Skill Learning:

Brain Systems, Eye Movements, Ageing, and Driver Behaviour

Jennifer Louise Mills

Department of Psychology

Royal Holloway, University of London

Thesis submitted in fulfilment of the Degree of Doctor of Philosophy

August 2017

Declaration of Authorship

I, Jennifer Louise Mills, hereby declare that this thesis and the work presented in it is entirely my own work. Where I have consulted the work of others, this is always clearly stated. No part of this thesis has been submitted for a higher degree at another university or institution.

Signed: _____

Date: _____

Abstract

The aim of this thesis is to investigate the mechanisms of skill acquisition and the impact of aging on these processes in the laboratory and during driving. This has a range of applications, including training older drivers to decrease their crash risk. Methods used include functional magnetic resonance imaging, eye tracking and driving simulation.

Chapter 2 investigates the neural mechanisms that support the cognitive control of eye movements during visual sequence learning. Areas of the cerebellum that communicate with the prefrontal cortex showed activity changes that corresponded with performance increases as subjects became better at rehearsing information in working memory.

Chapters 3 and 4 investigate the effects of ageing on visual skill learning. Using a novel spatial Stroop paradigm, Chapter 3 shows that in the face of conflicting information, performance decreases in older but not younger subjects. Chapter 4 uses an oculomotor adaptation of the Useful Field of Vision test, which examines the amount of information extracted from central and peripheral vision. Accuracy on a central visual task decreased as a concurrent peripheral visual task was conducted at higher radial eccentricities. Performance on the task conducted in central vision was significantly worse in older than younger subjects when the peripheral task was at the furthest distance.

The effects of route familiarity on driving are explored in Chapter 5. Results show that driver behaviour can be performed earlier, and with less hesitation in familiar environments. Younger drivers benefitted from this more than older drivers. Hazard perception skill was facilitated by increased familiarity with an environment.

This thesis reports the effects of practice on the cognitive control of eye movements during laboratory and real-world settings, and shows that they become increasingly skilled, probably supported by processes in the cerebellum. It also shows that the ability to acquire these skills reduces with age.

Dissemination of Findings

The work presented in Chapter 2 of this thesis forms the basis of a manuscript submitted for publication and peer-review in Journal of Neuroscience. It is now under revision.

Acknowledgments

First and foremost, I would like to thank my supervisor, Professor Narender Ramnani. In 2012, when choosing my Undergraduate project, my excitement to start doing Proper Science was due to Narender's genuine love and knowledge of his field. I am extremely thankful for being given the opportunity to pursue a PhD thereafter. Your support and encouragement has been invaluable, and your dedication to answering emails at 5am and putting up with my obscure questions have always been appreciated. Secondly, I would like to thank the Transport Research Laboratory for helping to fund the project and providing me with an invaluable opportunity to branch out beyond my field. In particular, I would like to thank Dr Shaun Helman, who took over supervising this project and has been the most patient, supportive and genuinely inquisitive second supervisor. I would also like to thank Dr Georgios Argyropoulos for his daily (hourly) support, particularly in the early days of the project, especially with my (many) MATLAB woes, and for continuing to be a constant source of help even after moving to a different job. My most heartfelt thanks also go to Dr Cat Sebastian, whose endless time, guidance and encouragement guaranteed I finished this PhD, and Professor Johannes Zanker, whose wise words were always timely and whose logistical help guaranteed these ideas could be realised.

Sincere thanks to Ari Lingeswaran for his MRI knowledge and to all the staff at TRL whose help and advice was invaluable for completing Chapter 5. In particular, I would like to thank Lena Weaver for all the logistical help and for answering my many questions, and Dr Simon Wilson, whose technical mastery made the collection of experiments in Chapter 5 possible and who provided great company for all my days in the Sim (thanks for the coffee, not so much for the haircut).

One of the best parts of doing a PhD is the people you meet. I've been lucky enough to be encouraged and inspired by some *fantastic* scientists. My deepest thanks go to Saz, whose patience, intelligence and humility has been my lifeline for these years. Thank you for the support, the company, and all the counselling sessions on the train. I wouldn't have wanted to share this journey with anyone else. Rachel, thank you for the DC breaks, the phone calls in times of crisis and for being the most kind, understanding and supportive friend to us all. Hannah Harvey, you have been the most fantastic comrade in study, work and politics. Your support in both equal rights and eye tracking have been integral to my work and my life. I would also like to thank all my PhD friends past and present. In

Contents

List of Tables

List of Figures

Figure 65: Average braking onsets for drives seen previously one, two or three times (see section 2.2) driven either with (L) or without (R) a pedestrian hazard. Error bars: +/- 1 SEM. * denotes significant differences, ** denotes a significant interaction.   *222*

Chapter 1: General Introduction

1.1   What is automaticity?

'When we learn a complex action by repeating it, the performance becomes increasingly automatic and stereotyped' (Fitts, 1964).

Before discussing the neural basis of skill learning, in particular visual skill learning, and its applied elements, it is important to accurately define what parameters constitute a 'skill'. A skill, whether cognitive or motor in nature, is generally defined as a behaviour which becomes quicker and more accurate over time as it is practiced. That is, skilled behaviours develop automaticity – after time, they can be triggered almost always by the same sensory events in the environment, and can be executed with a low degree of conscious control (Ashby, Turner & Horvitz, 2010).

In order to navigate life efficiently, the human brain relies on the automatic execution of cognitive processes. Automatic performance is beneficial because it provides us with the ability to execute a well-known process whilst, at the same, being able to attend to other things. For example, we must be able to attend and respond to conversations with others in the environment whilst conducting a number of secondary tasks including walking, typing and, driving. An automatic process is broadly defined as an internal memory system that can always or nearly always be activated by an item or sequence of information which may be internal or external, and can be activated without the conscious attention of the subject (Keele, 1973; Shiffrin & Schneider, 1977). Automatic processes are 'fast, feedforward, accurate and dependent on prior experience rather than ongoing feedback' (Ramnani, 2014, p. 256). Further, 'once learned, an automatic process will be difficult to suppress or alter' (Shiffrin & Schneider, 1977, p.56).

In contrast, controlled processes are under the constant attention of the subject due to a limited capacity, and each new activation of the behaviour requires the re-application of attention (Shiffrin & Schneider, 1977). Ramnani (2014)

conceptualises controlled processes as being 'effortful, dependent on a limited capacity working memory system and prone to disruption by concurrently performed tasks' (Ramnani, 2014, p.256). It is suggested that the two systems work together, and processes that are initially controlled can become automatic and unconscious over time (Evans, 2008; Ramnani, 2014).

This chapter will start by introducing models of automaticity in the realm of cognition and attention, and will provide a background into the neural basis of automatic processes, how these change with age, and how they impact human performance in the real world.

1.2   Models of automaticity

Many models have been used to explain how behaviours can be automatically executed. Arguably the most prominent of these was developed by Shiffrin & Schneider (1977). They proposed a two-process framework to explain human information processing which focused on automatic and controlled processing. In this model, a series of parallel automatic processes may occur first in order to encode information about the sensory inputs. In some cases, an automatic response may be executed based on prior learning, for example if we hear our own names, an automatic response would be to turn towards it. This requires no further level of controlled processing. In other cases, where an automatic process cannot be executed due, for example, to conflict as to where attention must be directed, controlled processes are used. These controlled processes help us to direct attention either to produce a novel response or find and execute a previously learned automatic response. However, it is not always the case that automatic processes precede controlled processes, in some cases, both automatic and controlled processes can occur in parallel such as during classic dual-task situations. Nor is it the case that behaviours necessarily always fall into one of the two processes. The two-process framework provides an adaptive framework to explain how we learn new behaviours. Shiffrin & Schneider (1977) suggest that as situation become familiar (for example, when the same behaviour must be repeated in the same environment over many occasions), controlled processes can transition into skilled,

automatic processes. In these instances, the attention demands of the automatic behaviour decrease, allowing other controlled operations to be executed simultaneously.

Other cognitive models overlap with the model outlined above. Deutsch & Deutsch (1963), Neisser (1967), Norman (1968; 1969) and LaBerge (1973; 1975) have all suggested models in which incoming sensory information is analysed in parallel and the results of this level of processing are used to choose which stimuli are further processed for memory or response. These do not necessarily contradict the previous model discussed, which broadly makes the same two-step process argument, but provide more specificity with regards to the actual roles of each level of processing. In particular, both Neisser (1967) and LaBerge (1973; 1975) outline automatic or 'preattentive' systems which are recruited early in the encoding process. These are similar to the automatic processing level in the Shiffrin & Schneider (1977) model, and both models also suggest that practice could lead to the automatic allocation of attention to processes, allowing these to become learned over subsequent repetitions (see above for an explanation with regards to Shiffrin & Schneider's (1977) model).

More recently, Kahneman (2011) suggested there are two systems that control the way humans process information. System 1 is rapid, automatic, stereotyped, subconscious, not sensitive to feedback and is difficult to suppress or alter. On the other hand, System 2 is a slow, effortful system which is highly sensitive to feedback and is flexible, but is less frequent and requires conscious cognitive input. Examples of System 1 behaviours include emotional reactions and reading. System 2 behaviours include navigating new social situations, new physical activities and completing complex logical reasoning tasks (Kahneman, 2011). The two systems model proposed by Kahneman (2011) fits very intuitively with Shiffrin & Schneider (1977)'s two process model. System 1 is the automatic process and System 2 is the controlled process that becomes involved when a behaviour cannot be automatically executed based on prior learning. The neural mechanisms of

automatic and controlled processes are outlined in detail in Ramnani (2014) and will be discussed below.

1.3   The neural basis of automaticity

1.3.1 The neural basis of automaticity

Traditional literature suggests that a mixture of long-term potentiation and long-term depression of neural activity (respectively, the strengthening and decreasing of strength between synapses) in the basal ganglia, in particular within the striatum, is intrinsically responsible for skill learning, alongside changes in activity across the cortex (Lehéricy et al., 2008; Poldrack et al., 2005). Research has shown that with extended training, activity in the associative striatum that is present during the early stages of learning declines to background levels (Poldrack et al., 2005), and, conversely, activity in the sensorimotor striatum responds more strongly after a sequence has become automatic (Miyachi, Hikosaka, & Lu., 2002). Such a view is, even superficially, too simplistic in nature because automaticity, and the learning of skilled behaviours, is characterised by changes in widely distributed neural networks, rather than in one single brain region (Ashby et al., 2010). Literature also suggests that the cerebellum is a candidate area for skill learning. The cortico-basal ganglia and cortico-cerebellar systems have similar structures and properties, and as such, both areas are likely to contribute to the automatic control of skilled behaviours (Ramnani, 2014). The structure of the cerebellum, and its contributions to skill learning will now be discussed.

The cerebellum is a small but computationally powerful structure containing around 50 billion neurons, roughly half the total number of neurons in the human brain (Zagon, McLaughlin, & Smith, 1977), and has a distinctive anatomical nature. The cerebellum has a cortex which is organised into a highly regimented, lattice-like structure that is split into three layers; a molecular layer, a Purkinje cell layer, and a Granular layer (Braitenberg & Atwood, 1958; Apps & Garwicz, 2005). This cortical sheet contains 4 types of neuron; Purkinje cells, Granule cells, Golgi cells and stellate or basket cells (Voogd & Glickstein, 1998). Purkinje cells are the prime computational unit of the cerebellum. Purkinje cells receive inputs from the pontine

nuclei by way of parallel fibres and from the inferior olive via climbing fibres, and they send the only outputs from the cerebellar cortex to the cerebellar and brainstem nuclei (Crepel, Mariani, & Delhaye-Bouchard, 1976; Fox & Barnard, 1957; Voogd & Glickstein, 1998).

The traditional view of the cerebellum, or 'little brain', is as a purely motor structure, and this view provided much of the focus of the early literature. Cortico-cerebellar connections between the cerebellum and cortical motor structures such as Brodmann areas 4 and 6, or the primary motor cortex and premotor cortex, respectively, are well documented (Middleton & Strick, 2000; Ramnani, 2006). Studies using both anterograde and retrograde cross-synaptic neurotropic tracer technology have shown dense afferent (towards) and efferent (away from) projections between the motor areas of the cerebral and cerebellar cortices. Although no studies have shown the collateralization of fibres from the prefrontal cortex in the pontine nuclei itself, it is likely that these areas form closed loops that relay information from the cerebellar cortex, through the thalamus to the cerebral cortex and then back to the cerebellum through the pontine nuclei, the main input nuclei of the cerebellum (Ramnani, 2014). That the same areas of the cerebellar cortex (namely lobules HIV through to HVI in the cerebellar hemispheres) both project to, and receive projections from the same motor cortical area suggests that these cortico-cerebellar loops form closed circuits (Kelly & Strick, 2003).

Logic dictates that such a closed circuit should perform specific computations, and this has been supported by evidence in the literature. Activity within this loop is responsible for the co-ordination of movements and motor memory, involving a transfer of information processing from the anterior cerebral cortical motor areas, which are responsible for the conscious control of movements, to the more anatomically posterior cerebellar cortical motor areas, which then control a movement once it has been well learned, or practiced. That is, when a movement has become an automatic, skilled behaviour. This is in keeping with the traditional view of the cerebellum, as outlined by Marr (1969) and Albus (1971), that the cerebellum processes information in a feed forward manner. Activity in the

cortical areas that consciously control a particular behaviour in the learning stages decreases as a function of learning over time, and control of these behaviours becomes the function of the cerebellum. The cerebellum controls behaviour using internal models (see later) that are executed automatically and unconsciously, and can be evoked when the same context arises in the future.

Why is it proposed that such learning is likely to occur in the cerebellum, as well as other structures? The cytoarchitecture - or cellular makeup - of the cerebellum has inspired its involvement in a number of theories of learning. Marr (1969) suggested that the strengthening of synapses between parallel fibres and the dendrites of Purkinje cells occurs through Hebbian learning. In short, this is when pre-synaptic neurons and post-synaptic neurons that are stimulated at the same time wire together, thereby increasing their synaptic efficacy when activated in the future. This results in a decrease in neural activity which is argued to underpin learning. In support of this, recordings from Purkinje cells from cerebellar lobules III, IV and V of non-human primates have found a high frequency of spike activity at the start of learning, which declined to background levels as learning progressed (Gilbert & Thach, 1977). Integral to this process, and the reason why it is believed to be a facet of the cerebellum, are error signals which are relayed by the climbing fibres in the cerebellum.

It has been suggested that complex spikes or 'error signals' relayed by climbing fibres specifically act on the synapses between parallel fibres and Purkinje cells, thereby decreasing their connectivity (Ramnani, 2006). Over time, Purkinje cells may learn to respond to signals from parallel fibres under the guidance of a teaching signal from climbing fibres (Ramnani, 2006). Evidence for this has been shown, though not consistently, by electrophysiological studies of cellular activity in the cerebellum in animal models in response to errors (Ebner, Johnson, Roitmain, & Fu, 2002; Horn, Pong, & Gibson, 2004; Krupa, Thompson, & Thompson, 2008).

Control theoretic accounts of information processing have been proposed to explain how these error signals underpin motor learning. The translation of motor

commands from higher cerebral cortical areas into actual, real-time movements operated by lower order motor control centres, such as the spinal cord, results in a set of sensory consequences including sensory and proprioceptive feedback. These contribute to the working of internal models. Internal models are neural representations of behaviours that are acquired through feedback, and can be used to reproduce behaviours have been previously conducted (Ramnani, 2006). There are two types of internal model – forward models, which are representations of previously conducted actions and inverse models, which provide the motor commands required to reach the desired state and implement the simulated behaviour (Wolpert, Miall, & Kawato, 1998). Forward models are fundamental to information processing by the cerebellum. Inputs to forward models are made from 'efference copies' of the motor commands that generate movements, and these efference copies of movements are used by forward models to predict the ideal state of the body after the movement has been made successfully (Ramnani, 2006). The outputs of these models are the predicted sensory consequences of the movements that are going to be executed. The discrepancy between the actual and predicted sensory consequences of a movement is assessed, and error signals based on these are used to alter consequent predictions so they may be made more accurately (Ramnani, 2006; 2014, and see below for a fuller discussion on the neural basis of forward models). As such, forward models are essentially input-output mappings for specific behaviours which are learned over time using error feedback, as outlined above (Miall & Wolpert 1996). The representations are then used to execute these actions automatically in the future.

In neural terms, the storage of information in the form of forward models is suggested to be located in the cerebellar cortex, due to research showing it is an important site for learning-related neural plasticity (Ito, 2001). Further, studies of cerebellar circuitry have shown that fibres from the motor cortex, which pass into spinal cord, form collaterals that pass into the pontine nuclei of the cerebellum, and then project to the cerebellar cortex (Ramnani, 2014; Uglioni & Kuypers, 1986). This suggests that forward models which involve cortico-pontine projections that arise in the motor cortex and carry information to the cerebellar cortex may use

copies of motor commands that are generated by the primary motor cortex to compare the actual and predicted consequences of current motor behaviours (Wolpert, Miall & Kawato, 1996). In addition to this neural mapping, it has been suggested that the possible site of the 'comparator' (the neural structure that analyses the discrepancy between the actual and predicted sensory consequences of a movement based on internally generated forward models, as outlined above) is the inferior olive. The inferior olive is closely associated with the cerebellum, as there are pathways that transmit information from the forward models' predictions either directly from the cerebellum to the inferior olive, or via the red nucleus, a structure that receives dense inputs from the cerebellum (Courvile & Otabe, 1974; Ralston, 1994; Ruigrok, 1997).

1.3.2 The cerebellum and cognition

The cerebellum is a dense and complex structure, and so more recent research has focused on whether these mechanisms of skill learning in the cerebellum are applicable outside the motor domain, and whether this structure plays a role in cognition.

Historically, due to its cortico-cerebellar connections, the cerebellum was seen as a motor structure (see above). Much of the early literature focused on the effects of cerebellar lesions on motor performance. Sherrington (1906) proposed that lesions to the cerebellum prevent input to the motor system and cause deficits of posture and movement. Dow (1949) was an early proponent of the cognitive cerebellum. He suggested that different patterns of activation in different areas of the cerebellum, including the inferior olive and the spino-cerebellar pathway, shows the cerebellum responds to sensory information separately from motor information. Though this idea was initially rejected, Leiner, Leiner & Dow (1986) later argued that phylogenetically different areas of the cerebellar dentate nucleus may project to different areas of the cerebral cortex, and this may underpin the differential cognitive and motor functions of the cerebellum. They suggested that older areas of the dentate nucleus may control motor behaviours through their connections with the motor cortex and the new areas of the dentate nucleus may control the more

recently evolved cognitive functions through their connections with the frontal association areas of the cerebral cortex. Such evidence would provide a rationale for the cerebellum dealing with the cognitive and motor demands of behaviour separately. Anatomical and functional evidence in favour of this argument will be explored in the following sections and throughout the rest of this thesis.

Connections between the cerebellum and prefrontal areas of the cerebral cortex have also been shown in anatomic tract-tracing literature. The previously mentioned body of work by Kelly & Strick (2003) has also shown closed, reciprocal loops that run between dorsal areas of the prefrontal cortex (Walker's Area 46) and Crus I and Crus II and vermal lobules VII and IX and with ventral portions of the dentate nucleus of the cerebellum. That these distinct loops run in parallel, but do not overlap, between the motor and cognitive areas of cerebral cortex and the cerebellum suggests that as well as processing information relating to action, the cerebellum processes cognitive information at a greater level of abstraction. Such information is likely to be rule-based and concerned with the abstract information used to instruct and guide actions, rather than implement the actions themselves (Ramnani, 2006). Indeed, elements of and inputs to both the cortical and cerebellar parts of this prefrontal loop have expanded disproportionately in the human brain when compared to components of the motor loop (see below).

Newer, event-related fMRI data supports this assertion. In relation to this topic, fMRI studies have explored cerebellar contributions to cognition by using first-order rule learning paradigms, which measure the ability to acquire associations between symbolic instructions, actions and consequences, as a typical example of the kinds of learning process that underpin primate cognition. Through the use of feedback, these rules are learned over time and therefore develop automaticity. Event-related fMRI methods allow the authors to time-lock activity related precisely to rule-processing, meaning such activity cannot be explained by activity underpinning movement. Balsters and Ramnani (2011) conducted an event-related fMRI study investigating the activity evoked by associating symbolic information cues with actions. In this study, arbitrary associations were formed

between symbolic instruction cues and the movement of individual digits in a button press task. The study involved a degree of training prior to scanning in order to compare rules that became automatic at different rates. The authors found significant activation related to the processing of symbolic instructive cues in prefrontal area 9/46 and, most importantly, correspondingly in Crus I of lobule HVIIA of the cerebellum which, as previously stated, forms reciprocal loops with the prefrontal cortex. This study also showed that activity in Crus I which is time-locked to the processing of symbolic cues decreases more rapidly for rules that become learned, or automated, more rapidly due to higher levels of reinforcement. That is, rules which received consistent, non-ambiguous feedback were learned more rapidly and the correspondingly more rapid decrease in processing activity in Crus I reflects the learning-related decreases in synaptic activity that are characteristic of Hebbian learning mechanisms and underpin the feed-forward control of behaviour (Ramnani, 2006; Balsters & Ramnani, 2011). Over and above the literature suggesting that activity in prefrontal-projecting areas of the cerebellum is evoked by first-order rule learning, it has also been shown that activity in areas such as Crus I and Crus II can be evoked by second-order rule learning tasks, which involve the processing of information at an even higher level of abstraction through the learning of primary rules which specify secondary rules which then go on to dictate action (Balsters, Whelan, Robertson & Ramnani, 2013).

Sequence learning is often used as a model to study prefrontal and cerebellar contributions to the acquisition of both motor and cognitive behaviours. Willingham (1998) defines motor sequence learning as the gradual increase in performance accuracy through repetitions of a serial pattern and typically, motor sequence learning is tested using button press tasks (Seidler, 2006). As such, sequence learning studies provide us with a kind of rule learning in which subjects learn the temporal order of rules that arbitrarily link movements, and these rules become more well-learned with practice. Research has shown that cerebellar activity decreases as motor sequence learning increases (Bernard & Seidler, 2013; Grafton et al, 2002; Toni et al, 1994; Tzvi et al, 2014). Some suggest that this is due to a transition in control from cerebellar circuitry to later control in the striatum

(Doyon & Benali, 2005). However, it is also possible that this decrease in activity reflects the representation of sequences of movements that are novel and require controlled processing, as opposed to those which are well learned (Wolpert et al, 1998). This is in keeping with the research, outlined above, suggesting that the cerebellum plays a role in automating the rules used to guide manual actions (Balsters & Ramnani, 2008; 2011). Further, research has shown that patients with damage to the cerebellum are able to implement sequences of movements when directly cued, but suffer when rules linking stimuli and responses are changed (Dirnberger, Novak & Nasel, 2013; Spencer & Ivry, 2009). Taken together, this adds to the extant literature suggesting that not only is the cerebellum a likely candidate for the storage of learned representations, but also that activity decreases in the cerebellum with increased motor sequence learning are more likely to be reflective of the acquisition of cognitive elements of behaviour, rather than movement itself.

This emerging body of literature provides direct evidence that the cerebellum is not just involved in the execution of learned movements, but that prefrontal-projecting cerebellar circuits play some kind of role in the automatic execution of well-learned cognitive rules that are used to guide action. The experimental work in this thesis aims to investigate whether this can also be applied to the oculomotor domain, and whether the cerebellum is involved in the control of eye movements. The theory behind this will be described in the next section.

1.3.3 The cerebellum and the oculomotor system

It has been suggested that the cerebellar activity associated with cognitive tasks during fMRI studies, such as the ones discussed above, is largely related to eye-movement behaviour, as research has shown that the cerebellar vermis is involved in eye movement control (Batini et al, 1978; Glickstein & Doron, 2008; Thier et al, 2002). However, the role of the cerebellar hemispheres in the automatic control of oculomotor behaviours is not as well understood. It has been claimed that in primates, the "least understood cerebellar region implicated in the control of eye movements is a large and ill-defined region in the hemispheres, adjoining vermal

lobule VII and loosely referred to as HVII" (Dash and Thier, 2014). The frontal eye fields are involved in the control of eye movements through their dense connections with the superior colliculus (Bruce & Goldberg, 1985; Schall, 2004). Anatomical tracer and lesion research in non-human primates shows that there are direct connections between the frontal eye fields, located in the prefrontal cortex, and Lobule HVII of the cereberellar hemispheres (Ohki et al, 2009; Xiong, Hiramatsu, & Nagao, 2002). Further anatomical research in non-human primates also shows connections from the dentate nucleus of the cerebellum to the frontal eye fields (Middleton & Strick, 2000). Taken together, these studies suggest that these areas of the cerebellum may play a role in the automatic control of learned eye movements, as has been shown in motor and cognitive control, outlined above. At present, this has not been tested in human subjects. Indeed, not only have patterns of activity connecting prefrontal-projecting areas of the cerebellum and areas of the prefrontal cortex itself been found in first-order rule learning paradigms that dictate actions using manual effector control, but further work from Ramnani and colleagues has also shown that first order rule learning tasks that dictate oculomotor behaviours result in decreases in Lobule HVIIA of the cerebellum, which decreases more rapidly when more consistent reinforcement creates more rapidly acquired knowledge of the rules that guide the eye movements (Argyropoulos, Mills & Ramnani, manuscript in preparation).

This thesis hopes to contribute to the emerging literature outlining the neural basis of automatic behaviours. Ramnani (2014) suggests that control theory (outlined above) provides a candidate model for understanding the neural basis of the relationship between automatic (System 1) and controlled (System 2) behaviours as outlined by Kahneman (2011). System 2 processes which are slow, sensitive to feedback, and require conscious cognitive input are supported by activity in the prefrontal cortex and over time, these transfer to System 1. Therefore, when repeated behaviours become automatic and thereby faster and more accurate, control is taken over by the cerebellum through its connections and interactions with the neocortex. The data outlined in this section and in Ramnani (2014) fit this proposal. However, the role of the cerebellum in the automation of rule-based

oculomotor behaviours is unclear and the literature in this area is just emerging. As such, this thesis hopes to help contribute to this area by using eye-tracking and brain imaging methods to investigate whether pathways running between Lobule HVIIA and cognitive areas such as prefrontal area 46, and visual areas such as the frontal eye fields mediate the transition to automatic, cognitive control of oculomotor behaviours separately from their motor commands, as outlined by Ramnani (2014).

1.3.4 Eye movements and cognition

In the same way that manual actions are shown to relate to cognition, research shows that cognitive processes are both influenced by eye movements, and eye movements are influenced by cognitive information such as knowledge, memories, and prior goals (Yarbus, 1965). Not only are eye movements argued to be the most common of all human behaviours, but they are also the result of a unique and close relationship between cognition and perception (Richardson & Johnson, 2008). As such, the studies of eye movements can help provide a detailed view of many human cognitive processes such as reading, reasoning, problem solving and overt visual attention (Jacob & Karn, 2003; Mele & Federici, 2012).

Eye tracking technologies are used to study eye movements, and they provide benefits over and above manual response methods which rely on a single button press because they provide high quality, high speed, reliable, real-time information that can be sampled continuously online at a higher rate than in manual response tasks. As such, eye tracking methods can provide a series of data points that give experimenters a more subtle insight into the cognitive processes that support the acquisition and execution of responses, rather than a single data point that captures behaviour at only one point in time (Richardson & Johnson, 2008). Further, it has been suggested that these processes are largely, though not entirely, out of the control of the subjects (Liversedge & Findlay, 2000; Spivey, Richardson & Dale, 2009).

Despite the close relationship between eye movements and cognition, few tasks that involve visual skill are conducted using eye tracking methods. Chapters

2 to 4 in this thesis aim to bridge this gap in the literature. Firstly, in Chapter 2, eye tracking methods are used in conjunction with functional magnetic resonance imaging to examine eye movements during a visual sequence learning task as sequences become more familiar. Further, in Chapters 3 and 4 eye tracking methods are used to investigate the change in automatic visual behaviours during the ageing process with respect to the Stroop task and the Useful Field of Vision task. These will be discussed in the following sections of this Chapter.

1.4   Ageing and skilled behaviour

1.4.1 Neural changes in the ageing population

The neural connections of the cerebellum and the prefrontal cortex, outlined above, are involved with shifting behaviours from an attentionally demanding state, mediated by the prefrontal cortex, to a more automatic state, mediated by the cerebellum. Such behaviours are considered to be automatic as they require less attention and less conscious input from the prefrontal cortex than new behaviours to execute (Lang and Bastian, 2002). An example of this can be seen in the cerebellar patient Gordon Holmes, who remarked that 'the movements of my left arms are done subconsciously, but I have to think out each movement of the right (affected) arm' (Holmes, 1939). Due to this shift, it is said that automatic behaviours, driven by the cerebellum, can be performed with 'little or no interference by a demanding secondary task' due to decreased dependency on active attentional mechanisms in the prefrontal cortex (Poldrack et al, 2005). Such automaticity is beneficial as it frees up attentional resources to focus on new problems that cannot be solved by previously learned information.

