & Avery, 2001; Mapstone, Dickerson, & Duffy, 2008; Kavcic et al., 2011). Given the differences in the types of tasks employed in these studies (e.g. detection vs. discrimination in noise), the effects of aging on radial motion perception currently remain unclear

Allen et al. (2010) also assessed the effects of age on radial and rotational global motion patterns under varying levels of visibility (dot contrast). Similar to their findings for translational motion, age-related impairments in sensitivity to radial and rotational motion were evident at low dot contrasts only. Again, this finding likely reflects an age-related change in contrast sensitivity rather than in global motion perception *per se*.

1.6.3.2. Biological motion

The perception of biologically relevant motion, such as that elicited by movements of the human body, has been shown to be associated with processing in the posterior superior temporal sulcus (pSTS) (e.g. Grossman et al., 2000; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; Grossman, Battelli, & Pascual-Leone, 2005) and is simulated in laboratory settings with the use of point-light

walker displays. Few studies have examined the effects of age on biological motion perception, however, the existing evidence suggests that the processing of this motion type remains relatively well preserved with age. Norman, Payton, Long and Hawkes (2004) examined age-related changes in biological motion perception by comparing young (mean age = 20.0 ± 1.9 years) and old (mean age = 72.6 ± 5.7 years) observers' sensitivity to point-light walkers that simulated physical activities such as walking, jogging and skipping. In a series of experiments, motion direction (forward vs. backward), stimulus duration (120 vs. 400ms) and visibility of the dot patterns (i.e. patterns were either 0, 50, or 85% occluded) were manipulated; participants were required to identify the movement type presented on each trial. The results of this study reveal that for biological motion carried out in the forward direction, young and old participants performed similarly. However, at short motion sequence durations, older observers made more errors in their judgments of point-light walker activity. Moreover, when the displays were partially occluded, older observers were less accurate in their judgments of activity type than younger observers.

In the presence of noise, older populations demonstrate greater impairments in sensitivity to biological motion. For example, Billino et al. (2008) presented point-light walkers embedded in noisy displays (i.e. dots that moved at random) to young and old participants and found the ability to detect the point-light walkers was moderately impaired in older participants. In agreement, Pilz, Bennett, and Sekuler (2010) demonstrated that older observers could identify the direction of point-light walker motion with comparable accuracy to young observers when the dot patterns were presented in the absence of noise. However, when noise was

included in the stimulus or when the stimulus was inverted, older observers were less accurate in their direction judgements. Together, the findings of these studies suggest that biological motion discrimination is relatively well preserved with age except when stimulus durations are short, when there is a disruption in the motion sequence, or in the presence of noise.

In summary, psychophysical evidence demonstrates that older populations differ from their younger counterparts on a number of perceptual tasks that require motion processing. Reductions in sensitivity to motion detection and discrimination have been demonstrated in older individuals and this is often exacerbated by stimulus parameters such as speed and contrast. Secondly, whilst the majority of research has focused on changes in sensitivity to translational motion, age-related reductions have been reported for more complex motion types as well. There is also some evidence to suggest that motion processing is more severely impaired in older women, particularly for the processing of motion information relevant for global motion and speed perception. Finally, although our understanding of the effects of normal aging on motion perception has greatly advanced in the last 30 years, there remain many questions about the mechanisms responsible for these changes and how these changes affect the daily lives of older populations.

1.7. Prelude to this thesis

Within this thesis, well-established psychophysical techniques were used to examine the effects of age on visual function, primarily motion perception. The aim of the experiments carried out in Chapters 3-6 was to further our understanding of the behavioural consequences of aging on sensitivity to motion information. A short summary of each chapter is provided below.

Chapter 3 (Experiments 1-4) examined age-related changes in the ability to discriminate orientation and direction in noisy displays and sought to describe these changes in terms of sampling efficiency and equivalent input noise by employing the Linear Amplifier Model. The results of this investigation indicate that older observers are less sensitive to orientation and direction information in the absence of noise and when noise is present in low levels. These differences were found to be due to increases in equivalent input noise only, and likely reflect a reduction in GABAergic inhibition within the motion-processing pathway.

Chapter 4 assessed the role of speed and spatial displacement in sensitivity to translational global motion throughout adulthood. The aim of the experiments carried out in this chapter was to clarify the discrepant findings in the existing literature and provide greater insight into the underlying causes of age-related changes in the perception of this motion type. The results of Experiments 5-7 suggest that performance on tasks of global motion is largely driven by the spatial displacements employed in the task. Only observers 70-79 years of age demonstrated reductions in global motion sensitivity. Furthermore, under some

experimental conditions, older female observers demonstrated greater reductions than their male counterparts, alluding to a gender difference in aging.

Chapter 5 (Experiments 8 & 9) examined the role of gender and age in spatial vision using tasks of contrast sensitivity and visual attention. The aim of this chapter was to determine whether the gender-specific deficits that have been observed in some tasks of motion perception extend to spatial vision as well or whether these deficits reflect changes in motion processing abilities. The results of these experiments indicate that gender does not mediate performance for measures of contrast sensitivity and visual attention, thereby supporting a motion-specific gender difference in aging.

Finally, Chapter 6 (Experiment 10) examined the effects of age on second-order (contrast-defined) global motion for translational, rotational and radial motion types. The aim of this chapter was to extend our understanding of second-order mechanisms and their susceptibility to age-related degradation. The findings presented within this chapter suggest there may be a selective impairment in the processing of second-order radial motion whilst the perception of second-order translational and rotational motion remains relatively well preserved with age.

Chapter 2

General Methods

The methodology and apparatus employed throughout this thesis are described below. Specific details are given in the experimental chapters that follow where appropriate.

2.1. Observers

Observers included in the following experiments ranged from 18 to 82 years of age. All observers reported normal or corrected-to-normal vision, and were free of eye and/or neurological disease. For each experiment, observers were given clear instructions and completed several practice trials prior to testing. Additionally, observers were provided with rest breaks throughout the studies at their request. Informed consent was obtained from all participants. All experimental procedures adhered to the tenets of the Declaration of Helsinki and the ethical procedures of the School of Psychology, University of Leicester.

2.1.1. Volunteer recruitment

Young volunteers were University of Leicester undergraduate students recruited through the School of Psychology Experimental Participation Requirement scheme. Students were granted credits for their participation in each experiment.

Older observers were recruited from the wider Leicester community. Studies were advertised in community centres, libraries, adult education centres and in the local media. Volunteers from the Leicester community received an honorarium upon completing an experiment.

2.1.2. Inclusion based on visual acuity

In addition to volunteers' self-reported visual health status, visual acuity was used as a screening measure for all experiments. Visual acuity was measured using the Freiburg Visual Acuity Test (FrACT), which is an open-access visual test that uses psychometric methods to measure visual acuity (Bach, 1996). FrACT has been used in a number of non-clinical and clinical studies and has been shown to provide a robust measure of visual acuity (e.g. Mund, Bell, & Buchner, 2010; Straube, & Fahle, 2011; Bennett, Elliott & Rodacki, 2012; Nielson & Hjortdal, 2012).

During the FrACT acuity task, observers were required to identify the orientation of the gap in Landolt C optotypes using a key press. A staircase procedure was used to decrease the size of the optotypes until a measure of the observer's spatial resolution limit was obtained. Each observer was given verbal instruction and completed one practice trial to familiarise themselves with the task and the keypad. Once testing commenced, visual acuity was measured twice and a mean was taken. Any observer whose mean best-corrected decimal acuity was ≤ 0.5 , the minimum visual acuity required to attain a driving license in the UK (Department of Transport, 2013), was excluded from the study.

2.1.3. Inclusion based on cognitive ability

In order to ensure that the performance of older observers was not influenced by the presence of any cognitive impairment the Mini Mental State Examination (MMSE) (Folstein, Folstein, & McHugh, 1975) was administered to all participants 60 years of age and older. The MMSE is a short questionnaire that assesses individuals on a number of key skills such as orientation to time and place, verbal memory and recall, and construct ability. Volunteers completed the questionnaire prior to psychophysical testing. Any individual with a score of 26 points or less, out of a possible 30, was not included as an observer due to the greater likelihood of cognitive impairment. All observers included in Experiments 1-10 demonstrated normal cognitive ability and scored within the normal range (27-30 points).

2.2. Image processing hardware

Unless otherwise stated, stimuli were generated using the C programming language in OpenGL on Macintosh G4 computers. Stimuli were either presented on a 21-inch Formac ProNitron CRT monitor (monitor resolution: 1024 x 768 pixels, refresh rate: 75 Hz) or a 21-inch Dell CRT monitor (monitor resolution: 1024 x 768 pixels, refresh rate: 75 Hz). Each set up was gamma corrected in the manner described below (see Section 2.3). A Cambridge Research Systems Bits++ attenuator was also included in each setup in order to increase the luminance dynamic range (i.e. the number of intensity levels available) of the graphics system from 8 to 14 bits. This allowed high-resolution grey-scale images to be presented

on the colour monitor by amplifying the monochrome signal and sending the same signal to the red, blue and green guns of the display.

2.3. Calibration

The displays described in Section 2.2 were gamma corrected in the following manner. Gamma was measured for 256 pixels, ranging from 0 to 255, where 0 is “black” and 255 is “white” using a spot photometer (*LS100, Konika Minolta*). The luminance of a central, uniform, stationary, circular test patch (radius = 128 pixels) was measured three times for each pixel value, and a mean corresponding to each value was obtained. The contents of a gamma-correction look-up table (LUT) were changed using the following power function:

$$y = 255 (x / 255) ^ { 1 / g} \quad [2.1]$$

where y is the final output of the gamma correction LUT (0-255), x is the original input value and g is the gamma correction factor. An example gamma function is shown in Figure 2.1.

Upon correction of the display, psychophysical procedures can be used to confirm that any residual luminance non-linearities are minimised. This is generally carried out as an additional precaution and is an important control when an experiment requires the use of dynamic (moving or flickering) stimuli (Ledgeway & Smith, 1994; Nishida, Ledgeway, & Edwards, 1997). Psychophysical gamma-correction is carried out using motion sequences in which consecutive images

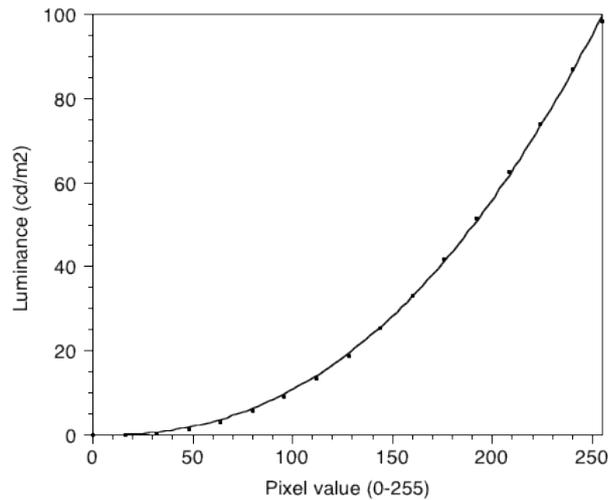


Figure 2.1. A power function describes the relationship between pixel value (range 0-255) and test patch luminance (in cd/m^2) prior to gamma correction.

alternate between a sinusoidal variation in the luminance (first-order) of a two-dimensional (2-d), broadband, static noise field (carrier) and an otherwise identical sinusoidal modulation in the contrast (second-order) of the noise field. When the spatial phases of the sinusoids in consecutive images differ by 0.25 spatial periods, observers cannot reliably determine motion direction unless a significant luminance non-linearity contaminating the second-order images is present (Ledgeway & Smith, 1994). Observer performance on such tasks can measure and/or check the efficacy of the gamma-correction applied to displays and variants of this technique have been widely used by other researchers (e.g. Papathomas, Gorea, & Chubb, 1996; Gurnsey, Fleet, & Potechin, 1998; Scott-Samuel & Georgeson, 1999; Lu & Sperling, 2001a).

Each display used within this thesis was gamma-corrected with a photometer and the psychophysical measurement procedure. For each display, the gamma values

obtained with these two methods were in good agreement (see Fig. 2.2 for an example).

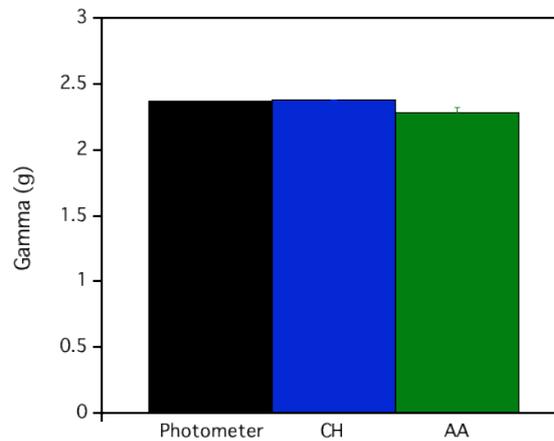


Figure 2.2. Comparison of the gamma values obtained by photometric and psychophysical (2 observers) methods.

2.4. Stimuli

With the exception of Experiment 9, the experiments presented within this thesis employed sinusoidal gratings or random dot kinematograms (RDKs) to investigate the effects of age on visual perception. These stimuli and their use in vision research are described below. Further details are provided in the appropriate experimental chapters.

2.4.1. Sinusoidal gratings

According to Fourier theorem, sinusoidal waveforms are the elementary units from which all complex waveforms can be composed. Based on this theorem, the visual system's response to sine waves of various spatial frequencies can be used to predict how the system would respond to an infinite number of inputs. Indeed, evidence has shown that the visual system behaves as a Fourier analyser and is tuned to a range of spatial frequencies (Campbell & Robson, 1968; Blakemore & Campbell, 1969; Blakemore & Sutton, 1969; Sachs, Nachmias, & Robson, 1971). As such, sinusoidal gratings are ideal stimuli to study the visual system and are widely used in behavioural studies.

An example of a luminance-defined sine grating is presented in Figure 2.3. Four key features define gratings: spatial frequency, contrast, orientation and spatial phase. The spatial frequency of a grating refers to the number of light and dark regions, created by the sinusoidal oscillation in brightness across the pattern, that are imaged within a given distance from the retina. Spatial frequency is expressed as the number of cycles per degree of visual angle (c/deg).

Contrast refers to the difference between the maximum and minimum intensities in the pattern of light and thus is a relative measure. Contrast is commonly described as the following:

$$\text{Michelson contrast} = (L_{\max} - L_{\min}) / (L_{\max} + L_{\min}), \quad [2.2]$$

where L_{\max} and L_{\min} are the maximum and the minimum luminances in the image, in the range 0-100 %.

The remaining two features orientation and phase refer to the axis of the grating bars and the position of the grating relative to some landmark (i.e. whether the first bar corresponds to peak luminance), respectively. As previously mentioned, sine waves can be considered to be the elementary units of complex waveforms thus, any visual pattern can be formed by summing a number of sine waves which vary in these four properties.

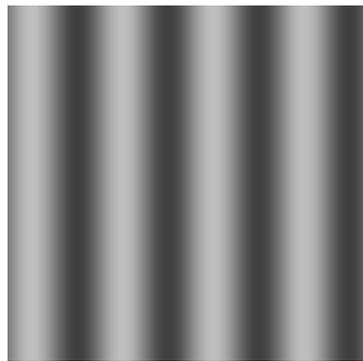


Figure 2.3. *A luminance-defined sinusoidal grating.*

2.4.2. Random dot kinematograms

Global motion stimuli were created with the use of random dot kinematograms (RDKs). RDKs are widely employed in studies of motion perception because they tap into global processing mechanisms whilst maintaining parameters such as luminance constant across the display. RDKs produce apparent motion through the rapid presentation of successive frames of dot patterns. In each display, a fixed proportion of dots move in a given ‘signal’ direction whilst the remaining dots act

as 'noise' and move at random. On any given trial, dots moving out of the aperture in one frame reappear at a new random position within the aperture on the subsequent frame (Edwards & Badcock, 1995). Global motion sensitivity can be measured by varying the signal intensity (i.e. varying the number of coherently moving 'signal' dots)(see Fig. 2.4). In the global motion tasks carried out in this thesis, coherence thresholds were measured for each observer in order to obtain a measure of sensitivity to global motion. A global motion coherence threshold refers to the minimum number of signal dots required to be moving coherently (i.e. in the 'signal' direction) in order for the overall direction of the dot pattern to be accurately identified. As such, lower coherence thresholds are indicative of greater sensitivity to global motion.

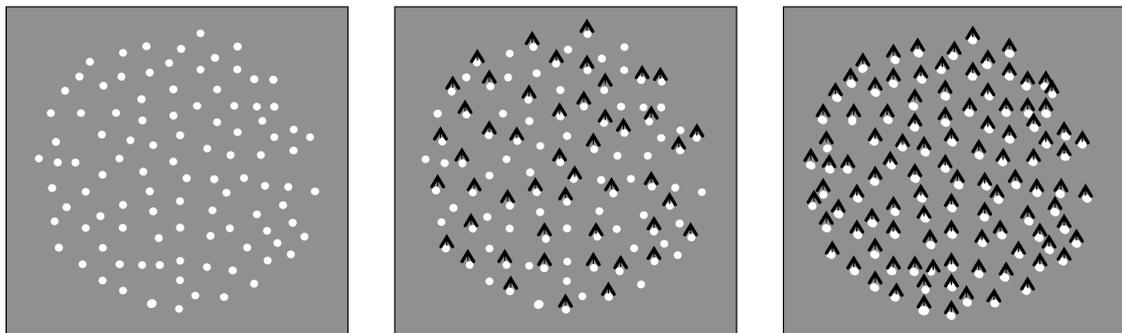


Figure 2.4. *RDKs of different coherence levels. In the display on the left all of the dots in the circular aperture are moving at random, in this case the coherence level of the display is 0% and there is no net motion. The centre display depicts a coherence level of 50%, with half of the dots moving in the signal direction (in this case upward) while the remaining dots create noise in the display. At a coherence level of 100%, as indicated in the right display, all the dots are moving in the 'signal' direction.*

2.5. Adaptive staircase procedures

Psychophysical thresholds were determined using adaptive staircase procedures. Often referred to as the 'method of ups and downs', an adaptive staircase provides a measurement of threshold by 'homing' in on the level of the independent variable at which an observer attains a certain percentage of correct responses. In all adaptive procedures the stimulus intensity on each trial is governed by the responses of previous trials. In general, errors made by the observer lead to increases in stimulus strength (i.e. the task becomes easier) and correct responses lead to decreases (i.e. the task becomes more difficult), with each change in staircase direction referred to as a 'reversal'. The procedure continues until the responses reach an asymptotic level where the staircase values hover until testing is terminated. The threshold is then calculated as the mean of a predetermined number of values from the plateau. An example of an adaptive staircase procedure is given in Fig. 2.5. Full details about the specific staircase procedures employed in Experiments 1-10 are given in the appropriate experimental chapters.

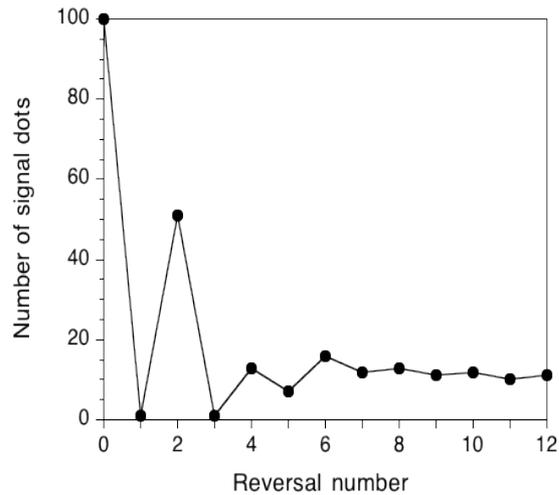


Figure 2.5. An example adaptive staircase used to determine the number of signal dots required to discriminate the direction of coherent global motion tracking 79% accuracy. Initially, all 100 dots in the display moved in the same direction, on each subsequent reversal the number of signal dots was halved until performance reached an asymptotic level. Testing was terminated after a total of 12 reversals and motion coherence thresholds were taken as the mean of the last 6 reversals.

Chapter 3

Age-related changes in the discrimination of orientation and direction in noise

3.1. Introduction

Neurophysiological studies that have examined the effects of aging on neuron function in visual cortical areas have revealed a number of consistent, reproducible and species-independent functional differences in neuron properties between young and old animals (see Chapter 1, Section 1.4 for a full description). Amongst these differences are changes in neuron selectivity for orientation and direction. Specifically, aged neurons in the primate and feline visual systems exhibit reduced orientation and direction selectivity, responding more vigorously to both optimal and non-optimal stimuli (Schmolesky, Wang, Pu, & Leventhal, 2000; Hua et al., 2006; Yu, Wang, Li, Zhou, & Leventhal, 2006; Liang et al., 2010; Fu et al., 2010). These reductions are accompanied by an increase in the baseline (spontaneous) activity of these cells, and have been attributed to a general unmodulated increase in neuron responsiveness due to a breakdown in intracortical inhibition within the aged visual pathway (e.g. Schmolesky et al., 2000; Hua et al., 2006; Yu et al., 2006; Liang et al., 2010). Similar findings have also been demonstrated in the rodent visual system, however unlike in monkeys and

cats, peak visually driven response rates do not differ with age in these species (Wang, Xie, Li, Chen, & Zhou, 2006).