Areas of the cortico-cerebellar system involved in this process are susceptible to deterioration during the healthy ageing process. Functional imaging studies have shown that the prefrontal cortex experiences the highest amount of atrophy during normal ageing and less functional activity has been shown in these areas during tasks of working memory and attention in ageing populations (Cabeza et al, 1997; Raz et al, 1997; Raz, 2000). Similar effects have been shown in the

cerebellum. Large-scale MRI research has shown that after the age of 40, the cerebellum shows age-related atrophy in the vermis and areas such as the tegmentum, pretectum and the pons, which conveys signals from the cerebral cortex to the cerebellum (Oguro et al, 1998). Further, post-mortem analysis of the cerebella of 90 non-clinical individuals found that Purkinje cells, the main computational unit of the cerebellum, reduce in number by roughly 2.5% per decade of life, with this being most apparent after the age of 60 (Hall et al, 1975). The question arises, what effect does the healthy ageing process have, therefore, on the ability to acquire and maintain automatic processes? This thesis will use the neural literature to form a basis to answer these questions using behavioural investigations.

1.4.2 The Stroop task, ageing and automaticity

Paradigms which rely on the ability to resist interference from task-irrelevant information are used in the literature to test automaticity, as behaviours that are more well-learned and therefore more automatic should be more resistant to interference. A common task used to investigate this is the Stroop test. The classic colour-word version of the Stroop task involves identifying the colour of a word, whilst ignoring its semantic content (Stroop, 1935). For example, in a congruent condition, the word 'RED' would appear in the colour red, and in an incongruent condition, the word 'RED' would appear in green font. These two conditions are examples of automatic and controlled processing. For most adults, reading single words is a well-learned automatic process and in most situations can be conducted rapidly, without the need of conscious cognitive input. However, when a conflicting situation is encountered in the incongruent condition, controlled processes are enabled, which rely on attention processes much more heavily, and this causes the well-known Stroop effect, whereby the more automatic processes interferes with the less automatic process (Stroop, 1935).

The Stroop task has been widely used to test the effects of ageing on information processing. However, the research regarding how this changes with age is unclear. Some studies have shown that older adults are less able to inhibit task-

irrelevant information than younger adults, which is shown by poorer accuracy rates and larger reaction times in incongruent conditions of the Stroop task (Adólfsdóttir, Wollschlaeger, Wehling, & Lundervold, 2017; Andrés, Guerrini, Phillips, & Perfect, 2008; Aschenbrenner & Balota, 2015; Bugg, DeLosh, Davalos, & Davis, 2007; West & Baylis, 1998; West & Alain, 2000). However, these results are contested in the literature. Other studies using Stroop paradigms have shown that older adults are just as able to inhibit task-irrelevant information as younger subjects (Salthouse & Meinz, 1995; Verhaeghen, 1999, 2011; Verhaeghen & De Meersman, 1998; Williams et al., 2007).

There may be a number of explanations for this disparity in the literature. Firstly, some argue that rather than reflecting genuine cognitive decline, the ageing effect seen in the Stroop and other cognitive tasks may be explained more sufficiently by domain-general decreases in the speed at which cognitive operations can be performed (Salthouse, 1996; Salthouse & Meinz, 1995). Secondly, the Stroop literature is a large body of literature and m any variations of the Stroop paradigm have been developed and tested. Subtle differences in the experimental paradigms used may explain the variation in results. Thirdly, the methods used to study the Stroop ageing effect largely involve manual control responses. However, the Stroop task is a highly visual task. The close relationship between eye movements and cognition has been discussed previously (see above) and in highly visual tasks such as the Stroop task, the study of eye movements can help to explain how processes of oculomotor control can determine what we see, in a top-down fashion. As such, it is arguably more important to understand tasks such as the Stroop task in an oculomotor context than in a manual control context. Section 1.3.3 of this chapter explored the possibility that prefrontal-projecting areas of the cerebellum may underpin the automation of rule-based oculomotor behaviours. If these areas are susceptible to age-related deterioration, it is logical that eye movements may be altered during performance of visual tasks that rely on automatic processes, such as the Stroop task. Despite this, no studies to date have investigated the effects of ageing on eye movements during such a task.

This section shows that attempts have been made to outline how automatic information processing changes with age, but there are problems with the diversity of behaviours used to assess this. A large part of this thesis (Chapters 3 through to 5) seeks to expand upon this literature assesing the effects of age on automatic behaviours during the Stroop task (outlined above) and also on simulated driving performance and performance during the Useful Field of Vision task, which will be discussed in the following section.

1.5   Automaticity in Human Performance

1.5.1 Models of human performance

An important element of this thesis is the convergence between the fields of cognitive psychology and neuroscience outlined above, and applied behavioural psychology, in order to investigate the performance of learned, skilled behaviours across the human lifespan. A good example of a complex behaviour involving multiple cognitive, sensory and motor elements that becomes an automated, skilled behaviour with experience is driver behaviour.

Many models of human performance seek to outline levels of performance that underpin skilled human behaviours. Rasmussen (1983) proposed a three level model of human performance, distinguishing skill-based, rule-based, and knowledge-based categories. Skill-based behaviour represents the sensory-motor elements of behaviours which are smooth, automated, and take place below the level of conscious control. He suggested that once behaviours are learned, they become less sensitive to feedback for control, much like automatic, or System 1 behaviours. Rule-based behaviour is typically controlled by subsets of stored rules which are goal-oriented but occasionally require some degree of conscious, cognitive input based on feedforward control mediated by feedback based on previous experience. As such, rule-based behaviours are moving towards being akin to System 2 or controlled processes, because they are still sensitive to feedback and the value of reward on the basis of fulfilling a goal. Lastly, knowledge-based performance describes control of performance at a higher conceptual level, in which

performance is explicitly developed in the given moment based on current goals and conscious cognitive input. These behaviours require development of a goal-oriented plan, the effect of which is compared with the goal of the performance per se. As a model, this is an effective description of various levels of human performance as it takes into account behaviour based on error feedback within the model, and the structure allows the matching of categories of human performance to particular situations. This model converges well with Shiffrin & Schneider (1977) and Kahneman (2011)'s two systems model of the way humans think outlined in Section 1.2 of this chapter. The convergence between these models is depicted in Figure 1. The neural basis of these two processes are documented in Figure 1 and discussed in detail in Section 1.3.3 (see also Ramnani, 2014).

Further models of human performance can also be applied to both the models outlined above, and driver behaviour specifically (Brouwer, 2002). Michon (1985) outlined a hierarchical task analysis of driver behaviour with three levels: the strategic level, the tactical level and the operational level. When applied to driving, the strategic level comprises general decisions that must be made a priori about a specific trip such as goals, routes, risks and costs. These are slow, effortful, long-term decisions that are tailored to each individual trip. As such, they are controlled behaviours that are comparable with System 2, controlled behaviours (see Figure 1).

Michon (1985) also outlined the tactical level of performance, which is an interim level between novel and highly skilled performance. This level involves behaviours that must be manipulated whilst driving, including manoeuvres which must be undertaken but cannot be entirely prepared for such as overtaking and passing other vehicles, as well as adjustments in speed and position which are dependent on environmental circumstances, but which can be anticipated based on previous knowledge. This level of performance maps onto Rasmussen's (1983) rule-based performance, which depends on both stored, rule-based knowledge on how to react in these situations given past experience, but also requires some degree of conscious manipulation in response to unanticipated situations. As such, both of

these levels are more akin to System 2 processes, due to their dependency on flexibility and responsivity to feedback (see Figure 1).

Finally, Michon (1985) outlines the operational level of performance. These are automatic action patterns that are completed within milliseconds, for example to avoid acute danger. Behaviour on this level relies on previous knowledge to make rapid adjustments and, as such, are similar to Rasmussen (1983)'s skill-based behaviour, automatic processing in Shiffrin & Schneider's (1977) model, and Kahneman's (2011) System 1 behaviours, which may depend heavily on neural input from the Cerebellum. The relationship between these models and real-world human performance will be explored in Chapter 5 of this thesis, which will address the effect of route familiarity on driver behaviour and the transition of driving performance from a controlled to an automatic state.
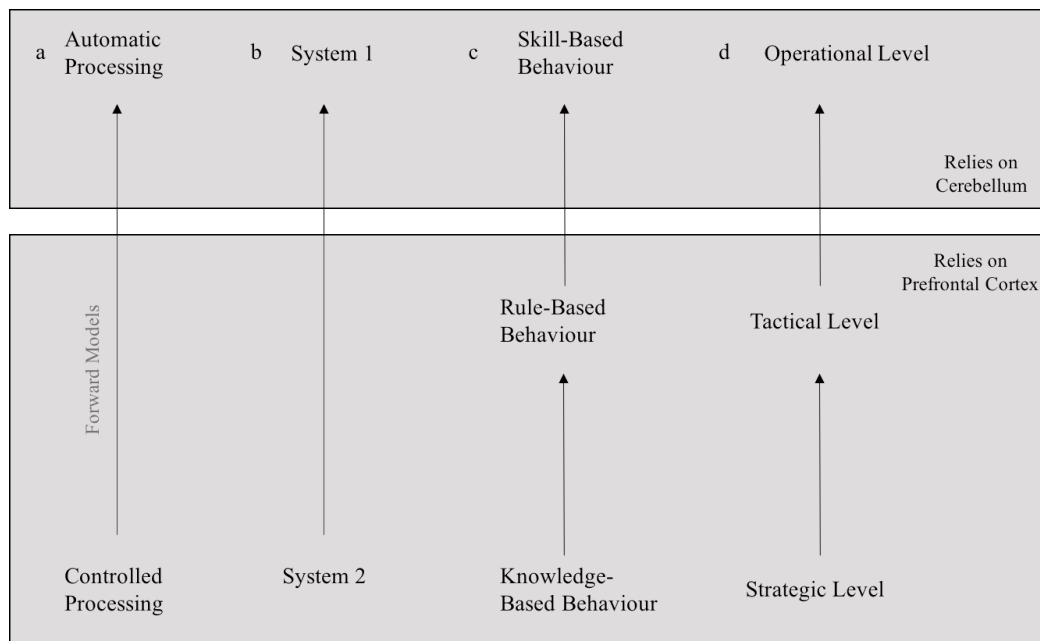
Figure 1: Convergence between models of Information Processing and Human Performance, and their proposed neural basis. a: Shiffrin & Schneider (1977), b: Kahneman (2011), c: Rasmussen (1983), d: Michon (1985). For a fuller discussion of the convergence between models a and b, see Ramnani (2014).

1.5.2 Typical accidents in ageing drivers

Chapter 5 in the thesis will use driving as a skilled behaviour to test whether there are age-related changes in the ability to perform learned behaviours in novel and familiar environments. Driver behaviour is an important area to study for applied behavioural psychologists with an interest in ageing due to the ever increasing life expectancy rates in the Western world and, subsequently, the increasing population of elderly people living more functional lifestyles. Research suggests that alongside the increasing population of older drivers, they are prone to particular types of crash. These two factors will now be addressed in turn.

In Britain in 2013, it was estimated that 16.6% of the population was aged over 65, and 2.3% were aged over 85 (Mitchell, 2013). Statistics from the United States show that between 1983 and 2008, the number of younger drivers holding a valid driving license has decreased; whereas the number of drivers aged 50 and above holding a valid US driver's license has increased consistently across the period, with the largest increases seen in the 65-59 and 70+ age groups (Sivak & Schoettle, 2011). Further analysis has shown generally the same pattern of decreases in license-holding younger drivers and increases in license-holding older drivers in many other countries, including Sweden, Norway, Great Britain, Canada, Japan, South Korea and Germany (Sivak & Schoettle, 2011), though the data used to draw these conclusions differed slightly in nature (age groupings, timing of data collection) between countries. Regression analysis of the data from these countries showed that median age was a significant predictor of the percentage of persons holding a valid driver's license (Sivak & Schoettle, 2011). Analysis of driving license holders in Great Britain specifically has shown a clear, consistent increase in license holders aged 70 and over since 1975 (Mitchell, 2013), a trend which is predicted to continue, particularly for women aged over 70, until 2030 (Siren et al, 2001). The same data by Mitchell (2013) also shows that these numbers may be ameliorated given evidence that the number of individuals, in particular women, that voluntarily surrender their driving licenses increases after the age of 70, though this could be due to unintentional pressure from the legislative processes involved in renewing a license, discouraging older but unimpaired drivers from feeling able to renew their licenses, rather than self-declaration of hazardous impairment (Ross,

Browning, Luszcz, Mitchell & Anstey, 2011). Accordingly, some evidence suggests that older drivers, up to the age of 75-80, are no more likely to be involved in fatal crashes than any other age groups, and that older drivers are involved in fewer pedestrian fatalities than younger drivers (Mitchell, 2013) but such evidence is often based on raw numbers, and therefore fails to account for the statistics showing that older drivers still constitute a smaller proportion of drivers in total, and that they often engage in disproportionate amounts of self-regulation (by avoiding driving in more hazardous situations such as at night time or in hazardous weather conditions), and so may not accurately represent the proportionally higher fatality rates in older drivers (Rolison, Hewson, Hellier & Husband, 2013).

Indeed, along with the increased trend for road-legal older drivers comes a large body of research showing they are over-represented in the accident data. Regression analysis of crash data in Britain between 1989 and 2009 by Rolison et al (2012) which used number of trips made by road users to calculate risk of fatal injury found that risk of fatal injury was highest for elderly drivers, elderly passengers and elderly pedestrians. Further, analysis of police reported crash data in the US between 1983 and 1995 has shown that fatal crash involvement for drivers aged 70 and over per capita increased by 34% but fatal crash involvement in the same period for drivers aged 16-69 reduced by 4% (Lyman, Ferguson, Braver & Williams, 2002). These authors also found that per vehicle miles travelled, fatal crash involvement rates started to rise after the age of 65, and this increase became much more substantial after the age of 70 (the same results have also been found by Li, Braver & Chen, 2003). Lyman et al (2002) also used the average annual police reported crash and fatal crash rates per licensed driver from 1990-1999 to predict the number of crash involvements for older drivers (aged 65 and over) in 2010, 2020 and 2030 and found that expected percentage contribution to fatal crash involvements to rise from 14% in 1999 to 15% in 2010, 20% in 2020 and 25% in 2030. More detailed analysis of over 4 million crash injuries in Texas over a 25-year period found that when compared with drivers aged 55-64, drivers over 65 were 1.78 times more likely to die in a fatal car crash, drivers over 75 were 2.59 times as likely to die and drivers over 85 were 3.72 times as likely to die (Griffin,

2004), though it may also be argued that higher fatal casualty rates may be due to frailty in the elderly population.

As well as data showing that older drivers are represented in the crash data in general, research also suggests that older drivers disproportionately experience particular types of road traffic accident. In particular, older drivers experience problems in real-world situations that rely on divided attention and decision making processes when they are placed under strict time constraints, including at intersections. Approaching an intersection requires analysis of one's own speed and position - both current and intended, traffic signs and signals and speed and location of oncoming traffic (Dotzauer, Caljouw, De Waard & Brouwer, 2013). It has been suggested that age-related depletion of attentional capacities, as described above, particularly at times when there is large amounts of visual information, could be responsible for older drivers' involvement in accidents that involve the manipulation of multiple variables for successful performance (Owsley et al, 1998). These limits on attentional mechanisms leave older drivers unable to engage in the operational behaviours (also known as System 2 or knowledge-based behaviours as outlined by the models of human performance, see Figure 1) which are important for driver safety. Detailed analysis of the crash data from Texas from 1975 to 1999, described above, also showed that drivers aged over 65 were 1.26 times more likely to be involved in a crash at a left turn, drivers aged over 75 were 1.4 times as likely and drivers aged over 85 were 1.5 times as likely than drivers in a control group aged 55 to 64. Research suggests that not only might this be due to decreased attentional abilities, other factors also play a role in older drivers' inability to manoeuvre safely at intersections such as reduced neck flexibility and reduced visual search capacity in situations requiring the manipulation of information from multiple visual areas at once (Dukic & Broberg, 2012). This research found that older drivers tend to focus more on visual information in the centre of the visual field such as road markings than younger drivers, who were more able to focus on dynamic information surrounding them such as the position of other vehicles. It seems logical, therefore, that specific inabilities such as these leave older adults prone to collision in situations where oncoming traffic must be navigated, such as

at an intersection. Older drivers even self-report experiencing particular issues more than other age groups when approaching intersections including not seeing oncoming vehicles, that is, they claim that they 'looked but did not see' other vehicles, and miscalculating the distance to turn causing a failure to yield (Braitman, Kirley, Ferguson & Chaudhard, 2007; Staplin, Lococo & Byington, 1998).

1.5.3 Factors underlying driving performance in the ageing population

Many suggest that age alone is an inappropriate indication of driver safety, as many other variables can impact on driver behaviour (Sommer, Falkmer, Bekiaris & Panou, 2004). In a systematic review of the driving literature as coded by 5 experts in the field, Vichitvanichphong, Talaei-Khoei, Kerr, & Ghapanchi (2015) found that factors underlying the decline in driving performance with increased age (outlined above) fit into three broad categories: physical, cognitive and visual abilities. The effects of ageing on driving performance were found to be due, in part, to age-related changes in motor abilities. These include musculoskeletal changes such as decreased neck rotation and limb and foot damage as well as physical reaction time. Cognitive decline affects older adults' ability to manage multiple tasks at once, which is a vital requirement for successful driving. Changes in cognitive abilities such as selective and divided attention and speed of information processing may relate to crash statistics in older drivers. Finally, changes in visual abilities such as colour vision, acuity, speed of visual search and Useful Field of Vision have been shown across the literature to correlate with older adults' driving abilities. For the sake of brevity in relation to this thesis, only cognitive and visual changes will be discussed in this section.

In general, on-road driving performance has been shown to correlate with a number of cognitive tests such as the Trail Making Test and the Wechsler Adult Intelligence Test (De Raedt & Ponjaert-Kristoffersen, 2000; Schanke & Sundet, 2000). Decline in performance during such tests have been widely associated with declines in driving performance in older adults. Mathias & Lucas (2009) conducted a meta-analysis of 21 studies assessing the on-road driving performance or previous

crash history of drivers aged 55 and over. They found that declines in tests of visuospatial awareness, memory span, movement perception, attention and reaction time were related to failure in either on-road or simulated driving tests. Further, older drivers with a history of driving offences were found to score more poorly in attention tasks such as the Stroop test, the Trail Making Test, the Useful Field of Vision task and also the Wechsler Adult Intelligence Test. The Useful Field of Vision Test (UFOV, see below and Chapter 4 of this thesis for a fuller discussion) was the only significant predictor of all three variables: on-road driving performance, simulated driving performance and previous accident history. Similar results were also found in an experimental study by Adrian, Postal, Moessinger, Rascale & Charles (2011). The authors studied 42 subjects aged 60-82 years old and found driving performance was associated with low scores on tasks of attention and task switching such as the Trail Making Task and the Plus-Minus task, and the Operation Span task, which assess cognitive updating abilities.

Driving involves the integration of multipl2e behaviours in parallel, and adapting to continually changing environment cues. As such, it relies on controlled processes, supported by the executive functions outlined above (Shallice, 1982; Norman & Shallice, 1986). As particular driving environments are encountered more times, driver behaviour may become more automated. As such, it is logical that drivers should benefit from previous experience when driving in familiar locations. If this process is impaired, such as during ageing, subjects may not be able to benefit from the learning process. This may help to explain why older drivers report avoiding driving in unfamiliar routes and locations (Burns, 1999; Joly, Frigon, & Daigneault, 2002; Older Drivers Task Force). Some research has investigated the extent to which familiarity with an environment affects driving in general, but this literature is conflicted.

Some research suggests familiarity increases performance in driving tasks. Read et al (2011) showed drivers who reported being more familiar with a route in their local area are less likely to commit navigation errors, less likely to commit safety errors, and less likely to get lost during a wayfinding task. However, some

research suggests that familiarity with a route leads to poorer driving performance, due to 'inattentional blindness' (Yanko & Spalek, 2013). This is when familiarity with a behaviour leads to mind wandering, leaving subjects less able to successfully complete the task at hand. Some research suggests that in familiar environments, drivers are more likely to engage unsafe behaviours such as driving faster, allowing smaller gaps with a pacer car and are less able to notice and react to novel stimuli in the environment (Charlton & Starkey, 2012; Colonna, Intini, Berloco, & Ranieri, 2016; Intini, 2016; Yanko & Spalek, 2013;). To our knowledge, only one study has addressed the effect of ageing on this process. In Read et al (2011)'s study, drivers aged 65 and above took longer to complete the task, and were more likely than younger drivers to commit navigation and safety errors, even when familiar with the route. To some extent, these effects were ameliorated by familiarity, but the older drivers continued to perform more poorly than younger drivers. To our knowledge, no other studies have addressed this topic. This is surprising given the wealth of evidence outlined above suggested older adults experience cognitive decline which can negatively impact driving performance, and that older adults self-report avoiding driving in unfamiliar environments.

Many agree that the decision of whether older adults should continue driving should not be based on cognitive tests alone (Withaar et al, 2000; Brooks & Hawley, 2005). It is estimated that 90% of the sensory information that is processed during driving is visual (Hills, 1980). It is well known that overall, vision deteriorates with increasing age (Attebo, Mitchell, & Smith, 1996).

Visual acuity is one of the most commonly used tests of visual function. Visual acuity is measured using the Snellen chart and categorises visual impairment from mild to moderate. Visual acuity has shown to decrease with increasing age, with particularly large levels of deterioration seen after age 70 (Burg, 1968; Attebo et al., 1996). However, the literature regarding the relationship between visual acuity and driving performance across the lifespan is conflicted. Some research suggests that poor visual acuity is related to crash risk, and that licensing drivers based on tests of visual acuity can help reduce fatal crash rates in older drivers

(Hofstetter, 1976; McGwin et al, 2008). However, others suggest there is little evidence to show any relationship between visual acuity and safety or performance of older drivers (Burg, 1967; Owsley & McGwin, 2010).

Other common measures of visual functioning, including binocular vision, dynamic visual acuity and colour vision have also been suggested to relate to driving performance in older adults. Though some studies have found scores on such measures relate to driving performance, the literature is equivocal, and those that do find correlations between these measures show they predict relatively small amounts of the variance (see Stoneley, Harrison, Manning & Haunton, 2014 and Wood, 2002 for reviews of the literature). The reasoning for this may be three-fold. Firstly, the tests used to assess visual function may not be closely related enough to real-world visual behaviours to predict driving outcomes (Bohensky, Charlton, Odell, & Keeffe, 2008). Secondly, many measures of both visual function and previous crash history rely on self-report (see Kline et al, 1992 for an example), which must be interpreted with caution. Inconsistencies between self-reported measures and official statistics have been shown in the literature surrounding previous crash history in older drivers (Owsley & McGwin, 2010), and research suggests around 50% older adults do not regularly undergo eye tests so may be unaware of deteriorating visual health (McGwin, Khoury, Cross, & Owsley, 2010). Thirdly, research shows that older adults who have visual impairments may self-regulate their driving, and so may not be represented appropriately in the statistics (Gilhotra, Mitchell, Ivers, & Cumming, 2001; Stoneley et al, 2014).

One test of visual function remains to be discussed. The Useful Field of Vision (UFOV), also known as the useful field of view or the 'functional visual field' is a concept first defined by Sanders (1970) and is defined as the area of the visual field from which information can be acquired from one fixation, in the absence of additional eye or head movements. Inspired by classic visual search tests, the conceptualisation of this was accompanied by a well-known computer based test within the ergonomics literature, known as the UFOV assessment (Ball & Owsley, 1993). This is a particularly useful test to combine with the human

performance models described above and with research into the roles of the prefrontal cortex and the cerebellum in the execution of learned behaviours, as it also provides a convergence between purely oculomotor and cognitive behaviours. The UFOV test relies on both the quality of processing of visual sensory information in the eyes and brain, but also, much like driving, on the individual's capacity to deal with selective and divided attention tasks in parallel (Ball, Owsley & Beard, 1990).

The UFOV task involves completing a selective attention task in the central visual area such as discriminating between two shaped targets and in parallel performing a divided attention task in the peripheral visual field, such as discriminating the location of a visual stimulus. Early vision research showed that visual acuity decreases as stimuli become more peripheral (Aubert & Foerster, 1857), and so the further away the peripheral target is from the central task, the more difficult the UFOV task becomes. The task sheds light into visual abilities over and above those tested in a standard ophthalmological exam using standard visual field tests as it measures both acuity in the central and peripheral visual fields as well as the ability to manipulate this into meaningful information which can be used to guide behaviour. Research shows the convergence of these two tasks results in an increased attentional and cognitive load, resulting in decreases in performance when compared with conducting a peripheral visual field tasks on its own in younger populations (Abernethy & Leibowitz, 1971; Ikeda & Takeuchi, 1975). Moreover, these performance decreases are even more marked in older adults, who make larger mistakes than younger subjects, particularly when secondary stimuli are located at larger radial eccentricities (Ball, Beard, Roenker, Miller & Giggs, 1988; Ball, Owsley & Beard, 1990; Edwards et al, 2006; Sekuler, Bennett & Mamelak, 2000).

This body of work may explain why older adults who otherwise show no clinical deficits experience systematic issues with specific parts of daily life, such as driving, which relies on integrating multiple streams of information in order to successfully complete the task. Performance on the UFOV task has been shown to

be a good predictor of crash involvement in older adults (Stoneley et al, 2014). A meta-analysis of studies using UFOV tests and either measures of retrospective driving abilities, current driving abilities, on-road driving or driving simulator performance in older drivers across eight studies consistently found that poor UFOV performance predicted negative driving outcomes, with a robust effects across the different measures of driving performance (Clay et al., 2005). Similar results have been shown by numerous other studies, which show performance on the Useful Field of Vision task is a better predictor of previous motor vehicle accidents in older drivers than other cognitive factors such as cognitive status, eye health and visual processing abilities (Ball, Owsley, Sloane, Roenker, & Bruni, 1993; Quigley, 1993; Owsley, McGwin & Ball, 1998; Mathias & Lucas, 2009). The only exception to this was in a study of drivers aged 55-87 years, Owsley, McGwin, & Ball, 1998) found that glaucoma was a significant predictor of previous injury during a motor vehicle accident, as well as UFOV performance.

1.5.4 Ageing and hazard perception

Hazard perception is a crucial element of safe driving. Hazard perception is defined as the ability to predict dangerous situations on the road (Wetton et al., 2010). Hazards can take many forms, but are generally defined as 'any object, situation, occurrence, or combination of these that introduce the possibility of the individual road user experiencing harm. Hazards may be obstructions in the roadway, a slippery road surface, merging traffic, weather conditions, distractions, a defective vehicle, or any number of other circumstances' (Haworth et al, 2001, p. 3). In general, hazard perception research tends to focus on the differences in performance between novice and experienced drivers. Research suggests that experienced drivers, generally defined as those who have had a full driving license for over 3 years, are able to predict hazards earlier than novice drivers, and this may help to explain why driving experience negatively correlates with crash risk (Crundall, 2016; Jackson et al, 2009; Kinnear, Kelly, Stradling., & Thomson, 2013; McCartt, Shabanova, & Leaf, 2003; McKenna & Crick, 1994; McKenna & Crick, 1997). A number of hazard perception tests have been developed, with the aim of predicting possible accident liability in all drivers. These tests are beneficial as they

are short, have high reliability, and have been successfully incorporated into the UK Driving Test. The process of creating hazard perception tests that predict capability for licensing is beyond the scope of this thesis, but a comprehensive review can found by Grayson & Sexton (2002). An important caveat to current hazard perception research is that it largely overlooks other variables that may impact hazard perception ability.

It has been suggested that during driving, situations of high cognitive load, where a competing task demands a large amount of cognitive resources, should affect controlled but not automatic processes (Engström, Markkula, Victor & Merat, 2017). This cognitive control hypothesis is in keeping with models of automaticity outlined in Section 1.2 of this chapter, which argue that an important aspect of automatic behaviours is that they require fewer conscious cognitive resources. Therefore, automatic behaviours can be completed without interference from a secondary task or situation of high cognitive load, as there is a larger amount of spare capacity that can be devoted to dealing with this information (Fitts & Posner, 1967; Poldrack et al, 2004). As such, when certain driving situations become well automated, for example when familiarity with a given environment increases, this leaves more scope for attention to be allocated to additional controlled processes with a high cognitive load. Therefore, hazard perception ability should be better when driving in familiar locations, because drivers should have more spare attentional capacity to be able to notice novel incidents in the environment. Some research suggests that novice drivers' hazard perception reactions were significantly slower when the subjects were asked to complete a secondary verbal task in parallel (Horswill & McKenna, 1999), but McKenna & Farrand (1999) found that when compared with novice drivers, experienced drivers' hazard perception performance suffered even more in the face of a competing secondary task. Much like most of the evidence in the ageing literature, research here is conflicted. Whilst some show that hazard perception declines with increasing age (Quimby & Watts, 1981), others show that hazard perception abilities in older drivers are equal to those of younger drivers (Olson & Sivak, 1986; Underwood, Phelps, Wring, van Loon, & Galpin, 2005; Borowsky, Shinar & Oron-

Gilad, 2010). This contradiction in the literature may be due to differences in familiarity with the environments in which the drivers' hazard perception abilities were tested. A number of the studies outlined tested hazard perception in older drivers in environments with which they were already familiar, which may have facilitated their performance. As explored in section 1.5.3 of this Chapter, changes in executive processing with increased age may leave older drivers less able to automate new behaviours, which may also subsequently impact their hazard perception ability in new environments. To date, no studies have directly investigated how hazard perception changes as environments become more familiar and driver behaviour arguably becomes more automated, nor have they investigated the differences between hazard perception abilities of older drivers in novel and familiar environments.

1.6 Summary and the current thesis

The present chapter outlines the current theory, research and application of skilled behaviour and automatic processing in humans. Since the development of the two-process model of human information processing by Shiffrin & Schneider in the 1970s, and subsequent models based on this (see Figure 1), much research has been conducted into automatic and controlled processing, the neural basis of these mechanisms, and how they change with age. This thesis aims to expand this literature, and merge the fields of cognitive psychology and neuroscience with the field of human performance.

Chapter 2 seeks to add to the literature investigating the neural basis of automatic visual processing. Previous research suggests that the development of both cognitive and motor skills, which are automatic in nature, is supported by neural changes in areas of the cerebellum that reciprocally connect with distinct areas of the cerebral cortex (Marr, 1969; Albus, 1971; Kelly & Strick, 2003). Anatomical research shows such reciprocal connections exist between areas known to be involved in oculomotor control, such as the frontal eye fields, and the same areas of the cerebellum, namely Lobule HVII (Xiong, Hiramatsu, & Nagao, 2002; Ohki et al, 2009). Using fMRI and eye tracking methods, Chapter 2 seeks to address

whether, consistent with previously established mechanisms of long-term depression, reduction in activity in neurons in Lobule HVIIA of the human cerebellum also underpins the automatic, cognitive control of learned eye movements, separately from their motor commands. Most sequence learning paradigms rely on manual button-press responses (Bernard & Seidler, 2006), but this study aimed to test, for the first time, the neural mechanisms that underpin eye movements during an *explicit* visual sequence learning task. In this chapter, the hypothesis that decreases in activity in Crus I and Crus II Lobule HVIIA would support eye movements as they became more familiar was tested using a novel paradigm involving the presentation and rehearsal of a series of visual sequences.

Chapters 3-5 then seek to elucidate how the typical ageing process affects our ability to learn and maintain automatic behaviours. Based on previous research outlining the neural degeneration in both the prefrontal cortex and cerebellum that occurs in typical ageing, Chapter 3 investigates the automatic priming of eye movements during the Stroop task, and how these are affected by the ageing process. Previous research using the Stroop task has provided conflicting evidence regarding the effect of the healthy ageing process on response inhibition, and this research remains equivocal. In Chapter 3, the hypothesis that ageing increases susceptibility to the classic Stroop effect is tested using a novel spatial Stroop paradigm which relies on non-linguistic but informative cues. Performance on this task was tested in groups of young adults and healthy older adults. The use of eye tracking methods also allowed, for the first time, an investigation into the effects of age on the kinematics of eye movements during a spatial Stroop task.

Chapter 4 investigates this in the context of the Useful Field of Vision task. Previous research suggests that the ability of older adults to use selective and divided attention mechanisms to complete both a central and peripheral visual task in parallel is poorer than in younger adults. Further, this deterioration has been shown to relate to crash risk in older drivers. This chapter seeks to use eye tracking methods in groups of younger and ageing adults to address methodological caveats in the extant literature, which lack methodological diversity. In this Chapter, the

hypothesis that the Useful Field of Vision decreases with increased age is tested using a novel Useful Field of Vision task which relies solely on eye movements for task completion. This allowed, as above, the simultaneous investigation of the kinematics of eye movements during the Useful Field of Vision task.

Finally, Chapter 5 continues to investigate the effects of ageing on the skilled performance of human behaviours across three experiments using driving simulation methods. Route familiarity is a prime candidate for investigating changes in skilled performance of driver behaviours. Previous research provides conflicting evidence surrounding the effect of familiarity with a visual environment on driver behaviour, and the literature testing this in ageing drivers is very limited. The first two studies aim to address this debate by investigating changes in features of driving performance such as steering during manoeuvres at junctions in urban environments and lane changes in motorway environments. These are tested in both younger and older drivers as visual environments transition from being novel to familiar. Building on the previous two experiments, the third experiment in this chapter aims to utilise the familiarity developed in the first experiment to investigate whether hazard perception skill in younger and older drivers is facilitated by increased familiarity with a visual environment.

Chapter 2: Memory-guided Oculomotor Sequences: Prefrontal and Cerebellar Working Memory Mechanisms

2.1   Introduction

In order to navigate everyday life in the most efficient manner possible, we rely on the rapid implementation of previously learned behaviours. This is important for behaviours which rely on past actions such as the use of oculomotor patterns for safe driving. Theoretical accounts have long held that that cerebellar circuitry may be capable of plasticity which can support the acquisition of motor skills (Albus, 1971; Ito, 1982; Marr, 1969). They predict that learning is accompanied by a reduction in synaptic efficacy between Purkinje cells and their inputs, and consequently a reduction of around 50%, to below baseline, in Purkinje cell activity during motor learning (Gilbert & Thach, 1977; Jirenhed, Bengtsson, & Hesslow, 2007). Control theoretic accounts propose that cerebellar circuitry may automate motor behaviours through the acquisition and storage of 'forward models' of action, which are representations of previously conducted actions. These are then used to allow pre-learned movements to be deployed efficiently and with reduced use of attentional resources in the future (Marr, 1969; Thach, 1998; Wolpert, Miall & Kawato, 1998). These models require cerebellar circuits to communicate with the motor cortex (Allen and Tsukahara, 1974; Ramnani, 2006, 2014l Wolpert et al, 1998).

In Chapter 1, the neural basis of automatic and controlled processing was discussed. It was suggested that controlled, conscious System 2 processes would be supported by activity in the cerebral cortex but as these become automatic, control (system 1 processes) would be taken over by the cerebellum. Indeed, in the primate brain, candidate areas for the storage of motor memory are thought to include specific parts of the cerebellar cortex, and these reciprocally connect with the primary motor cortex (Kelly and Strick, 2003). The primary motor cortex has been shown to form reciprocal connections with cerebellar lobules V, VI, VIIb, and VIIIa, and this loop is understood to support motor learning (Kelly & Strick, 2003; Middleton & Strick, 2000). It is now widely accepted that in non-human primates,

other areas of the frontal lobe such as the prefrontal cortex similarly communicate with different parts of the cerebellum, specifically, vermal and hemispheral parts of lobule HVIIA, which take up around 47% of the human cerebellum (Diedrichsen, Balsters, Flavell, Cussans, & Ramnani, 2009; Kelly and Strick, 2003). If activity decreases in the motor cortico-cerebellar loop subserve motor learning, it is possible that this prefronto-cerebellar system may support the acquisition of forward models that support the development of cognitive skills, given the role of the prefrontal cortex in the processing of rule-related information (Miller & Cohen, 2001; Ramnani, 2006, 2014; Wallis et al, 2001).

Recent literature supports this suggestion. Two behavioural models have been particularly useful for developing our understanding of prefrontal and cerebellar involvement in learning the rules used to select actions. First, sensory cues can be arbitrarily paired with specific responses through instrumental trial-and-error learning using feedback. This ability depends, amongst other areas, on the prefrontal cortex and cerebellum (Wise and Murray, 2000). In Chapter 1, previous research surrounding the role of Crus I of Lobule HVIIA in the processing of rule-related symbolic cues, independently of movement–related activity (Balsters and Ramnani, 2008; 2011), and the relationship between such activity and computational models of cerebellar learning (Albus, 1971) was discussed. Such findings are consistent with the view that as well as being involved in the execution of learned motor behaviours, the physiological processes in prefrontal-projecting areas of the cerebellar cortex also support the acquisition of cognitive skills used to guide manual actions.

The second behavioural model used to understand prefrontal and cerebellar contributions to behaviour is sequence learning. Motor sequence learning is defined as the gradual increase in performance through repetition of a serial pattern (Willingham, 1998). It is widely understood that the early stages of implicit and explicit sequence learning rely on the cerebellum (Doyon et al, 2003; Bernard & Seidler, 2013; Tszvi, Munter & Kramer, 2014). Some have suggested that the process of motor sequence learning involves a shift from cerebellar circuitry to later

dependency on sensorimotor representations in areas of the striatum (Doyon and Benali, 2005), whilst others have suggested that dependency shifts between different cortico-cerebellar and cortico-basal ganglia loops: from those that communicate with the prefrontal cortex, to those that communicate with the motor cortex (Hikosaka et al, 2002). Many suggest that there is a decrease in cerebellar activity as motor sequence learning progresses (Grafton et al, 2002; Toni et al, 1994; Tzvi et al, 2014). Some suggest this activity is related to the processing of prediction errors, the rate of which decrease when a motor sequence is well learned (Tzvi et al, 2014), whilst others suggest that this activity reflects the processing of stimulus-response associations that are to be learned, as compared to those which are already learned (Wolpert et al, 1998). Therefore, while there is agreement that the cerebellar cortex plays an important role, its specific contributions are not clear. This chapter seeks to expand upon this literature.

The role of the cerebellum in motor eye movement control is well documented. Research shows that the cerebellar vermis is involved in the control of eye movements (Batini et al., 1978; Thier et al., 2002). Saccades are commonly used to study motor learning. Saccades are made at high speeds, so are largely unable to rely on real-time sensory feedback to adjust the online control of movement, and tend to be made in an anticipatory manner, using predictive mechanisms which are likely to have import loci in the vermal cerebellum (Dash & Thier, 2014; Optican, 1995). The role of the cerebellar hemispheres in the control of eye movements is less well understood. Anatomical research in non-human primates shows that cortico-pontine fibres from the frontal eye fields synapse with cells in the pontine nuclei that project to lobule HVII of the cerebellar hemispheres, suggesting that the cerebellar hemispheres, particularly areas Crus I and Crus II may also play a role in the voluntary control of eye movements (Xiong, Hiramatsu, & Nagao, 2002). Indeed, Ohki et al (2009) show lesions in Lobule HVII result in delayed onsets and more variable amplitudes in both smooth pursuit and visually guided saccades. The authors also found that prior to lesion, learned visually-guided saccades had shorter durations, which returned to the normal range after lesion, perhaps suggesting that this area is involved in predicting eye movements based on

prior learning, and the benefits of learning may be negated by damage to the lobule HVII of the cerebellar hemispheres. This evidence is not conclusive, however, as lesions in Ohki et al (2009)'s studies were not precise and included both hemispheric VIIa and VIIb, both of which take up a large area of the cerebellum (see Diedrichsen et al, 2009), so it is uncertain whether one or both these areas contribute to the control of eye movements. Further, the same results have not been shown in human subjects because the same manipulations have not been applied in humans.

The present study attempts to address the following unresolved issues. First, most previous studies have used visually guided manual sequences with responses delivered by the finger or hand, in which oculomotor sequence learning must play a significant role (Miyashita, Miyachi & Hikosaka, 1996). To date, only one previous study has used eye movements to investigate cerebellar contribution to visuomotor sequence learning and this was in an implicit rather than an explicit sequence learning paradigm (Bernard & Seidler, 2013). During explicit sequence learning, the subject is aware of the intended outcome of the task, whereas during implicit sequence learning, sequences are often embedded as part of a larger task so the subject is not aware that they are learning the sequence. In the context of automation, this is important as behaviours that are more automatic are argued to occur below the level of conscious awareness, but behaviours that are more controlled are argued to rely more on conscious processing (see above). An important aim of this study is provide a detailed understanding of the parts of Lobule HVIIA that contribute to the cognitive control of eye movements.

Second, it could be argued that most experimental approaches to investigating sequence learning have involved the use of visual cues to guide eye movements, a process that is critically dependent on cerebellar circuitry (Stein and Glickstein, 1992). It could therefore be argued that cerebellar involvement may be due to the oculomotor rather than the cognitive control of sequence learning. Here, functional MRI was used to test the hypothesis that reduced activity would be shown in lobule HVIIA as subjects rehearsed oculomotor sequences that became

increasingly familiar, and therefore arguably more automatic. Elements of the experimental design presented in this Chapter required subjects to do so purely from working memory, without visual guidance, so oculomotor sequences were memory-rather than visually guided, relying on automatic, System 1 rather than controlled, System 2 processes.

2.2   Methods

2.2.1   Subjects

Sixteen subjects were used in the study (12 females; mean age = 24 years; standard deviation (SD) = 5.93). All subjects had normal or corrected-to-normal vision, were right-handed, and reported no neurological or psychiatric diagnoses. They were recruited from the student population of Royal Holloway, University of London. Subjects gave written, informed consent, and the study was approved by the Royal Holloway, University of London Psychology Departmental Ethics Committee. The study also conformed to the requirements of the Combined Universities Brain Imaging Centre (CUBIC) Rules of Operation (http://www.pc.rhul.ac.uk/sites/cubic/). All subjects received £10 for their time. Two subjects were removed prior to analysis due to poor quality eye-tracking data and low quality calibration of the eye tracker during the experimental session.

2.2.2   Apparatus

Subjects lay supine in a 3 Tesla Siemens Trio MRI scanner (http://www.pc.rhul.ac.uk/sites/cubic/) with their heads firmly stabilised within the head coil using cushioned pads. Stimuli were back-projected onto a screen behind the subjects and viewed through a mirror, which was positioned on the head coil above the subjects' eyes. An MRI-compatible Eyelink 1000 camera and infrared illuminator (SR Research Ltd, Canada) were positioned 60cm behind the subjects' head and used to track movements of subjects' right eye monocularly. Eye movements were sampled at a rate of 1 kHz.

The Eyelink 1000 system creates output files that automatic parse fixations, saccades and blinks and these can be used to calculate other eye movement kinematics. For Chapters 2, 3 and 4 of this thesis, these measurements were used. An online parser in the system uses velocity and acceleration-based saccade detection methods. A saccade is a short, ballistic eye movement. Velocity and acceleration are detected continuously online and when a threshold of 30° per second is reached, a saccade event is detected. Online analysis of gaze also allows Eyelink to detect fixation events. These were detected by sampling the gaze at a regular interval of 100ms. If the gaze is stable, a fixation event is detected. The onsets and offsets of these events and the X and Y co-ordinates of the gaze are recorded.

Experimental events were controlled using Experiment Builder software (SR Research Ltd, Canada) which ran on a dedicated Windows PC and automatically stored behavioural results in a log file. These events were precisely synchronised with scan onset times (transistor-transistor logic pulses from the MRI system were conveyed to Experiment Builder via a parallel port interface). In addition, experimental events and scan onset times were continuously sampled on an independent system at a frequency of 1 kHz using (A/D 1401 unit with Spike2 software on a separate Windows PC; Cambridge Electronic Design).

2.2.3 Experimental design

Table 1: Visual Sequence Learning Experimental Design Table

Block	Presentation (training for Rehearsal)						Rehearsal					
Learning Level	Novel			Familiar			Novel			Familiar		
#Rehearsals per block	1	2	3	1	2	3	1	2	3	1	2	3

Subjects were required to rehearse and execute a spatial oculomotor sequence purely from memory, in the absence of any spatial cues. Subjects were

familiarised with the behavioural requirements before the start of the experiment (see below).

Prior to entering the MRI unit and completing consent forms, subjects were given written task instructions. These instructions gave a written description of the task and, importantly, encouraged subjects to only move their eyes when the grid was displayed on the screen, not while the screen was blank. After entering the MRI unit but prior to entering the scanner, subjects were further reminded of the task instructions using a visual presentation on Microsoft PowerPoint. This presentation contained an accurate visual representation of the screens that would be presented during the experimental session, and a guided example of how and when eye movements should be made.

Blocks:
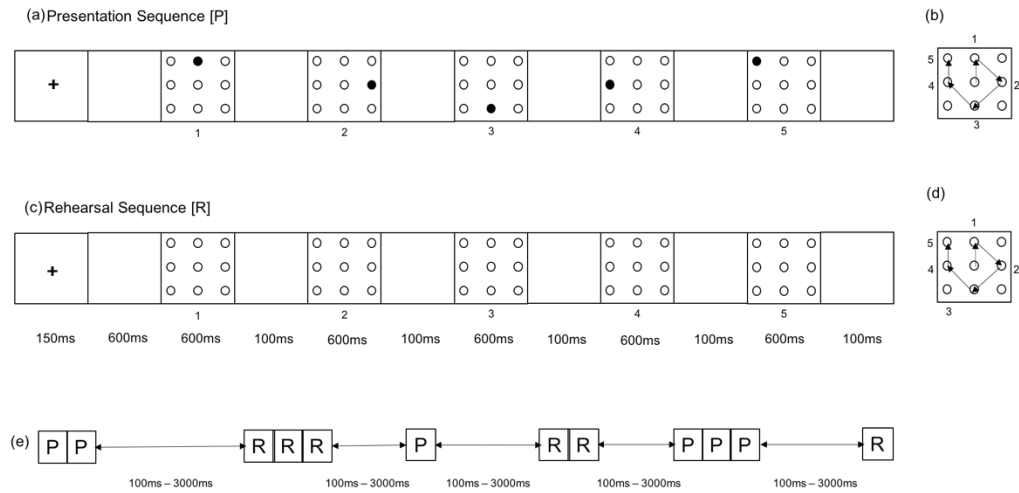
Figure 2: Experimental Design for Presentation blocks (a) and subsequent Rehearsal blocks (c) with timing details (b) and (d): Desired eye movements during Presentation and Rehearsal blocks respectively on a given trial. Eye movement behaviour during both blocks was intended to be the same, with equivalent motor demands. The only difference between these blocks was the presence or absence of visual cues (e): Trial structure with included jitter locations and durations (randomly distributed). Each Presentation and Rehearsal sequence was pseudorandomly repeated 1, 2 or 3 times consecutively as shown in (e).

Subjects were given successive pairs of 'Presentation' and 'Rehearsal' blocks, within which there were a series of sequence element trials (see below). During Presentation blocks, a sequence was learned under guidance of a spatial cue (filled circle) that moved across a 3 x 3 grid of nine empty circles (see 'Trials' below for details; Figure 2). There was a variable delay lasting 100ms-3000ms, during which the word 'Rehearsal' was displayed to inform subjects that the corresponding Rehearsal block would follow. During Rehearsal blocks, subjects were required to execute the same sequence purely from memory, without the guidance of spatial cues. We manipulated the level of learning by exposing subjects either to a Novel sequence (45 different sequences, not repeated from block to block), or a highly Familiar sequence (A single, highly Familiar sequence repeated across 45 blocks). Novel and Familiar sequences were pseudorandomly intermixed. The length of each block was variable, depending on the number of times that the sequence was presented: once, twice or thrice, pseudorandomly ordered, to facilitate within-block learning and ensure that there was sufficient behavioural data to make analysis

feasible (see below). Rehearsal blocks always followed Presentation blocks, but the order in which blocks of different repetition number were presented was pseudorandomised (see Figure 2e). Therefore, two factors were systematically manipulated. First, the extent to which the sequences were learned in the presentation block, and second, whether the sequences were Novel or Familiar.

Eye-tracker calibration:

The accuracy of eye-tracking depends on the quality and frequency of calibrations. In this study, steps were taken to maximise the accuracy of eye-tracker recording during scanning by using a nine-point calibration and validation sequence. At each point, the gaze of the subject as they fixated on the calibration point was recorded. These were manually accepted by the experimenter using the enter key on the keyboard. If the recorded gaze did not correspond with the calibration point on the screen, calibration for that point was repeated. This process was then repeated again to validate the calibration. After the validation, the Eyelink software evaluates the calibration and grades it as either 'GOOD' or 'FAILED'. Where calibration for a subject was failed, this was repeated until sufficient calibration was reached. 4 calibration blocks were included, which took place every 20 blocks. The timings of these blocks were similarly recorded, and in GLMs these blocks were modelled as confounds (see below).

Trials:

'Trials' were the onset of each sequence element. All trials in all conditions followed the same basic structure. A 3 x 3 grid of unfilled circles was presented in the centre of the subjects' visual field (see Figure 2 a-d). In Presentation trials, one of the empty circles was filled for 600 ms. The 3 x 3 grid disappeared for 100 ms before reappearing, with the filled circle in a new location. This served to pace the movements from location to location, and also to indicate the location to which subjects should direct their gaze. Although subjects were strongly encouraged verbally and through both sets of formal instructions not to move their eyes until

the grid was on the screen, this allowed for analysis of Anticipatory saccades. This dot appeared in a sequence of five locations (see Figure 2a). In response, subjects made saccades to these dots which were recorded by the MRI-compatible eye-tracker (see Figure 2b). In the following 'Rehearsal' block, the same grid was presented in the same way. Subjects were required to replicate the sequence that they had just observed by moving their eyes to the same locations in the same order. The critical difference was that the subjects were required to direct their gaze to each location in the sequence on the basis of memory, rather than on the basis of a visual cue (circles remained unfilled so there were no spatial cues, see Figure 2c). The grid onset and offset times were identical to the Presentation blocks (although there was no spatial cue), and served as a pacing cue to indicate when they were required to move to the next point in the sequence.

Two behavioural measures of learning were used. First, learning was measured as the proportion of correct saccades made towards the target placeholder within each block. Second, we analysed the proportion of correct decisions that were made with 'anticipatory' saccades (before the pacing cue, despite instruction to wait for the pacing cue), and the proportions that were made with 'reactive' saccades (after the pacing cue, as a reaction to the visual stimulus).

Pre-scanning training:

It was important to ensure that subjects became familiar with the behavioural requirements of the task prior to scanning, particularly the timings of visual events. Subjects practiced the task in the scanner immediately before the experiment during the acquisition of the T1 anatomical scan (see below). This ensured that the context of the experiment and training session were matched. The task was identical in all respects to that described above, but the sequences themselves were different. In order to ensure that all subjects received the same training, every subject was given two Presentation and Rehearsal blocks. This sequence was repeated for the exact same length and duration for each subject, to ensure all subjects received the same level of exposure to the task constraints, and

all were trained to the same criterion (10 consecutive trials performed correctly). Subjects were informed that the sequences in the experimental session would be different from those in the training session, and that block lengths would vary because sequences would be repeated.

2.2.4 Behavioural data analysis

Behavioural data for this experiment and throughout the thesis were analysed using IBM SPSS Statistics 21. To assess behavioural performance, a response was deemed to be correct if subjects fixated a target placeholder to within a straight line distance of 50 pixels from the placeholder. Two independent variables were analysed. First, the familiarity of the sequence (Novel vs. Familiar) and second, the number of repetitions of each sequence within a block (1, 2 or 3). There were two dependent variables. First, changes in the frequency of correct responses (accuracy) for Presentation and Rehearsal were assessed separately. Second, for Presentation blocks changes in the type of saccade were assessed: the frequency of anticipatory and reactive saccades, i.e. those that occurred before or after the time of stimulus onset, respectively. A series of two two-way repeated measures Analyses of Variance (ANOVAs) were conducted, one for Anticipatory saccades, and one for Reactive saccades (Familiarity, 2 levels; number of repetitions, 3 levels). For each type, the frequency of correctly executed saccades was assessed as the dependent variable.

Data were normally distributed and no statistically significant outliers were found. ANOVAs are reported with Greenhouse-Geisser correction to correct for violations of the the assumption of sphericity where appropriate. T-tests and pairwise comparisons are reported with an appropriate Bonferroni alpha level correction. Effect sizes are reported using partial eta squared values.

2.2.5 Experimental timings

The timings of blocks in this experiment were manipulated to optimise GLM modelling of fMRI data by reducing rank deficiency (see below), and also to optimise the sampling of haemodynamic activity. Each Presentation block took

place over the course of 2 TRs (repetition time; TR = 2s, see below). Rehearsal blocks took place over the course of the subsequent two TRs. The length of time separating the onsets of the Presentation and Rehearsal blocks and their immediately preceding TRs was varied in order to optimise the sampling of haemodynamic activity time-locked to these blocks. The range of the variable delay between the end of one block and the onset of the next ranged from 100-3000 milliseconds, and the range of the variable delay between the Presentation and Rehearsal blocks also ranged from 100-3000 milliseconds. The range of the delays was randomly distributed across trials. A series of pilot studies using this approach were run prior to the experiment to ensure that these timings resulted in GLMs which were optimal for statistical analysis (see below). The design of the experiment was varied three times, with three subjects per iteration. After the behaviour paradigm and experimental timings were optimised, an fMRI pilot was undertaken with two further subjects to optimise scanning parameters, check experimental timings in the scanner, and to develop good practice for eye tracking in the scanner (as previous pilots had used eye tracking methods in the laboratory). Data from these pilots was not included in the final analysis. The timings entered into the GLM were normalised against the timing of the first TR for each experimental run.

2.2.6 Functional imaging and analysis

Data Acquisition

1180 echo-planar imaging (EPI) scans were acquired from each participant using a 3 Tesla Siemens Trio Scanner (Royal Holloway, University of London). The start of the experiment was triggered after T1 equilibration was reached. The field of view covered the whole brain: 192 x 192 mm (64 x 64 voxels); 30 axial slices were acquired (25% slice gap, 0.9 mm; voxel size of 3 mm x 3 mm x 5 mm; TR = 2s; echo time (TE) = 32ms; flip angle = 80°). The functional sequence lasted 35 minutes. Prior to the functional scans, high-resolution T1-weighted structural anatomical images were acquired at a resolution of 1 mm x 1 mm x 1 mm using an MPRAGE sequence.

Image Preprocessing:

Scans were pre-processed in SPM8 (http://www.fil.ion.ucl.ac.uk/spm/) on MATLAB R2014a (MathWorks Inc.) (PC, Intel Core i5-3470 CPU 3.20 GHz processor; 8.00 GB RAM; 64-bit operating system; Windows 8). Each EPI was realigned to the first image of the series, and a mean image was calculated. Images were normalised to the reference space defined by the ICBM EPI template of the Montreal Neurological Institute (MNI) (Friston et al, 1995a). The registration of normalised images was visually checked against the T1-weighted single-subject canonical MNI image. A Gaussian kernel of 8mm was applied to spatially smooth normalised images (Friston et al, 1995b, c). Anatomical images were normalised to the reference space using SPM12 in MATLAB R2014a (PC, Intel Core i5-3470 CPU 3.20 GHz processor, 8:00 GB RAM, 64-bit operating system; Windows 8). The registration of images for each subject was visually checked using the CheckReg tool in SPM.

Statistical Analysis

First- and second-level analyses were performed in SPM12 in MATLAB 2015b (iMac, Intel Core i5 3.2 GHz processor; 8GB RAM).

First-level single-subject analysis

The primary aim of this analysis strategy was to model rehearsal-related activity across various sustained periods of time. Novel and Familiar sequences were modelled separately, in order that comparisons across these could be made. All other events were modelled as confounds. This approach resulted in the construction of twenty-three regressors (eight regressors of interest and a further fifteen regressors that modelled confounds; see below).

Regressors describing activity sustained over the time course of blocks were constructed by convolving boxcar functions that describe the timings of blocks of various lengths with a canonical haemodynamic response function. However, previous neurophysiological and fMRI studies have shown that sustained activity is almost always accompanied by activity that is transient in nature which is phase-locked to the start of such blocks, but is not sustained over the time course of the block (Courtney, Ungerleider, Keil & Haxby, 1996; Visscher et al., 2003). Given that the inferences in the hypotheses relate to sustained rather than transient activity, it was important that confounding transient activity be explicitly modelled so that it could be disambiguated from sustained activity. To achieve this, delta functions corresponding to the start time of the blocks were convolved with the same haemodynamic response function and incorporated into the same GLMs. As in previous studies that have taken this approach (Vilberg and Rugg, 2012), pilot studies allowed the timings in the experimental design to be modified to ensure that the proportion of shared variance between the two types of regressor was minimised (helped by the fact that the lengths of sustained blocks varied, but transient activity did not).