Behavioural (psychophysical) evidence supports neurophysiological findings that the normal aging process is accompanied by reductions in visual selectivity to direction and orientation. Older adults exhibit impaired performance across a range of tasks that require accurate motion detection and direction discrimination (e.g. Ball & Sekuler, 1986; Trick & Silverman, 1991; Wojciecowski, Trick, & Steinman, 1995; Snowden & Kavanagh, 2006; Bennett, Sekuler, & Sekuler, 2007). Age-related changes in the processing of orientation information have also been shown (Betts, Sekuler, & Bennett, 2007).

3.1.1. Psychophysically-motivated models of age-related cortical decline

To better understand the neurophysiological changes that take place within the aged visual system and the consequent behavioural impairments, sub-optimal human performance can be compared to that of an ideal observer with a technique that manipulates the external noise added to a stimulus. The ideal observer predicts the best possible performance in a task (in this case not perfect performance because of the added noise), and begins with a calculation known as a cross-correlation. This is also known as the Linear Amplifier Model (LAM) (e.g. Barlow, 1978; Legge, Kersten, & Burgess, 1987; Pelli, 1990). The performance of real observers will deviate from that of the ideal observer, and the external noise technique allows for the analysis of mechanisms that degrade performance of real observers to be grouped into two separable factors: (1) those that lead to increases in equivalent (or internal) noise; and/or (2) decreases in sampling (or

calculation) efficiency. Equivalent (or internal) noise refers to all the additive¹ random noise within the system being assessed (in this case the aged visual system), and can be optical (e.g. light scatter) or neural (e.g. increased spontaneous firing). Generally sampling efficiency refers to how well the system is able to use the relevant information it is provided. For example, in the modelling associated with this paradigm, it is commonly assumed that the first step in visual perception is to measure the direct match of the stimulus with an internal representation of the signal, often called a template. A better match of the stimulus with the template indicates a greater likelihood of signal presence. Differences in sampling efficiency would be represented as differences in the quality of the template, with lower sampling efficiencies indicating poorer templates. For example, if an observer used a small template to locate a large signal, this would be less efficient than using a larger template closer to the actual size of the signal.

The external noise technique requires targets in a display to be embedded in external noise and is based on the assumption that at low levels of external noise, noise intrinsic to the visual system (i.e. equivalent noise) dominates, rendering the addition of external noise to have little or no effect. Higher levels of external noise lead to the eventual “swamping” of the internal noise. The more external noise required to swamp a visual system, the more intrinsically ‘noisy’ that system is. The benefit of equivalent noise and sampling efficiency paradigms is that

¹ Note that equivalent noise assesses all internal noise that is *additive*, or noise that is constant with the varying levels of external noise. Noise that varies with the external noise is considered *multiplicative*, and affects the sampling efficiency (Ahumada, 1987; Burgess & Colborne, 1988).

performance loss can be more fully described than as a simple decrease in accuracy or signal-to-noise ratio. A corollary is that the measures of equivalent noise and sampling efficiency can be more easily related to neural responses, for example, those associated with aging described earlier. As outlined above, increases in spontaneous neural firing would be represented as an increase in equivalent noise. For sampling efficiency, the concept of templates has been used extensively and successfully in the modelling of visual receptive fields. In these models, neural responses are the direct results of the match of a neuron's template (as determined by the receptive field) and the stimulus. The external noise technique has been used to account for human performance across a range of visual tasks at threshold, near threshold and suprathreshold, including retinal processing (e.g. Barlow, 1956), change detection (e.g. Barlow, 1978), reaction times (e.g. Simpson, Findlay, & Manahilov, 2003) and perceptual learning (e.g. Chung, Levi, & Tjan, 2005). It has also been applied to investigate a number of age-related changes in visual performance (e.g. Pardhan, Gilchrist, Elliott, & Beh, 1996; Bennett, Sekuler, & Ozin, 1999; Pardhan, 2004; Betts et al., 2007).

In the context of aging, the external noise technique has predominantly been used to tease apart the relative contributions of optical and neural factors to the well-established decline in contrast sensitivity with age (e.g. Derefeldt, Lennerstrand, & Lundh, 1979; Owsley, Sekuler, & Siemsen, 1983; Sloane, Owsley, & Alvarez, 1988; Elliott, Whitaker, & MacVeigh, 1990). For example, Pardhan et al. (1996) employed a spatial two-alternative forced choice detection task to examine age differences in contrast sensitivity to 6 c/deg sinewave gratings embedded in static Gaussian white noise. Analysis of sampling efficiency and equivalent noise levels in each age

group indicated that only differences in sampling efficiency were apparent between the two groups, leading the authors to suggest that the age-related loss in contrast sensitivity at low levels of illumination was due to neural, rather than optical factors. Pardhan (2004) extended this analysis across a wider range of spatial frequencies (1, 4 & 10 c/deg). In agreement with previous studies (e.g. Elliott et al., 1990) in the absence of external noise, contrast detection thresholds were worse in older adults relative to younger adults, at 4 and 10 c/deg, but not at 1 c/deg. With the addition of external noise, changes in sampling efficiency and equivalent noise were spatial frequency dependent; at 1 and 4 c/deg older observers were found to have lower sampling efficiencies than their younger counterparts whilst at 10 c/deg only changes in equivalent input noise were significant. Pardhan (2004) concluded that neural factors were the leading cause of age-related declines in contrast sensitivity at low to intermediate spatial frequencies whilst optic factors were responsible for losses at higher spatial frequencies. A caveat is that Pardhan and colleagues (1996; 2004) classified changes in sampling efficiency and equivalent input noise as strictly neural and optical, respectively. However, this classification may be too rigid as factors that affect equivalent input noise can be neural (such as changes in the spontaneous activity of neurons in visual pathways) or optical (such as optic blur or intraocular scatter).

Bennett et al. (1999) also assessed the effects of age on contrast sensitivity for 1, 3 and 9 c/deg gratings embedded in external noise. Under low noise conditions, older observers had higher detection thresholds than young observers at the highest spatial frequency (i.e. 9 c/deg) only. However, under high noise conditions,

older observers performed worse at all three spatial frequencies. Estimates of sampling efficiency and equivalent noise were subsequently computed for each age cohort. For all conditions included, older observers had lower sampling efficiencies than their younger counterparts but did not differ systematically with respect to equivalent noise. A control task ruled out the possibility that optic factors, specifically reduced retinal illumination, were responsible for this performance difference thereby alluding to a neural origin. Together, the results of these studies suggest that age differences in contrast thresholds for the *detection* of sinewave gratings presented in external noise reflect reductions in sampling efficiency with age.

This technique has also been employed by Betts et al. (2007) to assess age-related differences in orientation discrimination. In their study, young and older participants were required to discriminate the orientation of Gabor patterns embedded in static noise across a range of spatial frequencies (0.75 – 3 c/deg). For both age groups, thresholds increased as external noise level increased. There was a recurring interaction at each of the spatial frequencies between age and noise level, with older participants having markedly higher thresholds in low levels of noise than their younger participants. Unlike previous studies (e.g. Pardhan et al., 1996; Bennett et al., 1999; Pardhan, 2004), when the relationship between performance and noise level was evaluated with respect to the contributions of equivalent noise and sampling efficiency, older adults' performance was found to be reflective of age-related increases in equivalent noise. Simulating reduced retinal illumination in young participants increased equivalent noise but fell short of adequately explaining the increase observed in the aged. Thus, the authors

concluded that the differences in orientation discrimination must have a neural basis.

3.1.2. The aim of Experiments 1-4

Whilst the effects of external noise on psychophysical performance for discriminating the orientation of static stimuli have been evaluated (Betts et al., 2007), the effects of noise on direction discrimination have yet to be elucidated. The aim of the experiments outlined in this chapter was to examine the relative effects of additive noise on performance for discriminating direction and orientation in young and older participants under equivalent experimental conditions. Additionally, the external noise technique has previously been used to assess age-related changes in central vision only. As such, a secondary aim of this study was to extend this analysis to include direction and orientation discrimination in the periphery, therefore the effects of additive noise were assessed in both central (Experiments 1 & 2) and peripheral (Experiments 3 & 4) vision.

3.2. Methods

3.2.1. Observers

Twenty-six observers took part in the study and were assigned to 'young' or 'older' age groups. Young observers ranged from 18-29 years of age and older observers ranged from 65-79 years of age. Observer demographics including mean decimal acuities are presented in Table 3.1. Each participant completed all components of

the study (i.e. both direction and orientation discrimination tasks) with the exception of one older participant who was unavailable for the orientation discrimination task. For additional participation criteria see Chapter 2: General Methods.

Table 3.1
Observer demographics for Experiments 1-4

Age Group	Sample Size (n)	Mean Age \pm S. D.	Mean dec. VA \pm S. D.
Young	13	19.7 \pm 1.7	1.11 \pm 0.27
Older	13	69.8 \pm 3.2	0.79 \pm 0.24

3.2.2. Apparatus and Stimuli

Experimental stimuli were generated using a Macintosh G4 and presented on a Formac ProNitron CRT monitor with an update rate of 75 Hz. The mean luminance of the display was ~ 40 cd/m². The monitor was the only light source. Images were viewed binocularly at a distance of 139 cm. One screen pixel subtended 0.016° resulting in a display that subtended 6°. In Experiments 1 and 2, stimuli were presented in the centre of the screen. In Experiments 3 and 4, stimuli and procedures were identical to those stated above with the exception that stimuli were presented 10° in the left periphery.

Stimuli were either luminance-defined sinusoidal gratings (L) or luminance gratings with additive noise (L_n). L_n stimuli were constructed by adding a sinusoidal grating to a field of noise (Figure 3.1). The noise was composed of a field of 2-d, binary, dynamic random visual noise in which individual pixel elements were assigned to be either 'black' or 'white' with equal probability. The noise had a Michelson contrast of 10, 20, 40 or 80% and was resampled on every

frame. The luminance contrast (amplitude) of the pattern could be varied according to Eq. [2.2]. When noise was present, L_{\max} and L_{\min} corresponded to the maximum and the minimum mean luminances averaged over adjacent noise elements with opposite polarity in the image. All stimuli had a spatial frequency of 1 c/deg and drifted at a temporal frequency of 1 Hz. A stimulus schematic is shown in Figure 3.1.

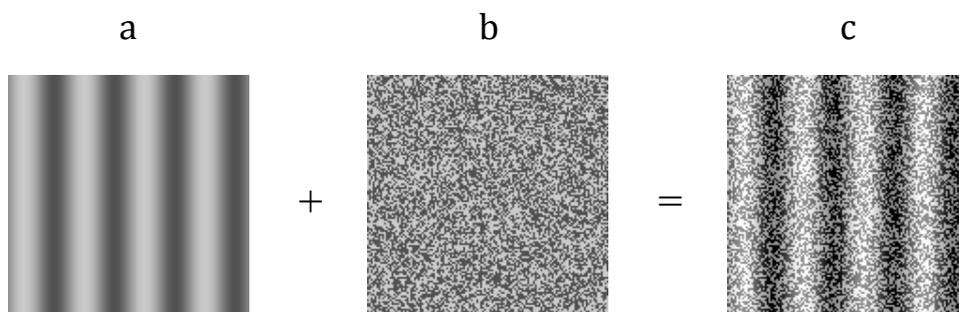


Figure 3.1. Schematic of the stimuli used in Experiments 1-4. (a) A luminance-defined sinusoidal grating. (b) A 2-dimensional dynamic binary noise field made up of randomly assigned pixels of opposite polarity (i.e. “black” or “white”). The polarity of the pixels changed on each frame of the motion sequence (i.e. if they were black they became white or if they were white they became black). The contrast of the noise field was either 10, 20, 40 or 80%. (c) Luminance-defined noise. Luminance-defined noise was created by adding (a) the luminance-defined grating to (b) the binary noise field. All patterns were 1 c/deg and drifted at 1 Hz.

3.2.3. Procedure

A single-interval, forced-choice procedure was employed. On each trial, participants were presented with a fixation cross, followed by the presentation of a moving stimulus. After the presentation of the stimulus, participants had to

judge either stimulus direction or orientation. For the direction discrimination task, the grating pattern was always vertically oriented and participants had to judge whether the pattern moved to the left or to the right. The direction of movement was chosen at random on each trial. For the orientation discrimination task, participants had to judge whether the pattern was vertical or horizontal. In the orientation discrimination condition, the pattern orientation was randomised on each trial and direction of movement was always orthogonal to its orientation.

The luminance contrast of the test stimulus was varied from trial to trial according to a modified 1-up 3-down staircase designed to converge on the contrast corresponding to 79.4% correct (Wetherill & Levitt, 1965; Levitt, 1971). Threshold estimates were taken as the mean of the last 4 reversals in each staircase. Each observer completed 2 staircases for each condition and the order of testing was randomised.

3.3. Results: central vision

3.3.1. Experiment 1: direction discrimination

Figure 3.2 shows mean contrast thresholds for discriminating stimulus direction without and with additive noise for young (circles) and older (squares) participants. In both age groups, contrast thresholds increased (i.e. performance became worse) as the contrast of the noise increased. This was confirmed using a two-way (noise, 5 levels; age, 2 levels) Greenhouse-Geisser corrected analysis of variance (ANOVA), which revealed main effects of noise ($F(1,310, 31.438) = 129.133, p < .001$) and age ($F(1,24) = 11.364, p < .05$). As can be seen in Fig. 3.2,

adding noise differentially affected the performance of young and older participants. Young observers were more sensitive to the addition of external noise within the display; as noise contrast increased performance deteriorated more rapidly in the young than in the older age cohort. However, there was no significant interaction between the two factors ($F(1.310, 31.438) = 1.429, p = .249$).

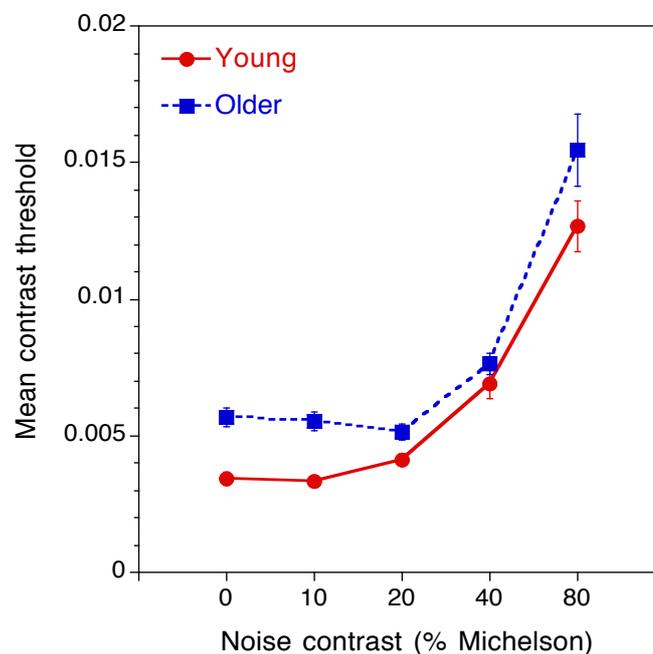


Figure 3.2. Mean contrast thresholds for discriminating the motion direction of luminance-defined gratings and luminance-defined noise. Data are shown for young (circles) and older (squares) participants. Error bars represent ± 1 S.E.M.

3.3.2. Experiment 2: orientation discrimination

Mean contrast thresholds for discriminating stimulus orientation at each additive noise level for young (circles) and older (squares) participants are shown in Figure 3.3. Findings were similar to those found in Experiment 1 for direction discrimination in noise. Contrast thresholds increased with increasing noise contrast for both young and older participants, albeit to a lesser extent than in the direction discrimination task. This was confirmed using a two-way (noise, 5 levels; age, 2 levels) ANOVA with a Greenhouse-Geisser correction, the results of which revealed a main effect of noise ($F(1.741, 40.050) = 169.143, p < .001$) and a main effect of age ($F(1, 23) = 15.740, p < .05$). Contrast thresholds were lower in young participants for luminance gratings and luminance-defined noise at low contrasts. As additive noise contrast increased, young participants' thresholds increased more rapidly, however performance differences diminished at higher noise contrasts. This effect was confirmed by ANOVA, which showed a significant interaction between age and noise level ($F(1.741, 40.050) = 4.206, p < .05$). Subsequent Bonferroni corrected *t*-tests revealed significant performance differences ($p < .01$) at all but the highest noise level (Table 3.2).

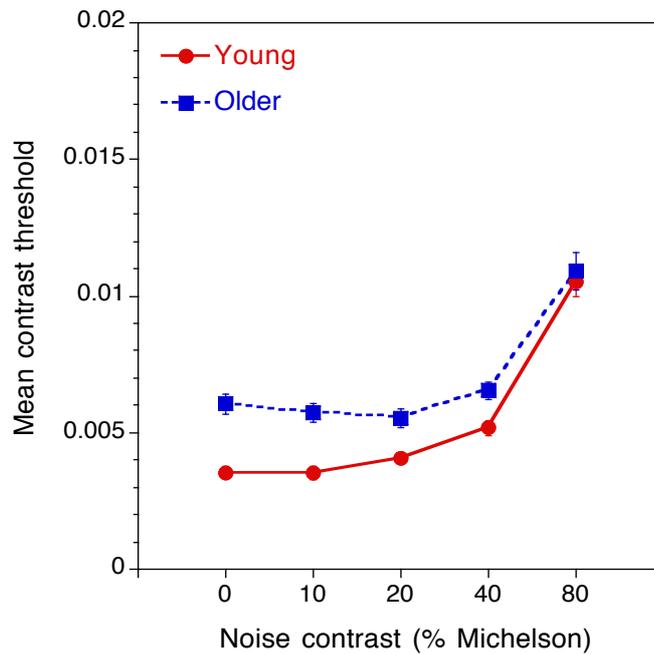


Figure 3.3. Mean contrast thresholds for discriminating the spatial orientation of luminance-defined gratings and luminance-defined noise. Data are shown for young (circles) and older (squares) participants. Error bars represent ± 1 S.E.M.

Table 3.2
t-Test results for orientation discrimination in central vision

Noise contrast (% Michelson)	<i>t</i>	df	<i>p</i> -value
0	-5.924	23	< .001
10	-5.354	23	< .001
20	-3.795	23	< .01
40	-3.147	23	< .01
80	-.465	23	.646

3.3.3. The contributions of equivalent noise and sampling efficiency to direction and orientation discrimination in central vision

To assess equivalent noise and sampling efficiency, contrast thresholds and noise contrast were transformed into threshold contrast signal energy and noise spectral density (*NSD*), respectively. Threshold contrast signal energy ($E_{threshold}$) is equal to the square of threshold contrast ($C_{threshold}$), integrated over space (in degrees) and time (in seconds), or

$$E_{threshold} = \iiint C_{threshold} dx dy dt \quad [3.1]$$

and has the units of deg² sec. Noise spectral density (*NSD*) is given as:

$$NSD = C_{noise}^2 * pixel\ size * frame\ duration \quad [3.2]$$

in which C_{noise} = noise contrast, *pixel size* = the size of a single pixel in deg², and *frame duration* = the duration of each frame in seconds; *NSD* also has the units of deg² sec. The reason for employing this transform is that it yields the following linear relationship:

$$E_{threshold} = k(NSD + N_{eq}) = k * NSD + k * N_{eq}, \quad [3.3]$$

in which N_{eq} = equivalent noise, and $(d')^2/k$ = sampling efficiency (Legge, Kersten, & Burgess, 1987). The value d' (d -prime), a standard measure of sensitivity from Signal Detection Theory (Green & Swets, 1966), is the normalized distance between the two Gaussian distributions of equal variance (one for the signal and

one for the nonsignal) assumed to describe the internal responses of the observer (the 'equivariance model'); for a 2AFC task at 79.4% correct, $d' = 1.16$. Thus, equivalent noise is given as $-1 \times x$ -intercept, and sampling efficiency is a scalar of the reciprocal of the slope of this linear relationship.

Fits were performed on the group means² with weighted linear regressions to account for heteroskedasticity (unequal variance). Data for zero noise contrast were excluded in this analysis. Estimates of the variance for the x-intercepts and the slopes (and thus assessing the equivalent noise and the sampling efficiency) of these fits were found using 50,000 iterations of Monte Carlo resampling, which is similar to bootstrapping (Efron & Tibshirani, 1993; Shimozaki, 2010). Each iteration consisted of a weighted linear regression fit of newly selected data points; these new data points were randomly chosen from Gaussian distributions with the same means and standard errors as the original data points. Estimates of the variance for the x-intercepts and the slopes were then taken from the 50,000 iterations.

Figure 3.4 and Table 3.3 give the results with threshold contrast signal energy and noise spectral density. Correlations of the fits were all above 0.90 (corresponding to R^2 values above 0.831). The results indicate that the young and aged participants did not differ significantly in their sampling efficiencies (as indicated

² In a previous study (Bennett et al., 1999), fits to individual observers sometimes led to spurious results of negative equivalent noise values due to measurement error. To avoid this issue, fits were performed on the group means, as opposed to each observer individually.

by the slopes in Figure 3.4) for either the motion direction or the orientation task. However, the young and aged participants did differ significantly in their equivalent noise (as indicated by the x-intercepts) for both tasks, with the aged having higher levels of equivalent noise.

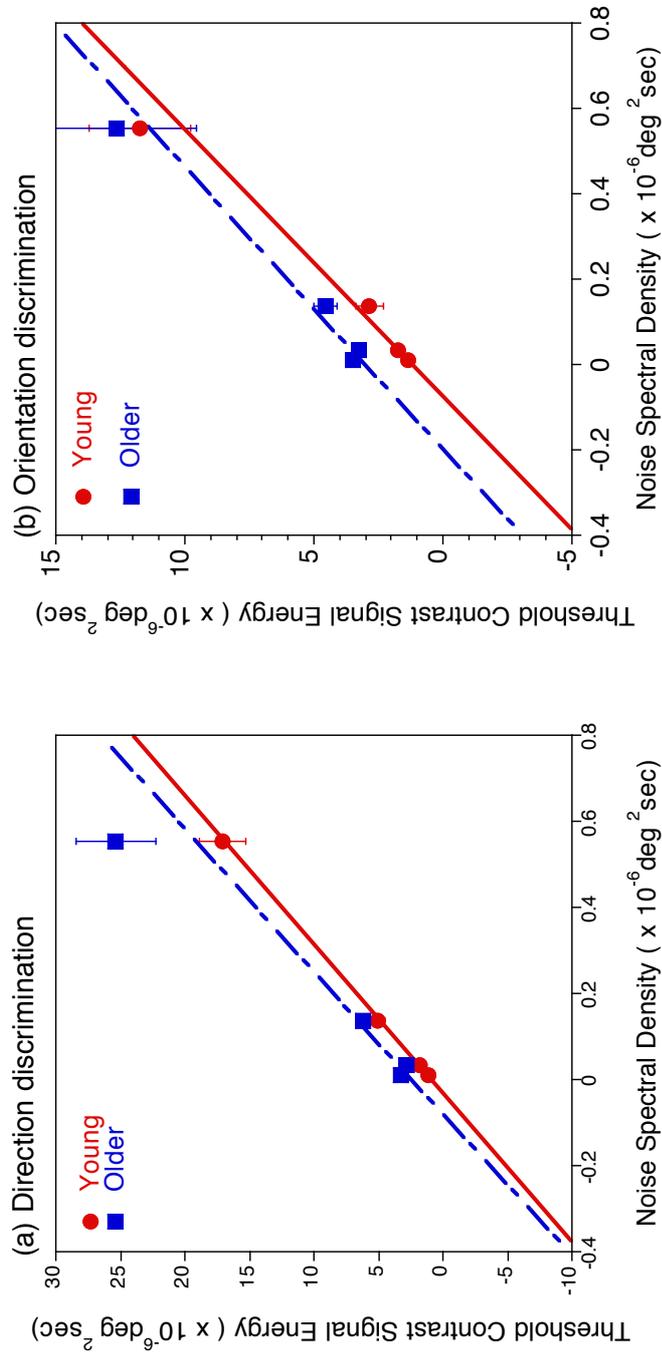


Figure 3.4. Threshold contrast signal energy as a function of noise spectral density for discriminating the (a) motion direction and (b) spatial orientation of centrally presented stimuli. Data are shown for young (circles) and older (squares) participants. Error bars represent ± 1 S.E.M. Best-fitting lines are shown as solid (young) and dashed (older) lines.

Table 3.3
Estimated sampling efficiencies and equivalent noise values in central vision

Condition	Age Group	R ²	k			x-intercept		
			Mean	S.E.M.	p-value	Mean	S. E.M.	p-value
direction	young	0.9977	28.84	2.51	n.s.	-0.0307	0.0055	p < .05
	older	0.9118	30.22	3.34		-0.0742	0.0145	
orientation	young	0.9695	15.97	1.24	n.s.	-0.0718	0.0102	p < .01
	older	0.9562	15.12	1.87		-0.1915	0.0359	

$k = (d')^2 / \text{sampling efficiency} = \text{slope (of contrast energy vs. noise spectral density) linear function, } d' \text{ for } 79.4\% \text{ in a 2AFC} = 1.16$

$x\text{-intercept} = -1 * N_{eq}$

Units for the x-intercept are $10^{-6} \text{deg}^2 \text{sec}$, $N_{eq} = \text{equivalent noise}$

Note that values were derived from fits to 4 data points per age group at noise spectral densities of 0.0086, 0.0345, 0.138 & 0.553 ($\times 10^{-6} \text{deg}^2 \text{sec}$)

3.3.4. The relative effects of additive noise on direction and orientation discrimination in central vision

To compare the relative effects of additive noise on direction and orientation discrimination, contrast thresholds at each noise level are plotted in Figure 3.5 for (a) young and (b) older participants. The findings are comparable for both age groups. Contrast thresholds for direction and orientation discrimination were equivalent when no noise was present (luminance-defined grating) and at additive noise contrasts of 10 and 20%. However when additive noise contrast was 40% and higher, contrast thresholds for direction discrimination were elevated relative to those for orientation discrimination in the same observer. This was the case for young and old observers alike. Table 3.4 presents the results of paired samples *t*-tests for each age group. After correcting for multiple comparisons using Bonferroni methods, only the difference between performance on the direction and orientation tasks at 40% noise was significant for young observers. Differences in sampling efficiency between direction and orientation discrimination were also noted. Efficiency is an absolute measure of performance, relative to the ideal observer (as outlined in Section 3.1.1), where efficiency values span 0-1, 1 being the ideal observer. In this instance, efficiency is a scalar of the reciprocal of parameter *k* in Table 3.3. Efficiencies for direction were markedly lower (by a factor of around 2) than those for orientation. This was the case for both young [direction sampling efficiency: 0.0467 (± 0.0042 SE); orientation sampling efficiency: 0.0843 (± 0.0067 SE); $p < .001$] and older [direction sampling efficiency: 0.0445 (± 0.0052 SE); orientation sampling efficiency: 0.0890 (± 0.0118 SE); $p < .01$] age groups.

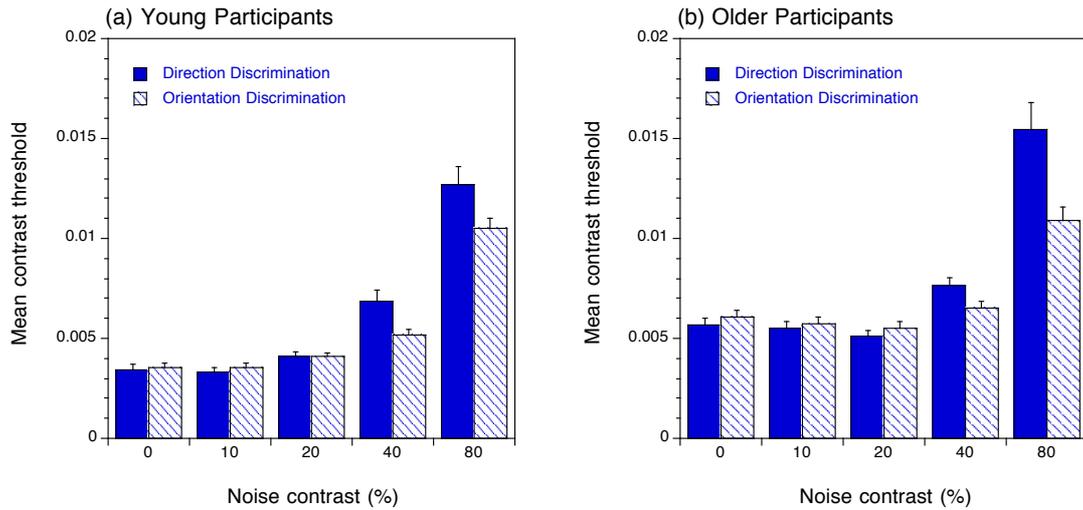


Figure 3.5. Mean contrast thresholds for direction and orientation discrimination in (a) young and (b) older participants. Error bars above each column represent + 1 S.E.M.

Table 3.4

t-Test results for paired comparisons of the effects of additive noise on direction and orientation discrimination

Noise Contrast (% Michelson)	Young			Older		
	<i>t</i>	df	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value
0	-.534	12	.603	-1.057	11	.313
10	-.764	12	.459	-.718	11	.488
20	.193	12	.850	-1.267	11	.231
40	4.841	12	<.001	2.356	11	.038*
80	2.090	12	.059	2.779	11	.018*

* not significant at the corrected α value ($\alpha = .01$)

3.4. Results: peripheral vision

3.4.1. Experiment 3: direction discrimination

Mean contrast thresholds for discriminating the direction of peripherally presented stimuli at each additive noise level for younger (circles) and older (squares) participants are shown in Figure 3.6. Similar to the findings in central vision, young participants were sensitive to the addition of low levels of external noise, whilst performance in older participants remained relatively unaffected by noise, except at the highest noise level. These findings were confirmed using a two-way (noise, 5 levels; age, 2 levels), Greenhouse-Geisser corrected analysis of variance (ANOVA), which revealed a main effect of noise ($F(2.806, 67.334) = 81.536, p < .001$) and a main effect of age ($F(1,24) = 13.568, p = .001$). Unlike the findings in central vision, the interaction between noise and age was significant ($F(2.806, 67.334) = 5.053, p < .05$). Subsequent Bonferroni corrected *t*-tests indicate significant age-related difference ($p < .01$) at all but the highest noise conditions (Table 3.5).

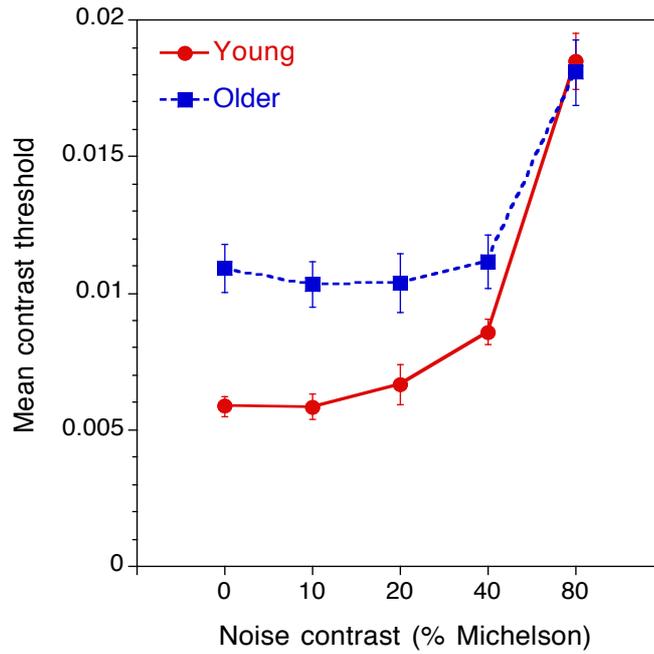


Figure 3.6. Mean contrast thresholds for discriminating the motion direction of peripherally presented luminance-defined gratings and luminance-defined noise. Data are shown for young (circles) and older (squares) participants. Error bars represent ± 1 S.E.M.

Table 3.5
t-Test results for direction discrimination in peripheral vision

Noise contrast (% Michelson)	<i>t</i>	df	<i>p</i> -value
0	-5.314	24	< .001
10	-4.696	24	< .001
20	-2.843	24	< .01
40	-2.352	24	.031*
80	.253	24	.646

* not significant at the corrected α value ($\alpha = .01$)

3.4.2. Experiment 4: orientation discrimination

Mean contrast thresholds for discriminating stimulus orientation at each additive noise level for young (circles) and older (squares) participants are shown in Figure 3.7. Unlike the findings in Experiment 3, orientation thresholds in both age groups were less affected by the addition of external noise. A two-way (noise, 5 levels; age, 2 levels) ANOVA with a Greenhouse-Geisser correction, revealed a main effect of noise ($F(2.599, 59.778) = 61.979, p < .001$) and a main effect of age ($F(1, 23) = 17.911, p < .001$). Once again the interaction between age and noise level was significant ($F(2.599, 59.778) = 3.849, p < .05$). Bonferroni corrected t -tests revealed significant performance differences ($p < .01$) between young and older observers at all but the highest noise level (Table 3.6).

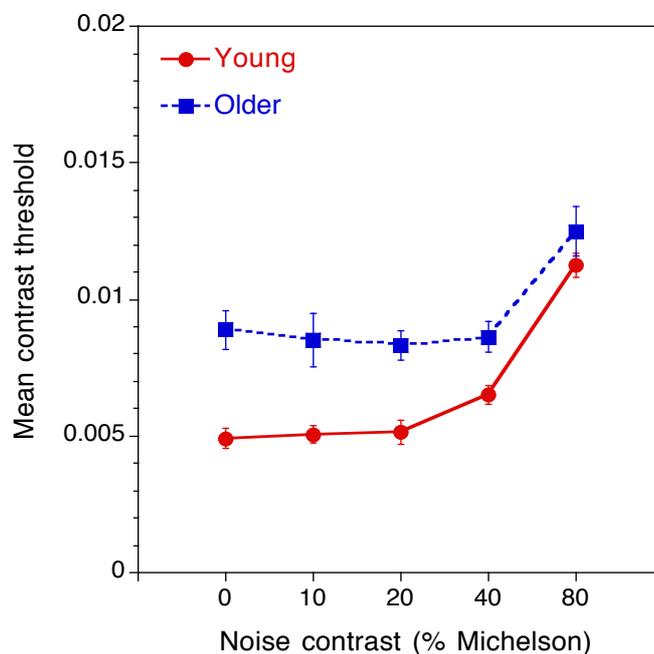


Figure 3.7. Mean contrast thresholds for discriminating the spatial orientation of peripherally presented luminance-defined gratings and luminance-defined noise.

Error bars represent ± 1 S.E.M.

Table 3.6*t*-Test results for orientation discrimination in peripheral vision

Noise contrast (% Michelson)	<i>t</i>	df	<i>p</i> -value
0	-5.073	23	< .001
10	-3.438	23	< .01
20	-4.686	23	< .001
40	-3.264	23	< .001
80	-1.293	23	.209

3.4.3. The contributions of equivalent noise and sampling efficiency to direction and orientation discrimination in the periphery

To assess direction and orientation discrimination for peripherally presented stimuli in terms of equivalent noise and sampling efficiency methods were identical to those stated in Section 3.3.3. The results of this analysis are presented in Figure 3.8 and Table 3.7 and are similar to the results obtained in central vision. Once again, correlations of the fits were above 0.90. For both the motion direction and orientation discrimination tasks, sampling efficiencies did not differ between young and older participants. However, age-related differences in equivalent input noise were significant for the direction task ($p < .01$) and approached significance for the orientation discrimination task ($p = .053$).

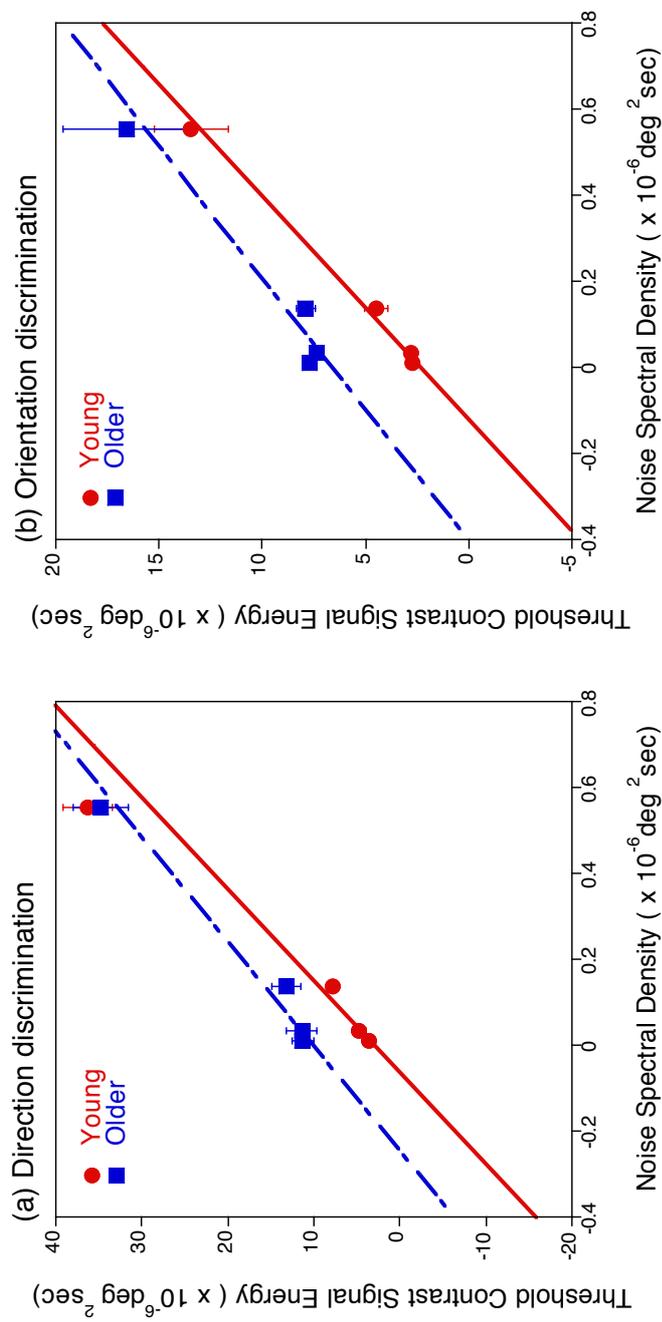


Figure 3.8. Threshold contrast signal energy as a function of noise spectral density for discriminating the (a) motion direction and (b) spatial orientation of peripherally presented stimuli. Data are shown for young (circles) and older (squares) participants. Error bars represent ± 1 S.E.M. Best-fitting lines are shown as solid (young) and dashed (older) lines.

Table 3.7.
Estimated sampling efficiencies and equivalent noise values in peripheral vision

Condition	Age Group	R ²	k			x-intercept		
			Mean	S.E.M.	p-value	Mean	S. E.M.	p-value
direction	young	0.952	0.0288	0.0025	n.s.	0.0593	0.0117	p < .01
	older	0.965	0.0328	0.0054		0.2413	0.0581	
orientation	young	0.991	0.0700	0.0050	n.s.	0.1194	0.0164	p = .053
	older	0.948	0.0823	0.0203		0.3982	0.1274	

$k = (d')^2 / \text{sampling efficiency} = \text{slope (of contrast energy vs. noise spectral density) linear function, } d' \text{ for } 79.4\% \text{ in a 2AFC} = 1.16$

$x\text{-intercept} = -1 * N_{eq}$

Units for the x-intercept are $10^{-6} \text{deg}^2 \text{sec}$, $N_{eq} = \text{equivalent noise}$

Note that values were derived from fits to 4 data points per age group at noise spectral densities of 0.0086, 0.0345, 0.138 & 0.553 ($\times 10^{-6} \text{deg}^2 \text{sec}$)

3.4.4. The relative effects of additive noise on direction and orientation discrimination in peripheral vision

As in Section 3.3.4, the relative effects of additive noise on direction and orientation discrimination were compared for peripherally presented stimuli. Mean contrast thresholds for direction and orientation tasks in each age group are presented in Figure 3.9. Contrast thresholds for direction and orientation discrimination were elevated in the periphery relative to those obtained in central vision, and unlike the findings in central vision, both age cohorts generally demonstrated greater sensitivity on the orientation task. Paired samples *t*-tests, which were corrected for multiple comparisons, indicate that young observers differed significantly in their performance on direction and orientation discrimination tasks at high levels of additive noise ($p < .01$). Similar differences were obtained for older observers (see Table 3.8). Therefore, regardless of age or visual field location, direction discrimination appears to be more adversely affected by high levels of additive noise. Differences in sampling efficiency between direction and orientation discrimination were once again noted. In young observers this difference was significant [direction sampling efficiency: 0.0288 (± 0.0025 SE); orientation sampling efficiency: 0.0700 (± 0.0050 SE); $p < .001$] whilst it approached significance in older observers [direction sampling efficiency: 0.0328 (± 0.0054 SE); orientation sampling efficiency: 0.0823 (± 0.0203 SE); $p = .055$].

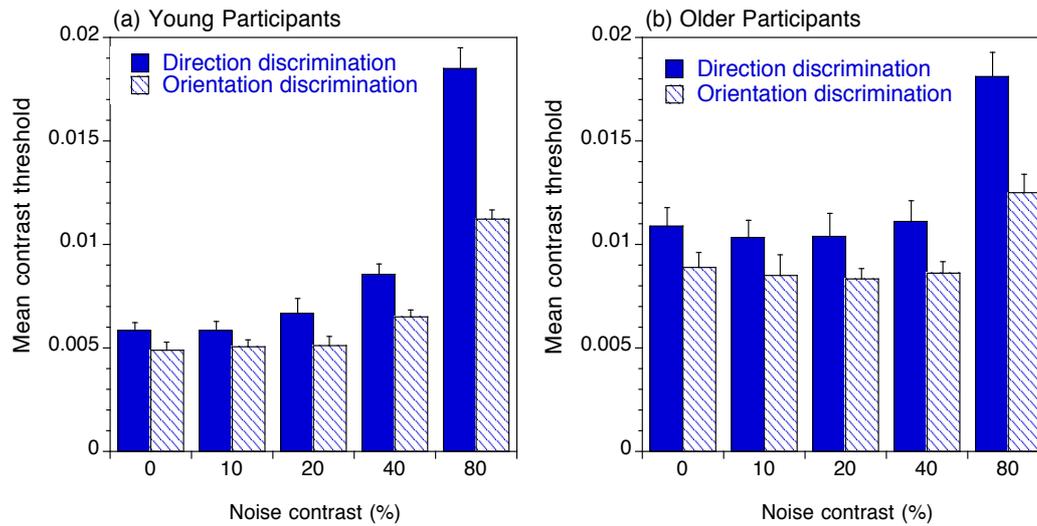


Figure 3.9. Mean contrast thresholds for direction and orientation discrimination in the periphery for (a) young and (b) older participants. Error bars above each column represent + 1 S.E.M.