Two additional categories of confound were modelled. First, activity that was time-locked to eye-tracker calibration events was separately modelled (see above). Second, six head motion regressors, calculated during the realignment preprocessing stage were included (three translations and three rotations).

The following events were therefore separately modelled as both sustained regressors, including activity across the entire block, and as transient regressors, modelling the transient activity associated with the start of the same blocks in the following regressors: Presentation Novel (1, 2, and 3 sequence repetitions together), Presentation Familiar (1, 2, and 3 sequence repetitions together), Rehearsal Novel (1 sequence repetition), Rehearsal Novel (2 sequence repetitions), Rehearsal Novel (3 sequence repetitions), Rehearsal Familiar (1 sequence repetition), Rehearsal Familiar (2 sequence repetitions), Rehearsal Familiar (3 sequence repetitions). Calibration blocks and rehearsal jitter durations were also included as a confound

regressor and six head motion regressors (translations and rotations in x, y and x planes).

GLMs for individual subjects were estimated, and SPM{t} images from regressors 1-8 from each subject were incorporated into a random effects, group-level analysis (One-Way ANOVA). Contrasts were calculated following estimation.

Thresholds and Masking

Cerebellar, prefrontal and premotor (included due to the proximity of the frontal eye fields to the premotor cortex, and to allow for the possibility that parts of the frontal eye fields may lie in the boundary between the two) activity for T-contrasts and F-contrasts during second-level group analysis were tested using small volume correction (SVC) for the cerebellum and the prefrontal and premotor cortices ($p < .001$). The cerebellar mask was generated using the SUIT toolbox in SPM12 (Diedrichsen, 2006; Diedrichsen et al 2009, 2011; Diedrichsen and Zotow, 2015). The prefrontal and premotor cortex mask was manually constructed by the author. A whole brain mask was created using the T1 canonical MNI structural image, from which the grey matter was segmented using SPM12. As there are no anatomical landmarks identifying the premotor cortex (Brodmann Area 6) from the primary motor cortex (Brodmann Area 4), an independent mask of Brodmann Areas 4a and 4p bilaterally was created by the author using probabilistic maps in SPM Anatomy Toolbox (Eickhoff et al, 2005; 2006; 2007) and then used the ImCalc function on SPM12 to subtract this from the whole brain masked. The author then used MRIcron (Rorden, Karnath, & Bonilha, 2007) to manually delete voxels posterior to the remaining area, leaving only frontal lobe cortex anterior to area 4a and 4p.

Localisation

Peak co-ordinates were localised to gross anatomical landmarks on the canonical brain of the MNI series, and verified on T1 structural images of the subjects included in this study, that have been normalised to the reference space of

the MNI template. The probabilities of cortical peak co-ordinates are reported in probabilistically defined cytoarchitectonic maps and the probabilities of cerebellar peak co-ordinates based on gross anatomy using the SPM Anatomy Toolbox (Eickhoff et al, 2005). The locations of peak haemodynamic activity are reported in terms of MNI co-ordinates, and these are attributed to sulcal and gyral landmarks using the terminology of the atlas of Duvernoy (1999). The nomenclature of Larsell (1970, 1972) is adopted when discussing the gross anatomy of the cerebellum.

2.3   Results

2.3.1   Behavioural results
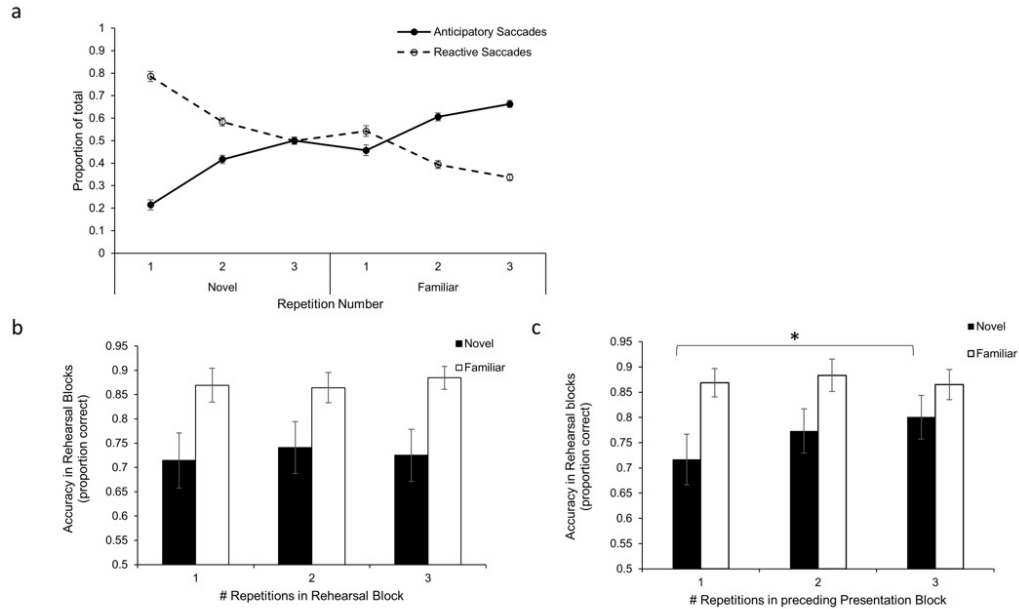
Figure 3: (a) Number of Anticipatory and Reactive saccades as a proportion of all correctly executed saccades The proportion of Anticipatory saccades were significantly higher in Familiar blocks than Novel blocks and further increased significantly with each additional sequence repetition. Further, the proportion of Reactive saccades were significantly higher in Novel than Familiar blocks and decreased significantly with each additional sequence repetition. (b) Rehearsal effects on accuracy in Rehearsal Blocks. Accuracy was significantly higher in Familiar than Novel sequences. However, in contrast with Presentation effects on accuracy in Rehearsal Blocks, accuracy was not significantly affected by Repetition Number. (c) Presentation Effects on Accuracy in Rehearsal Blocks. This study tested whether learning effects during Presentation Blocks were unmasked when visual cues were removed in the subsequent Rehearsal Blocks. Accuracy was significantly higher in Familiar than Novel sequences. Further, a significant interaction was found between Familiarity of the Sequence (Novel vs Familiar) and Sequence Repetition (1 vs 2 vs 3 Repetitions). T-tests revealed the source of this interaction. Significant differences were found between 1 vs 3 Repetitions in Novel Sequences* (Bonferroni corrected $p <$ .025) but not in Familiar Sequences. All Error Bars: +/- 1 Standard Error of the Mean.

Performance in Presentation Blocks

Presentation effects upon Accuracy in Presentation Blocks:

The proportion of correct responses was significantly higher in Familiar (mean = 0.75, SE = 0.54) blocks than Novel (mean = 0.61, SE = 0.61) blocks (F$_{(1,15)}$ = 34.723; $p <$ .001; η^2 = .698). There was a significant overall main effect of

Familiarity by this measure. However, the proportion of correct responses did not appear to change as a function of sequence repetition (F $_{(1.540,23.104)}$ = 2.831; p = .091; η^2 = .159). There was also no significant interaction between these two main effects (F (2,30) = .022; p = .979; η^2 = .001). During Presentation blocks, saccades always were guided by the presence of visual cues, thus reducing the scope for errors. The presence of the cues during Presentation may have masked learning-related performance changes to some extent in those blocks. The underlying behavioural effects of training were unmasked in two ways. First, the effects of sequence Familiarity and repetition number on behaviour are examined *before* the cue onset, using the frequency of Anticipatory (and conversely Reactive) saccades as a dependent variable. Second, the impact of any training in Presentation would also have been present on accuracy rates in immediately subsequent Rehearsal blocks in which there were no visual cues. Therefore, this Chapter assessed the effects of Repetition number and sequence Familiarity in Presentation blocks upon accuracy rates in the immediately subsequent Rehearsal blocks (see below).

Anticipatory and Reactive Saccades during Presentation Blocks:

There was a significant main effect of sequence Familiarity on type of saccade made during Presentation blocks (see Figure 3a). There were significantly more anticipatory saccades during Familiar blocks (mean = .434, SE = .044) than in Novel (mean = .226, SE = .018) blocks (F $_{(1,14)}$ = 47.220; p < .001; η^2 = .771). There were also significantly more reactive saccades during Novel blocks (mean = .417, SE = .056) than Familiar (mean = .346, SE = .055) blocks (F $_{(1, 14)}$ = 6.209; p = .026, η^2 = .307).

Furthermore, the number of anticipatory saccades made increased significantly with each additional sequence repetition (F $_{(1.359, 19.027)}$ = 61.958; p < .001, η^2 = .816, η^2 = .636). There were significantly more anticipatory saccades in the third repetition (mean = .424, SE = .035) and the second repetition (mean = .352, SE = .035) than the first repetition (mean = .214, SE = .023). Further, there were significantly more anticipatory saccades in the third repetition than the second.

However, there was no significant interaction between sequence Familiarity and repetition number on the frequency of anticipatory saccades ($F_{(2, 28)} = 1.874$; $p = .172$, $\eta^2 = .118$).

The number of reactive saccades made also decreased significantly with each additional presentation repetition ($F_{(1.118, 15.649)} = 24.477$; $p < .001$). There were significantly fewer reactive saccades in the third (mean = .308, SE = .046) and second (mean = .349, SE = .053) repetitions than the first repetition (mean = .488, SE = .067). There were also significantly fewer reactive saccades in the third repetition than the second repetition. No significant interaction was found between sequence Familiarity and Repetition number upon reactive saccade frequency ($F_{(1.448, 20.277)} = .908$; $p = .389$, $\eta^2 = .061$).

Performance in Rehearsal Blocks

Rehearsal effects on Accuracy in Rehearsal Blocks:

Learning-related performance during Rehearsal was entirely from memory because no visual cues were present. Accuracy rates during these blocks presented a clear picture of learning for Familiar and Novel sequences. As expected, there was a significant main effect of sequence familiarity on accuracy during the Rehearsal period (accuracy was significantly higher in the Familiar (mean = .873, SE = .028) than the Novel (mean = .727, SE = .054) sequences as expected; $F_{(1, 15)} = 14.229$; $p = .002$; $\eta^2 = .487$; Figure 3b). It was expected that a large proportion of the learning would take place in Presentation, rather than subsequent Rehearsal blocks. Consistent with this view, no significant effect of number of sequence repetitions during Rehearsal blocks on Rehearsal accuracy was found ($F_{(2, 30)} = .697$; $p = .506$, $\eta^2 = .044$), and furthermore no significant interaction between sequence familiarity and repetition number ($F_{(2,30)} = 1.070$; $p = .356$, $\eta^2 = .067$).

The influence of Presentation upon Accuracy in Rehearsal Blocks:

This chapter also tested for the possibility that the number of times sequences were presented in Presentation blocks would influence performance in immediately subsequent Rehearsal blocks (note that the number of repetitions in Presentation blocks did not systematically vary with the number in subsequent Rehearsal blocks). To determine whether performance accuracy during the rehearsal period changed as a function of sequence learning during the presentation block immediately preceding the rehearsal block, 2 x 3 repeated measures ANOVA was conducted, with sequence familiarity (Novel and Familiar) and Presentation sequence repetition number (1, 2 and 3) as factors. Accuracy was significantly higher during Familiar (mean = .874, SE = .029) than Novel (mean = .763, SE = .045) blocks (F $(1,15)$ = 20.671; p < .001, η^2 = .579; Figure 3c), and this also increased significantly with each additional sequence repetition: (F $(2, 30)$ = 6.762; p = .004, η^2 = .311). Accuracy was significantly higher during the third (mean = .835, SE = .034) and second (mean = .829, SE = .036) repetitions than the first repetition (mean = .791, SE = .038). However, there was no significant difference between the second and third repetitions (p = 1.000). There was a significant interaction between these main effects (F $(1.371, 20.560)$ = 5.401, p = .022, η^2 = .265).

Figure 3c suggests that the interaction between sequence familiarity and repetition number comes from an increase in accuracy for Novel sequences, as compared with a relatively consistent accuracy rate regardless of the number of repetitions for the Familiar sequences. Two *post-hoc* t-tests were applied to investigate this possibility, by testing for differences between 1 vs 3 repetitions for each of the two levels of Familiarity (Novel and Familiar sequences). There was a significant difference between 1 and 3 sequence repetitions in the Novel condition (t $_{(15)}$ = -5.015, p < 0.000) but no such differences were found in the Familiar condition (t $_{(15)}$ = -.104, p = .918). In both cases, a *post-hoc* Bonferroni correction was applied (alpha level, 0.025).

This analysis confirms that for Novel sequences, increases in the number of sequence presentations in Presentation blocks were accompanied by corresponding increases in the accuracy rate in immediately subsequent Rehearsal blocks. In contrast, accuracy rate for Familiar sequences was consistently high, and independent of the number of sequence presentations in Presentation blocks. This evidences suggests a fundamental difference in the status of representations used in Novel and Familiar blocks. In the former, the ability to execute sequences correctly from memory was dependent upon a memory of the sequence built up in immediately preceding Presentation blocks. However, in the latter, sequences were independent of such processes and instead depended upon more resilient, longer-term representations which benefited from extensive block-to-block training. The experimental design presented in this Chapter captures a process of transition, where with each repetition during Presentation, the representation used in subsequent Rehearsal is increasingly likely to yield higher accuracy, into a state in which this representation becomes relatively independent of short-term learning. This finding has been exploited in the fMRI analyses to test whether cerebellar activity decreases in proportion to this increasing independence (see the following section 2.3.2).

2.3.2   Functional imaging results

The aim of this experimental design was to test the following hypotheses. First, consistent with the connectional organisation of the cortico-cerebellar system, the rehearsal of sequences from long-term memory would activate parts of the cerebellum (lobule HVIIA) known to be interconnected with the prefrontal cortex. Second, consistent with theories of cerebellar learning, it was predicted that sequences which were Novel and less well-known to subjects would evoke greater cerebellar activity than those which were Familiar. Third, consistent with previous experimental work, it was predicted activity related to working memory in area 46 of the prefrontal cortex, and in the Frontal Eye Fields in which neurons become active during the cognitive control of eye movements.

The experimental design enabled us to model Novel and Familiar Blocks in Presentation and Rehearsal conditions. Within Rehearsal conditions, blocks that contained 1, 2 or 3 sequence repetitions were modelled separately. These allowed three contrasts to be run:

i)   Presentation-related activity: Familiar blocks <> Novel blocks (F contrast)

ii)   Rehearsal-related activity: Familiar blocks <> Novel blocks (F contrast)

iii)   Rehearsal-related activity: Graded, accuracy-related changes (T contrast).

Although the principal aim of this study is to test hypotheses related to the operation of working memory in memory-guided sequences (activity in Rehearsal blocks), this experimental design presents the opportunity to investigate activity in presentation as well as rehearsal blocks.

Presentation blocks - Familiar < > Novel sequences:

A small volume correction was applied to the part of the frontal lobe containing prefrontal and premotor cortices given hypothesised involvement of the frontal eye fields and prefrontal cortex. Results outside this region were corrected for family-wise error (FWE). An activation was present in an anterior portion of the right middle frontal gyrus (40, 42, 28). This coordinate is likely to lie in area 46, homologous to area 46 in macaque monkeys which is known to contain memory fields that exhibit delay period activity during working memory (Constantinidis, Franowicz, & Goldman-Rakic, 2001). This area is posterior to probabilistic representations of area 10 in the frontal pole (FP1; Bludau et al., 2014). Rajkowska & Goldman-Rakic (1995) have analysed the cytoarchitecture of the middle frontal gyrus and also describe the the central portion of the middle frontal gyrus as area 46 (Rajkowska & Goldman-Rakic, 1995). While Brodmann (1908,1909) referred to this location as area 9, Petrides & Pandya, (1999) reported it to have

cytoarchitectonic properties that were similar to those of classical area 46, and so referred to it as area 9/46.

An activation was also found in the posterior part of the right superior frontal gyrus near the junction with the precentral sulcus (24,2,58; Figure 4a,b). Although the precise location of the human frontal eye fields is still unclear, it has been suggested that it is situated in the superior precentral sulcus (Percheron et al, 2015), at the junction with the superior and/or middle frontal gyri (Blanke et al., 2000; Tehovnik et al, 2000). Indeed, Paus (1996) identified such a region very close to the coordinates reported here which was also modulated by oculomotor demands across a set of different experiments (31, -2, 47 [SDs: 11mm, 5mm, 5mm, respectively]). Gitelman, Parrish, LaBar, & Mesulam (2000) also suggest that activity in this region reflects frontal eye field activity during both covert (-36, 3, 54; 30 -3, 54) and overt eye movements (-36, 3, 54; 33 -3, 48). The coordinates found fall broadly within these coordinate ranges.

An activation was also found on the medial wall, above the cingulate sulcus in a posterior part of the superior frontal gyrus (6, 14, 52; Figure 4 c,d). This is likely to represent activation in the supplementary eye field (SEF). This coordinate sits within the coordinate range for the SEF and cingulate eye field (CEF) identified by Grosbras, Lobel, Moortele, LeBihan, & Berthoz (1999) (x range: 4mm – 12mm; y range: -2mm -24mm; z range: 48mm – 54mm). When this activation is overlaid on the normalised T1 anatomical scans of the subjects included in this study, this coordinate lies rostral to the paracentral sulcus, which forms the rostral border of the paracentral lobule, and dorsal to the cingulate sulcus, suggesting that this is in the SEF rather than the CEF. Although Amiez & Petrides, (2009) suggest that the SEF is located in the paracentral sulcus, the current results do not concur with this view. Whilst the coordinates found concur with the conclusions of other imaging studies (see above), allowing us to conclude that this activation is likely to represent the SEF, the coordinate reported does not lie in this sulcus.
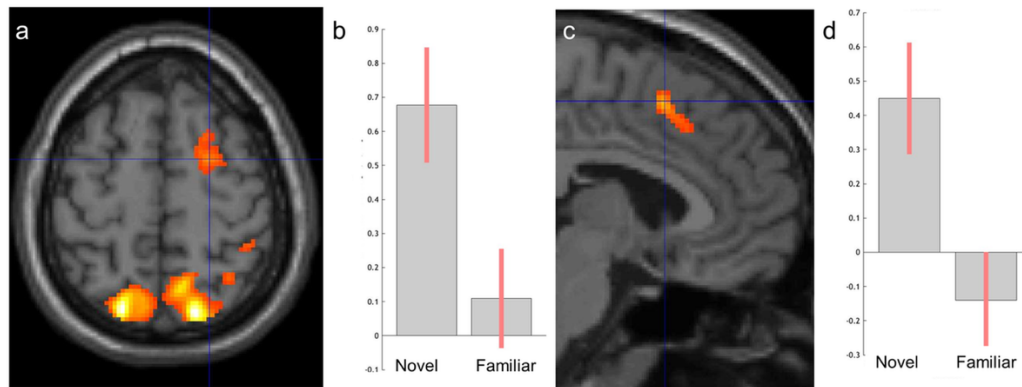
Figure 4: Activity evoked during Presentation blocks. SPM{F} contrast specifying a difference in activity between all Novel and all Familiar conditions. Locations of activations in (a) frontal eye field (lateral part of posterior superior frontal gyrus, near junction with precentral sulcus) and (c) supplementary eye field (medial posterior part of superior frontal gyrus). Crosshairs pass through peak voxels. SPM{F} contrast image overlaid onto the canonical brain of the MNI series. Parameter estimates of these areas plotted in (b) and (d), respectively.

Activations were also shown in the superior parietal lobe bilaterally (18, -72, 58; -18, -70, 58, see the bottom of Figure 4a), the right inferior parietal lobe (40, -40, 48). Such activity in the parietal lobes may reflect visual attention (Desimone & Duncan, 1995). Activity was also shown in the right superior occipital gyrus (26, -66, 46). No evidence of such differences were found in the cerebellum for Presentation blocks (although see below for cerebellar findings in Rehearsal blocks).

Table 2: Presentation, Novel <> Familiar F-contrast peak voxels (*SVC uncorrected p < .001; **FWE-corrected for multiple comparisons p < .05). Negative X co-ordinate values indicate activity in the Left Hemisphere.

	F	Z	Co-ordinates (x,y,z)	Probabilistic Cytoarchitecture (if available)
Frontal Lobe **Prefrontal**				
Lateral orbital gyrus / anterior insula junction*	21.30	4.27	30, 22, -6	n/a
Superior frontal gyrus/superior frontal gyrus junction*	17.49	3.87	24, 2, 58	n/a
Middle frontal gyrus*	16.26	3.73	40, 42, 28	n/a
Posterior medial frontal gyrus*	15.92	3.69	0, 18, 48	n/a
Superior frontal gyrus*	13.66	3.40	18, 36, 54	n/a
Lateral orbital gyrus / anterior insula junction*	11.99	3.18	-32,24,-4	n/a
Premotor/Primary Motor Cortex				
Medial superior precentral sulcus*	20.24	4.16	6, 14, 52	n/a
Parietal Lobe				
Superior parietal gyrus**	37.07	5.55	18, -72, 58	Area 7P (49%), Area 7A (39%)
Superior parietal lobe**	36.43	5.51	-18, -70, 58	Area 7P (63%), Area 7A (37%)
Inferior parietal lobe**	24.71	4.59	40, -40, 48	Area 2 (38%), Area hIP2 (34%) and Area 7PC (20%)
Intraparietal sulcus**	24.25	4.55	26, -66, 46	n/a

2.2 Rehearsal blocks - Familiar <> Novel sequences:

In contrast to Presentation blocks, during Rehearsal blocks subjects executed oculomotor sequences purely from memory, without the benefit of visual guidance. A significant activation is reported that overlaps the one in the same part of the middle frontal gyrus (area 46) in the previous contrast (and indeed differs by no more than 2mm in any plane; Figure 5a,b). Figure 5c shows that this area responds in the same way to Novel and Familiar sequences regardless of whether these are executed in Presentation or Rehearsal phases. Activity for Novel sequences is greater than that of Familiar ones. In addition, in common with some cerebellar activations (see below), the activity in Novel sequences declines in proportion to the number of times that sequences are rehearsed in the Rehearsal phase.
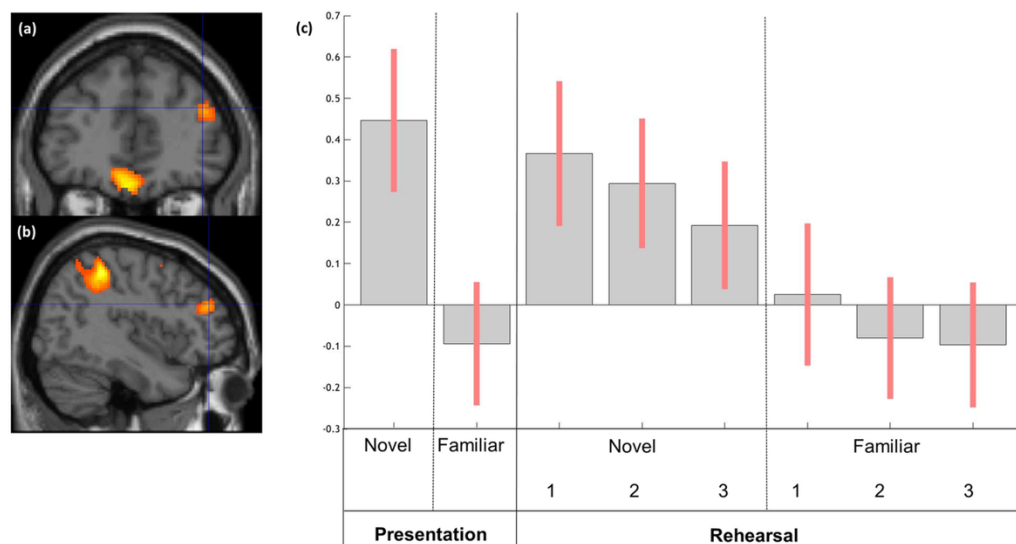
Figure 5: Prefrontal cortex activity evoked during Presentation and Rehearsal. SPM{F} contrast specifying a difference in activity between all Novel and all Familiar conditions (see Results 2.2). Peak location of activity in area 46 (42, 42, 26) in the coronal (a) and sagittal (b) planes of section. Image (a, b) and parameter estimates (c) are derived from Rehearsal (Novel v Familiar).

Additional areas of the prefrontal cortex were found that responded differently in Rehearsal than in Presentation. This included the medial part of the left and right polar prefrontal cortex in area 10 (-6, 64, 6; Öngür, Ferry & Price, 2003; Ramnani and Owen, 2004). This occupies a cytoarchitectonic area described as frontopolar area 2 (Fp2) by Bludau et al., (2014). Another activation was found

in an anterior part of the superior frontal gyrus in the left hemisphere (-10, 64, 30). This coordinate has a low probability of being situated in area 10 (FP1), and is therefore more likely to be placed in area 9 which lies immediately dorsal to it. These activations were sufficiently robust that they even survived a stringent FWE correction ($p < .05$). A fourth prefrontal activation was found in the gyrus rectus, in medial parts of the orbitofrontal cortex (area 14 of Brodmann; Fo1 of Henssen et al., 2016).

In addition, an activation was shown in a posterior part of the middle frontal gyrus (38, 6, 54) close to the area argued above to be the frontal eye field. Activations were also seen in the right inferior (48, -36, 50) and superior (18, -74, 58; -18, -70, 58) parietal lobes.

Activations were seen in set of three cerebellar locations. As hypothesised, an activation was found in left and right Crus II of lobule HVIIA (32, -82, -36; -26, -88, -34; Figure 6a). When projected onto the canonical brain of the MNI series it is difficult to distinguish whether the peak voxel lies in Crus I or in Crus II. Although the presence of learning-related differences in this area supports the anatomical hypothesis outlined, the directionality of parameter estimates contradicts the physiological aspects. Greater decreases were predicted for the Familiar sequences compared with Novel sequences, whereas the parameter estimates indicate the opposite (Figure 6d). This is elaborated upon in the Discussion.

The contrast also revealed differential activity in the depths of the posterior superior fissure, in approximately in lamella a of Crus I, lobule HVIIA (cr.Ia) on the canonical brain of the MNI series, and close to the lamella c' of lobule HVI (-28, -64, -30; Figure 6b). When this activation was overlaid on the normalised T1 images of the subjects included in this study, the activation was located in, or at the border of Crus I, in twelve of the sixteen subjects included in this study. When overlaid onto a cerebellar flatmap, it appeared immediately posterior to the superior posterior fissure in Crus I (Figure 6g, activation b). In the remaining four the

activation was in lobule HVI, close to the border of Crus I. The parameter estimates (Figure 6e) show that Novel sequences evoked greater activity than Familiar sequences. This finding is in line with both anatomical and physiological aspects of the hypotheses outlined previously. Interestingly, activity declined progressively with the level of learning, such that the least Familiar sequence (one repetition of Novel sequences) evoked the greatest activity, and the most Familiar sequence (three repetitions of Familiar sequences) evoked the least.