Table 3.8

t-Test results for paired comparisons of the effects of additive noise on direction and orientation discrimination in the periphery

Noise Contrast (% Michelson)	Young			Older		
	<i>t</i>	df	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value
0	-1.844	12	.090	-2.337	11	.039*
10	-2.039	12	.064	-2.502	11	.029*
20	-2.525	12	.027*	-1.748	11	.108
40	-4.458	12	<.01	-2.034	11	0.67
80	-7.612	12	<.001	-3.052	11	.01

* not significant at the corrected α value ($\alpha = .01$)

3.5. Discussion

Experiments 1-4 investigated the effects of additive dynamic noise on contrast thresholds for coarsely discriminating motion direction and spatial orientation in young and older participants. Compared to their young counterparts, older adults demonstrated reduced sensitivity (higher thresholds) on direction and orientation tasks, but required a greater increase in external noise to elicit a corresponding reduction in sensitivity. This was true for stimuli presented in both central and peripheral visual fields. Calculations of sampling efficiency and equivalent noise for each age group attributed age differences to increases in equivalent noise only. Once again, this was the case for both direction and orientation discrimination.

The finding that age-related differences in sensitivity to orientation and direction were best described by increases in equivalent input noise in older observers supports neurophysiological evidence which suggests there is greater internal noise within the aged visual pathway due to age-related increases in spontaneous activity and responsiveness to non-optimal stimuli (e.g. Schmolesky et al., 2000; Hua et al., 2006; Yu et al., 2006; Liang et al., 2010; Zhang et al., 2008; Fu et al., 2010). Despite the higher thresholds obtained by both age groups for the discrimination of direction and orientation information in the periphery, age differences were also attributed to increased equivalent input noise in older, relative to younger observers. These results suggest that age differences in the discrimination of direction and orientation in central and peripheral vision are constrained by similar mechanisms.

These findings are also in good agreement with Betts et al. (2007), which examined the effects of age on orientation discrimination using Gabors presented within static 2-D Gaussian noise. For orientation discrimination of these static displays, performance differences were also attributable to increases in equivalent noise with age. After ruling out the role of reduced retinal illumination due to degraded optics (i.e. changes in pupil size and lens opacity) in older observers, Betts et al. (2007) proposed that their findings may reflect neural changes in the aged visual system. Despite the difference in noise (i.e. static noise in Betts et al. (2007) vs. the use of dynamic noise in this study) the findings of Experiments 1-4 are consistent with Betts et al. (2007), and add weight to the notion that increased neural noise has a particularly detrimental effect on visual discrimination.

When the relative effects of additive noise were compared between direction and orientation tasks, observers demonstrated greater sensitivity to orientation than direction in high noise conditions. Sampling efficiencies were also found to be higher for orientation discrimination than for direction in each age group under all viewing conditions. These findings may, at least in part, reflect differences in the proportion of neurons selective for direction and orientation. Some neurophysiological evidence for example suggests a higher proportion of orientation selective neurons than direction selective neurons in area V1 of the monkey. This is the case in young and aged animals (Leventhal, Wang, Pu, Zhou, & Ma, 2003) and may go some way to explaining why, at the highest additive contrasts, thresholds for discriminating direction were particularly affected. Specifically, adding high levels of noise effectively reduces the signal-to-noise ratio of the population of neurons selective for a particular stimulus attribute (in this

case direction and orientation). If fewer neurons are responsive to a given attribute in the first instance, the effects of adding noise are likely to be more marked. It may also be possible that differences in discriminative abilities for direction and orientation reflect the visual system's need for at least two spatially and temporally separable stimulus samples in order to determine the correct direction of a moving stimulus whereas for orientation discrimination, one stimulus sample is potentially sufficient.

3.5.1. Accounting for these findings in the context of the GABA hypothesis

A number of behavioral studies have attributed age-related changes in visual sensitivity to reductions in GABAergic inhibition in the aged visual cortex (e.g. Andersen & Ni, 2008; Betts, Taylor, Sekuler, & Bennett, 2005; Allen, Hutchinson, Ledgeway, & Gayle 2010). The findings of the current set of experiments fit well with this hypothesis. GABA has been shown to control direction and orientation selectivity in visual cortex neurons (e.g. Rose & Blakemore, 1974, Sillito, 1975; Tsumoto, Eckart, & Creutzfeldt, 1979; Leventhal et al., 2003; Li et al., 2008; Jirrmann & Pernberg, 2009; Katzner, Busse, & Carandini, 2011). For example, early studies showed that the GABA_A antagonist bicuculline reduces cortical inhibition in cat visual cortex, leading to increased spontaneous firing rates and decreased orientation and direction selectivity (e.g. Rose & Blakemore, 1974; Sillito, 1975; Tsumoto et al., 1974). These findings have recently been confirmed by Katzner et al. (2011) who examined the role of GABA_A inhibition in the primary visual cortex of the cat by measuring the effects of gabazine, a selective GABA_A antagonist, on neuron selectivity and responsiveness. Gabazine markedly increased neuron firing rates, broadened tuning bandwidths and decreased selectivity for stimulus

orientation and direction. In terms of the tuning of GABA inhibition, it appears to be closely mapped to that of the excitatory drive (e.g. Katzner et al., 2011). Removing inhibition therefore leads to an increase in the neuron's excitatory drive. This reduces the ability of neurons to keep responses to irrelevant information below threshold, leading to increased neural noise and decreased selectivity to stimulus parameters such as orientation and direction.

There is compelling evidence to support age-related reductions in GABAergic inhibition in the visual cortex. Leventhal et al. (2003) temporarily restored the orientation and direction selectivities of aged V1 neurons in primates after the electrophoretic application of GABA and/or the GABA_A agonist muscimol. After GABA/muscimol administration aged neurons were more narrowly tuned, had lower peak responses and less spontaneous activity. Conversely, the application of the GABA_A antagonist bicuculline was shown to severely diminish the selectivity of young V1 neurons, temporarily inducing an 'aged-like' state in these cells. There is also direct evidence to suggest that aged brains have lower concentrations of GABA. For example, there is a decrease in the number of GABA-immunoreactive neurons in the aged feline visual cortex (e.g. Hua, Kao, Sun, Li, & Zhou, 2008; Diao, Xu, Li, Tang, & Hua, 2009). Furthermore, two different enzymes involved in the synthesis of GABA, glutamic acid decarboxylase (GAD) and GABA alpha-ketoglutaric transaminase (GABA-T), have been shown to decrease in the aged brain (Fonda, Acree, & Auerbach, 1973; McGeer & McGeer, 1976; 1978).

Whilst the GABA hypothesis has been lent much support in recent years, it is important not to overlook the possible roles of other neurotransmitters in age-

related changes in visual function. Both excitatory and inhibitory inputs drive neuron response, thus changes in multiple neurotransmitters may create a shift in the excitation-inhibition equilibrium leading to increased noise within the visual system. Few studies have examined the effects of age on neurotransmitters other than GABA, but the results of those which have suggest that GABA may not be the only neurotransmitter found in lower concentration in the aged brain. In the cat visual cortex, for example, glutamatergic receptors NMDA and AMPA have been shown to be involved in maintaining direction selectivity and complex cell response (Rivadulla, Sharma & Sur, 2001). In these species, Diao et al. (2009) demonstrated that age-related reductions in striatal GABA were accompanied by a loss in glutamic acid immunoreactive neurons (Glu-IR) although to a lesser extent. In aged macaques, Gazzaley, Siegel, Kordower, Mufson, and Morrison (1996) reported a loss of excitatory glutamatergic N-methyl-D-aspartate receptor subunit 1 (NMDAR1) in the dendrites of the dentate gyrus. Acetylcholine (ACh) has been shown to directly activate GABAergic interneurons (Javoy, Scatton, & Ruberg 1989; Schroeder, Zilles, & Luiten, 1989). At the retinal level, starburst amacrine cells encode motion and direction information via the co-release of GABA and ACh (Lee, Kim & Zhou, 2010) and in the visual cortex, ACh has been shown to reduce response variability (Sato, Hata, Hagihara & Tsumoto, 1987). Thus far, it has been shown that concentration of acetylcholinesterase (AChE), the enzyme required to break down ACh, is lower in the visual cortex of aged cats (Sirvio, Pitkanen, & Paakkonen, 1989). It has also been shown that cholinergic neurons projecting to the visual cortex via the basal forebrain decrease in size during aging (Mesalun, Mufson, & Rogers, 1987). Therefore in order to further our understanding of the underlying causes of age-related changes in neuron selectivity it is imperative to

focus attention on the cumulative effects of age-related reductions in these neurotransmitters.

3.5.2. Conclusions

Experiments 1-4 have shown that, although external noise as a deleterious effect on the ability to discriminate stimulus direction and orientation, its effects are less marked in older adults. These findings were attributed to increased internal (equivalent) noise in aged visual system and are in agreement with previous neurophysiological findings for reduced direction and orientation selectivity in single neurons in aged mammalian visual cortex (e.g. Schmolesky et al., 2000; Wang et al., 2005; Yu et al., 2006; Zhang et al., 2008; Yang et al., 2008; Liang et al., 2010) and human psychophysical performance for orientation discrimination in noise (Betts et al., 2007). These findings also fit well with the hypothesis that age-related reductions in GABA lead to decreased signal-to-noise ratios in direction- and orientation-sensitive neurons in visual cortex however future studies should more closely examine the cumulative effects of neurotransmitter reductions with age.

Chapter 4

Investigating changes in the spatial and temporal integration of global motion across adulthood

4.1. Introduction

Global motion refers to instances in which the individual trajectories of local moving elements in a visual scene come together to create a larger, more global, stimulus. Although the individual elements move along different local trajectories, their combined direction appears to move coherently. Real world examples include the movement of a swarm of bees, a flock of birds, or a school of fish. Other examples include leaves blowing on a tree, the movement of ripples on the surface of water or the gross movement of blades of grass in fields, all of which permit detection of wind direction. Given the necessity for accurate global processing in everyday life, it is not surprising that age-related impairments in the perception of this motion type have been the focus of a number of studies (e.g. Trick & Silverman, 1991; Gilmore, Wenk, Naylor, & Stuve, 1992; Andersen & Atchley, 1995; Wojciechowski, Trick, & Steinman, 1995; Atchley & Andersen, 1998; Tran, Silverman, Zimmerman, & Feldon, 1998; Snowden & Kavanagh, 2006; Bennett, Sekuler, & Sekuler, 2007; Billino, Bremmer, & Gegenfurtner, 2008; Allen, Hutchinson, Ledgeway, & Gayle, 2010).

To date, the majority of studies that have investigated the existence of age-related changes in global motion perception have done so using patterns in which local dots cohere along a translational (up or down, left or right) trajectory. However, the precise effects of age on the ability to encode motion of this type are presently unclear; whilst some studies have found evidence for age-related deficits, others have not (see Table 4.1 for a summary). This apparent discrepancy in the literature may be due to the speed of RDK patterns employed in each study. For example, Trick and Silverman (1991) measured global motion sensitivity for dot patterns traveling at a speed of $5.8^\circ/\text{s}$ in adults ranging from 25 to 80 years of age and found that motion sensitivity decreased almost linearly with age. However, in a similar study, Gilmore et al. (1992) presented young and older observers with RDK patterns travelling at a speed of $3.9^\circ/\text{s}$ and failed to find evidence of a general decline with age. Rather, motion impairments were only evident in older female observers. More recently, Snowden and Kavanagh (2006) used RDKs of different speeds ($0.045 - 4^\circ/\text{s}$) to show that age-related performance deficits on a direction discrimination task were specific to local element speeds below $1^\circ/\text{s}$. At higher dot speeds (i.e. $> 10^\circ/\text{s}$) there is compelling evidence of an age-related decline in motion sensitivity (e.g. Wojciechowski et al., 1995; Atchley & Andersen, 1998; Billino et al., 2008).

There is also some evidence that deficits in global motion perception in the elderly may be influenced by a reduced ability to integrate visual signals over space. Andersen and Ni (2008) employed a kinetic occlusion task in which observers had to determine the 2D shape of a stimulus whilst the amount of visual information

Table 4.1
A synopsis of previous investigations of age-related changes in global motion perception

Study	Local dot speed (°/s)	Effect of age?	Points of note
Trick & Silverman (1991)	5.8	YES	
Gilmore et al. (1992)	3.9	NO	No overall age difference, but older females more impaired
Andersen & Atchley (1995)	2.4	YES	In addition to an age difference there was also a gender × age interaction, older females demonstrated greatest impairments
Wojciechowski et al. (1995)	28	YES	
Atchley & Andersen (1998)	4.8 & 22	YES	At 4.8 °/s, only older females were impaired in central vision. At 22 °/s, older observers impaired relative to young, except at a viewing eccentricity of 40°.
Tran et al. (1998)	2.5	YES	
Snowden & Kavanagh (2006)	0.045-4	YES	Age-related deficits only evident at speeds ≤ 1 °/s. Gender difference but this did not interact with age.
Billino et al. (2008)	6.6 & 18.6	YES	Age-related deficits apparent for both dot speeds
Allen et al. (2010)	5.6	YES	Age-related deficits only at low dots contrasts

available, and the duration of such information, was manipulated. The results demonstrate that older observers exhibited impaired performance relative to younger observers on tasks that required the spatial integration of kinetic occlusion information. Conversely, older observers did not exhibit any age-related performance deficits in temporal integration. Using a two-frame apparent motion stimulus in which dot spatial displacement and inter-stimulus-interval (ISI) varied, Roudaia, Bennett, Sekuler, and Pilz (2010) investigated the spatial and temporal integration limits of age-related motion processing deficits. The authors found that spatial displacement had a much greater adverse effect on performance in older adults than the length of the ISIs between frames. This was particularly evident at low and high displacements.

Studies of motion perception that have employed RDK stimuli have often manipulated the speed of apparent motion by changing the spatial offset (displacement) of local dots on each successive frame of the motion sequence whilst keeping the frame rate constant. As such, it is not possible to tease apart the relative contributions of dot speed and spatial displacement. Therefore, the observed age-related deficits at low and high dot speeds could equally reflect deficits in the processing of small and large spatial displacements, and may be indicative of an age-related deficit in spatial integration. In addition, because previous studies have often focused comparisons between two discrete age categories (i.e. young vs. old), with the inclusion criteria for the “old” age group varying between studies, the age at which changes in global motion perception become apparent is currently unresolved.

The purpose of the following experiments was to assess the relative effects of local dot speed and spatial displacement on age-related deficits in global motion processing across the adult lifespan.

4.2. Methods

4.2.1. Observers

Fifty-six observers, ranging from 20-79 years of age, took part in Experiments 5-7 and were grouped by decade. Observer demographics including mean decimal acuities for each age cohort are presented in Table 4.2. Unless otherwise stated, each observer took part in all experiments.

Table 4.2
Observer demographics for Experiments 5-7

Age Group	Sample Size (n)	Mean Age \pm S. D.	Mean dec. VA \pm S. D.
20-29	11	23.0 \pm 2.9	1.00 \pm 0.29
30-39	8	35.1 \pm 2.1	1.23 \pm 0.37
40-49	8	42.5 \pm 1.9	0.92 \pm 0.23
50-59	8	54.4 \pm 2.2	0.90 \pm 0.42
60-69	10	63.5 \pm 2.7	0.82 \pm 0.17
70-79	11	73.6 \pm 2.7	0.80 \pm 0.34

4.2.2. Apparatus and stimuli

RDK patterns were generated on a *Macintosh G4* and presented on a *Formac ProNitron 21/650* CRT monitor (resolution: 1024 x 768 pixels). The monitor had a refresh rate of 75Hz and was gamma-corrected as described in Chapter 2: General Methods.

RDKs were composed of 100 (30% Michelson contrast) non-overlapping dots which were presented centrally within a 10° (diameter) circular aperture at a viewing distance of 130 cm. Each dot had a diameter of 0.27° and was presented on a mid-grey background of mean luminance 28.57 cd/m^2 . Each RDK was composed of a sequence of images which, when presented consecutively, produced continuous dot motion (motion sequence). The total duration of each motion sequence was 0.856 s and was kept constant across all experimental conditions. Each dot was displayed on-screen at a given spatial position for the duration of one frame, after which it moved to a new position. The lifetime of each dot was that of the motion sequence.

4.2.2.1. Experiment 5: varying dot speed & spatial displacement

Previous studies have typically manipulated local dot speed by manipulating the spatial displacement of each dot on each frame of the motion sequence. To allow for comparisons with previous work, Experiment 5 co-varied dot speed and spatial displacement from 0.625 to $10^\circ/\text{s}$, and 0.067 to 1.068° , respectively. In this experiment, the motion sequence was made up of 8 consecutive images, each 0.107 s in duration. The dot speeds employed are well within the range of those examined in previous aging studies and include speeds above and below $3^\circ/\text{s}$, which has been shown to be the optimal stimulus speed (Watson & Turano, 1995). In Exp. 5-7 dot speeds $\leq 1.25^\circ/\text{s}$ were classified as low, $2.5^\circ/\text{s}$ as intermediate and $\geq 5^\circ/\text{s}$ as high.

4.2.2.2. Experiment 6: varying dot speed

To assess the effects of dot speed in the absence of potentially confounding effects of dot spatial displacement, dot spatial displacement remained constant across all conditions at 0.267° and dot speed varied from 0.625 to $10^\circ/\text{s}$. This was achieved by manipulating (in octave steps) the number (2 to 32, respectively) and duration (0.427 to 0.027 s, respectively) of the individual frames that comprised the motion sequence. All other experimental parameters (including total motion sequence duration) remained unchanged.

4.2.2.3. Experiment 7: varying dot spatial displacement

To assess the effects of dot spatial displacement in the absence of potentially confounding effects of dot speed, dot speed remained constant across all conditions at $2.5^\circ/\text{s}$ and dot spatial displacement was varied from 0.067 to 0.534° ³. This was achieved by manipulating (in octave steps) the number (32 to 4, respectively) and duration (0.027 to 0.213 s, respectively) of the individual frames that comprised the motion sequence. Once more, motion sequence duration remained unchanged.

4.2.3. Procedure

Stimuli were viewed binocularly in a darkened room where the monitor display was the only light source. Global motion coherence thresholds were measured

³ Under the conditions employed in Experiment 7, none of the observers, irrespective of their age, were able to reliably discriminate motion direction at the largest dot displacement used in Experiment 5 (i.e. $1.068^\circ/\text{frame}$). This is likely due to the correspondence problem (e.g. Williams & Sekuler, 1984), and was exacerbated by the fact that only 2 images per motion sequence (1 dot jump) were required to maintain a speed of $2.5^\circ/\text{s}$ when dot displacement was set to $1.068^\circ/\text{frame}$. As such, only 4 dot displacements were included Experiment 7, the largest of which was $0.534^\circ/\text{frame}$.

using a direction discrimination procedure in which observers had to choose between two alternative directions (up vs. down). Motion coherence thresholds were calculated using an adaptive staircase procedure (Edwards & Badcock, 1995) in which the proportion of signal dots presented on each trial varied according to the observer's recent response history. The staircase terminated after 12 reversals and threshold values (corresponding to 79% correct performance) were taken as the mean of the last 6 staircase reversals. Each observer completed 4 staircases and a mean was taken for each experimental condition. Experimental conditions were presented in a pseudorandom order.

4.3. Results

4.3.1. Experiment 5: varying dot speed & spatial displacement

Mean motion coherence thresholds (expressed as the percentage of signals dots required to produce 79% correct performance) were measured for each age group as a function of local dot speed and spatial displacement (Figure 4.1). Low speeds corresponded to low spatial displacements and high speeds to high spatial displacements. A two-way (speed/spatial displacement, 5 levels; age, 6 levels) analysis of variance (ANOVA) with a Greenhouse-Geisser correction yielded a significant effect of speed/spatial displacement, ($F(2.293, 114.634) = 334.778, p < .001$), and age, ($F(5, 50) = 6.093, p < .001$). The age \times speed/spatial displacement interaction was not significant ($F(11.463, 114.634) = 1.719, p = .075$). Furthermore, Bonferroni corrected post hoc analysis revealed that age-related deficits did not impact upon performance (relative to the youngest age cohort - 20s) until observers were in their 70s ($p < .001$).

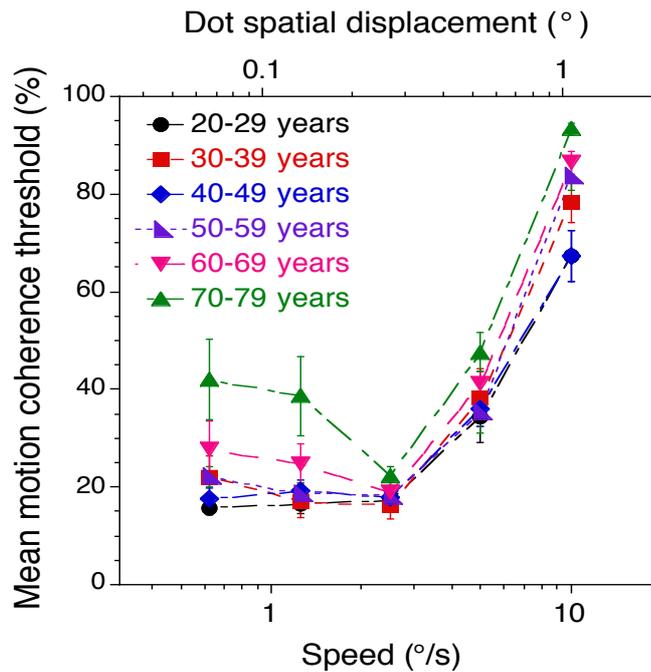


Figure 4.1. Mean motion coherence thresholds obtained in Experiment 5. Thresholds for each age cohort are presented as a function of speed (0.625 – 10 °/s) and dot spatial displacement (0.067– 1.068 °/frame). Error bars = ± 1 S.E.M.

4.3.2. Experiment 6: Varying dot speed

Figure 4.2 shows mean motion coherence thresholds for each age group as a function of local dot speed. Dot spatial displacement remained constant at 0.267°. A two-way (speed, 5 levels; age, 6 levels) ANOVA that was Greenhouse-Geisser corrected for within-subjects effects revealed a main effect of speed ($F(3.290, 164.497) = 69.547, p < .001$) but no main effect of age ($F(5, 50) = 1.635, p = .168$) and no speed \times age interaction ($F(16.450, 164.497) = 1.247, p = .239$). Thus, although performance appeared to improve as local dot speed increased, it was not significantly affected by the aging process.

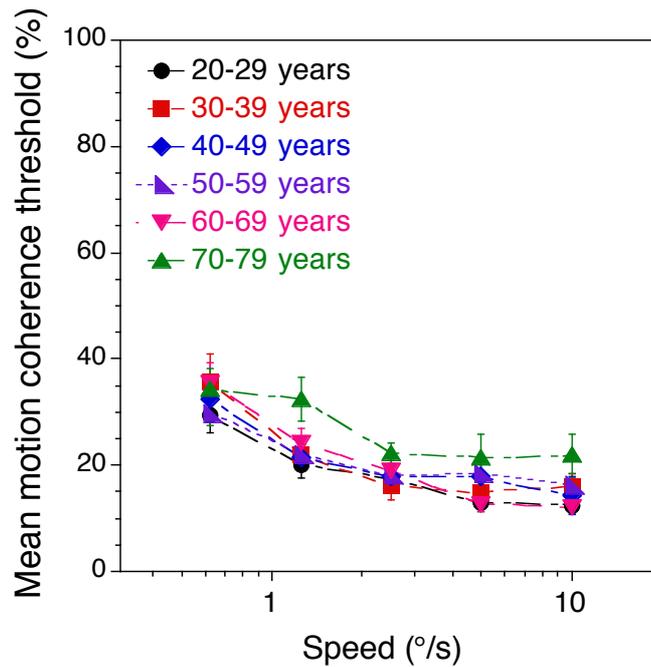


Figure 4.2. Mean motion coherence thresholds of each age cohort in Experiment 6. Speed ranged from (0.625 – 10 °/s) and dot spatial displacement remained constant at 0.267 °/frame. Error bars = ± 1 S.E.M.

4.3.3. Experiment 7: varying dot spatial displacement

Figure 4.3 shows mean global motion coherence thresholds for each age group as a function of local dot spatial displacement. Dot speed remained constant at 2.5 °/s. A two-way (displacement, 4 levels; age, 6 levels) ANOVA using a Greenhouse-Geisser correction identified a significant effect of displacement, ($F(2.165, 108.263) = 164.472, p < .001$) and age ($F(5, 50) = 3.192, p < .05$). The displacement × age interaction was not significant ($F(10.826, 108.263) = 1.020, p = .434$). Bonferroni Post hoc analysis revealed no significant effects of age on performance (relative to the youngest age cohort) until the age of 70 ($p < .05$). These findings suggest that the speed-dependent effects obtained in Experiment 5 were heavily mediated by dot displacement.

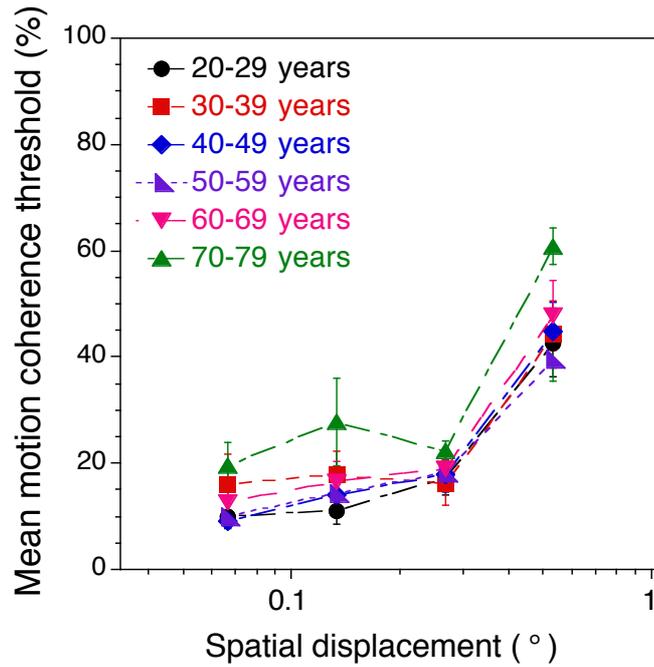


Figure 4.3. Mean motion coherence thresholds for each age cohort in Experiment 7.

Dot spatial displacement ranged from (0.067– 0.543 °/frame) and dot speed remained constant at 2.5 °/s, error bars = ± 1 S.E.M.

To verify the robustness of these findings, 16 additional observers in the 60s ($n= 8$, mean age = 66.7 ± 0.6 years, mean decimal acuity = 0.82 ± 0.11) and 70s ($n= 8$, mean age = 76.5 ± 1.1 years, mean decimal acuity = 0.75 ± 0.05) age cohorts completed the task under the same experimental conditions in Experiment 7. Figure 4.4 shows mean global motion coherence thresholds as a function of local dot spatial displacement for observers aged 20-59 years (the original data in Experiment 7), 60-69 years (original and additional data sets: $n=18$) and 70-79 years (original and additional data sets: $n=19$) cohorts.

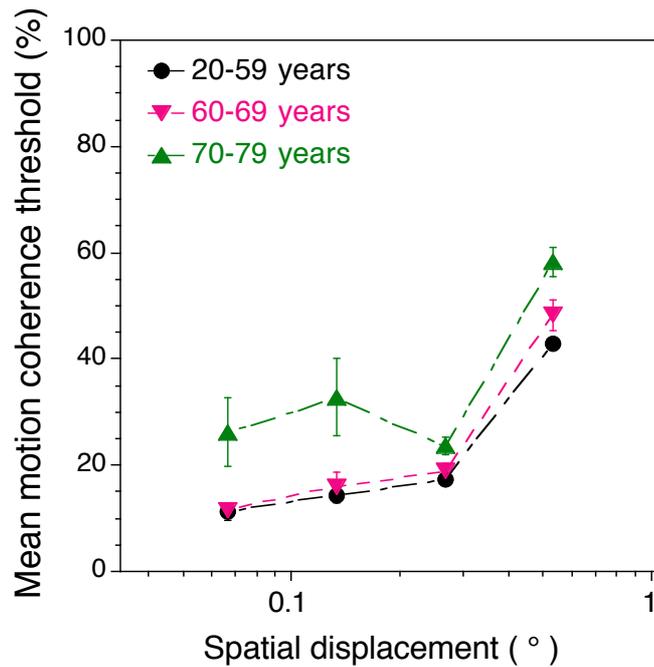


Figure 4.4. Mean motion coherence thresholds with the inclusion of 16 additional observers aged 60-79 years. Thresholds are presented for each displacement included in Experiment 7. Error bars = ± 1 S.E.M.

Difference contrasts confirmed that the 60s cohort did not differ from the younger population ($p = .423$) but significant performance differences were observed for the 70s cohort relative to the younger population ($p < .001$). When the 60s cohort was included in the 'younger' population group, the 70s cohort still differed significantly from the population as a whole ($p < .001$), therefore subsequent analyses were carried out between 'young' (20-69 years) and 'older' (70-79 years) age groups. A two-way (age, 2 levels; spatial displacement, 4 levels) ANOVA revealed a significant interaction between spatial displacement and participant age ($F(1.943, 135.983) = 3.075, p = .051$). Bonferroni corrected t -tests revealed significant performance differences between observers 20-69 years and 70-79 years at the two largest displacements assessed (Table 4.3).

Table 4.3*Experiment 7 independent t-test results*

Dot spatial displacement (°)	<i>t</i>	df	<i>p</i> -value
0.0667	-2.286	18.894	.034*
0.1335	-2.416	19.245	.026*
0.267	-3.335	70	< .0125
0534	-4.153	70	< .001

* not significant at the corrected α value ($\alpha = .0125$)

The findings of some studies suggest that global motion perception may be particularly impaired in older women (e.g. Gilmore et al., 1992; Andersen & Atchley, 1995; Atchley & Andersen, 1998). However the extent to which older women are impaired, relative to older men, is unclear. To investigate this notion in the context of the present study, global motion coherence thresholds were compared for male (closed symbols) and female (open symbols) observers aged 20-69 years, (circles; 28 males & 25 females) and 70-79 years (triangles; 9 males & 10 females) as a function of local dot spatial displacement (Figure 4.5). A $2 \times 2 \times 4$ (age \times gender \times displacement) mixed-design ANOVA with a Greenhouse-Geisser correction confirmed main effects of displacement ($F(2.014, 136.939) = 119.388, p < .001$), age ($F(1,68) = 24.019, p < .001$) and gender ($F(1, 68) = 10.103, p < .05$). There were also significant displacement \times gender ($F(2.014, 136.939) = 4.699, p < .05$), and age \times gender ($F(1,68) = 6.248, p < .05$) interactions. The interaction between displacement and age approached significance ($F(2.014, 136.939) = 2.941, p = 0.56$), whilst the displacement \times age \times gender interaction was not significant ($F(2.014, 136.939) = 2.786, p = .065$). These findings suggest that there are gender differences in global motion sensitivity when RDK speed is mediated by dot spatial displacement. As can be seen in Fig. 4.5, these gender differences

become more pronounced with age. Older female observers demonstrate the greatest reductions in sensitivity to coherent global motion.

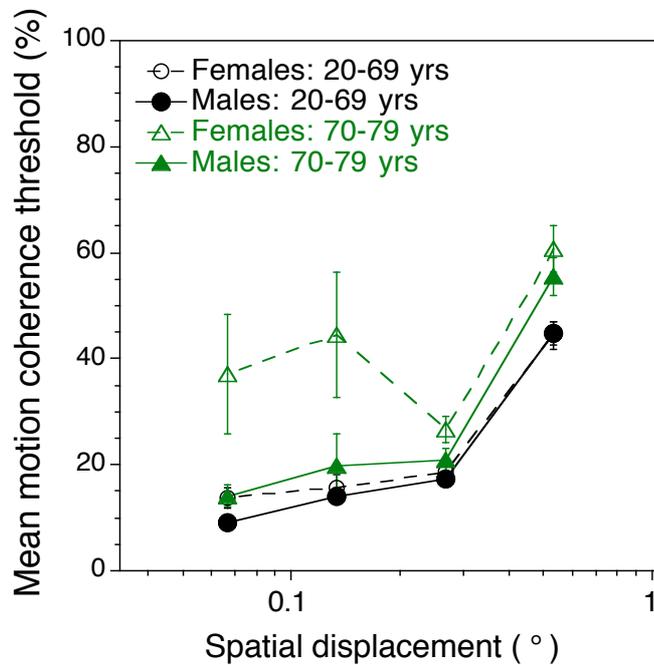


Figure 4.5. Comparison of the mean motion coherence thresholds in Exp. 7 based on gender. Performance of male (closed symbols) and female (open symbols) observers aged 20-69 and 70-79 years age at each spatial displacement assessed in Experiment 7 (0.067– 0.543 °/frame). Error bars = ± 1 S.E.M.

4.4. Discussion

The findings of Experiments 5-7 have shown that age did not lead to a gradual or general decline in global motion perception. Age-related deficits were only evident in the oldest age cohort (70-79 years), were parameter-dependent and appeared to be more pronounced in females. The findings of Experiment 5 suggested that older observers (i.e. 70 years +) were impaired, compared to their younger

counterparts, across the range of speeds/spatial displacements assessed. However, when the relative effects of dot speed (Experiment 6) and dot spatial displacement (Experiment 7) were examined, only variations in spatial displacement yielded differential age effects. When the results from Experiment 7 were analysed on the basis of gender, gender differences were apparent at low dot displacements. These differences became more pronounced in the oldest age cohort, with female observers in their 70s exhibiting the most marked deficits. The implications of each finding are addressed below.

There is some disagreement regarding whether age-related deficits in global motion processing reflect a gradual decline throughout adulthood or a sudden onset in old age, particularly in the 8th decade of life. This is an important issue because aging studies tend to include a broad range of age cohorts to represent their 'old' sample. Whilst the findings of some studies suggest that global motion perception declines steadily with normal aging (e.g. Trick & Silverman, 1991; Wojciechowski et al., 1995; Billino et al., 2008), others (e.g. Bennett et al., 2007) suggest that global motion perception is relatively well preserved through the adult lifespan, until around 70 years of age. The findings of the present study are in agreement with those of Bennett et al. (2007) and suggest that, at least under the current testing conditions, age-related impairments only manifest themselves after 70 years of age. This finding has important implications for what should be deemed as an 'older sample' in experiments investigating the effects of age on visual processing.

The finding that age-related deficits in global motion perception were heavily mediated by the spatial displacement of the dots that made up the RDK stimulus suggests that the ability to integrate signals over space may be a more fundamental part of motion perception than the ability to integrate signals over time, and more markedly affected by the normal aging process. This notion is in agreement with previous studies that have shown that older adults exhibit impaired performance, relative to their younger counterparts, on tasks that require spatial integration in both stationary (e.g. Roudaia, Bennett, & Sekuler, 2008) and moving displays (e.g. Andersen & Ni, 2008; Roudaia et al., 2010).

Watamaniuk and Sekuler (1992) have examined the temporal integration time for global motion perception in 'normal', i.e. non-aged, vision. In their study, performance for discriminating the direction of global motion was assessed as a function of the duration of the motion sequence (150 to 1250 ms) by increasing the number of frames from 3 to 25. They found that the temporal integration limit for global motion was around 0.465 s, corresponding to 9.3 frames. In Experiment 6 dot speed was manipulated by manipulating the number of frames that made up the motion sequence. Specifically, a one-octave increase in speed (within the range 0.625 to 10 °/s) corresponded to a one-octave increase the number of frames (within the range 2 to 32). As such, in assessing the effects of speed on motion coherence thresholds, Exp. 6 also assessed the effects of the number of frames. As shown in Fig. 4.2, motion coherence thresholds decreased initially as speed increased from 0.625 to 2.5 °/s, after which performance plateaued. This corresponds to an initial improvement in performance as the number of frames increased from 2 to 8, followed by an asymptote between 8 and 16 frames. These

findings are in agreement with those reported by Watamaniuk and Sekuler (1992), despite the differences in other RDK parameters. Moreover, the number of frames over which performance asymptoted was unaffected by age.

The findings of Experiment 7 suggest that, especially in the case of female observers, age may lead to a narrowing of the range over which older observers can integrate moving signal across space. This narrowing appears to be marked by an increase in D_{\min} and a decrease in D_{\max} , the minimum and maximum spatial displacements over which accurate direction discrimination is possible. Indeed, Roudaia et al. (2010) have recently found age-related reductions in the range of spatial displacements over which motion integration can take place. Wood and Bullimore (1995) estimated D_{\min} increased at a rate of 0.07 log min arc per decade. Hess, Baker, and Zihl (1989) have shown similar findings in the case of a motion blind patient who suffered bilateral damage to motion-sensitive cortical areas. Using a two-frame apparent motion stimulus, they found that D_{\min} was around a factor of 3 higher in the motion blind patient compared to control observers and D_{\max} was around a factor of 3 lower. In the context of aging, the narrowing of the range of resolvable displacements may reflect age-related changes in the properties of neurons in different parts of the motion-processing pathway. In the case of small displacements, elevated thresholds in the elderly may reflect changes in the properties of area V1 (Baker & Braddick, 1985) and/or age-related deficits in the magnocellular-processing pathway. Deficits at large displacements may reflect age-related changes in V5/MT where it has been shown that D_{\max} is largest (Van Essen & Maunsell, 1983). Although the observers that took part in the above experiments were nonglaucomatous, the finding that thresholds were particularly

elevated at low dot displacements is comparable to motion processing deficits in glaucoma. Bullimore, Wood, and Swenson (1993) for example found that patients with glaucoma exhibited a larger impairment in motion sensitivity for D_{\min} than for D_{\max} . In this context, elevated motion coherence thresholds may potentially provide a biomarker for later development of the disease.

The finding that women in their 70s appear to be particularly susceptible to age-related deficits in global motion perception supports evidence from previous studies (e.g. Gilmore et al., 1992; Andersen & Atchley, 1995; Atchley & Andersen, 1998) and may reflect the importance of sex hormones such as oestrogen in age-related deficits in visual perception. For example, there is psychophysical evidence that postmenopausal women exhibit lower contrast sensitivity than premenopausal women and that after menopause, it continues to decline (Siesky, Harris, Patel et al., 2008). Moreover, hormone replacement therapy has been shown to lead to contrast sensitivity improvements (Guaschino et al., 2003).

In conclusion, the findings of Experiments 5-7 indicate that age-related deficits in global motion perception are best described as being parameter-dependent (in this case specific to dot spatial displacement) rather than being representative of a general age-related perceptual decline. They also suggest that the neural mechanisms underlying spatial integration in global motion perception are relatively well preserved in later stages of life, at least until the age of 70 years. This finding has important implications in terms of how 'old' populations are defined in aging studies, in that the inclusion criteria for such populations should be selected with caution, as a broader age range (i.e. < 70 years) may lead to an

underestimation of perceptual deficits. Moreover, women in their 70s seem to be more deleteriously affected by age than their male counterparts, highlighting a possible role of sex hormones in age-related changes in visual perception.

Chapter 5

Investigating the relationship between age, gender and spatial vision

5.1. General Introduction

There has been a great deal of research dedicated to understanding the influence of gender in visual perception. Gender differences have been established for a number of visual tasks including visual acuity (e.g. Burg, 1966; McGuinness, 1976), visual persistence (e.g. McGuinness & Lewis, 1976), texture (e.g. Li, Asano, Asano, & Okajima, 2013), and colour (e.g. Pardo, Pérez, & Suero, 2007) perception. In the context of aging, there is evidence to suggest that changes in visual function may be mediated by gender. Specifically, older female observers have demonstrated greater impairments, relative to their male counterparts, in the perception of translational global motion (Schieber, Hiris, White, Williams, & Brannans, 1990; Gilmore, Wenk, Naylor, & Stuve, 1992; Andersen & Atchley, 1995; Atchley & Andersen, 1998; Conlon & Herkes, 2008) direction-of-heading (Raghuram & Lakshminarayanan, 2011), biological motion (Pilz, Bennett, & Sekuler, 2010) and speed (Norman, Ross, Hawkes, & Long, 2003; Raghuram, Lakshminarayanan, & Khanna, 2005).

Perhaps the most compelling evidence for gender differences in aging comes from studies of global motion perception. Along with the findings of Experiment 7, a number of studies have noted a more pronounced decline in sensitivity to translational global motion in older women. For example, Gilmore et al. (1992) found that age differences in motion sensitivity were driven by the performance of older female observers. Whilst older men attained coherence thresholds comparable to those characteristic of young observers, older females performed significantly worse than all other groups. Thus the authors concluded that age-related losses in motion sensitivity were gender-specific. Andersen & Atchley (1995) replicated Gilmore et al.'s (1992) study and once again older females demonstrated a marked decrease in performance. However in this instance, older males did show some degree of reduced sensitivity. Conlon & Herkes (2008) have also found that older female participants can be less sensitive to global motion than older males. Furthermore, they showed that performance was correlated with participants' reports of poor perceptions of other vehicles and road signs while driving.

These gender differences are not restricted to tasks which measure sensitivity to random dot displays, rather age-related changes in speed perception have been established using both sine gratings and RDKs. For example, Raghuram et al. (2005) assessed the effects of age on speed discrimination for drifting gratings presented at either 500ms or 1000ms and found that, not only did older observers demonstrate reduced performance relative to their younger counterparts at both stimulus durations, but there was an interaction between age and gender as well. Older female observers were found to be less sensitive to differences in speed

relative to older males. Similar gender differences were demonstrated in older observers when speed discrimination was assessed for limited-lifetime dot patterns (Norman et al. 2003).