An activation is also reported in lobule HVIIIA (-32, -44, -46; most likely in lamella c of this lobule, this being the lamella immediately adjacent to the adjoining lobule HVIIB; see Figure 6c). Parameter estimates show that Novel sequences evoked increases in BOLD activity that were greater than those evoked by Familiar sequences (Figure 6f and g, activation c). A similar pattern was found in a smaller activation in lobule HVIIB, adjacent to the posterior parts of Crus II (cr.IIp).
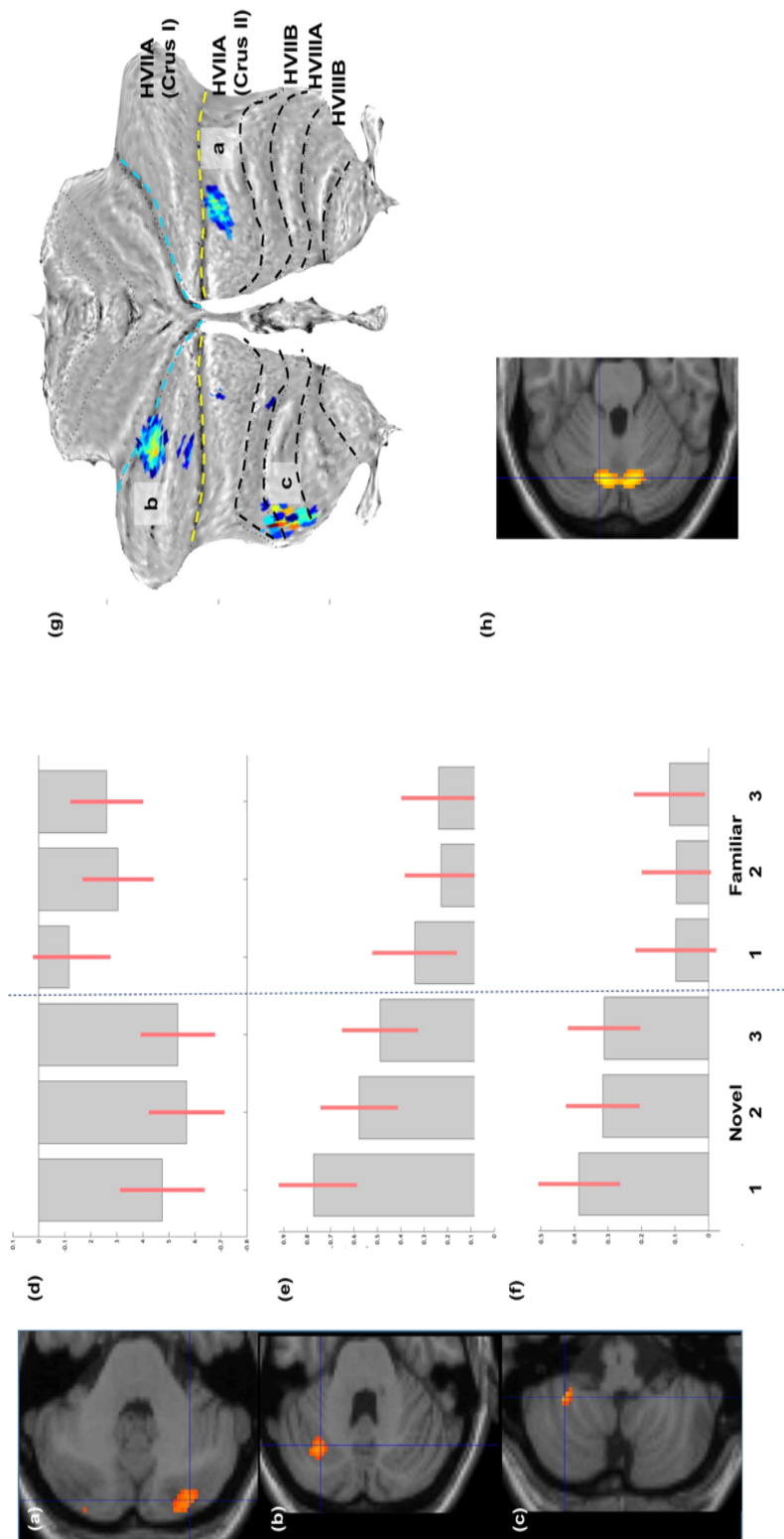
Figure 6: Cerebellar activity evoked during Rehearsal blocks. SPM{F} contrast specifying a difference in activity between all Novel and all Familiar conditions. Locations of activations in (a) right Lobule HVIIA, Crus II [32, -82, -36], (b) left lobule HVIIA Crus I [-28,-64,-3]). and (c) left lobule HVIIIA [-32,-44,-46]. (d)-(f) show parameter estimates for peak voxel in each of these locations. Figure (g) shows thresholded SPM{F} contrast image overlaid onto cerebellar flatmap (lobules HVIIA – HVIIIB labelled on the right; activations labelled individually, a-c as in anatomical sections. Conjunction of T contrasts for all Rehearsal conditions: Bilateral activation in oculomotor vermis (crosshair at -12, -72, -24; Z = 4.56; T=4.78). Activity is centered at the border of lobules VI and VII

Table 3: Rehearsal, Novel <> Familiar F-contrast peak voxels (*SVC uncorrected p < .001; **FWE-corrected for multiple comparisons p < .05) Negative X co-ordinate values indicate activity in the Left Hemisphere.

	F	Z	Co-ordinates (x,y,z)	Probabilistic Cytoarchitecture (if available)
Frontal Lobe **Prefrontal**				
Superior frontal gyrus*/**	30.37	5.06	-10, 64, 30	Fp1 (5%)
Frontal pole (frontopolar gyrus)*/**	27.88	4.86	-6, 64, 6	Fp2 (57%), Fp1 (43%)
Lateral orbital gyrus / anterior insula junction */**	25.89	4.69	32, 22, -8	n/a
Middle frontal gyrus*	17.82	3.90	42, 42, 26	n/a
Medial superior frontal gyrus*	13.75	3.42	6, 26, 42	n/a
Medial orbital gyrus*	11.71	3.14	-30, 38,-12	Area Fo3 (23%)
Superior frontal gyrus/superior frontal gyrus junction*	12.02	3.18	38, 6, 54	n/a
Parietal Lobe				
Postcentral gyrus*	13.27	3.35	46, -32, 54	BA2 (70%), BA1 (30%)
Postcentral gyrus*	13.20	3.34	42, -40, 60	BA1 (40%), BA2 (26%)
Superior parietal lobule**	34.53	5.37	18, -74, 58	Area 7p (61%), Area 7a (26%)
Superior parietal lobule**	28.84	4.94	-18, -70, 58	Area 7a (63%), Area 7p (37%)
Inferior parietal lobule**	28.60	4.92	48, -36, 50	Area PFt (21%), Area 2 (13%), Area PFm (11%)
Inferior parietal lobule**	24.31	4.55	-40, -44, 40	Area hIP1 (33%), Area hIP3 (31%), Area hIP1 (31%)
Temporal Lobe				
Middle temporal gyrus**	23.87	4.51	-62, -10, -16	n/a
Subcortical Areas **Cerebellum**				
Cerebellum Lobule HVIIIA (46%), Lobule HVIIB (20%), Lobule HVIIIB (12%)*	17.78	3.90	-32,-44,-46	
Cerebellum Lobule HVIIA Crus I (50%), Lobule HVI (50%)*	16.92	3.80	-28,-64,-30	
Cerebellum Lobule HVIIA Crus I (94%)*	16.42	3.74	32,-82,-36	
Cerebellum Lobule HVIIA Crus I (52%), Lobule HVIIA Crus II (48%)*	12.83	3.29	-26,-88,-34	
Cerebellum Lobule HVIIB (90%), Lobule HVIIA Crus II (10%)*	12.05	3.19	-20,-74,-50	

Decreasing learning-related activity during Rehearsal, weighted by performance

Above, it is shown that the rehearsal of Novel and Familiar sequences from memory evoked differential activity in a set of cerebellar areas, most of which showed greater activity for Novel compared with Familiar sequences. This supports previous suggestions that, consistent with computational models of cerebellar plasticity, cerebellar activity decreases during the course of learning (Balsters and Ramnani, 2011; Ramnani, 2014). Similar patterns were observed in the prefrontal cortex. Inspection of parameter estimates shows that in a subset of those areas, activity appeared to change in a *graded* manner (Novel > Familiar and within these, one repetition > three repetitions; Figure 5c. Higher levels of Rehearsal block accuracy appeared to exhibit proportionately lower levels of cerebellar activity. It should be noted that behaviourally, there were no such graded changes related to Rehearsal *per se.* but there were graded changes in accuracy for Rehearsal blocks if those blocks were reordered according to the number of sequence repetitions in their corresponding Presentation blocks (see Behavioural Results). It is argued above that this may reflect a transition of control from mechanisms that were dependent upon the degree of exposure of the sequence in the immediately preceding Presentation phase, to those which were independent of such mechanisms, and reliant instead on longer-term representations. The fMRI results above are supplemented by statistically testing for activity which varied specifically in proportion to these particular behavioural outcomes (see Behavioural Results; Figure 3). Such activity reflected the rehearsal of sequences in working memory under conditions that were, in varying degrees, dependent either on short-term memories established by immediately preceding events, or upon longer-term learning.

This relationship was tested by weighting each of the six Rehearsal regressors with a measure of accuracy as reported in the behavioural results section (see also Figure 3), such that higher performance related to proportionately lower activity.

Significant effects were found in a set of prefrontal areas. Some of these were present in areas found to be active in both of the previous contrasts. These include a part of the middle frontal gyrus which it has been previously suggested includes area 46 (46, 46, 24) and the junction of the lateral orbital gyrus in the orbitofrontal cortex and the anterior parts of insular cortex (30, 22, -8). On the medial wall, there was also such an effect in the superior frontal gyrus (8, 28, 42). These prefrontal areas were therefore more active during Novel than Familiar sequences, regardless of the presence of cues, and Rehearsal-related activity was inversely proportional to accuracy when measured in terms of the number of sequence repetitions in immediately preceding Presentation blocks. In addition, activity which varied in relation to accuracy in this manner was also found in areas not revealed in previous contrasts. These included a more dorsal, posterior part of the middle frontal gyrus (36, 8, 42), and a part of the inferior frontal gyrus immediately dorsal to the ascending ramus of the Sylvian fissure (50, 18, 24).

Performance-related activity differences are also shown in six main locations across four lobules of the cerebellar cortex (Figure 7). As hypothesised, two effects were seen in lobule HVIIA. The most significant of these was in a location almost identical to that reported in the previous contrast (-30, -66, -32). The other was located in medial parts of right and left lobule HVIIA in Crus II (10, -76, -32; -12, -80, 34). Additional effects were found in lobule HVIIB bilaterally and in lobule HVIIIA unilaterally. The parameter estimates for all of these areas are in line with the model used to test the hypothesis. This suggests that learning-related effects are not only present in lobule HVIIA (as hypothesised in this chapter), but also beyond this lobule in HVIIB and HVIIIA. The absence of activity in vermal parts of lobule VII (oculomotor vermis) when looking for differences in Rehearsal was noted. However, it likely that given the same eye movement demands in all Rehearsal conditions (irrespective of different learning levels) such activity was more likely to be revealed by a conjunction across the different Rehearsal conditions. Such activity was found bilaterally (see Figure 6h).

In summary, a large number of cerebellar cortical locations were found in which Novel and Familiar conditions elicit differential responses. Some of these are within areas known to connect with the prefrontal cortex in monkeys. There are a number of areas which show such differences for which point-to-point connectivity with the prefrontal cortex is yet to be established. While a number of cerebellar areas showed decreasing activity in proportion to increasing levels of learning, some areas showed other trends (e.g. 6d). This suggests that multiple cerebellar circuits can become engaged in the maintenance and manipulation of sequences for a range of different reasons.
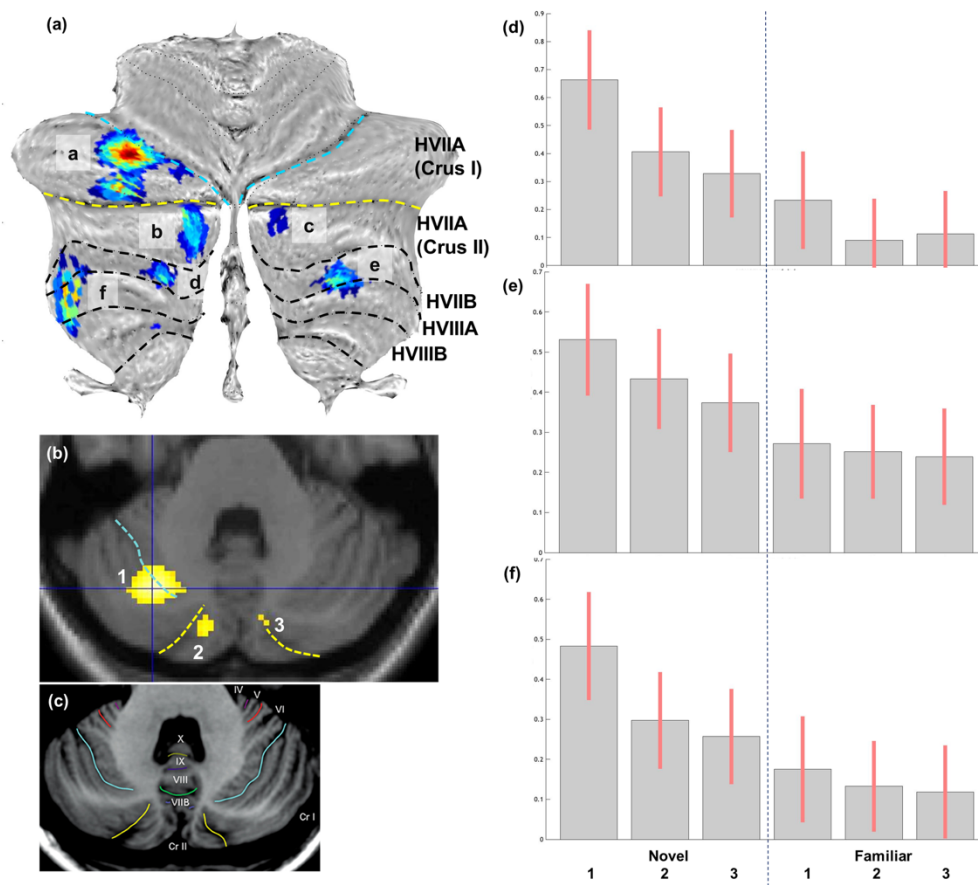
Figure 7: Cerebellar activity evoked during Rehearsal blocks. SPM{t} contrasts over the six regressors were weighted by accuracy scores sorted by the number of repetitions in immediately preceding Presentation blocks. (a) Thresholded SPM{t} contrast image overlaid onto cerebellar flatmap (lobules HVIIA – HVIIIB labelled on the right; activations labelled individually. a: left lobule HVIIA (Crus I); b and c located in right and left lobule HVIIA (Crus II); d and e located in lobule HVIIB; f located in lobule HVIIIA. Black lines indicate fissures between lobules. Superior posterior fissure indicated by light blue line, and horizontal fissure by yellow line. Colour coding applies to fissures denoted in (b) and (c). Activity overlaid onto the canonical brain of the MNI series. Numbering scheme for activations consistent with (a). The horizontal section passes through the peak voxel of activations 1 and 3. (c) Atlas image from Schmahmann et al. (2000). Horizontal section comparable with plane of section in (b). Parameter estimates from activations [peak coordinates]: (d) Left HVIIA (Crus I) [-30, -66, -32]; (e) Right lobule HVIIA (Crus II) [10, -76, -32]; (f) Right lobule HVIIB [26, -66, -50].

Table 4: Rehearsal, T-contrast weighted by accuracy scores in Behavioural Results peak voxels (*SVC uncorrected p < .001; **FWE-corrected for multiple comparisons p < .05). Negative X co-ordinate values indicate activity in the Left Hemisphere.

	T	Z	Co-ordinates (X Y Z)	Probabilistic Cytoarchitecture (if available)
Frontal Lobe **Prefrontal**				
Lateral orbital gyrus / anterior insula junction */**	5.15	4.89	30, 22, -8	n/a
Middle frontal gyrus*	4.35	4.19	44, 42, 24	n/a
Postcentral gyrus*	3.71	3.61	46, -32, 54	Area 2 (70%), Area 1 (30%)
Middle frontal gyrus*	3.66	3.56	38, 8, 40	n/a
Medial superior frontal gyrus*	3.65	3.55	8, 28, 42	n/a
Inferior frontal gyrus*	3.50	3.41	50, 18, 24	Area 45 (14%)
Lateral orbital gyrus / anterior insula junction*	3.31	3.24	-32, 22, -10	n/a
Postcentral gyrus*	3.30	3.22	-48, -36, 56	Area 2 (60%), Area 1 (36%), Area PFt (11%)
Middle frontal gyrus*	3.24	3.16	50, 26, 36	n/a
Middle frontal gyrus*	3.21	3.14	38, 8, 46	n/a
Parietal Lobe				
Postcentral gyrus*	3.41	3.32	42, -40, 60	Area 1 (40%), Area 2 (26%)
Inferior Parietal Lobule**	5.07	4.82	48, -36, 50	Area 2 (13%), Area PFt (21%), Area PFm (11%)
Subcortical Areas **Cerebellum**				
Cerebellum Lobule HVIIA Crus I (99%)*	4.54	4.35	-30,-66,-32	
Cerebellum Lobule HVIIIA (46%), Lobule HVIIB (20%), Lobule HVIIIB (12%)*	4.05	3.91	-32, -44, -46	
Cerebellum Lobule HVIIB (90%), Lobule HVIIA Crus II (10%)*	3.83	3.72	-20, -74, -50	
Cerebellum Lobule HVIIB (48%), Lobule HVIIIA (23%)*	3.82	3.71	26, -66, -50	
Cerebellum Lobule HVIIA Crus II (82%), Lobule HVIIA Crus I (9%)*	3.75	3.64	-12, -80, -34	
Cerebellum Lobule HVIIIB (58%), Lobule HIX (30%)*	3.38	3.30	-14, -60, -50	
Cerebellum Lobule HVIIA Crus I (58%), Lobule HVI (13%), Lobule HVIIA Crus II (9%)*	3.24	3.17	10, -76, -32	
Cerebellum Lobule HVIIB (30%), Lobule HVIIA Crus II (6%)*	3.21	3.14	32, -60, -50	
Cerebellum Lobule HVIIB (68%), Lobule HVIIIA (27%)*	3.21	3.14	16, -72, -50	
Cerebellum Lobule HVIIIA (22%), Lobule HVIIB (19%), Lobule HVIIA Crus II (12%)*	3.19	3.12	34, -52, -50	

2.4   Discussion

This chapter aimed to investigate the dissociation between activity generated by visually-guided and memory-guided sequences, and how this altered with sequence familiarity. This allowed, for the first time, an investigation of which areas of the cerebellar hemispheres contribute to the automatic motor and cognitive control of eye movements during visual sequence learning in humans. At present, this is the first experiment to investigate this process using eye movements during explicit sequence learning. As hypothesised, during both Presentation and Rehearsal phases, eye movements were performed more accurately during Familiar sequences than Novel sequences. Results also revealed a novel observation which suggests that performance of Familiar and Novel sequences was dependent on fundamentally different forms of memory. It can be argued that qualitatively different types of memory underpin performance in these conditions because behavioural data shows that for Novel sequences, higher numbers of sequence repetitions in Presentation blocks resulted in progressively higher recall accuracy during immediately subsequent Rehearsal blocks (see Figure 3). This did not vary for Familiar sequences, suggesting that they were relatively independent of training in presentation (see Figure 3). Therefore, this suggests that although Novel sequences were dependent on shorter term representations, Familiar sequences were dependent on longer-term memory systems.

An important characteristic of automatic behaviours is that they are executed below the level of consciousness, resulting in faster and more accurate behaviours than those under the influence of controlled processes (Kahneman, 2011; Schneider & Shiffrin, 1977). Accordingly, results showed that during Presentation blocks, the amount of Anticipatory saccades made prior to the onset of the pacing cue increased in accordance with increased sequence familiarity and repetition number, whilst the amount of saccades made as a response to visual cues decreased, suggesting that not only accuracy but the speed of eye movements changes as sequences become more familiar.

The experimental design presented also allowed BOLD activity related to Rehearsal blocks to be modelled separately from that in immediately preceding 'Presentation' blocks in which sequences were learned under visual guidance for later rehearsal. The principal aim of the study was to test the hypothesis that the automatic execution of Familiar and the less automatic execution of Novel sequences purely from memory result in, respectively, lower and higher activity in areas of the cerebellar cortex which connect with the prefrontal cortex. Consistent with this view, such activity was found to be present in Crus I of lobule HVIIA. This effect was the most significant of all those found in the cerebellum. Not only was there less activity in Familiar than Novel sequences, but activity also decreased progressively as the number of repetitions (and hence, the degree of familiarity and automaticity) increased. The effects cannot be ascribed to differences in sensory processing or to oculomotor control as has been previously argued (see Glickstein & Doron, 2008; Doron et al, 2010), because oculomotor demands were directly comparable across conditions. There are two possible explanations for this activity, both of which are learning-related. First, it was argued in the Introduction of this Chapter that physiological excitability decreases are a marker of the cerebellar plasticity that supports learning. Second, the decrease may reflect a change in activity evoked by error signals. The methods and design used in this Chapter are not able to disambiguate these possibilities completely, but the former is consistent with other findings (Balsters and Ramnani, 2011), and the latter is a less likely possibility, because there were no visual cues during rehearsal to indicate to subjects that they had selected an incorrect movement.

Decreasing activity was also found in area 46 of the prefrontal cortex during presentation blocks (see Figure 5). It could be argued that such decreases in activity might be relation to either the implementation of the oculomotor movement or the execution of the rules that guide these movements. The location of the activation, in area 46, suggests the latter is most likely as this area has no direct anatomical output to the musculoskeletal system, only indirect outputs. Previous research suggests this area is more related to the rules that guide action (see Ramnani 2014 for a review) and the results from this study align most strongly with this argument.

Beyond this primary result, evidence showed that cerebellar areas beyond lobule HVIIA showed differential BOLD activity related to Familiar and Novel sequences. Some areas of the cerebellar cortex also showed learning-related activity differences in the direction opposite to that predicted, although these were infrequent. This observation highlights the possibility that there may be multiple forms of cerebellar plasticity in different cerebellar cortical areas that support learning (d'Angelo, 2014). These results also contribute to our currently sparse understanding of the organisation of the oculomotor cerebellum. The 'oculomotor' vermis (parts of vermal lobule VII) is widely regarded as an important part of the eye movement system that connects with oculomotor nuclei of the brainstem (Noda et al, 1990; Thier et al, 2002; Yamada and Noda, 1987), and results showed activity here that is common to all rehearsal-related conditions in which the execution of saccades is a common feature (lobule HVII; Figure 6h). However, no significant learning-related differences were observed in this area.

In Chapter 1 of this thesis, the unknown role of the cerebellar hemispheres in the control of eye movements was discussed. This study of the memory-guided rehearsal of oculomotor sequences provides an opportunity to shed light on the location of these areas in the human brain. Lobule HVIIA contains cells which fire in relation to the voluntary control of goal-directed eye movements (Mano, Ito, & Shibutani, 1991; Marple-Horvat & Stein, 1990). This chapter shows three main areas within lobule HVIIA in which BOLD response amplitudes differ depending on whether oculomotor sequences are familiar or novel. The most anterior of these lies in Crus I (see above), but there are a further two locations within Crus II. One of these, a paravermal area, appears to show a similar pattern of decreases (Figure 6f) to those in Crus I. The other is localised more laterally (Figure 6a,d,g-a) and shows decreases that are greater for Novel sequences than Familiar ones. Given that these areas respond differentially to the degree of familiarity of sequences, it may be the circuitry in these areas acquires and uses forward models of processes initiated in the prefrontal cortex that relate to the execution of sequences. It is possible that there may be two separate loops involved in the control of eye

movements: a first that hypothetically links eye movement areas in the prefrontal cortex such as the FEF with the oculomotor vermis (Voogd et al, 2012), creating a motor oculomotor loop, and a second that links the same areas of the prefrontal cortex to Lobule HVIIA in the cerebellar hemispheres, creating a cognitive oculomotor loop (see Figure 8). Point-to-point anatomical data for the first loop remains to be shown, but given evidence that there are direct connections between HVIIA and the FEF (Xiong & Nagao, 2002), this suggests that a secondary oculomotor loop with a differential function in the cognitive rather than the motor control of behaviour may exist.

Manual Loop	Prefrontal Loop	Oculomotor Loop 1	Oculomotor Loop 2
Primary Motor Cortex	Area 46	?	Frontal Eye Fields
↓ ↑	↓ ↑	↓ ↑	↓ ↑
Cerebellar Lobules HIV, HV, HVI	Cerebellar Lobule HVIIA (Crus I + II)	Cerebellar Vermal Lobule VII	Cerebellar Lobule HVIIA (Crus I + II)
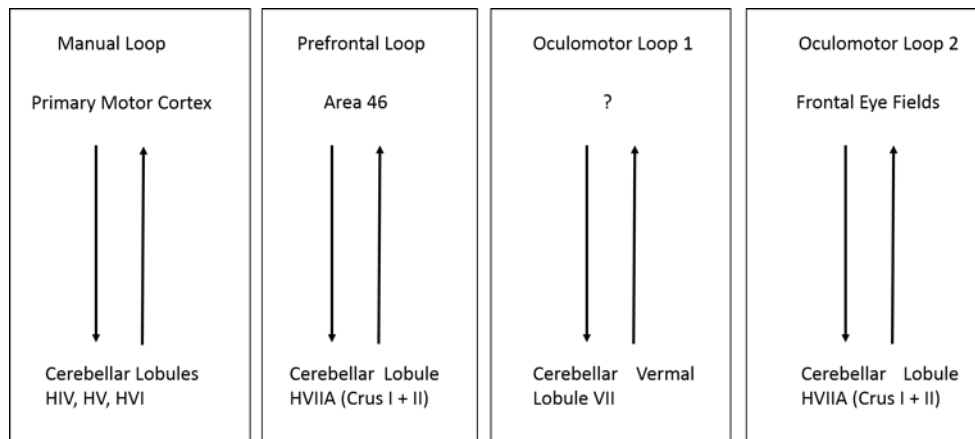
Figure 8: A new model for the motor and cognitive control control of oculomotor behaviours.

Although these areas may be specialised for the cognitive control of eye movements, it is important to note that they may have more domain-general roles that do not tie them to the cognitive control of specific effector systems. Previous studies have reported very similar activations to those reported in this chapter in Lobule HVIIA on the border of Lobule VI and Crus I (32, -64, -28; 38, -72, -38), and activity very close to the site of the more lateral activation in Crus II related to the automation of symbolic rules used to guide manual actions (Balsters and Ramnani, 2008; 2011). Future work is needed to clarify this matter, in order to determine whether Lobule HVIIA has a general role in the cognitive control of behaviours or whether different areas of this lobule may control the automation of rules used to guide manual and oculomotor behaviours separately.

It has been argued previously (Ramnani, 2014) that motor and non-motor skill learning involves a transition from "controlled" to "automatic" processing, dependent, respectively, upon prefrontal and cerebellar circuitry and their interactions. Flexible prefrontal operations may be used to resolve novel problems (such as the acquisition of Novel sequences in this study). However, they demand the use of limited capacity working memory, are effortful and prone to failure if their limited capacity is exceeded by the demands of a concurrently performed task. The cerebellar cortex may provide a mechanism to deal with these shortcomings, in the form of a second, long-term store for forward models of the same operations (such as the structure of sequences in this study). Although less flexible, it could operate automatically, with less effort and concurrently with other tasks ongoing in working memory without disrupting them. The behavioural results presented in this Chapter support the conclusion that performance is initially reliant on working memory, whereas it transitions to dependency on longer-term memory stores, and become less dependent on working memory.

The results presented in this Chapter suggest that the cerebellar areas identified are likely to work in concert with a set of connected prefrontal areas. Processing Familiar (vs. Novel) memory-guided sequences was associated with activation in the mid-portion of the middle frontal gyrus (area 46; figure 4) and the frontal pole (Fp2, area 10), both of which communicate with the cerebellum via the pontine nuclei (Schmahmann and Pandya, 1997). Area 46 is specifically known to send outputs to lobule HVIIA and "oculomotor" lobule VII (Kelly and Strick, 2003) and has a known role in the maintenance of information in working memory (Petrides, 2000; Constantinidis et al, 2001). In this study, Novel sequences activated Area 46 in both visually- and memory-guided conditions (activity also decreased as familiarity increased). It is therefore likely that area 46 supports short-term, working memory-related processes, and becomes less involved as sequences come to depend upon longer-term stores, possibly in cerebellar circuitry. A number of studies have implicated cerebellar circuitry in working memory operations (Desmond, Gabrieli, Wagner, Ginier, & Glover, 1997; Küper et al., 2016; Peterburs, Cheng & Desmond, 2015; Sakai, Rowe & Passingham, 2002; Thürling et al.,

2012b). Indeed, Küper et al., (2016) report activations in a set of areas very similar to those found in this Chapter and dependent upon working memory load. Similarly, Peterburs et al (2015) found increased activity again in a similar set of areas. This study additionally shows that they play a role in the rehearsal of sequences, purely on the basis of memory and unaided by visual cues.