Thus far, evidence suggesting age-related differences in visual perception are mediated by gender has come primarily from studies of motion perception. Whether gender mediates age-related declines in spatial aspects of vision is less clear. This is an important issue given that the ability to effectively attend to, and distinguish between, salient information across the visual field is a fundamental aspect of vision in everyday life. Moreover, it is important to understand whether age-related gender differences are restricted to, or extend beyond, motion processing. This may provide insight into the mechanisms underlying motion perception and the role gender may have in increasing susceptibility to age-related degradation within this pathway. As such, the purpose of Experiments 8 and 9 was to compare the performance of young and older adults on tasks of spatial vision, specifically in contrast sensitivity and visual attention, to examine whether the interaction between age and gender observed in tasks of motion processing extend to the spatial domain.

5.2. Experiment 8: age, gender and contrast sensitivity

It is well known that the normal aging process has a selectively deleterious effect on contrast sensitivity (e.g. Owsley, Sekuler, & Siemsen, 1983; Ross, Clark, & Bron, 1985; Elliott, Whitaker & MacVeigh, 1990; Norton, McBain, & Chen, 2009). The contrast sensitivity function of older adults is particularly degraded, relative to

their younger counterparts, at spatial frequencies ≥ 2 c/deg and is characterised by a more pronounced high frequency fall-off. These age-related losses in contrast sensitivity may be exacerbated in low levels of illumination (e.g. Sloane, Owsley, & Alvarez, 1988; Scheffrin, Tregear, Harvey, & Werner, 1999; Jackson & Owsley, 2000) and/or in the presence of temporal modulation (e.g. Whitaker & Elliott, 1992; Clark, Hardy, Volbrecht, & Werner, 2010).

It is currently unclear whether gender mediates age-related losses in contrast sensitivity. Therefore the aim of Experiment 8 was to measure contrast sensitivity in young and old observers to determine whether age-related gender differences exist on this spatial task.

5.2.1. Methods

5.2.1.1. Observers

Seventy-nine observers were included in the study. Forty-one were assigned to the ‘young’ age group (18-28 years) and thirty-eight to the ‘older’ (70-82 years) age group. The mean age and decimal acuity of each age group is presented in Table 5.1. For additional participation criteria refer to Chapter 2: General Methods.

Table 5.1
Observer demographics for Experiments 8 and 9

Age group	Gender	Sample size (n)	Mean age (± 1 SD)	Mean decVA (± 1 SD)
Young	Female	21	20.71 (± 2.61)	1.36 (± 0.23)
	Male	20	22.15 (± 2.91)	1.35 (± 0.35)
Older	Female	20	74.05 (± 2.82)	0.80 (± 0.16)
	Male	18	74.56 (± 3.88)	0.87 (± 0.31)

5.2.1.2. Apparatus & Stimuli

Stimuli were either 4 or 16 c/deg stationary sinusoidal grating patterns that subtended 6° horizontally and vertically. Stimuli were generated on a Macintosh G4 and presented on a Dell monitor with a refresh rate of 75 Hz. The mean luminance of the display was approximately 49.7 cd/m². Images were viewed binocularly at a distance of 139 cm and in a darkened room where the monitor was the only light source. To minimise spatial transients, patterns were spatially windowed in the horizontal dimension according to a half cycle of a raised cosine function. Stimulus contrast in the plateau region of the window varied according to Eq. [2.2].

5.2.1.3. Procedure

Contrast thresholds were calculated using a temporal two-interval forced choice procedure and an adaptive staircase routine. Each trial contained two intervals, one containing the grating stimulus and the other blank (mean luminance). Participants were asked to identify which interval contained the grating stimulus. A stimulus schematic is given in Figure 5.1. Each trial began with a central fixation cross presented onscreen for 750 ms, after which the first interval was presented for 750 ms. At the end of the first interval, the fixation cross reappeared, again for 750 ms. This was followed by the second interval (duration 750 ms), after which the fixation cross re-appeared. The participant was then cued to respond with a key press. The interval that contained the grating was randomised on each trial. On each trial the contrast of the grating varied according to a modified 1-up 3-down staircase designed to converge on the luminance contrast corresponding to 79.4 % correct performance (Wetherill & Levitt, 1965; Levitt, 1971). At the

beginning of each run of trials the contrast of the grating pattern was set to around 6 dB above threshold and the initial staircase step size was chosen to be half this value. On subsequent reversals the step size was halved and testing was terminated after a total of 16 reversals. Threshold estimates were taken as the mean of the last 4 reversals in each staircase. Each observer completed two runs of trials (i.e. 2 staircases) for each spatial frequency and the order of testing was randomized.

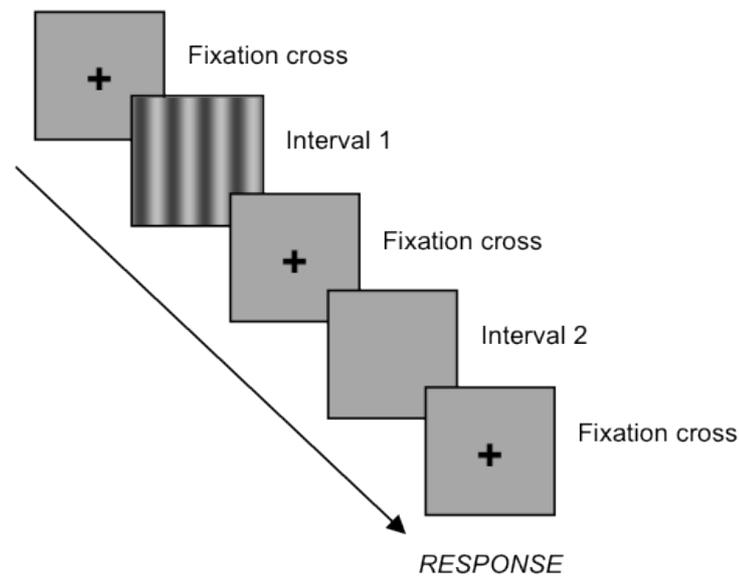


Figure 5.1. Schematic of the experimental set-up for Experiment 8. Observers were presented with a fixation cross, followed by two intervals, one of which contained a sinusoidal grating and the other a blank field. The observers' task was to identify the interval in which the grating appeared. The contrast of the grating varied until participants attained a level of 79 % correct performance.

5.2.2. Results and discussion

Figure 5.2 shows log contrast sensitivity for young and older female and male observers at 4 and 16 c/deg. A three-way (age, 2 levels; gender, 2 levels; spatial frequency, 2 levels) analysis of variance (ANOVA) confirmed a main effect of spatial frequency ($F(1, 75) = 138.848, p < .001$). Within each age group, contrast sensitivity was higher at 4 c/deg than at 16 c/deg. The effect of age was also significant ($F(1,75) = 58.341, p < .001$); older adults exhibited poorer contrast sensitivity than their younger counterparts at both spatial frequencies. At 16 c/deg older adults were particularly poor at detecting gratings, as indicated by a significant interaction between spatial frequency and age ($F(1,75) = 7.070, p < .05$). The effect of gender was not significant ($F(1,75) = .087, p = .769$). There was no interaction between spatial frequency, age and gender ($F(1,75) = .411, p = .523$), spatial frequency and gender ($F(1,75) = 1.062, p = .306$), or age and gender ($F(1,75) = .011, p = .915$).

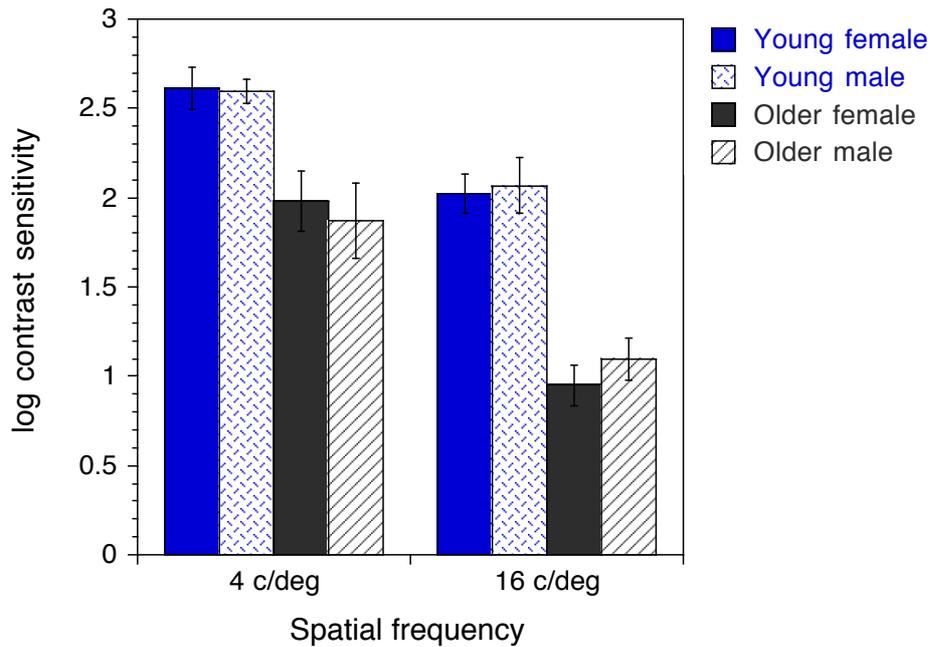


Figure 5.2. Gender-based comparison of young and older adults' log contrast sensitivity at 4 and 16 c/deg. Error bars represent ± 1 S.E.M.

In accordance with the human spatial contrast sensitivity function (Campbell & Robson, 1968), all observers demonstrated higher sensitivity at 4 c/deg than at 16 c/deg. In agreement with previous studies (e.g. Ross et al., 1985; Elliott et al., 1990; Whitaker & Elliott, 1992; Norton et al., 2009), older adults demonstrated reduced contrast sensitivity in comparison to their younger counterparts, with sensitivity loss greatest for 16 c/deg gratings. That these findings did not interact with gender suggests that, at least on low-level visual tasks, age-related differences are not gender-dependent.

In young adults, Brabyn and McGuinness (1979) measured contrast thresholds for spatial frequencies ranging from 0.4 - 10 c/deg and found evidence of an interaction between gender and spatial frequency. At low spatial frequencies (i.e.

0.4 - 0.8 c/deg) females were more sensitive to contrast than their male counterparts, whereas males demonstrated greater sensitivity at the highest spatial frequencies (i.e. 8 -10 c/deg). For mid range frequencies (i.e. 1-7 c/deg), contrast thresholds were similar between male and female observers. This pattern of results was obtained when both static and dynamic displays were employed. Other studies however, have failed to find evidence to support gender differences in contrast sensitivity, even when a similar range of spatial frequencies was examined (e.g. Higgins, Jaffe, Caruso, & deMonasterio, 1988; Owsley et al., 1983; Solberg & Brown, 2002). The results of Experiment 8 are in agreement with these studies and suggest that, irrespective of age, contrast sensitivity is not mediated by gender.

5.3. Experiment 9: age, gender and visual attention

The Useful Field of View (UFOV) test assesses age and/or pathology-related changes in cognitive function. Comprised of three subtests, each subtest builds upon the former, increasing the cognitive load for each task, and allowing for measures of visual processing speed (i.e. how fast the visual system can identify a presented target), divided attention (i.e. the ability to simultaneously attend to multiple elements in a visual scene) and selective attention (i.e. the ability to attend to specific elements in a visual scene whilst ignoring other non-relevant information), to be obtained respectively. The UFOV has repeatedly been shown to be a robust measure of visual attention, is sensitive to small changes in attention throughout the lifespan (Sekuler, Bennett & Mamelak, 2000), and is widely

employed experimentally and clinically to assess visual attention in older adults. As such, Experiment 9 employed the UFOV to assess the role of gender in visual attention in young and older observers.

5.3.1 Methods

5.3.1.1. Observers

The same observers who took part in Experiment 8 took part in Experiment 9. See Table 5.1 for observer demographics.

5.3.1.2. Apparatus & Stimuli

The UFOV® program (Posit Science) was run on a PC and presented on an Iiyama Vision Master monitor with a refresh rate of 60 Hz⁴. Participants viewed the screen at a distance of 57 cm such that targets appeared in a 20° region of space. Stimuli were viewed binocularly and in a darkened room where the monitor was the only light source.

5.3.1.3. Procedure

The three UFOV subtests were presented in sequential order for all observers. For each subtest, observers were provided with both oral and written instruction. Observers also completed at least four practice trials prior to commencing each task. Subtest One (Test of Visual Processing Speed) required observers to identify a flashing central target with the use of a computer mouse (i.e. observers had to

⁴ In Experiment 9, the Bits++ attenuator was not required. As such, it was not included in the experimental set-up.

indicate whether the target was a car or a truck). In Subtest Two (Divided Attention Task), observers once again had to identify a centrally presented target (as in Subtest One targets could either be a car or a truck), as well as indicate the radial position of a simultaneously presented peripheral target. In all cases the peripheral target was a car and observers were asked only for the location of the target in the periphery. Subtest Three (Selective Attention Task) was similar to Subtest Two, again requiring both the identification of a central target (car vs. truck) and the localization of a periphery target (the position of the car); however, in order to increase the attentional load of the task, the peripheral target was embedded in distractors (triangles). For each subtest, a measure of threshold was obtained by varying presentation duration according to a 2-down 1-up adaptive procedure tracking 75% correct performance.

5.3.2. Results and discussion

Figure 5.3 shows young and older female and male participants' performance on each subtest of the UFOV. Two-way (age x gender) ANOVAs were performed for each UFOV subtest (processing speed, divided attention & selective attention). Across all subtests, there were significant main effects of age (Subtest 1: [$F(1, 75) = 7.800, p < .05$]; Subtest 2: [$F(1, 75) = 28.078, p < .001$]; Subtest 3: [$F(1, 75) = 111.943, p < .001$]). However, there were no significant main effects of gender (Subtest 1: [$F(1, 75) = 2.269, p = .136$]; Subtest 2: [$F(1, 75) = .095, p = .759$]; Subtest 3: [$F(1, 75) = .514, p = .475$]), and no significant interactions between age

and gender (Subtest 1: [$F(1, 75) = 2.890, p = .093$]; Subtest 2: [$F(1, 75) = .074, p = .786$]; Subtest 3: [$F(1, 75) = .005, p = .943$]).

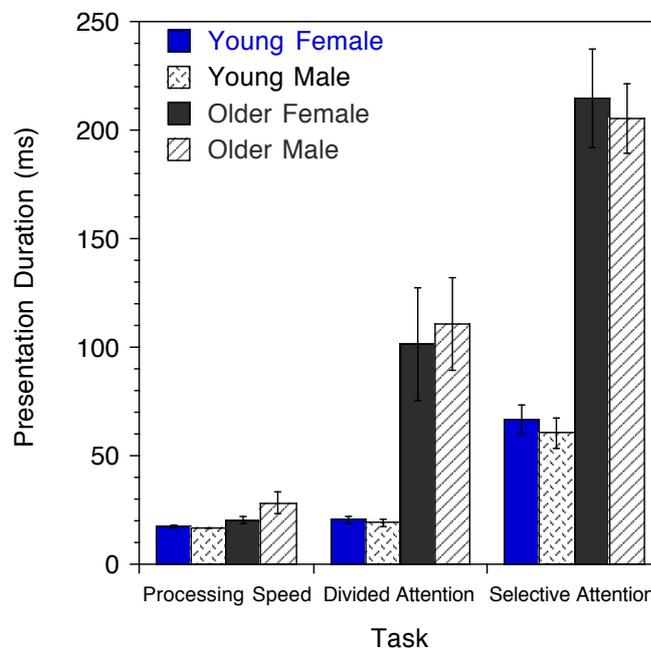


Figure 5.3. Gender-based comparison of young and older adults' performance on the three subtests of the UFOV (Processing Speed, Divided Attention & Selective Attention). Error bars represent ± 1 S.E.M.

The results of Experiment 9 are in accordance with past research that suggests performance on the UFOV is impaired with age (e.g. Sekuler et al., 2000; Edwards et al., 2006; Lunsman et al., 2008) As can be seen in Figure 5.3, age differences became more pronounced as the cognitive demands of the task increased. These findings suggest that older adults may be less able to carry out daily tasks when attentional demands are high (i.e. tasks such as driving a vehicle). Gender did not affect UFOV performance in either of the age cohorts assessed, further supporting evidence that the performance of older adults is not mediated by gender (e.g.

Edwards et al., 2006; Lunsman et al., 2008). Given the findings in both age cohorts, it can be concluded that performance on the UFOV is not mediated by gender at any point throughout adulthood.

5.4. General Discussion

Experiments 8 and 9 compared spatial visual processing in younger and older adults by measuring contrast sensitivity and visual attention, respectively. Findings showed that, whilst there was a deleterious effect of age on contrast sensitivity and performance on the UFOV, there were no gender-based performance differences. Thus, the age-related gender differences observed for global motion perception in Experiment 7, do not appear to extend to these spatial aspects of vision.

The findings of Experiments 8 and 9, in conjunction with those presented in Experiment 7 and others (e.g. Schieber et al., 1990; Gilmore et al., 1992; Andersen & Atchley, 1995; Norman et al., 2003; Raghuram et al., 2005; Conlon & Herkes, 2008; Pilz et al., 2010; Raghuram & Lakshminarayanan, 2011) suggest there may be a gender-specific deficit in the magnocellular processing stream in normal aging. The M-pathway has been shown to be particularly sensitive to information concerning motion (e.g. Merigan, Byrne, & Maunsell, 1991; Schiller, Logothetis, & Charles, 1990; Callaway, 2005), and is therefore a likely candidate for these gender-specific deficits. Gilmore et al. (1992) were among the first to establish that older men and women differ in their sensitivity to coherent global motion. In order to assess the mechanisms responsible for this interaction between age and gender,

Gilmore et al. (1992) carried out an additional experiment in which observers completed a motion coherence task as well as Witkin's Embedded Figures Test (EFT; Witkin, Oltman, Raskin, & Karp, 1971). The EFT provides a measure of field dependence, and is a task that requires figures to be discriminated from their background. According to Livingstone and Hubel (1987) both motion processing and figure-ground discrimination are associated with the M-pathway. As such, performance on these two tasks was used to assess whether gender differences reflect deficits in the M-pathway. As predicted, gender differences were apparent amongst older observers, on both tasks older females demonstrated reduced sensitivity relative to their male counterparts. These findings support a gender-specific deficit in the M-pathway and may account for the lack of an interaction between age and gender in the contrast sensitivity task carried out in Experiment 8; age-related losses in contrast sensitivity have largely been attributed to deficits in the P-pathway (Crassini, Brown, & Bowman, 1988).

Whilst gender differences in aging have been shown for visual tasks that involve motion processing, not all motion types elicit these performance differences. For example, Atchley and Andersen (1998) examined the effects of age on sensitivity to components of optic flow, specifically lamellar (translational) and radial flow. The results of this investigation indicate that gender differences obtained for older observers for translational motion do not extend to the processing of radial motion. In order to provide a more detailed explanation for the interaction between age and gender for translational global motion only, Atchley and Andersen (1998) proposed a three-stage model of motion processing. The first stage of this model involves the extraction of 2-D motion signals with the use of

Reichardt-like motion detectors. Following this, the 2-D information is processed by one of two separate pathways; the first pathway is responsible for the processing of the differential invariants of optic flow proposed by Koenderink and van Doorn (1977) (i.e. curls, divergences, and deformations). The second pathway is responsible for the analysis of global velocity information and is dependent upon the visual system's ability to accurately integrate velocity information across the visual field. Finally, the third stage of this model involves the processing required to carry out a perceptual task, the inputs of which depend upon the nature of the task. According to Atchley and Andersen (1998) the selective age-related gender differences observed for the perception of translational motion likely reflect a gender-specific deficit in the pathway responsible for global velocity analysis. This model provides an adequate explanation for the gender differences observed in the processing of global motion (e.g. Schieber et al., 1990; Gilmore et al., 1992; Andersen & Atchley, 1995; Atchley & Andersen, 1998; Conlon & Herkes, 2008), biological motion (Pilz et al., 2010), and speed (Norman et al., 2003; Raghuram et al., 2005). Even Raghuram and Lakshminarayanan (2011) suggest their finding of a gender difference amongst older observers for the perception of heading direction may reflect the processing of lamellar (translational) components of their stimuli and thus would be in line with a selective deficit in global velocity analysis.

In the context of Atchley and Andersen's (1998) model, and more generally, it is unclear why older females would be particularly impaired in the processing of motion information. Pakkenberg and Gundersen (1997) found males typically have more cortical cells than females, however age-related cell loss was similar

between the sexes. In primates, Giannaris and Rosene (2012) found V1 neuron number and volume did not decline with age for either sex; males and females differed solely in total brain weight. Neurophysiological studies in rodents suggest that older *male* rodent populations demonstrate greater declines with age. Specifically, spontaneous activity levels were found to be higher in visual cortex neurons of old male rats, in comparison to older females, leading to greater declines in signal-to-noise ratios in males (Wang, Chen, Wang, & Zhou, 2010). Thus there is currently no clear evidence to explain why older female populations demonstrate greater reductions in sensitivity to motion perception. This is an issue that has significant implications for aging populations, especially given the gender difference in lifespan, and therefore warrants further investigation.

In conclusion, the results of Experiments 8 and 9 indicate that gender-related age differences observed in motion perception do not extend to tasks of spatial vision. Specifically, contrast sensitivity, processing speed, selective and divided attention. These findings, in conjunction with previous research, suggest that motion-processing pathways in older women may be particularly susceptible to age-related degradation. However, further investigation is required to provide a more comprehensive understanding of visual deficits that develop with age and how these changes may be mediated by gender.

Chapter 6

The effects of age on the perception of second-order global motion

6.1. Introduction

Studies of global motion perception in the aged have focussed on changes in sensitivity to luminance-defined (first-order) motion (e.g. Gilmore, Wenk, Naylor, & Stuve, 1992; Wojciechowski, Trick, & Steinman, 1995; Snowden & Kavanagh, 2006; Allen, Hutchinson, Ledgeway, & Gayle, 2010). In everyday life however, non-luminance based features such as contrast, texture and depth can also define motion. In such instances, the motion created is generally referred to as 'second-order' motion (Cavanagh & Mather, 1989). The processing of second-order stimuli has been the topic of much debate (for reviews see Baker, 1999; Burr & Thompson, 2011) as there are fundamental differences in the manner in which first-order and second-order motions are analysed. From a computational perspective, second-order motion lacks energy in the Fourier plane, rendering Reichardt-like motion detectors such as those proposed by Adelson and Bergen (1985) unable to extract motion energy. It has therefore been argued that an additional non-linear rectification stage is required to transform the motion energy of second-order stimuli for detection (e.g. Chubb & Sperling, 1988). As

such, second-order motion is likely to require more complex levels of analysis by the visual system than first-order, luminance-defined motion. On that basis, it has often been proposed that, at least in early stages of visual processing first- and second-order information are encoded separately, with second-order motion processing relying on a network of distinct and perhaps 'higher order' extrastriate brain areas (e.g. Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Wenderoth, Watson, Egan, Tochon-Danguy, & O'Keefe, 1999; Vaina & Soloviev, 2004).

A number of lines of evidence from normal and clinical populations converge to suggest early separate processing mechanisms exist for first- and second-order motion. For example, in normal populations, motion sequences comprised of interleaving frames of first- and second-order information have failed to produce a compelling impression of motion direction (Mather & West, 1993; Ledgeway & Smith, 1994). Moreover, the effects of cross-adaptation between first- and second-order stimuli have been shown to be minimal. Adaptation to a first-order stimulus only diminished observers' responses to stimuli that were also first-order, having little to no effect on responses to second-order stimuli. Likewise, only sensitivity to second-order stimuli was altered when the adapting stimulus was second-order (Nishida, Ledgeway, & Edwards, 1997; Ashida, Lingnau, Wall, & Smith, 2007). In the context of amblyopia, Simmers, Ledgeway, Hess and McGraw (2003) have shown greater deficits for second-order (contrast-defined) global motion processing than for first-order (luminance-defined) global motion processing, relative to a normal population. Furthermore, studies of motion perception in patients with focal cortical brain lesions have revealed selective impairments in first- or second-order motion perception whilst perception of the other motion

type remained intact (Vaina, Makris, Kennedy, & Cowey, 1998; Vaina, Cowey, & Kennedy, 1999; Billino, Braun, Bremmer, & Gegenfurtner, 2011). These findings in brain-injured patients provide evidence of a double dissociation between the processing of these two motion types.

A dissociation between first- and second-order motion processing mechanisms is also apparent in early development. For example, Elleberg et al. (2003) compared sensitivity to first-order and second-order local motion in 5 year olds and adults and found that children demonstrated reduced sensitivity, relative to adults, for both first- and second-order local motion. However there was a much smaller discrepancy in first-order local motion sensitivity than second-order local motion sensitivity. This was especially true at high stimulus velocities where the difference between the children's and adults' sensitivity to second-order local motion was eight times greater than the difference in sensitivity to first-order local motion. Elleberg et al. (2004) subsequently investigated differences in the development of sensitivity to global first-order and second-order motion. Global motion coherence thresholds were measured for 5 year olds and adults using limited lifetime random Gabor kinematograms that contained either first-order or second-order cues to motion presented at three speeds (1.5, 6 & 9°/s). Elleberg et al. (2004) found that, in general, performance for both first-order and second-order motion was much worse in 5 year olds than in adults. In particular, the difference in performance between 5 year olds and adults was more pronounced at 1.5°/s than for the faster speeds and this discrepancy in performance was especially large for second-order motion. Together, these findings suggest that the mechanisms responsible for the perception of second-order motion are not only

separate from those which process first-order stimuli, but may also develop at a slower rate throughout childhood.

Few studies have investigated the effects of age on second-order information. Habak and Faubert (2000) compared contrast thresholds for detecting static and drifting first-order and second-order gratings in young (21 – 26 year of age) and older (64 – 70 years of age) adults. Thresholds for detecting the orientation of a first-order static pattern were the same in young and older observers. For moving first-order patterns thresholds for detecting orientation and drift direction were around 1.5 times greater for the older than for the younger observers. For all second-order conditions, thresholds for detecting orientation and drift direction were around 2 times higher for older observers. These findings led Habak and Faubert (2000) to propose that second-order motion perception becomes more degraded with age due to the fact that more processing steps are required in the analysis of these stimuli. In support of these findings, Tang and Zhou (2009) investigated modulation sensitivity for first- and second- order grating patterns in individuals 19-79 years of age and found that the ability to accurately discriminate the direction of second-order grating patterns declined earlier in the aging process than sensitivity for first-order grating patterns. Therefore, at least for drifting sinusoidal gratings, there is a more adverse effect of age on second-order motion perception.

The effects of age on the perception of global motion patterns in which dots are defined by characteristics other than luminance have yet to be examined. Like first-order (luminance-defined) RDKs, second-order (contrast-defined) RDKs can

also provide a compelling impression of global motion. Such patterns are defined by an ensemble of random dots, each of which modulates the contrast of a (first-order) carrier and movement is of the dots, not the carrier pattern. Furthermore, few studies have examined the effects of age on RDK patterns in which dots move along more complex trajectories such as those associated with optic flow during self-motion, and the results have been mixed for those that have. For example, evidence suggests sensitivity to radial expansion is preserved with age (Atchley & Andersen, 1998; Billino, Bremmer, & Gegenfurtner, 2008). Conversely, on tasks that required observers to discriminate between expanding and contracting dot patterns in noisy displays, older individuals were found to have elevated motion coherence thresholds relative to young observers (O'Brien, Tetewsky, & Avery, 2001; Kavcic, Vaughn, & Duffy, 2011). Allen et al. (2010) also found age-related declines for radial and rotational global motion, but only when the dot contrast was low and close to its own detection threshold. The authors attribute this sensitivity reduction to the age-related loss in contrast sensitivity. Given that an abundance of physiological evidence exists that indicates neurons in MST are selective for radial and rotational motions (Tanaka & Saito, 1989; Duffy & Wurtz, 1991), age-related changes in sensitivity to these motion types may reflect deficits beyond MT.

The following experiment (Experiment 10) sought to examine the effects of age on the processing of second-order global motion. In addition to investigating whether age differentially affects the perception of first and second-order global motion for translating patterns, Experiment 10 also assessed second-order motion sensitivity for rotational and radial motion types.

6.2. Methods

6.2.1. Observers

Twenty-nine observers were included in Experiment 10 and were grouped as ‘young’ (20-29 years) or ‘older’ (65-79 years)⁵. Most participants completed all components of the experiment (i.e. all motion types) over two sessions. In some instances a participant was only available for one session. In these cases, performance was measured for one motion type only. For each motion type, participants were required to complete both first-order and second-order components of the study. Observer demographics for each motion type (translational, radial & rotational) are outlined in Table 6.1.

Table 6.1
Observer demographics for Experiment 10

Motion Type	Age Group	Sample size (n)	mean age \pm S. D.	mean decVA \pm S. D.
<i>Translational</i>	Young	11	21.46 \pm 1.97	1.37 \pm 0.24
	Old	11	69.91 \pm 2.51	1.12 \pm 0.26
<i>Rotational</i>	Young	9	21.89 \pm 1.97	1.41 \pm 0.22
	Old	9	68.33 \pm 2.45	1.17 \pm 0.22
<i>Radial</i>	Young	10	21.70 \pm 1.95	1.39 \pm 0.18
	Old	10	68.80 \pm 2.86	1.21 \pm 0.20

⁵ Although the findings of Experiment 5 indicate that changes in global motion perception emerge in the 8th decade of life, the ‘older’ age category was extended to include observers 65-69 years of age because previous studies of second-order motion sensitivity (i.e. Habak & Faubert, 2000; Tang & Zhou, 2009) have demonstrated that age differences are evident earlier in the aging process.

6.2.2. Apparatus and stimuli

Stimuli were generated using a *Macintosh G4* computer and presented on a *Dell* monitor with a refresh rate of 75 Hz. The mean luminance of the display was 49 cd/m². Stimuli were presented within a circular window at the centre of the display that subtended 12° at a viewing distance of 92 cm.

Global motion stimuli were either first-order (luminance-defined) or second-order (contrast-defined) RDK patterns (Figure 6.1). In each instance, 50 non-overlapping dots were presented within the display aperture. This aperture contained a carrier composed of spatially 2-d, static, random visual noise in which individual pixel elements were assigned to be either 'black' or 'white' with equal probability. The noise had a Michelson contrast of 0.1 (before modulation by the dots, see below). The remainder of the screen was set to mean luminance.

Each RDK was generated anew immediately prior to its presentation and was composed of a sequence of 8 images, which when presented consecutively produced continuous apparent motion. The duration of each image was 53.3ms, resulting in a total stimulus duration of 426.7ms. Dot density was 0.44 dots/deg² and the diameter of each dot was 0.235°. At the beginning of each motion sequence, the position of each dot was randomly assigned. On subsequent frames, each dot was shifted by 0.3°, resulting in a drift speed, if sustained, of 6°/s. When a dot exceeded the edge of the circular display window it was immediately re-plotted in a random spatial position within the confines of the display aperture.

RDKS were high contrast, with dot modulation depth set to 0.3 (in the range 0-1) for first-order dots and 0.8 (range 0-1) for second-order dots⁶.

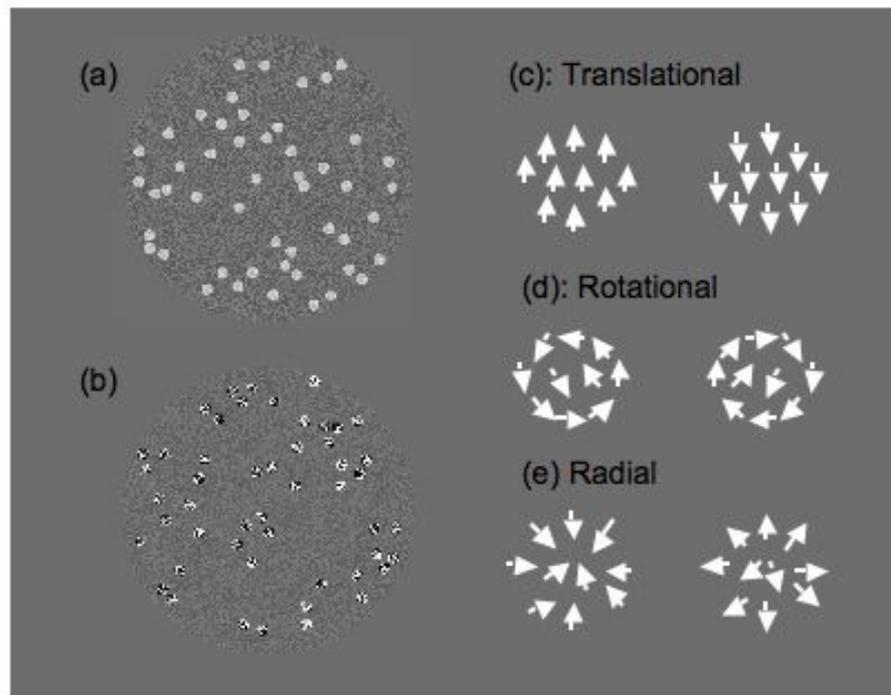


Figure 6.1. Example of the stimuli employed in Experiment 10. (a) First-order (luminance-defined) and (b) second-order (contrast-defined) dot fields were presented within a static noise carrier. Mean motion coherence thresholds were obtained for (c) translational (upward vs. downward), (d) rotational (anti-clockwise vs. clockwise) and (e) radial (contraction vs. expansion) motion trajectories.

⁶ Second-order dots were presented at a higher modulation depth (contrast) than first-order dots because of the marked differences in sensitivity to first- and second-order motion (e.g. Lu & Sperling, 1995; 2001b; Hutchinson & Ledgeway, 2006; Aaen-Stockdale, Ledgeway, & Hess, 2007; Schofield, Ledgeway, & Hutchinson, 2007). The modulation depths used for first-order and second-order dots were the maximum that could be represented against the background of mean luminance.

Dots were created by increasing the mean luminance of the noise carrier within the dots, relative to that of the noise carrier in the background region (c.f. Simmers et al., 2003), using the following equation:

$$\text{Dot modulation depth} = (DL_{\text{mean}} - BL_{\text{mean}}) / (DL_{\text{mean}} + BL_{\text{mean}}), \quad [6.1]$$

where DL_{mean} and BL_{mean} are the mean luminances of the carrier within the dots and background, respectively.

For second-order dots, the mean contrast of the noise carrier within the dots was increased with respect to the mean contrast of the noise carrier in the background as follows:

$$\text{Dot modulation depth} = (DC_{\text{mean}} - BC_{\text{mean}}) / (DC_{\text{mean}} + BC_{\text{mean}}), \quad [6.2]$$

where DC_{mean} and BC_{mean} are the mean contrasts of the carrier within the dots and background, respectively.

The global motion coherence level of the stimulus was manipulated by constraining a fixed proportion of ‘signal’ dots on each image update to move coherently along a trajectory (either translational, rotational or radial) whilst the remainder (‘noise’ dots) move in random directions. For dots traveling along a translational trajectory, signal dot direction could be either upwards or downwards on each trial with equal probability (Fig. 6.1c). For rotational motion, signal dots travelled clockwise or anti-clockwise, again with equal

probability (Fig. 6.1d). Lastly, for radial motion, signal dots were displaced along trajectories consistent with either expansions or contractions with equal probability (Fig. 6.1e).

Following previous studies (e.g. Burr & Santoro, 2001; Simmers, Ledgeway, Mansouri, Hutchinson, & Hess, 2006; Aaen-Stockdale et al., 2007; Allen et al., 2010), the magnitude of the dot displacement was always constant across space in that it did not vary with distance from the origin as it would for strictly rigid global radial or rotational motion. This ensured that all stimuli were identical in terms of the speeds of the local dots. As such, performance for radial and rotational motion could be directly compared to performance for translational motion.

6.2.3. Procedure

All measurements were carried out under binocular viewing conditions. Motion coherence thresholds were measured using a single-interval, forced-choice, direction-discrimination procedure. On each trial participants were required to identify the direction of the moving dot patterns and were given two alternatives to choose from (i.e. up vs. down, clockwise vs. anticlockwise, or expanding vs. contracting). Performance was measured separately for each motion type and the order of testing was pseudorandomised. Data-collection was carried out using a 3-down, 1-up adaptive staircase procedure (Edwards & Badcock, 1995) that varied the number of signal dots present on each trial, according to the observer's recent response history, to track a 79.4 % correct response level (see Chapter 2: General Methods for more details). For each motion type, mean motion coherence thresholds for first-order and second-order RDKs were taken as the mean of 2

staircase procedures. Experimental conditions were presented in a pseudorandom order.

6.3. Results

Mean motion coherence thresholds (expressed as the percentage of signal dots required to produce 79% correct performance) for each stimulus type are presented in Figure 6.2. For clarity, each motion type has been plotted separately. As can be seen in the figure, motion coherence thresholds were generally higher for second-order stimuli in comparison to first-order stimuli. Differences between young and older observers appeared to be minimal for rotational motion. For translational RDKs, older observers were found to have slightly elevated thresholds particularly for first-order motion. However, the most pronounced age difference was observed for radial motion; relative to their younger counterparts, older observers had markedly elevated thresholds for second-order radial motion sequences. A 2 (stimulus type) × 3 (motion type) × 2 (age) mixed-design ANOVA with two between-subjects factors (motion type & age) identified main effects of stimulus type, motion type and age, as well as a significant interaction between the three factors. All other interactions were not significant (see Table 6.2 for a complete list of ANOVA results). Bonferroni corrected post hoc comparisons for motion type revealed significant differences in sensitivity to rotational and radial motion types ($p < .05$).

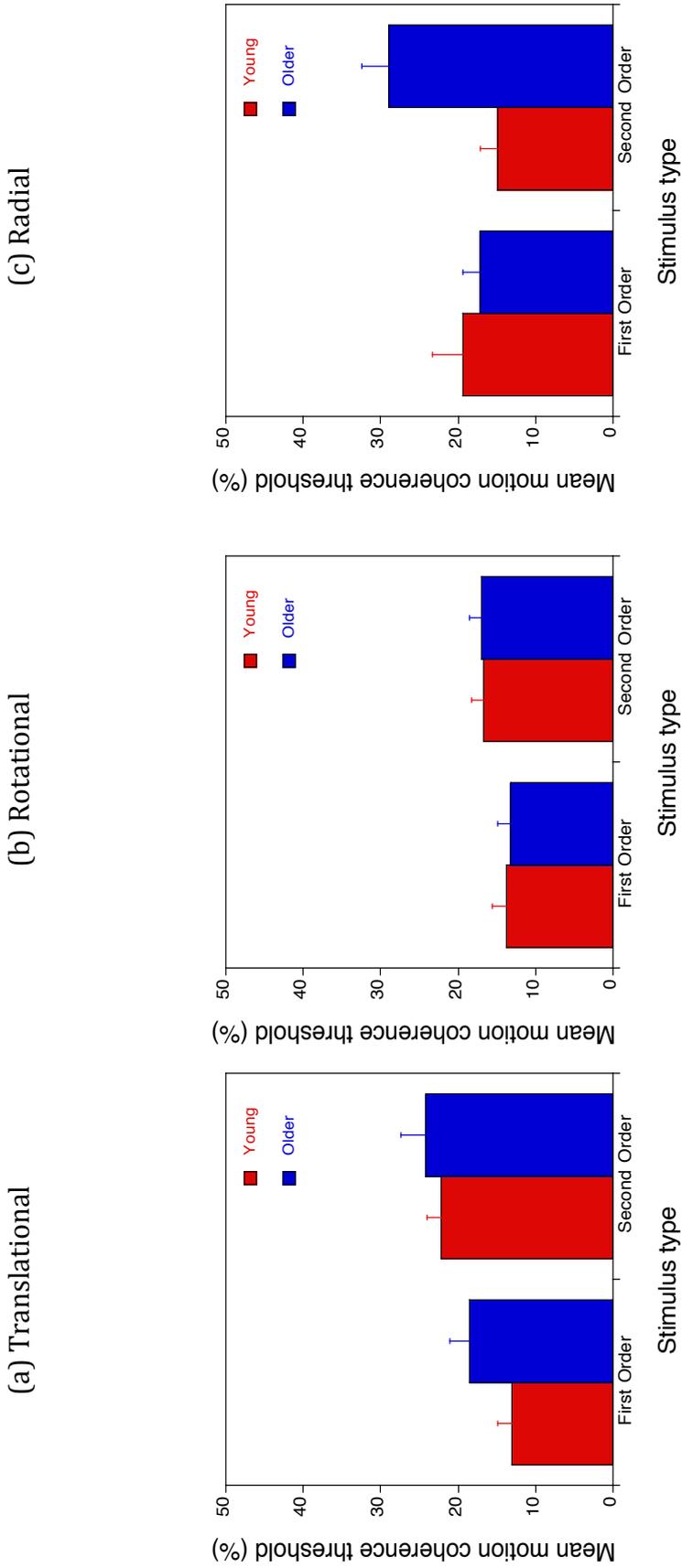


Figure 6.2. Mean motion coherence thresholds for first- and second-order global motion. Coherence thresholds of young (20-29 years) and older (65-79 years) observers are expressed as the percentage of signal dots required to attain 79% correct performance for (a) translational (b) rotational and (c) radial motion types. Error bars = ± 1 S.E.M.

In order to more closely examine the stimulus type × motion type × age interaction, *t*-tests were carried out to compare performance between young and old observers for first- and second-order RDKs for each motion type. The results are presented in Table 6.3 and indicate that young and older observers only differ in global motion sensitivity for second-order radial motion. Therefore, for high contrast global motion stimuli, sensitivity to second-order translational and rotational motion is preserved with age whilst sensitivity to second-order radial motion is reduced.

Table 6.2.
ANOVA results for Experiment 10

Factor	<i>F</i>	<i>p</i> - value
Stimulus type	$F(1, 54) = 11.574$	< .01
Motion type	$F(2, 54) = 3.959$	< .05
Age	$F(1, 54) = 4.428$	< .05
Stimulus type × motion type	$F(2, 54) = .869$.425
Stimulus type × age	$F(1, 54) = 2.553$.116
Stimulus type × motion type × age	$F(2, 54) = 4.627$	< .05
Motion type × age	$F(2, 54) = 1.291$.283

Table 6.3
Independent t-test results comparing young and older observers' sensitivity to first- and second-order global motion

Motion type	Stimulus type	<i>t</i>	df	<i>p</i> -value
<i>Translational</i>	First-order	-1.700	20	.105
	Second-order	-.504	20	.619
<i>Rotational</i>	First-order	.208	16	.838
	Second-order	-.154	16	.880
<i>Radial</i>	First-order	.468	18	.646
	Second-order	-3.379	18	< .005

6.4. Discussion

Experiment 10 compared the effects of age on first-order (luminance-defined) and second-order (contrast-defined) global motion sensitivity for translational, rotational and radial motion types. Two key findings were identified: (1) sensitivity to second-order motion was generally lower than first-order sensitivity and (2) age differences in global motion sensitivity were only apparent for second-order radial motion. Each of these findings will be addressed below.