The frontal lobe and parietal eye fields are also important parts of the oculomotor system, connected with each other (Barbas and Mesulam, 1981) and frequently shown to be engaged in the higher order, cognitive control of eye movements (Ferrera et al, 2009; Schall, Hanes, Thompson, & King, 1995; Schall et al, 2002). The FEF and IPS also send outputs to lobule HVIIA via the pontine nuclei (Xiong et al, 2002; Prevosto, Graf & Uglioni, 2010). It was therefore expected that rehearsal-related activations would be found in the FEF, SEF and intraparietal sulcus. However, these areas were activated only in the presentation blocks, and not in the rehearsal blocks (Figure 4; the FEF and SEF were more active during presentation Novel sequences than Familiar sequences). Although this seems to imply that the FEF and IPS are more concerned with stimulus-guided than memory-guided eye movements, that conclusion is contradicted by previous work showing that these areas are importantly engaged in memory-guided saccades (Brown et al., 2004; Dias and Segraves, 1999)

This chapter has shown activity related to cognitive and oculomotor demands during visual sequence learning in areas of the prefrontal cortex, the frontal and parietal eye fields, hemispheral parts of cerebellar cortical lobule HVIIA, and the oculomotor vermis. These areas can be organized into three cortico-cerebellar subsystems on the basis of their connectivity. First, it is argued above that the most likely system to be engaged in visual sequence learning is that which connects prefrontal Area 46 with lobule HVIIA of the cerebellum. Second, the least understood is the system which connects the oculomotor vermis, which did not show learning-related effects, with area 46 (Kelly and Strick, 2003), which did. Note that although some believe the oculomotor system to be connected with the cortical eye fields, no evidence to support this could be found in human subjects

(see Voogd et al, 2012), though this has been shown in non-human primates (Xiong et al, 2002). Third, the frontal lobe and parietal eye fields also connect with each other and with lobule HVIIA, and here the neocortical components of the system did not show learning-related effects. In order to close the gaps in our understanding, anatomical studies will need to produce a more detailed account of the connections between cerebellar and neocortical areas, and data from functional imaging and electrophysiology will need to characterise the exchange of information between them during the process of sequence learning.

Chapter 3: Conflict Resolution During a Spatial Stroop Task in Young and Ageing Populations

3.1   Introduction

Literature surrounding the effects of ageing on cognition tends to focus on clinical ageing, with a wealth of research investigating the effect of clinical diagnoses such as Alzheimer's, dementia and Mild Cognitive Impairment (MCI) on executive processes such as working memory and attention. Many early studies in this field focused on the effects of clinical ageing when compared to control groups of healthy ageing subjects because the decline in cognitive processes such as response inhibition are accelerated in older adults with Alzheimer's when compared with healthy older adults (Spieler, Balota, & Faust, 1996). Due to this, it is hard to distinguish the effects of healthy ageing on cognitive processing, and newer research is seeking to address this caveat.

An important aspect of human cognition is the ability to ignore conflicting information in order to focus on task-relevant information. In order to complete everyday tasks, the human brain must be able to negotiate many sources of information that may increase processing load, and to persevere with a goal in the face of information that is conflicting. This is seen in many real-world examples of human behaviour, such as maintaining attention to driving whilst passengers in a car are talking, or inhibiting the deleterious effects of visual information from static and dynamic road advertisements on driving performance. A common task used to study resistance to interference in human participants is the Stroop task. The classic version of this task involves identification of colour words e.g. RED or BLUE which appear in either a congruent manner (e.g. the word 'RED' appearing in red font) or an incongruent manner (e.g. the word 'RED' appearing in blue font), and subjects generally use verbal responses or manual responses to indicate the colour of the word they have been presented, whilst attempting to inhibit the linguistic content of the word itself (Stroop 1935).

Whilst novel behaviours require conscious attention and controlled processing, it has been suggested that automatic behaviours become faster and more reflexive with practice, occurring below the level of conscious awareness (Posner & Snyder, 1975; Ashby, Turner, & Horvitz, 2010). Shiffrin & Schneider (1977) suggest that in the cognitive sciences, automatic behaviours have two fundamental properties. Firstly, automatic behaviours are triggered by sensory cues, which almost always elicit the behaviour. Secondly, automatic behaviours can be successfully performed in the face of a secondary task without interference (Poldrack et al., 2005). It is often suggested that responses to linguistic cues in the colour-word Stroop task are hard to supress, due to the automatic nature of well-learned procedural behaviours such as reading. Such automatic processes require fewer attentional resources, and are prioritised due to their rapid implementation. Such processing will then 'interfere with processing other information about the word' (Anderson, 1990, p. 100) which relies on more controlled processes, thereby contributing to the classic Stroop effect.

Research into the effect of ageing on inhibitory processing has shown mixed results. It has been suggested that older adults are less able to inhibit interference from other sources of information than younger adults as information overloads the working memory of ageing populations more easily, leaving these older adults with less capacity with which to inhibit interference from conflicting stimuli (Hasher & Zacks, 1988). In the classic colour-word version of the Stroop task, this has been shown by increased error rates and longer reaction times in response to conflict in incongruent Stroop trials in older adults (Adólfsdóttir, Wollschlaeger, Wehling, & Lundervold, 2017; Andrés, Guerrini, Phillips, & Perfect, 2008; Aschenbrenner & Balota, 2015; Bugg, DeLosh, Davalos, & Davis, 2007; West & Baylis, 1998; West & Alain, 2000). However, these results have not been consistently replicated. Some studies show retained inhibitory processing across the lifespan in a domain general context (see Burke & Osborne, 2007 for a review), and others show no age-related deficits in Stroop performance specifically (Salthouse & Meinz, 1995; Verhaeghen & De Meersman, 1998; Verhaeghen, 1999, 2011; Williams et al., 2007). Some argue that Stroop effects in ageing populations can be reliably explained by the

general slowing of the speed at which the task is performed across the lifespan, and when they appropriately control for differences in speed of processing in their Stroop task data by, for example, regressing accuracy scores against measures of reaction time and processing speed, there are no significant ageing effects (Salthouse & Meinz, 1995; Verhaegen & De Meersman, 1998; Verhaegen, 2012).

Methodological differences in this body of research should be noted, and may explain the inconsistencies between studies outlined above. In particular, studies which do show Stroop effects tend to use the classic colour-word Stroop tasks (see above) whilst others showing no Stroop effects across the age span tend to use alternative Stroop paradigms, including number and position (Salthouse & Meinz, 1995) and spatial Stroop tasks (Verhaegen, 1999). This juxtaposition in the literature could be argued to represent a linguistic priming effect. Age-related changes in Stroop performance may be more convincingly explained by changes in semantic processing than more global changes in executive functioning, meaning they have more difficulty inhibiting information on the basis of semantic meaning rather than inhibiting response selection on the whole. Indeed, Brink & McDowd (1999) directly compared ageing effects in a classic colour-word Stroop task and a colour-block variation of the task. Subjects were presented with a colour patch to which they were asked to respond whilst inhibiting the name of a colour, either congruent or incongruent with the colour-patch, which was presented in black text either above or below the colour patch. The authors found no ageing effects in the colour-block Stroop task, but found age-related deterioration in performance on incongruent trials of the colour-word Stroop task.

There are exceptions to this argument. Graf & Uttl (1994) compared the performance of older adults in a classic colour-word variant and a picture-word variant of the task, where visual items were presented with a congruent or incongruent corresponding noun. They found significant age-related effects for the picture-word but not the colour-word task. Graf & Uttl (1994) suggest that this may be due to two reasons. Firstly, they suggest that previous studies may not have screened older adults appropriately for health problems, such as dementia. Global

processing deficits symptomatic of age-related disorders such as dementia may contribute to the interference effects found in some previous colour-word Stroop experiments but not others, and may explain the different findings in the literature. However, this is common practice in more recent literature which does show significant ageing effects in the colour-word Stroop task (e.g. West & Alain, 2000). Secondly, rather than using raw accuracy scores, the authors expressed performance during the Stroop test as a ratio index of interference relative to simple word reading speed. The authors suggest that this method of differentiating the effects of general slowing from cognitive interference may explain the different effects in their data and previous colour-word Stroop data which does not use such an index (Graf & Uttl, 1994). However, there may be a further important methodological difference which may explain this pattern of results. Graf & Uttl (1994) failed to include an appropriate control group of younger participants in their study. Other studies also fail to include a young control group (Aschenbrenner & Balota, 2015; Adólfsdóttir, Wollschlaeger, Wehling, & Lundervold, 2017) or an appropriate control or baseline measure such as a neutral condition as well as the incongruent/congruent conditions which would have allowed the authors to separate the experimental effects from the effects of either speed of processing changes or changes in semantic priming (Adólfsdóttir et al., 2017; Brink & McDowd, 1999; West & Bell, 1997). This may mean that any effects of ageing in these particular data sets are overstated as they do not have appropriate comparisons to measure against.

Instead, Brink & McDowd (1999) suggest the different patterns of results in different versions of the Stroop task may relate to the attentional resources each task variant requires. It has been suggested that there are two attention systems, the anterior and posterior attention systems (Posner & Petersen, 1990). The anterior attention system is required to focus on one of multiple sets of information which are physically integrated with distracting information, or cannot easily be processed separately based on peripheral cues such as shape, colour or location. The posterior attention system is responsible for focusing attention on particular visual information on the basis of easily detectable peripheral cues. The latter is less complex in nature and the use of this system may compensate for age-related

decline in the anterior attention system (Grady, 2008). Brink & McDowd (1999) suggest that in their study, the colour-word version of the Stroop task relies on the anterior attention system as the colour and word information is integrated in the same physical location. However, the colour-block version of the Stroop may benefit from the utilisation of the posterior attention system because the colour block and the colour word are presented adjacent to each other, so peripheral location cues can be used to complete the task. The same argument could be made for other non-typical variants of the Stroop task. For example, in the fish spatial Stroop task used by Williams et al (2007), the task was simplified so it could be used in a lifespan study to test children as young as 5 as well as older adults, up to the age of 76. In this task, subjects were required to identify the direction a fish was facing, which could be congruent or incongruent with its location on the screen e.g. the fish could be on the left of the screen and also facing leftward. It could be argued that peripheral cues such as the shape of the image could be easily separated from the location of the image, thereby relying on the posterior attention system, and facilitating the information processing.

The study presented in this Chapter seeks to resolve the issues outlined above by using a spatial Stroop paradigm which contains no linguistic information, with appropriate baseline measures and a control group. Further, it seeks to develop a novel spatial Stroop paradigm where target information was physically integrated with the distracting information in a more complex manner so that processing could not be facilitated by the posterior attention system and relies on the anterior attention system.

In the oculomotor domain, there is a distinction between endogenous and exogenous saccades. Endogenous saccades are controlled, goal directed saccades which require conscious manipulation. Exogenous saccades, on the other hand, are automatic, and occur with minimal involvement of conscious control (Berger, Henik, & Rafal, 2005; James, 1890). In the same way that manual actions are shown to relate to cognition, research shows that cognitive processes both influence, and are influenced by eye movements. It is generally accepted that the

oculomotor system processes information in concert with the cognitive system and eye tracking methods are used to study these behaviours. These provide benefits over and above other methods (e.g. manual response tasks) as they sample at a faster rate, thereby providing us with a more detailed, semi-continuous, real-time source of information about the perceptuomotor processes that support problem solving, and these processes are largely, though not all, out of the control of the subjects (Liversedge & Findlay, 2000; Spivey et al, 2009). Despite this, few studies have directly investigated the effects of the Stroop task on the automatic execution of saccades. Some studies have investigated the automatic priming of eye movements during Stroop tasks involving linguistic cues. These studies follow the task set up of the original Stroop task but use peripherally presented colour patches to invoke oculomotor responses to direction words or colour words. Eye movements during these tasks have shown longer saccade initiation latencies and larger error rates during incongruent than congruent trials (Hermens & Walker, 2012; Hodgson, Parris, Gregory, & Jarvis, 2009). During incongruent trials, these studies found a high frequency of corrective saccades with atypically short inter-saccadic intervals (usually of less than 100ms) after primary saccades towards the congruent location, indicative of the automatic implementation of prepotent oculomotor responses from linguistic cues during incongruent trials. This suggests that eye movements can be automatically guided by symbolic information, even if it is irrelevant to the task at hand (Hodgson et al, 2009). An important caveat to the current oculomotor Stroop literature is the lack of data on automatic priming of saccades outside of the linguistic domain. As previously discussed, reading is well-known to be an automatic, procedurally learned behaviour, and the automatic priming of saccades for linguistic cues may reflect semantic priming as a domain-specific phenomenon, rather than a general phenomenon. Manual response tasks have shown that non-linguistic symbolic cues such as directional arrows automatically cue visual attention in humans, likely due to their unambiguous, salient meaning in everyday communication (Hommel, Pratt, Colzato, Godijn, & Godijn, 2001). However, no studies could be found that have investigated the effect of ageing on automatic priming of saccades by non-linguistic symbolic information during spatial Stroop tasks, nor have they investigated the effect of aging on this process.

This Chapter aims to investigate two main hypotheses. Firstly, whether the suggested decline in inhibitory processing in ageing populations results in poorer performance during incongruent trials of a spatial Stroop task that does not rely on linguistic cues. This Chapter aimed to expand on previous work by using a spatial Stroop paradigm which investigated colour-direction conflict using well-known symbolic cues and arbitrarily learned colour-location mappings. It was hypothesised that the healthy ageing process would result in a decreased ability to persevere with these newly learned eye movements in the face of incongruent information represented by well-known symbolic cues. Secondly, this study aimed to investigate whether age-related differences in susceptibility to cognitive conflict had an effect on eye movement parameters. It was hypothesised that saccades during incongruent trials would have longer reaction times and larger saccade amplitudes and durations than saccades in congruent and control trials. Further, it was hypothesised that due to increased interference from incongruent information, these effects would be more pronounced in older subjects.

3.2   Methods

3.2.1   Subjects

Subjects were recruited from Royal Holloway, University of London and the surrounding residential area of Egham, Surrey. Subjects were divided into 2 groups, a young control group and an ageing experimental group. 26 young participants were tested, but 2 subjects were removed from the analysis stage (see below for exclusion criteria) leaving 24 younger subjects (22 females; mean = 18.79 years, range = 18-22 years, SD = 1.10). 20 older participants were tested, but 6 were excluded from the analysis leaving final n = 14 (6 females; mean = 63.86 years, age range = 59-72 years, SD = 4.97). All subjects gave written informed consent and the study was approved by the Royal Holloway, University of London Psychology Department Ethics Committee. All subjects had normal or corrected-to-normal vision and were free of colour vision impairment, neurological, psychiatric and cerebrovascular disorders as tested in a pre-screening session. All subjects were rewarded for the experimental session with either 2 research credits towards their

Departmental University Research Participation Scheme (for the control group of students) or £10 (for the ageing group). Subjects were recruited opportunistically either from students and workers at the University or people living or working in the local area.

Exclusion Criteria

Subjects were removed if they had problems with colour vision (control group, n = 1), did not complete the full experimental session (experimental ageing group, n = 1), or had insufficient eye tracking data (control group, n = 1, experimental ageing group, n = 5). Eye tracking data was considered insufficient if over 30% of the total number trials had to be excluded. Trials were excluded from analysis if no saccade was detected prior to final fixation point on the target placeholder (see Figure 9), an incomplete saccade was detected, with no completely sampled saccade seen between the central fixation point and the final fixation on the target placeholder (see Figure 10) or if lots of inconsistently sampled data were detected that did not comprise an identifiable, complete saccade (see Figure 11 for an example). Insufficient eye tracking data may have been caused by physical problems (e.g. many blinks, droopy eyelids, contact lenses, head movement) or technical reasons (reflection from corrective glasses, calibration errors).
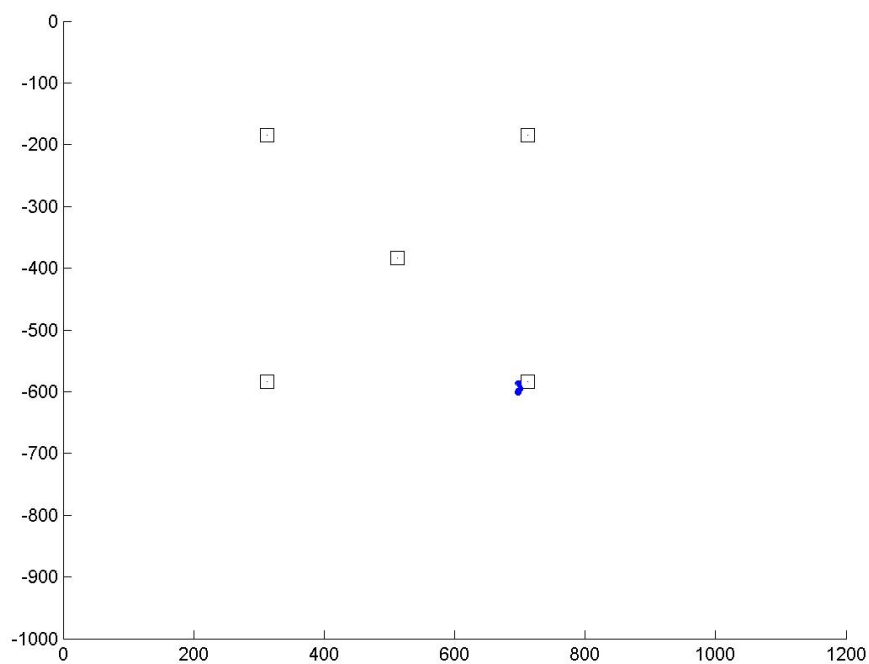
Figure 9: An example of a trial with a fixation but no detectable saccade. On these plots, the five squares mark the locations of the four corner placeholders and the central fixation cross. Axes represent screen pixels in the x and y co-ordinates. The blue dots represent gazes sampled every millisecond.
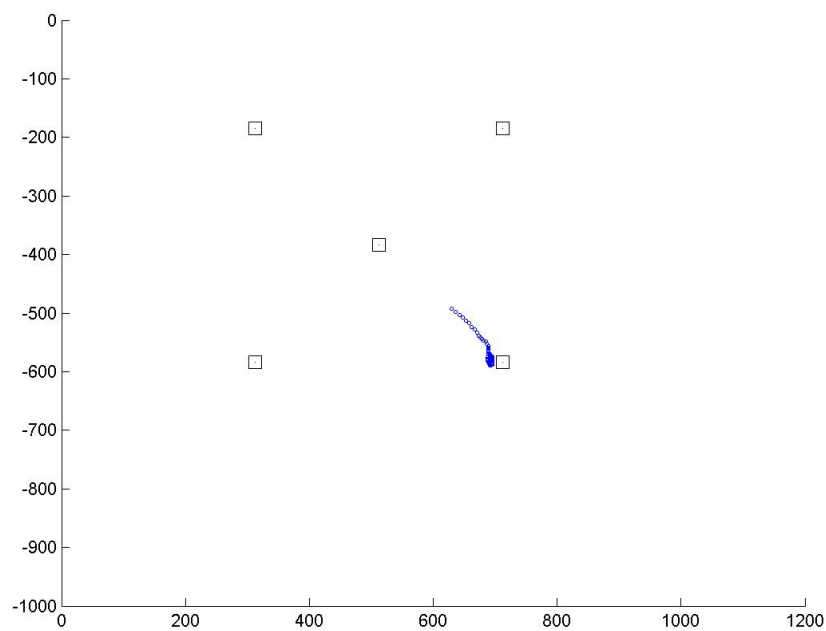
Figure 10: An example of a trial without a full saccade detected. Axes represent screen pixels in the x and y co-ordinates.
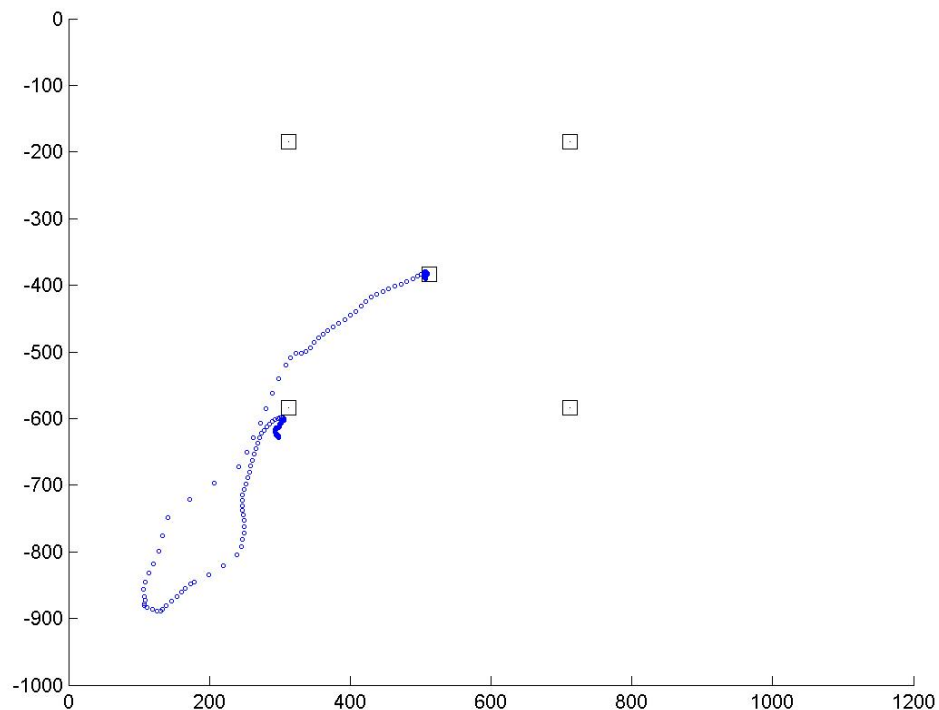
Figure 11: An example of a trial where weak calibration meant multiple gaze traces were detected and a full, complete saccade could not be tracked. Axes represent screen pixels in the x and y coordinates.

3.2.2 Apparatus

Subjects' heads were placed in an upright desktop head mount positioned 60 cm from the screen. The desktop head mount was equipped with both a chin rest and a forehead rest in order to stabilise the head and prevent subtle head movements from causing the appearance of gaze drift. An Eyelink 1000 eye-tracking system (SR Research Ltd) was used to track monocular vision from the subject's right eye at a sampling rate of 1kHz. A purposefully-dedicated personal computer with EyeLink software was used to collect and record oculomotor behaviours. The raw data took the form of a pupil centre/corneal reflection technique, rather than creating temporal video recordings of the eye per se for post-hoc analysis. Experiment Builder software recorded the timings of individual events which allowed the reaction times to be calculated off-line after the experiment had taken place. A separate personal computer running Experiment Builder software was used

for experimental programming and stimulus presentation alongside a 1024 x 768 pixel screen screen with a refresh rate of 60Hz).

3.2.3 Experimental design

This experiment aimed to investigate two main hypotheses. Firstly, it aimed to elucidate whether there were age-related differences in the ability to learn rule-based oculomotor behaviours and to conduct these in the face of the Stroop-related cognitive conflict. A spatial Stroop paradigm was used in which trials fitted into three conditions, which comprised the independent variable of trial type. These were control trials, congruent trials and incongruent trials (see below for details). Performance was measured using overall accuracy at implementing the rule-based oculomotor behaviours as a proportion of total trials in each of the three conditions. It also aimed to investigate whether age and incongruency of symbolic information resulted in changes in the following eye movement parameters: time taken to execute a saccade, saccade duration and saccade amplitude. Two groups of subjects were used to test the independent variable of age: a young control group and an ageing experimental group, comprised of older adults aged over 60. There were no differences between the conditions presented to the two subject groups; experimental timings and experimental setup remained consistent across conditions.

Task:

Subjects were required to use trial-and-error learning to learn the mappings between colours presented within an experimental stimulus and placeholders located in the four corners of the screen. Placeholders were located in the peripheral corners of the screen (see Figure 12), as it has been suggested that placeholders located immediately to the sides or above or below a central fixation point during oculomotor Stroop tasks may impede the spatial parameters of saccades (Hodgson et al., 2009). Subjects were informed at the beginning of the experiment that each colour they would see arbitrarily corresponded to one of the four peripheral

placeholders, and they had to begin by guessing, and use the feedback given to discover these relationships.

At the beginning of each trial, a fixation cross was presented in the centre of the screen. This was followed by the experimental stimulus which appeared in the centre of the screen. The experimental stimulus contained a diamond shape surrounded by four arrows, pointing towards four placeholders located in the top left, top right, bottom left and bottom right of the screen (see Figures 12-14). After the disappearance of a brief fixation cross in the centre of the screen, subjects were instructed to move their gaze towards one of the four placeholders. Once their gaze had settled on a placeholder, it would turn green if they had made a correct response and red if they had made an incorrect response. The advantage of this element of the experimental design was that feedback would be given in the location in which the subjects were already fixating, which maximised the visibility of the feedback. Subjects were instructed that if the placeholder turned green, this was a correct colour-location mapping, and they should look towards that placeholder every time they saw that colour appear within the experimental stimulus in the future. They were explicitly instructed to learn the relationships between colours and placeholders based on these rules, regardless of location.

Whilst the experimental stimulus was on the screen, one of the five sections (either the centre diamond or one of the four directional triangles, or 'arrows' in the four corners of the central stimulus, see Figure 12) would be filled in with a colour. The colours used in the experiment were blue, orange, yellow, pink, brown and purple. In the examples in Figures 12-14, red has been used as an example although this was not used in the final experiment. In order to examine whether there were age-related differences in the ability to resist conflicting cognitive information, this experimental stimulus allowed presentation of the colours to occur in three different conditions. For example, if the correct location for the red colour was the top left placeholder, the following conditions could occur:
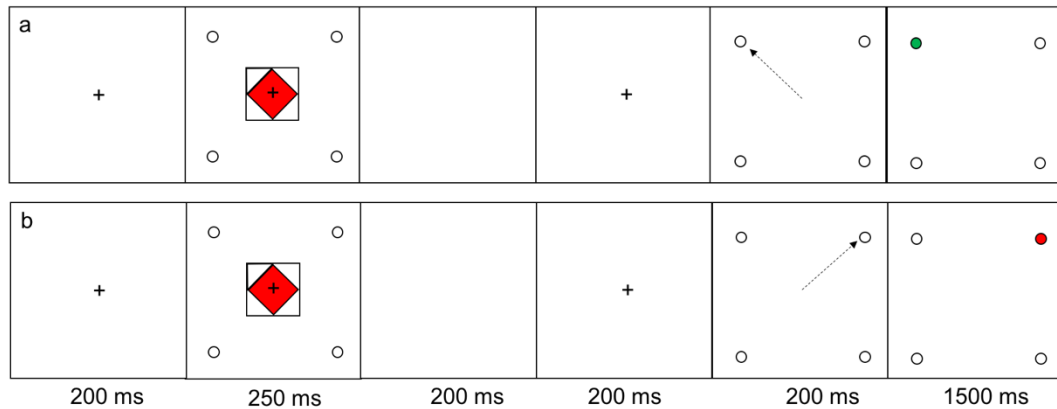
Figure 12: Example of a trial in the control rule-learning condition providing no directional information. In these graphs, the square with a coloured section in the centre of the screen represents the experimental stimulus and the circles in the four corners represent the peripheral placeholders. Each colour that was presented in the experimental stimulus corresponded with one of the four peripheral placeholders. After a go signal, subjects were required to move their eyes to the peripheral placeholder that corresponded with the colour presented within the experimental stimulus, regardless of which part of the experimental stimulus was coloured. The dotted line represents an eye movement from fixation location to peripheral placeholder. If the subject looked at the correct placeholder, it would turn green (a) and if the subject looked at the incorrect placeholder, it would turn red (b).
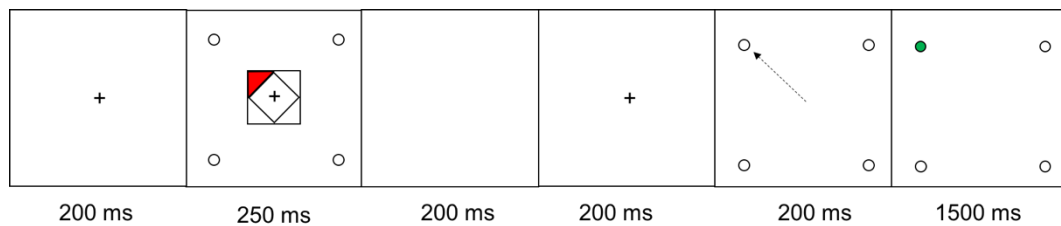
Figure 13: Example of a trial in the congruent condition, where the direction of the arrow corresponded with the colour-location mapping.
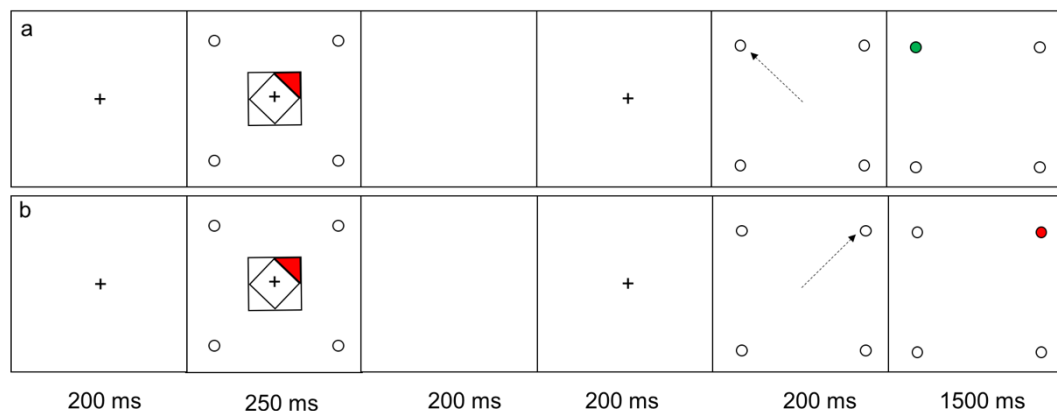
Figure 14: Example of a trial in the conflicting, incongruent Stroop condition where the direction of the arrow did not correspond with the colour-location mapping. In this condition, the colour corresponded with a placeholder in a different location. An example of a correct response (a) and an incorrect response (b).