The finding that coherence thresholds were elevated for second-order, relative to first-order, global motion is in line with the evidence that second-order motion requires more complex analysis by the visual system and is, at least initially, processed by separate mechanisms than first-order motion (e.g. Mather & West, 1993; Ledgeway & Smith, 1994; Lu & Sperling, 1995; Nishida et al., 1997; Dumoulin, Baker, Hess, & Evans, 2003; Vaina & Soloviev, 2004; Thibault, Dauxerre, & Vital-Durand, 2005; Allard & Faubert, 2006). These findings are also in agreement with previous reports of higher direction discrimination thresholds for second-order relative to first-order motion displays (Smith, Snowden, & Milne, 1994; Habak & Faubert, 2000; Aaen-Stockdale et al., 2007) and provide further support for the existence of early separate processing pathways.

For luminance-defined (first-order) stimuli age differences were not significant for any motion type. This likely reflects the speeds and spatial displacements employed in the study. Specifically, the results of Experiment 6 demonstrated that

sensitivity to translational global motion did not differ with age across a range of speeds (0.625-10 °/s) when dot spatial displacement was set to 0.267°. The current study employed a similar spatial displacement as Exp. 6 (i.e. 0.3°) and a speed of 6 °/s (within the range of those employed in Exp. 6) in order to isolate age-related impairments specific to second-order motion perception. Therefore the lack of age differences for translational first-order motion in this experiment are in accordance with, and further support, the findings of Exp. 6. Furthermore, the finding that sensitivity to first-order radial and rotational motion types did not decline with age at the speed/spatial displacement employed in this experiment may suggest that the parameter-dependent effects of age described in Chapter 4 for translational global motion extend to rotational and radial motion types as well, however further investigation is required to examine this in greater detail.

Past studies of second-order motion perception in the aged have measured contrast sensitivity for second-order gratings and have shown an age-related decline in the perception of this stimulus type (Habak & Faubert, 2000; Tang & Zhou, 2009). The current experiment assessed observers' ability to discriminate the global direction of second-order dot patterns presented at high contrasts (i.e. maximum modulation depths). The findings of this study indicate that for translational and rotational motion trajectories, the perception of stimuli defined by contrast (second-order) is well preserved with age. Conversely, aging affects the perception of second-order motion travelling along a radial trajectory, leading to a reduction in the ability to discriminate the global direction of these patterns. Therefore, at least when dots are presented at high contrast, age differences in

sensitivity to second-order global motion are not all encompassing, rather are specific to radial motion.

There are a number of possible explanations for this age-related decline in second-order radial motion perception. Firstly, there is evidence to suggest that the processing of first- and second-order global motion may remain separate up to the level of optic flow analysis. For example, Edwards and Badcock (1995) carried out a series of experiments investigating the interaction of first- and second-order stimuli in global motion displays by having observers complete a direction discrimination task for RDKS composed of dots defined by both luminance and contrast. The results of this investigation demonstrated that the addition of first-order dots to a second-order display impaired the perception of second-order coherent motion but the reverse was not true, that is, second-order dots did not impair the perception of first-order global motion. These findings suggest that first- and second-order motion processing remain separate at the level of global motion analysis. Similar paradigms have been used to show that separate first- and second-order motion processing mechanisms extend to the level of MST and in the processing of optic flow (Badcock & Khuu, 2001; Cassanello, Edwards, Badcock, & Nishida, 2011). Therefore, the age-related decline in second-order radial motion sensitivity observed in this experiment may reflect an impairment intrinsic to second-order pathways at the level of MST.

If area MST was particularly susceptible to the effects of aging, one may argue that sensitivity to rotational motion should show similar reductions as radial motion, however the processing of rotational and radial motions may be constrained by

different mechanisms. Whilst area MST is associated with the processing of both rotational and radial motion (Tanaka & Saito, 1989; Duffy & Wurtz, 1991), there is evidence to suggest these two motion types are processed independently. For example, it has been shown that rotational and radial motions do not mask each other (Freeman & Harris, 1992) and that radial motion is perceived to be faster than rotational motion (Geesaman & Qian, 1996). From a developmental perspective, infants demonstrate significant increases in sensitivity to radial motion between 2 and 3 months of age (Shirai, Kanazawa, & Yamaguchi, 2008a), without a corresponding increase in sensitivity to rotational motion during this time (Shirai, Kanazawa, & Yamaguchi, 2008b). Direct comparisons between rotational and radial motion sensitivities in infants 2 – 3 months of age indicate that sensitivity differences emerge when infants are 3 months old and result from a greater sensitivity to radial motion (Shirai et al., 2008b). These findings indicate a dissociation in the developmental time courses of these two motion types (Shirai et al., 2008b) and provide evidence in support of separate processing pathways for radial and rotational motions.

There is also evidence to suggest that rotational motion sensitivity may be preserved with age. Specifically, when examining first-order global motion sensitivity for translational, radial and rotational motion types, Allen et al. (2010) found an interaction between age and motion type, with older observers demonstrating the greatest sensitivity to first-order rotational motion RDKs. Furthermore, in Experiment 10 observers differed in their sensitivity to rotational and radial motion types. Motion coherence thresholds were markedly lower (i.e. sensitivity was greater) for rotational motion particularly in older observers.

Therefore, if rotational and radial motions are indeed processed separately, it is plausible that the effects of age may be more deleterious for second-order radial motion only.

Alternatively, age-related changes in temporal integration may underlie the reduction in second-order radial motion sensitivity demonstrated in Experiment 10. A recurring finding in the literature is that second-order motion requires longer presentation durations in order for observers to accurately perceive motion direction (Allen & Derrington, 2000; Ledgeway & Hess, 2002). For global motion stimuli, Aaen-Stockdale et al. (2007) compared young observers' perception of second-order RDKs for translational, rotational and radial motion across a range of modulation depths and found thresholds were consistently higher for second-order radial motion relative to the other motion types. Further investigation revealed that for second-order radial kinematograms longer stimulus durations (i.e. > 427 ms) were required to elicit comparable thresholds to those obtained for translational and rotational motion (Aaen-Stockdale et al., 2007). Thus in young observers, relative to other motion types, longer presentation durations are required for the integration of local second-order dot motion into a coherent percept of radial flow. In aging, these differences in temporal integration periods may be exacerbated. For example, electrophysiological evidence indicates visually evoked potentials (VEPs) in response to radial motion are delayed in older individuals (Fernandez & Duffy, 2012; Kuba et al., 2012). Furthermore, low contrasts have been shown to exacerbate the effects of temporal noise in older observers (Allen et al., 2010). In Experiment 10 stimulus duration was 426.7ms, identical to that employed by Aaen-Stockdale et al. (2007), therefore the elevated

thresholds observed in older adults for second-order radial flow may reflect reduced temporal integration in the processing of this motion type.

In conclusion, Experiment 10 sought to examine the effects of age on the perception of second-order translational, rotational and radial global motion stimuli. In comparison to first-order motion, observers generally demonstrated lower sensitivity to second-order RDKs. This finding further supports the evidence which suggests that, at least at early processing stages, the processing of first- and second-order information is constrained by different mechanisms. The effects of age on second-order motion sensitivity were found to be specific to second-order radial motion, leading to age differences in the perception of this motion type only. This age-related reduction in second-order radial motion sensitivity may reflect changes in the mechanisms underlying the perception of second-order radial motion that manifest earlier in the aging process than for other motion types. Further investigation is required to better understand the underpinnings of this decline.

Chapter 7

General Discussion

The purpose of this thesis was to use psychophysical methods to examine the effects of 'healthy' aging on visual perception, with a particular emphasis on furthering our knowledge of age-related reductions in the perception of motion. The results of Experiments 1-10 highlight four key findings: (1) increased internal noise in the aged motion pathway leads to reduced orientation and direction sensitivity in older adults (2) age-related impairments in global motion perception are mediated by reductions in spatial integration (3) age-related gender differences in visual perception do not extend to spatial tasks and may be motion-specific (4) there is a selective impairment in the processing of second-order radial motion in the aged. Each of these findings will be discussed below, along with their contribution to our knowledge of the aged visual system and future directions for research.

7.1. Evidence for reduced orientation and direction sensitivity

In Chapter 3 an external noise paradigm was used to demonstrate age-related reductions in orientation and direction discrimination in central and peripheral vision. In central vision (Exps. 1 & 2) older observers, relative to young observers, were less sensitive to the orientation and direction of drifting gratings in the

absence of external noise. When external noise was added to the displays, older observers were less sensitive to the added noise and required greater levels of noise to elicit an increase in their discrimination thresholds (i.e. reduce their performance) in comparison to their younger counterparts. When the performance of young and old observers was described in terms of sampling efficiency and equivalent input noise, age-related reductions in orientation and direction sensitivity were best explained by changes in equivalent input noise (i.e. increased internal noise) within the aged visual pathway. Similar age-related differences in orientation and direction sensitivity were established in the periphery and were also attributable to changes in equivalent input noise (Exps. 3 & 4). These findings are in agreement with a number of behavioural studies that have demonstrated an increase in internal noise in the aged visual system (e.g. Bennett, Sekuler, & Sekuler, 2007; Betts, Sekuler, & Bennett, 2007; Bower & Andersen, 2012), and are the first to demonstrate age-related declines in sensitivity to the orientation and direction of drifting gratings in central and peripheral vision.

Whilst the external noise paradigm is limited in the extent of information it can provide regarding the underlying determinants of performance on a psychophysical task (i.e. sampling efficiency and equivalent input noise represent categories of mechanisms that affect performance), when taken with the recent reports from neurophysiology, greater insights are gained into the changes that take place in the aged brain. For example, there is compelling physiological evidence that aged neurons in the visual cortex and extrastriate are less selective for orientation and direction in comparison to younger neurons (Schmolesky,

Wang, Pu, & Leventhal, 2000; Hua et al., 2006; Yu, Wang, Li, Zhou, & Leventhal, 2006; Liang et al., 2010; Fu et al., 2010). This decline in selectivity is accompanied by an increase in the overall activity of these neurons including increases in spontaneous firing rates and responsiveness to non-optimal stimuli, ultimately leading to lower SNRs in these cells and increased noise within the visual system (Schmolesky et al., 2000; Hua et al., 2006; Yu et al., 2006; Liang et al., 2008; Fu et al., 2010). At present, age-related changes in neuron selectivity and internal noise have been widely attributed to an age-related breakdown in intracortical inhibition within the visual pathway, due specifically to reductions in GABA concentration (e.g. Schmolesky et al., 2000; Wang, Xie, Li, Chen, & Zhou, 2006; Yu et al., 2006; Liang et al., 2008; Yang et al., 2008; Fu et al., 2010). GABA has been shown to have a key role in maintaining the orientation and direction selectivity of visual cortex neurons (e.g. Rose & Blakemore, 1974, Sillito, 1975; Tsumoto, Eckart, & Creutzfeldt, 1979; Leventhal, Wang, Pu, Zhou, & Ma, 2003; Li et al., 2008; Katzner, Busse, & Carandini, 2011) and is closely mapped to the excitatory drive of motion-sensitive neurons (e.g. Katzner et al., 2011). Decreases in GABA concentration may therefore result in a shift in the excitation-inhibition balance such that neurons demonstrate an increased responsiveness to sub-optimal stimuli leading to increased neural noise.

In addition to GABA, age-related changes in other neurotransmitters and their potential consequences on the excitation-inhibition balance should not be overlooked. For example, neurotransmitters such as ACh and glutamine have been shown to be involved in motion processing (e.g. Javoy, Scatton, & Ruberg, 1989; Schroeder, Zilles, & Luiten, 1989; Rivadulla, Sharma, & Sur, 2001; Lee, Kim, & Zhou,

2010) and there is evidence that the concentration of these neurotransmitters may also be reduced with age (e.g. Sirvio, Pitkanen, & Paakkonen, 1989; Diao, Xu, Li, Tang, & Hua, 2009). The effects of age-related changes in these neurotransmitters on neuron selectivity have yet to be examined and warrant further investigation. Moreover, it is likely that reductions in more than one of the aforementioned neurotransmitters underlie the age-related change in neuron selectivity therefore future work should focus on examining the cumulative effect of changes in these neurotransmitters.

7.2. The critical role of spatial integration in global motion deficits

Chapter 4 (Exps. 5-7) assessed the effects of aging on the perception of translational global motion across a range of speeds as well as the contribution of changes in spatial and temporal integration to age-related performance differences. In Exp. 5 when both speed and spatial displacement were varied, only individuals 70-79 years of age demonstrated reduced sensitivity to coherent global motion, differing from observers 20-69 years of age at each of the speeds/displacements examined. When speed was varied at a constant displacement (Exp. 6) there were no performance differences between any of the age cohorts. This differed from the findings of Exp. 7 (i.e. when spatial displacement varied whilst speed remained constant) where the 70-79 age cohort once again demonstrated performance impairments, especially female observers, suggesting that age-related reductions in sensitivity to coherent global motion such as those established in Exp. 5 were heavily mediated by the spatial displacement of the dots in the motion sequence. The results of these experiments

clarify the discrepancy in the current aging literature regarding changes in global motion sensitivity (e.g. Gilmore et al., 1992; Atchley & Andersen, 1998; Tran et al., 1998; Snowden & Kavanagh, 2006) and suggest that the mixed results were largely due to the different spatial displacements (and corresponding speeds) used in these studies. Additionally, the results of these experiments clearly indicate that sensitivity to translational global motion remains well preserved with age until the 8th decade of life. This too may provide a partial explanation for the mixed results in the literature as many studies have included much younger age cohorts in their older adult samples which may have masked underlying age differences.

The results of Experiments 5-7 demonstrate a reduction in the ability of the visual system to integrate motion information across space and are in agreement with previous work that has shown older populations demonstrate reduced spatial integration using kinetic occlusion (Andersen & Ni, 2008) and moving dot patterns (Wood & Bullimore, 1995; Roudaia et al., 2010). Furthermore, reduced integration of local orientation information has been shown for contour integration in the aged (Roudaia, Bennett, & Sekuler, 2008). Taken together, the findings suggest that whilst temporal integration is preserved with age, the visual system's ability to integrate information, particularly motion information, over space may be compromised.

Perceptual learning may provide an opportunity to ameliorate reductions in motion sensitivity that develop with age. The majority of research on perceptual learning has focused on the effects of training on young adult populations (see Sagi, 2011 for a review). However this technique has been used successfully in

clinical populations as well. For example, in patients with amblyopia perceptual training has been shown to strengthen the amblyopic eye, leading to improvements in visual acuity (e.g. Li & Levi, 2004; Li, Young, Hoenig, & Levi, 2005) and contrast sensitivity (e.g. Chung, Li, & Levi, 2006; 2008; Zhou et al., 2006).

Few studies have examined the effects of perceptual learning on age-related visual impairments; those which have (e.g. Richards, Bennett, & Sekuler, 2006; Andersen, Ni, Bower, & Watanabe, 2010; Mayhew, Li, Sotrrar, Tsvetanov, & Kourtzi, 2010) have shown that visual sensitivity in older adults can be improved with training. For motion-related impairments the findings, though limited, have been promising. For example, Ball and Sekuler (1986) trained young and old observers on a direction discrimination task over six sessions. Post-training results showed that the benefits of training were similar in both age groups. In fact, older participants' performance had improved such that it matched the young participants' pre-training performance level. Furthermore, the results of a follow up test carried out four weeks later suggest that the benefits of training were retained in older observers in the absence of any additional training. Bower and Andersen (2012) also demonstrated that older participants maintain the capacity for perceptual learning and exhibit a similar rate of learning as young observers. In this study, benefits of training were evident using both sine gratings and RDKs and were transferable. These findings suggest there is scope to utilize this training technique to minimise age-related impairments in motion perception.

7.3. Gender differences in aging: evidence for a motion-specific impairment?

In Experiment 7, older female observers demonstrated a greater decline in global motion sensitivity than older male observers at low spatial displacements. In order to examine this gender difference in greater detail, Chapter 5 examined the effects of age and gender on spatial vision. Gender differences in contrast sensitivity and visual attention were the focus of Experiments 8 and 9, respectively. Consistent with the current literature on contrast sensitivity and visual attention (as measured by the UFOV) in the aged (e.g. Owsley, Sekuler, & Siemsen, 1983; Whitaker & Elliott, 1992; Sekuler, Bennett, & Mamelak, 2000), older observers demonstrated reduced performance on both spatial tasks however there were no gender differences in performance. This was the case for young and old observers alike. Therefore, at least for tests of UFOV and contrast sensitivity for static displays, there are no gender differences nor any interaction between gender and age. The findings of Exps. 7 – 9, along with others (e.g. Schieber, Hiris, White, Willians, & Brannans, 1990; Gilmore et al., 1992; Andersen & Atchley, 1995; Atchley & Andersen, 1998; Norman, Ross, Hawkes, & Long, 2003; Raghuram, Lakshminarayanan, & Khanna, 2005; Conlon & Herkes, 2008; Pilz, Bennett, & Sekuler, 2010; Raghuram & Lakshminarayanan, 2011), suggest that older female observers may be more vulnerable to age-related declines in motion perception than their male counterparts.

It is unclear why older female observers may be particularly susceptible to age-related declines in motion processing and there has been little research to address this issue. There is some evidence that these gender differences may reflect

deficits in the M-pathway (e.g. Gilmore et al., 1992). Moreover, Atchley and Andersen (1998) proposed a three-stage model of motion processing, according to which, the sensitivity reductions exhibited by older female populations would reflect impairments in the pathway responsible for global velocity analysis. In order to gain insight into this gender difference that develops with age, it may be of interest to examine the role of sex hormones such as oestrogen in visual function. There is evidence that oestrogen is neuroprotective (e.g. Suzuki, Brown, & Wise, 2009; Gibbs, 2010; Simpkins, Yi, & Dykens, 2010) and that vulnerability to cortical decline increases post-menopause due to the lower levels of this sex hormone (e.g. Henderson, 2006; Bonomo et al., 2009), therefore age-related changes in motion sensitivity may be mediated by changes in this hormone. Animal models may provide an opportunity to examine sex hormones and their effects on visual function more closely. Whilst past studies have typically used primate models (e.g. Girard, Salin, & Bullier, 1992; Movshon & Newsome, 1996; Schmolesky et al., 2000) there is growing evidence that rodents may prove to be useful candidates to study the visual system (e.g. Douglas, Neve, Quittenbaum, Alam, & Prusky, 2006; Huberman & Niell, 2011; Busse et al., 2011).

7.4. Selective effects of aging on second-order radial motion

Chapter 6 examined the effects of age on second-order (contrast-defined) global motion. In Experiment 10, the effects of age on first- and second-order global motion were compared for high contrast RDK displays travelling along translational, rotational and radial trajectories. Consistent with the second-order literature (e.g. Smith, Snowden, & Milne, 1994; Aaen-Stockdale, Ledgeway, & Hess,

2007) observers were generally less sensitive to second-order motion. Interestingly, older observers only demonstrated age-related impairments in the perception of second-order radial motion. These results suggest there may be a selective impairment in the perception of second-order radial motion with age, at least for high contrast displays. As this was the first study to examine the effects of age on second-order global motion little is known as to why this impairment in second-order radial motion perception develops with age.

In order to more closely examine the effects of age on second-order radial motion, as well as the effects of age on other aspects of motion perception, it may be of value to combine classic psychophysical methods with other neuroscientific techniques such as electroencephalography (EEG) or functional magnetic resonance imaging (fMRI). In the past, a number of these techniques have been combined with psychophysics, the results of which have had profound impacts on our understanding of the visual system. For example, Beckers and Zeki (1995) demonstrated the critical role of MT in motion perception by performing transcranial magnetic stimulation (TMS) over V1 and MT whilst observers completed a motion task. Nakamura et al. (2003) also provided evidence for the role of MT in global motion perception using magnetoencephalography (MEG). More recently, Billino, Braun, Böhm, Bremmer, and Gegenfurtner (2009) used MRI and computer tomography (CT) scans to demonstrate that translational, radial and biological motions are processed by distinct mechanisms. Therefore, our understanding of the visual system has been greatly enriched by combining neuroscientific techniques to answer complex research questions. Future aging

studies should exploit these techniques to gain greater insights into age-related changes in visual function.

7.5. Conclusions

The objective of this thesis was to further our understanding of age-related changes in visual perception. The results of Experiments 1-10 illustrate the complexity of the visual system; whilst aging does not lead to a general decline in motion processing, there are a number of reductions in visual sensitivity which result from the 'normal' aging process. Future research should more closely examine the potential benefits of perceptual learning on minimising age-related reductions in motion sensitivity as well as the role of sex hormones in this decline. Furthermore, future studies should combine psychophysics with neuroscientific imaging and/or recording techniques such as fMRI, MEG or EEG to provide a more comprehensive understanding of the changes that take place within the visual system as we age.

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