The order of colours and conditions were randomised in order to prevent order effects from confounding learning effects. The identities and timings of oculomotor responses were logged and recorded by Experiment Builder software designed for compatibility with the Eyelink 1000 eye-tracking system.

Experimental Sessions:

All experimental sessions for each subject took place in the same behavioural set up during the testing period to ensure consistent environments across conditions. The Stroop task lasted roughly 25 minutes and contained 120 trials, split across three conditions (see Table 5). There were equal amounts of trials for each colour, and these trials were split evenly across centre (control), congruent and the remaining three incongruent placeholders. Therefore, there was a higher amount of incongruent trials, but these were divided evenly across all the remaining non-congruent target locations. A break was given every 20 trials to prevent fatigue in the subjects. Prior to the experiment and during each break prior to resuming the experiment, a 5-point calibration and validation was undertaken to optimally configure the eye tracker for the subject, and to allow for correction of gaze drift that may have occurred as a result of head movement (see Section 2.2.2 for a more detailed description of the calibration process).

Table 5: Spatial Stroop Trial Structure

Condition	Control Condition	Congruent Condition	Incongruent Condition
# of trials	24	24	72

Experimental Timings:

Experimental timings remained consistent across the two groups of subjects to ensure that any differences in behaviour could be attributed to the experimental manipulation rather than to confounding differences due to differential presentation

and response time windows. Due to the psychophysical aspects of this task, it was important that the presentation of stimuli and the collection of oculomotor responses was at a fairly rapid pace, in order to ensure that saccades were ballistic and natural and not mediated by the effects of manipulation at the level of alternative conscious cognitive processing.
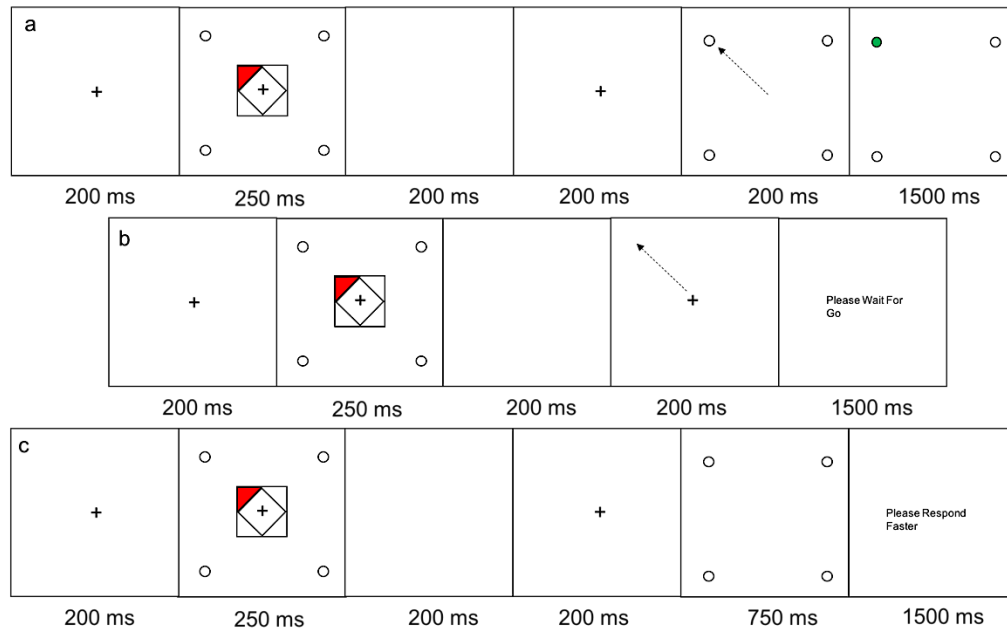
Figure 15: Trial design and trial timings for a correctly executed trial (a), a premature trial (b), and trial with no detected response (c).

After the experimental stimulus was displayed for a period of 250 ms, a fixation cross was displayed and subjects were instructed to respond when the cross disappeared from the screen and the four target placeholders appeared (see Figure 15). Responses were tracked in real time and if a valid response was made that lasted for 50 milliseconds (ms) within the 200 ms response period, the placeholder the subject fixation on would turn green for a correct response and red for an incorrect response. This feedback would last the length of the inter-trial interval, roughly 1500 ms. If no response was made within 750 ms, a 'Please Respond Faster' screen would appear. If a response was made that lasted for 50 ms or more prior to the disappearance of the central fixation cross, which acted as the 'Go' cue, a premature response screen would appear which read 'Please wait for Go'. These trials were removed prior to analysis. On average, there were 7.86 (6.55%)

premature trials for younger subjects and 5.36 (4.47%) premature trials for ageing subjects. There were 8.23 (6.86%) no response trials for young subjects and 9.93 (8.27%) no response trials for ageing subjects. There were no significant differences between age groups in frequency of premature or no response trials ($p > .05$).

Pilot Experiments:

Pilot experiments were used to determine the number of colour-location mappings used in the final version of the experiment. The original intention of the study was to include as many colour-location mappings as possible, to create the maximum amount of variation possible. A preliminary version of the experiment (Pilot experiment 1) used 8 colour-location mappings (blue, purple, yellow, orange, pink, brown, aqua, red), with each target placeholder having two corresponding colour mappings. Pilot experiments of this version of the experiment lasted around 40 minutes due to the long software loading time required for the high number of experimental stimuli, which was believed would be too long for the ageing subjects. When piloting the longer version of the experiment with 8 colours, the inter-trial interval was around 5 seconds long per trial and it was decided that this may cause the subjects to remove their heads from the headrest and look away from the eye tracker, as it appeared as though the experiment had stopped, which may have affected the quality of the eye tracking data as we could not recalibrate the eye tracker in between each trials. The use of four colour mappings was considered in order to reduce stimulus loading time and therefore reduce the length of the experiment. However, it was decided that four colour-location mappings would be too few as this would allow at least one mapping to be learned through elimination rather than trial and error. Therefore, six colour-location mappings were used in the final experimental paradigm as it allowed the most variation whilst maintaining a natural and unnoticeable inter-trial interval. A preliminary version of the experiment with 6 colours was conducted, with the experimental stimulus displayed for 350 ms and a 250 ms response window. These original timings were based on previous research. It is suggested that the average fixation duration is around 263 ms for younger adults and 329 ms for older adults (Paterson, McGowan & Jordan,

2013) and whilst the experimental stimulus was on the screen, the subjects were intended to keep their eyes fixated and not make any saccades, so a 350 ms fixation window was used for the first pilot experiment. Saccades take around 200ms to initiate (Purves et al., 2001) so any saccades that occurred prior to a 200ms time window were classed as premature saccades and a corresponding message was displayed (see Figure 15b).
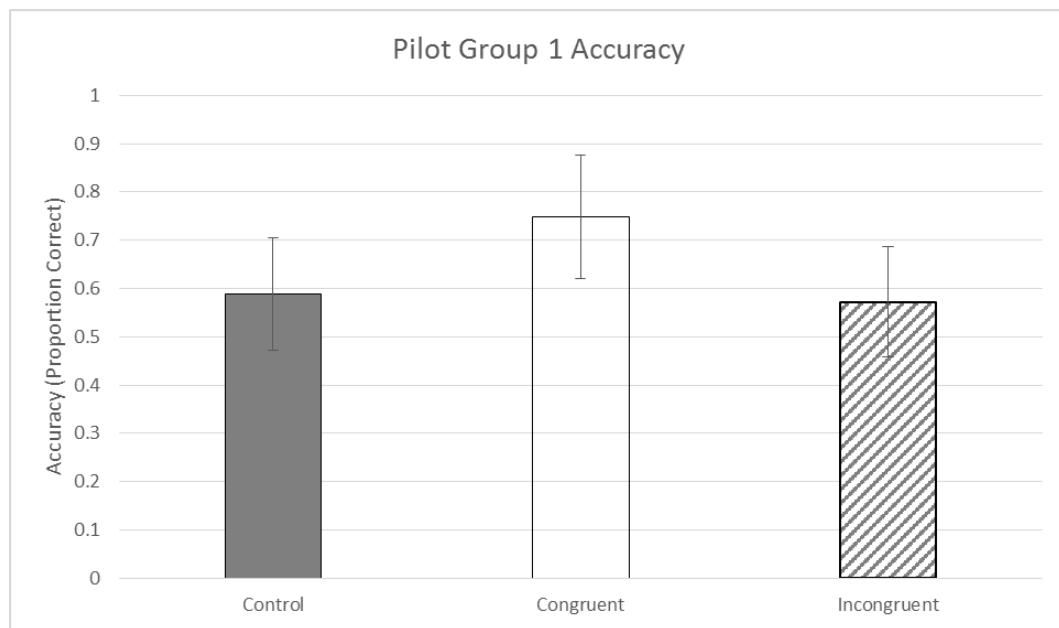
Figure 16: Accuracy data for young control subjects using Pilot experiment 1.

A further pilot experiment (Pilot experiment 2) was undertaken to determine whether a shorter response period may elicit more automatic responses and help increase the Stroop effect and help decrease the experiment length. In this version, the stimulus was displayed for 225 ms and the response period was 175 ms. The average duration of a saccade after onset is between 30ms and 100ms (Bahill, Clark & Stark, 1975) so a slightly longer duration window of 175ms was used during the initial pilot experiment just in case durations were elongated in older adults.
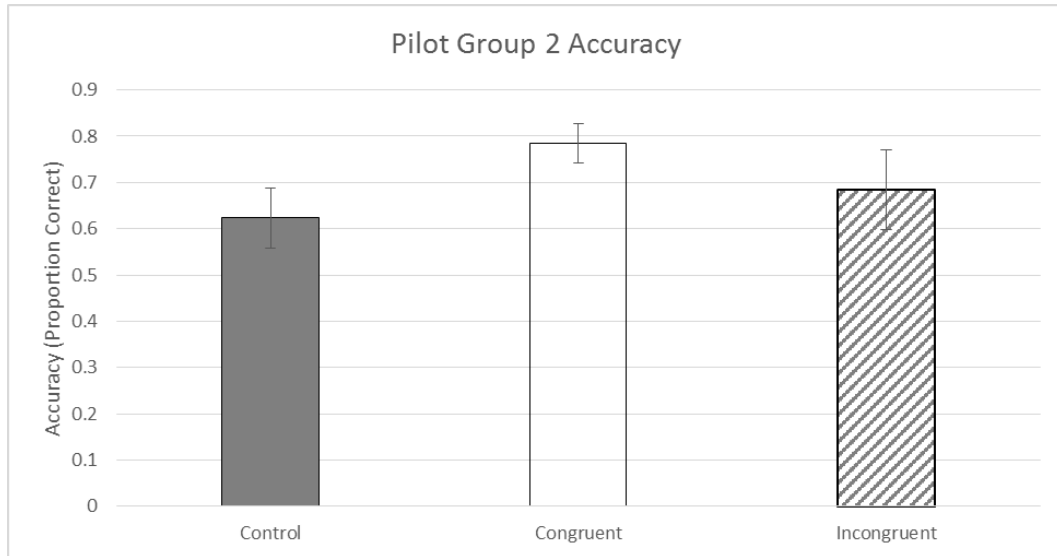
Figure 17: Accuracy data for young control subjects using Pilot experiment 2.

At this speed, data showed a less pronounced effect in the incongruent vs congruent condition than in the first pilot experiment (see Figure 16), so it was decided to display the experimental stimulus for 250 ms and allow a 250 ms response period. This experimental version was tested in a group of ageing participants, and we found the desired effect (see Figure 18). Therefore, these timings were used in the final experiments.
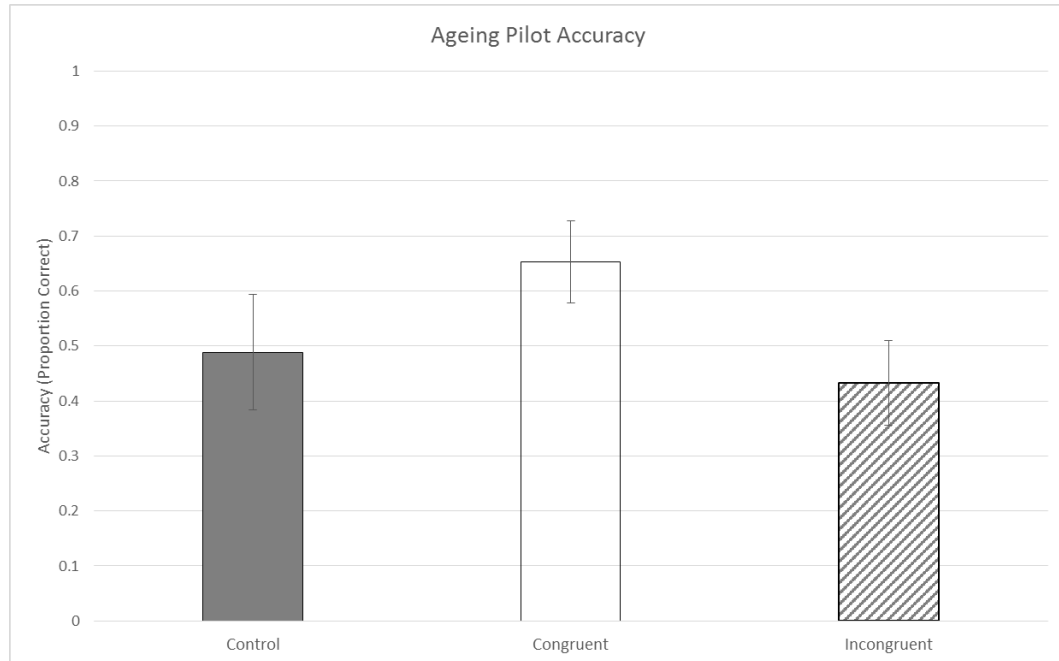
Figure 18: Accuracy data for the final version of the experiment tested on ageing subjects (error bars: +/- 1 SEM).

3.2.4 Preprocessing of oculomotor data

This study also aimed to investigate whether the effect of cognitive conflict during incongruent trials as compared to congruent and control trials could be seen in psychophysical measures. For this, a series of eye movement analyses were undertaken investigating reaction time, saccade duration and saccade amplitude. Due to this, the author was only interested in the effect of condition on eye movement parameters of correctly executed saccades, as we could be sure of where the subject was looking, and the cognitive processes that underpin the execution of these saccades were correctly performed. Therefore, incorrect trials were removed prior to these analyses. Three further subjects were removed from the final analysis for these measures, as once incorrect trials and trials with insufficient eye tracking data were removed (as outlined in *Exclusion Criteria*), there was at least one condition with no remaining valid data. For all variables tested (accuracy, reaction time, saccade duration and saccade amplitude) we tested for statistically significant outliers. In keeping with previous behavioural work in the field, data was defined as an outlier if it lay beyond 3 standard deviations above or below the age group

mean for each condition (Williams et al, 2007). No data satisfied this criterion, so no data points were removed.

3.2.5   Behavioural data analysis

A series of 3 x 2 Mixed Measures ANOVAs with two factors were conducted: Condition (3 levels: control rule mapping, congruent direction-rule mapping and incongruent direction-rule mapping) and age group (2 levels: a young control group and an ageing experimental group) were used to investigate overall accuracy, reaction time, saccade duration and saccadic amplitude. Overall accuracy consisted of number of correct trials as a proportion of all valid trials. Reaction time and saccade duration were measured in milliseconds. Reaction time was defined as the time between the onset of the go signal (disappearance of the fixation cross) and the onset of the saccade. Saccade duration was defined as the time between the onset of the saccade and the final fixation point. Saccade amplitude was defined as distance of the saccade from the onset of the saccade to the final fixation. Saccade amplitude can be measured in either pixels or degrees. For the analysis in this Chapter and in Chapter 4, pixel measurements were used because converting these raw measurements to degrees of visual angle would be confounded by the curvature of the saccade.

An important assumption of Analysis of Variance (ANOVA) is the normal distribution of scores for each variable, therefore this assumption was tested prior to analysis using the Kolmogorov-Smirnov (K-S) test. A significant ($p < .05$) K-S statistic indicates the assumption of normality is violated. Transformations were applied to correct the data where appropriate (an example is shown below). Transformations were applied using the 'TRANSFORM' function in SPSS. The aim of transforming the data is to change each value and each variable within the same analysis to correct the distribution and make the data as normally distributed as possible, without changing the relationship between the variables (Field, 2009). In some cases, different variables within the same analysis were skewed in different directions due to differences between young and ageing subjects (see below for an

example). In these cases, no transformations were applied, as the ANOVA is often argued to be robust to violations of their assumptions (see Glass, Peckham & Sanders, 1972).

Accuracy data showed a negative skew for younger subjects when tested for normal distribution, with more data points grouped towards the higher end of the accuracy scores (see Figure 19a).
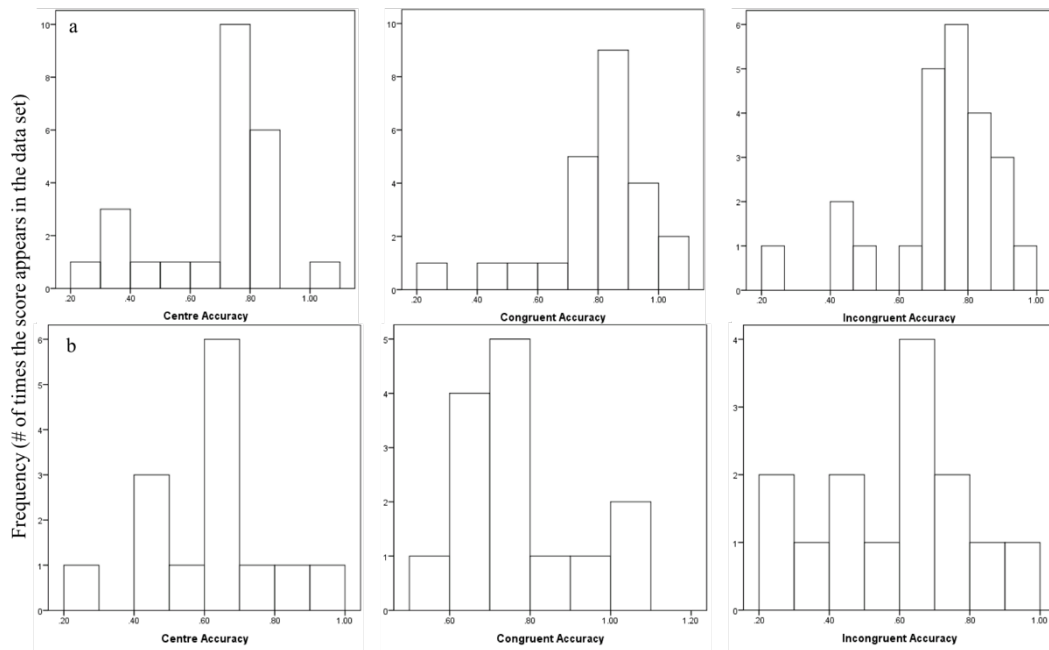
Figure 19: Raw frequency distributions for accuracy data for all conditions for younger subjects (a) and ageing subjects (b). Prior to transformation, data showed a negative skew for younger subjects (a), with data being group significantly towards the right of the frequency distributions.

When transformations were applied to reverse scored data in order to correct this, data for young subjects showed normal distributions, but reverse scored data for ageing subjects showed a negative skew for normal distribution in the congruent condition (see Figure 20b). For this reason, analysis was performed on non-corrected data, because the transformations introduced new problems.
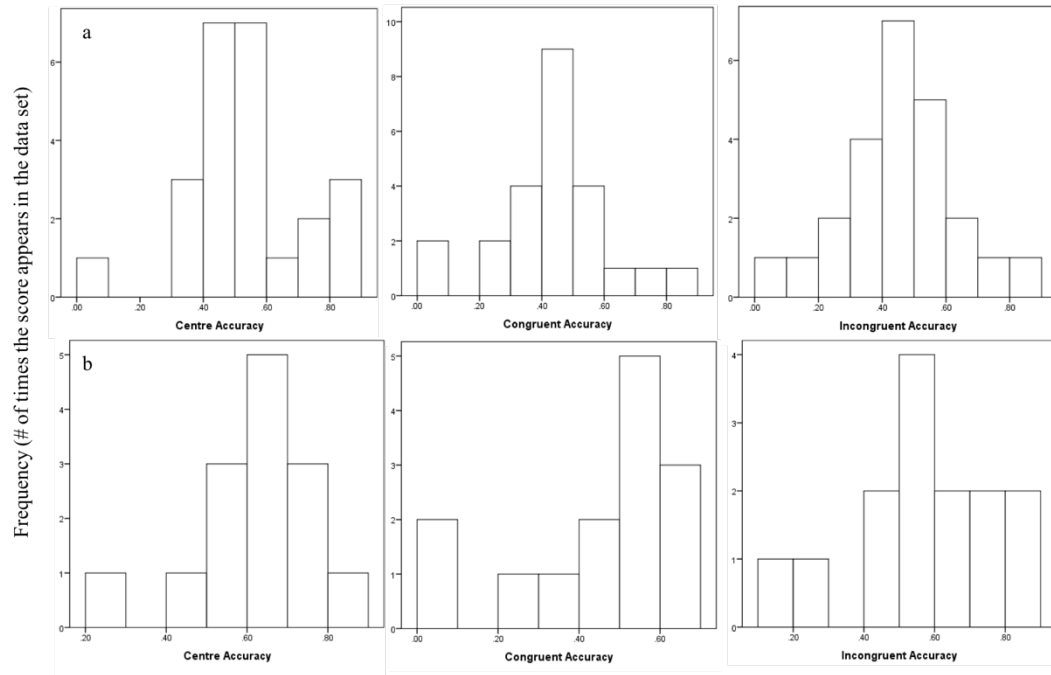
Figure 20: Square root transformed accuracy data. After transformation, data for younger subjects (a) became normal as tested by the K-S test, however data for older subjects (b) then became negatively skewed, with data grouped towards the right of the frequency distributions, which was not present prior to transformation (see Figure 19b).

Reaction time and saccade duration analyses showed a positive skew towards the lower data values when tested for normal distribution of the data (see Figure 21 for an example of skewed distributions prior to transformation). These analyses were therefore adjusted using base-10 logarithmic transformations prior to analysis to normalise the data (see Figure 22 for an example of corrected distributions after transformation).
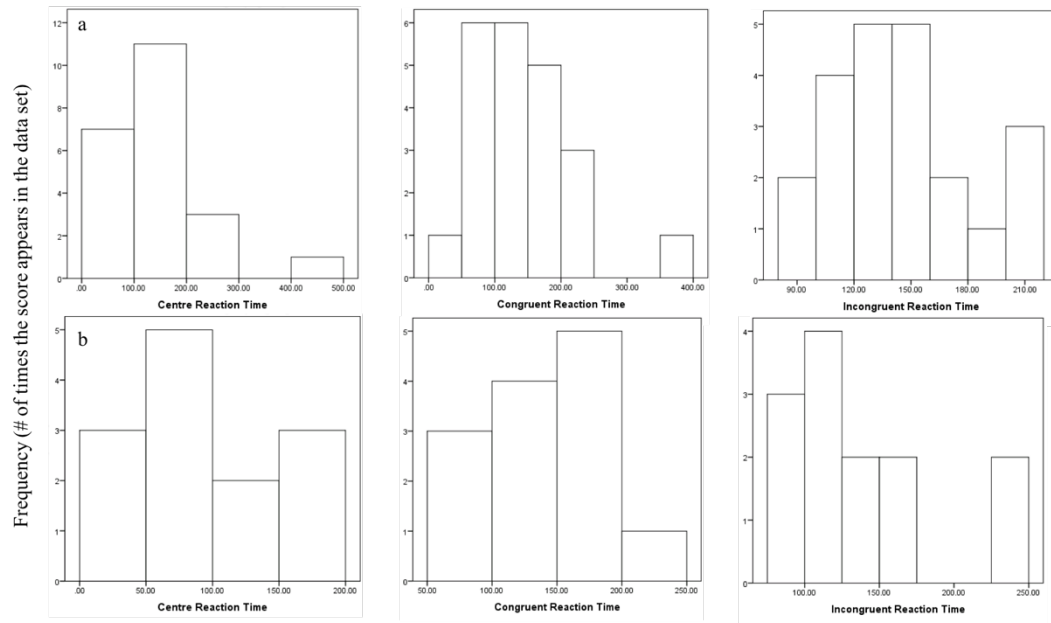
Figure 21: Reaction time frequency distributions for both young (a) and ageing (b) subjects prior to transformation.
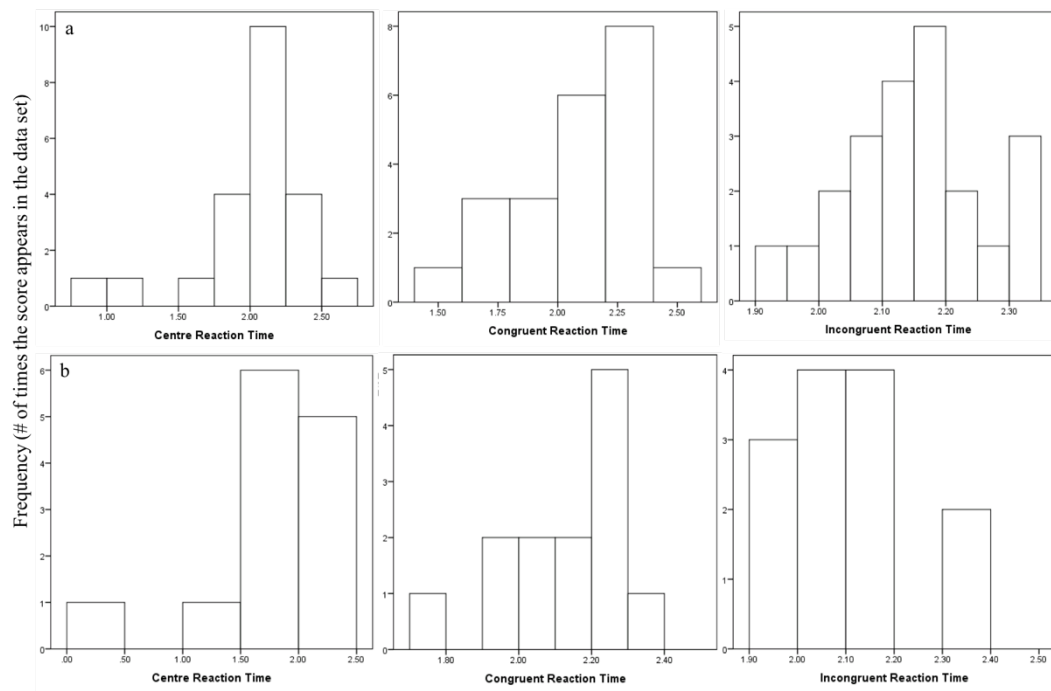
Figure 22: Reaction time frequency distributions for young (a) and ageing (b) subjects after base-10 logarithmic transformations were applied.

Comparisons and descriptive statistics within the Results section text are reported using data adjusted for non-normality, as outlined above. All ANOVAs are reported with a Greenhouse-Geisser correction where data violate assumptions

of sphericity, and *post-hoc* tests are reported with Bonferroni corrections for multiple comparisons. Effect sizes are report using the partial eta squared value.

3.3 Results

3.3.1 Accuracy

Data showed there was a significant main effect of condition: $F_{(2, 72)} = 20.525$, $p < .001$, $\eta^2 = .363$. Overall, accuracy was significantly higher in the congruent condition (mean = .776, SE = .027) than the control condition (mean = .647, SE = .032), $p < .001$). Accuracy was also significantly higher in the congruent condition than the incongruent condition (mean = .650, SE= .031), $p < .001$. Across both age groups, there were no significant differences between the control condition and the incongruent Stroop condition, $p > .05$. All pairwise comparisons were Bonferroni corrected for multiple comparisons.

There was a non-significant overall main effect of age group: $F_{(1, 36)} = 2.250$, $p = .142$, $\eta^2 = .059$. However, there was a marginally significant interaction between condition and age group: $F_{(2, 72)} = 3.023$, $p = .055$, $\eta^2 = .077$. To explore the source of this nearly significant interaction and consistent with the primary hypothesis of this experiment, one independent *post-hoc* t-test was conducted to investigate age differences in the incongruent Stroop condition. As only one t-test was conducted, there was no need to correct for multiple comparisons. There was a significant difference between the young control group and the ageing experimental group on accuracy scores in the incongruent spatial Stroop condition ($p = .039$, equal variances assumed, see Figure 23). To our knowledge, previous studies of the Stroop effect have found no notable differences between young and ageing subjects on measures of accuracy in a neutral condition, but instead focus on measures of reaction time for this difference, so this relationship was not considered for further investigation.
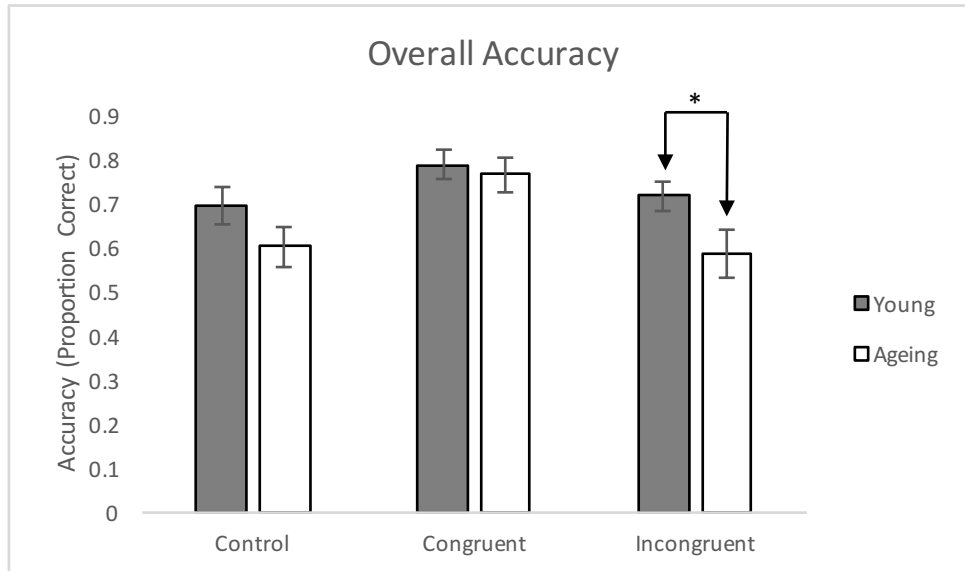
Figure 23: Overall accuracy data for young and ageing subjects, * represents significant differences in independent measures t-tests. Error Bars: +/- 1 SEM.

3.3.2 Reaction time
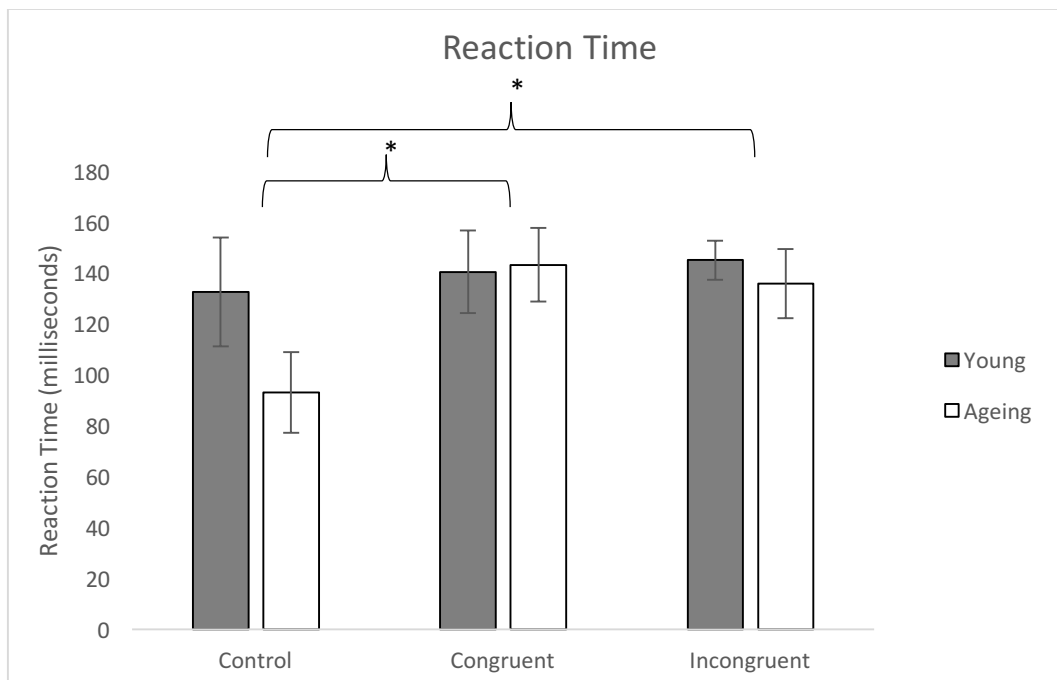
Figure 24: Untransformed Reaction Time data for young and ageing subjects. * represents significant differences in the main effect of condition. No significant differences between age groups were shown.

Reaction times were calculated in milliseconds as time between the disappearance of the fixation cross, which acted as the go signal, and the onset of

the principal saccade. (see Figure 25). Statistical tests were conducted on transformed data (see Methods), but raw reaction time data can be seen in Figure (21). There was a significant main effect of condition on reaction time, $F_{(1.401, 46.238)} = 6.986$, $p = .006$, $\eta^2 = .175$. Overall, reaction times were significantly longer in the incongruent (mean = 2.130, SE = .021, p = .019) and congruent (mean = 2.108, SE = .038, p = .034) conditions than the control condition (mean = 1.901, SE = .079, see Figure 24). There was no significant difference between the congruent and incongruent conditions. There was no significant main effect of age ($F_{(1,33)} = .855$, $p = .362$, $\eta^2 = .025$) nor was there a significant interaction between condition and age group ($F_{(1.401, 46.238)} = .233$, $\eta^2 = .044$).
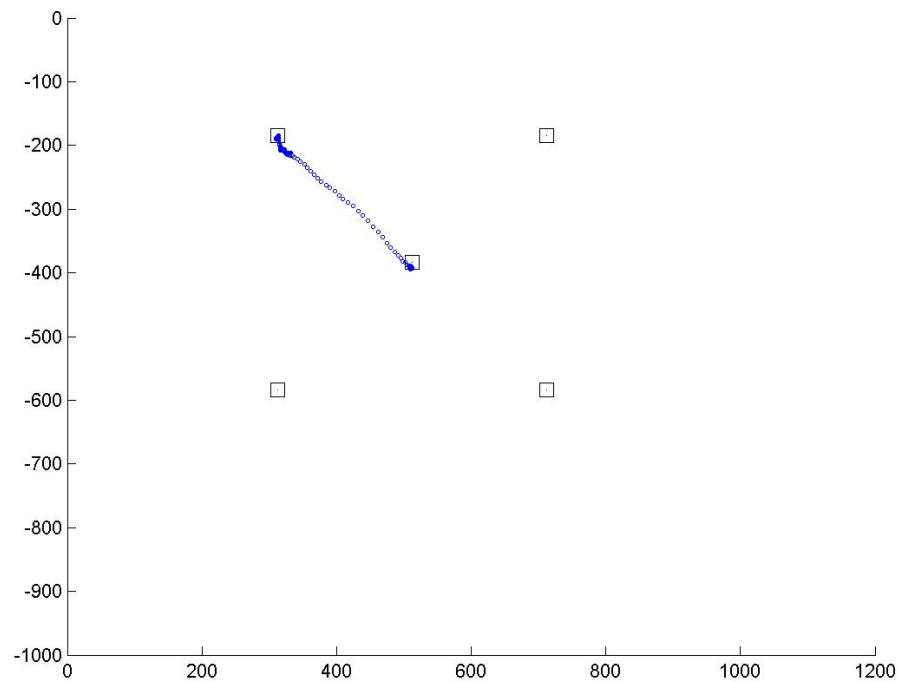
Figure 25: A typical example of a correctly executed saccade with the onset on the saccade marked in dark blue at the central fixation point and the final fixation points marked in dark blue at the peripheral target placeholder. The principle saccade is the saccade between these two identifiable fixation points. The blue circles represent gaze sampled every millisecond.

3.3.3 Saccade duration

Saccade duration was calculated in milliseconds. Data was transformed to correct for the lack of normal distribution. Statistical tests were conducted on transformed data. There was a significant main effect of condition on saccade duration, $F_{(1.337, 46.238)} = 9.291$, $p = .002$, $\eta^2 = .220$. Overall, saccade duration was significantly longer in the incongruent (mean = 1.633, SE = .023, p = .001) and congruent (mean = 1.625, SE = .023, p = .027) conditions than the control condition (mean = 1.537, SE = .031; See Figure 26). There was no significant difference between the congruent and incongruent conditions. There was no significant main effect of age ($F_{(1, 33)} = .017$, $p = .898$, $\eta^2 = .001$), nor was there a significant interaction between condition and age group ($F_{(1.337, 46.238)} = .731$, $\eta^2 = .006$).

Figure 26: Untransformed saccade duration data for young and ageing subjects. * represents significant differences in the main effect of condition. No significant age differences were shown.

3.3.4 Saccade amplitude

Data fitted criteria for normal distribution so no transformations were applied to the data. There was a significant main effect of condition on saccade amplitude, $F_{(1.354, 44.668)} = 12.404$, $p < .001$, $\eta^2 = .273$. Overall, saccade amplitude was significantly larger in the incongruent (mean = 177.24 pixels, SE = 9.456, $p < .001$) and congruent (mean = 164.261 pixels, SE = 9.887, $p = .020$) conditions than the control condition (mean = 120.237 pixels, SE =12.325). There was no significant difference between the congruent and incongruent conditions. There was no significant main effect of age ($F_{(1,33)} = .106$, $p = 747$, $\eta^2 = .003$), nor was there a significant interaction between condition and age group on saccadic amplitude ($F_{(1.354, 44.668)} = .620$, $p = .482$, $\eta^2 = .018$).

Corrective Saccades

Previous research has shown that during Stroop tasks using oculomotor responses, corrective saccades are made where a saccade is made to an incorrect location and this is followed by a fast saccade to the correct location (Hermens & Walker, 2012). Within the trials that were performed correctly (as the final, main fixation was on the correct target placeholder), there were frequent examples of such corrective saccades in the data presented in these chapters. In these trials, an initial saccade was made towards the placeholder in direction the arrow was pointing, before a corrective saccade was made towards the placeholder that corresponded with the colour presented. It is possible that the inclusion of trials with these corrective saccades affected the other results previously discussed. For example, the time taken to make a saccade in an incorrect direction and a corrective saccade to the correct location may increase the time taken to reach the final fixation point and therefore increase reaction times in some trials. Though analysis of such saccades is beyond the scope of this thesis, an example has been given in Figure 27. Further data analysis investigating the parameters of eye movements in trials with and without corrective saccades separately may provide a more accurate picture on the effect of cognitive conflict on eye movements during this Stroop task.
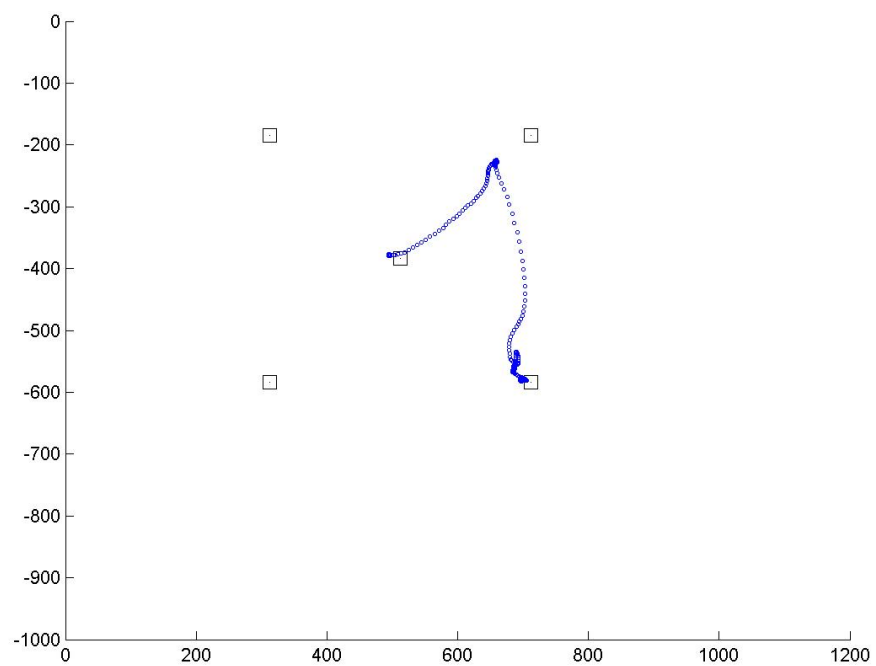
Figure 27: An example of a corrective saccade, where an initial saccade was made to the incorrect placeholder, but was corrected prior to the completion of the saccade.

3.4   Discussion

An important characteristic of automatic behaviours is that they are resistant to the interfering effects of a second task. Although this was not a classic dual-task paradigm in which there were two concurrent tasks to perform, subjects still had to navigate two different sets of rules, one of which was conflicting with the other so it was hypothesised similar effects would be present during this task. This Chapter aimed to investigate whether the healthy ageing process has deleterious effects on the ability to resist such interference. A spatial Stroop task involving non-linguistic symbolic cues was used to investigate two main hypotheses.

Firstly, it was hypothesised that the non-clinical ageing process would result in higher levels of cognitive interference from conflicting directional information during the incongruent trials of a colour-direction spatial Stroop task. Previous studies investigating the effects of ageing on the Stroop paradigm have found more significant effects during linguistic Stroop tasks than Stroop tasks using non-linguistic cues, which could be argued to reflect a semantic priming effect, rather than a domain general effect of cognitive conflict. Data showed accuracy was not significantly different between young and ageing participants for a control, baseline condition or the congruent condition. However, the interaction between age groups (young vs ageing) and Stroop condition (control vs congruent vs incongruent) was approaching significance. Importantly, this was explained by a significant age difference in accuracy during incongruent trials, where the direction of the arrow and the colour-location mapping were in conflict with each other. During these trials, but no other trial types, older subjects had significantly lower accuracy scores than younger subjects. In keeping with our first hypothesis, this suggests that whilst they were able to perform the behaviours equivalently, the older subjects were more susceptible to interference from task-irrelevant information.

Secondly, this study aimed to investigate whether this process had an effect on psychophysical parameters. Many suggest that oculomotor behaviours relate to cognitive processing (Spivey et al, 2009), and studies have found that the automatic

priming of eye movements in response to linguistic cues during Stroop tasks results in saccades with longer reaction times as well as larger error rates on incongruent trials (Hermens & Walker, 2012; Hodgson et al., 2009). However, to the author's knowledge, whether such an effect is seen outside of the linguistic domain, or in ageing populations, has never been tested. Data showed that when two separate rules had to be implemented during the congruent and incongruent trials, reaction times, saccade durations and saccade amplitudes increased when compared with control trials where only colour mappings had to be implemented. However, pairwise comparisons showed there were no significant differences between congruent and incongruent trials on any of these measures, suggesting that the Stroop effect did not influence the kinematic properties of the eye movements themselves. Further, despite the differences in overall accuracy described above, we found no significant effect of age on any of our eye movement parameters tested: reaction time, saccade duration or saccade amplitude. Possible explanations for these results will be discussed in further detail below.

An important difference between this study and previous studies in the field is that the effects of eye movements and their relation to cognitive processes during the Stroop task was assessed both with relation to age, and using eye tracking methodologies. This is important because eye movement behaviours are, on the whole, more rapid than manual responses, and eye tracking methods allow us to sample at a much higher rate. Due to their rapidity, eye movements have been argued to precede the onset of manual actions by up to 1 second, and can be used to guide the implementation of the next manual behaviour before the previous one has even been completed (Land, Mennie, & Rusted, 1999). Therefore, there is, arguably, more information in an eye movement that can tell us about internal states in the generation of responses than there is in responses relying on manual control. Although eye movements can be voluntarily controlled, it has been argued that the rapidity of eye movements (occurring roughly 5-6 times faster than manual behaviours) means these are more likely to occur without our subjective awareness before interference from conscious processes (Land et al., 1999; Liversedge & Findlay, 2000; Spivey et al, 2009). An important facet of automatic behaviours is

that they are able to rely on previously learned information, and therefore generally do not require feedback, and are less reliant on continuous monitoring from conscious mechanisms (Land et al., 1999). It has also been argued that shifts in attention occur before the onset of eye movements (Posner & Petersen, 1990). Therefore, when investigating the effects of interference during the execution of automatic behaviours in a task such as ours, the use of eye movements allows us to investigate how our attention can be disrupted by conflicting information, before we even aware this has occurred.

Age-related differences were seen in accuracy, but not in the eye movement parameters of correctly executed trials. Hermens & Walker (2012) have argued that no models exist to explain the kinematics of eye movements and the disparity in measurements such as reaction time and saccade trajectory in tasks such as this. Further, to our knowledge, no equivalent studies have been conducted in the ageing population to compare these results with. However, average reaction times in previous literature range from 340-400ms (Hermens & Walker, 2012) to 400-450ms (Hodgson et al, 2009). These are similar to the reaction times in this study, which include a preparatory window of 200ms prior to the Go signal, then an average time before the onset of the saccade of 100-160ms (see Figure 24). Although other studies have identified eye movement differences in the reaction times of incongruent trials in younger subjects (Hermens & Walker, 2012; Hodgson et al., 2009), these findings were not universal for all measures tested in their experiments. Contrary to their hypotheses, Hermens & Walker (2012) found no differences in the saccade trajectories (or amplitudes) during incongruent trials when responses were correctly executed. Given that the Eyelink 1000 system used in this experiment samples at one of the highest rates possible, and that previous studies with similar data collection and analysis methods as ours have also found similar results in young, healthy subjects (Hermens & Walker, 2012), methodological reasons for these differences are unlikely.

This finding has two important implications for the literature. Firstly, these results suggest that cognitive and motor control processes are differentially affected

by ageing. The difference in accuracy scores seen in the incongruent condition between young and ageing subjects suggests that at the higher level of decision making, older subjects but not younger subjects are more susceptible to conflicting information. It could be argued that older adults have an overreliance on automation, but this study shows that at the lower-level of motor kinematics, once behaviours have reached an automatic state – as indicated by the correct performance of incongruent trials, eye movement behaviours in the young and older subjects are performed equivalently. This suggests equal levels of automation between younger and older subjects. This is surprising given the wealth of evidence showing changes in performance during motor (see Seidler et al., 2010) and oculomotor control (see Owsley, 2011) with ageing. Hogdson et al. (2009) suggest that in keeping with manual response Stroop tasks, this suggests interference is limited to the cognitive processing that occurs prior to the initiation of the action, rather than during the execution of the action itself. Therefore, no differences are seen in the spatial characteristics of motor responses as they are performed (see also Logan & Zbrodoff, 1998). This study adds evidence to this argument, and suggests that such an effect exists even when the response modality is oculomotor. Further, this data suggests that in both younger and older adults, learned behaviours can be implemented within the same oculomotor parameters.

Secondly, that there were no age differences in the eye movement parameters tested directly contradicts the argument that the source of the differences in the Stroop effect across different age groups is due to differences in speed of processing. This study found that reaction time did not differ between young and ageing subjects on any of the conditions of our task (see Figure 24), which suggest that either there were no real differences in speed of processing in the older subjects which could contribute to performance differences in older subjects, or that older adults are able to use alternative cerebellar and prefrontal neural mechanisms to compensate for such a change, these will be discussed in detail below. A controversy remains in the Stroop literature as to whether poorer performance on incongruent trials in ageing subjects reflects deficits in executive control, as argued above, or delays in processing. Many studies have suggested that age-related

variation in Stroop task performance can be wholly or partially attributed to general slowing (Bugg et al., 2007; Graf, Uttl, & Tuokko, 1995; Müller et al., 2016; Verhaeghen & De Meersman, 1998) whilst others have shown that such effects are upheld, even when speed of processing is controlled for (Troyer, Leach, & Strauss, 2006; West & Baylis, 1998). The use of reaction time data in our study allowed us to address this issue. If poorer performance in the incongruent condition in this study were caused by general slowing in the speed of processing with increasing age, we would expect longer reaction times in the older subjects in all conditions, rather than just the incongruent condition and this was not the case (see Results). It is important to note that studies controlling for speed of processing usually use specifically designed reaction time measures, to act as a control variable. Whilst this study did not include such a measure, it suggests that future work replicating this task with such a measure would help strengthen this argument.

An interesting observation in the data were the lack of differences between the control, baseline condition and the incongruent condition. To the author's knowledge, this is the first time that a Stroop task has included trial and error rule learning. That is, the task involved using trial and error learning to find the correspondence between the colour presented and the placeholder this colour was associated with. This was a beneficial approach as the baseline condition was not a direct instruction cue, but instead involved using feedback to learn and implement an arbitrary rule between the stimulus and response (see Figure 12). This condition was, therefore, more computationally difficult than the direct instruction cues used in congruent trials, where the arrow the colour was presented in would always point in the direction of the correct placeholder (see Figure 13). This allowed this study to investigate more thoroughly whether there were cognitive as well as motor differences in the ability of older vs younger subjects to learn novel behaviours as well as resist cognitive interference. There were no significant age differences in the control condition, which suggests that older subjects were just as able to learn and implement novel responses to symbolic cues, however there were age differences in the incongruent condition, suggesting that even though these were learned to an equivalent level, older adults were less able to inhibit responses to

task-irrelevant information than younger subjects. That there were no significant differences between the control condition and in the incongruent condition in accuracy scores in younger adults or older adults is an elusive finding. In keeping with previous Stroop tasks, and due to the presence of conflicting information, it was expected that accuracy would generally be significantly lower in the incongruent condition than in both the congruent and control conditions and this was not found. However, this result has also been shown in previous work. Williams et al. (2007) found mean intra-individual standard deviations (ISDs) for reaction time data did not differ between their incongruent condition and their neutral condition for any age groups across the lifespan (ages 5 to 76). Further, these authors also found no age-related differences in ISDs in congruent and neutral conditions, or between incongruent and congruent conditions except for 9-11, 12-15 and 20-29 year olds. The authors concluded that their data did not support the hypothesis that differences in reaction time inconsistency could be explained by age-related differences in executive control. However, the significant differences young and ageing subjects in accuracy on incongruent, but not congruent trials in this chapter contradict this (see above for a fuller discussion). It is important to note that although these authors used a spatial Stroop paradigm similar to the present study, they explicitly focused on reaction time rather than overall performance or accuracy of performance during the Stroop task, so this may account for both similar and dissimilar results to the present study. No other studies have found the same pattern of results regarding incongruent vs control trials, so we are unable to resolve this difference until further research investigating the effects of age on both trial and error learning and Stroop interference using alternative Stroop paradigms is conducted. An important first step is to replicate this study in a larger sample. A large amount of data had to be removed prior to analysis, particularly for the older subjects, so it could be argued that this analysis did not have enough statistical power to observe a valid effect. However, partial eta squared values for the main effect of condition during accuracy analysis was very high. Partial eta squared (η^2) is a common test of effect size for ANOVA: .01 is seen as a small effect, .06 a medium effect and .13 a large effect (Bourne, 2017). A power calculation conducted in the present study showed that this analysis had an eta squared value of .363,

which constitutes a large effect size. More likely, the lack of differences in control and incongruent trials in both younger and older subjects may be due to differences in neural control mechanisms as behaviours become more automated. This will be discussed below.

In Chapters 1 and 2 of this thesis, previous research from Ramnani and colleagues outlining the role of the cerebellum in the automation of cognitive behaviours was discussed (see also Ramnani, 2006; 2014). As discussed, it has been argued that once behaviours have reached a level of automation, control may be taken over by the cerebellum, leaving the prefrontal cortex more able to take control of other processes such as managing interfering, task-irrelevant information. Indeed, research has shown that patients with damage to the cerebellum are more susceptible to the intrusive effects of distracting information (Lang & Bastian, 2002). Research has also shown that from the age of 50, areas of the cerebellum including the vermis and the pons, which relays neural signals from the cerebral cortex to the cerebellum, experience age-related grey matter atrophy as part of the healthy ageing process, with atrophy being most apparent after the age of 60 (Hall, Miller, & Corsellis, 1975; Oguro, Okada, Yamaguchi, & Kobayashi, 1998). Research has shown that older adults have a reduced ability to automate new skills (Rogers & Fisk, 1991), which we suggest may be explained by these age-related neural changes. This study found no differences in performance between the young and ageing groups on control or congruent conditions, so it cannot be directly argued that behaviours during this spatial Stroop task had not reached equivalent levels of automation. However, that the older subjects performed less accurately on incongruent trials overall suggests this may be the case. Further fMRI research will be needed to elucidate this argument. Previously, it has been shown that plastic mechanisms in Lobule HVIIA of the human cerebellum supports the learning of rule-based manual actions (Balsters & Ramnani, 2008; Balsters & Ramnani, 2011) and long-term cognitive representations that underpin oculomotor sequence learning (Chapter 2 of this thesis). Therefore, it could be argued that if older adults are less able to automate new behaviours, such as the colour-location mappings in this novel spatial Stroop paradigm, there will be less apparent decreases in activity

in Lobule HVIIA of the cerebellum and more prefrontal activity during control rule-based trials and incongruent trials in older adults, indicating the requirement of a higher level of conscious control. This may also explain why younger and older subjects showed similar performance in control and incongruent trials. As opposed to the congruent trials, these trial types had an arbitrary rule-learning element. If behaviours in younger subjects became highly automated and cerebellar driven, we would expect no differences in performance between control and incongruent trials. If, however, behaviours in the ageing subjects were still being compensated for by the prefrontal system, given they both have high cognitive demands, we would expect performance to be equivalent in control and incongruent trials as well, but incongruent performance to be poorer than in younger subjects, as was found in our data. That is, performance levels would be equivalent, but the neural profiles of these behaviour would be different in younger and older subjects.

It is important to consider the caveats and limitations of this study. A primary issue whilst conducting this study involved the use of eye tracking methods on elderly subjects. Removing poor quality eye tracking data is common in the literature (for an example, see Hermens & Walker, 2012), which tends to be conducted on healthy, young subjects. Due to physical changes in motor apparatus with age, it is understandable that the amount of insufficient quality eye tracking in these subjects would be higher, and this population more prone to data dropout due to head movement and eye problems such as droopy eyelids and large amounts of blinking. However, this caused two main issues in our data: a smaller (yet, as argued above, statistically adequate) sample size for the older subjects, and unequal sample sizes between young and ageing subjects. Whilst we have accounted for this in our analysis methods, future work replicating this work using large, equal sample sizes would be useful to help replicate and validate the results of this study.

Features of the task may also help explain some of the non-significant results found in eye movement parameter data. It has been suggested that averaging saccade amplitude across multiple target locations could reduce significant differences between congruent and incongruent conditions due to differences in the

degree of saccade curvature between saccades made in different directions. Hermens & Walker (2012) discuss this issue, as they found the same lack of effects in younger subjects. The authors suggest that larger deviations towards and away from distracting information are present for vertical than for horizontal saccades. Future work should consider including shorter trials, so that a larger amount of trials for each target location could be collected and data for each of these analysed separately. Such a design was not applicable to our data, as it would have significantly reduced statistical power for each analysis. Further, Hermens & Walker (2012) suggest that using two rather than four target locations could target inhibition mechanisms more accurately, as attentional processes would be less widely distributed. However, if there are fewer targets to select between, this may make the task too easy and cause ceiling effects. Future work should aim to explore this possibility.

It is possible that the measures used by this study were not sensitive enough to detect age-related effects in oculomotor behaviours, and other measures such as inter-saccadic intervals, and total movement time may be more sensitive to ageing. Eye tracking methods allow us to sample at a high enough rate to look at the oculomotor behaviours that precede manual responses, as well as the response itself. Hermens & Walker (2012) showed that during their saccadic Stroop study, a large amount of saccades were initially incorrectly made towards the cue and then were corrected and made towards the target. Whilst testing for this this was beyond the scope of this data set, examples of inter-saccade intervals were seen in these data (see Figure 27), and this may be a path for future research to investigate as eye tracking measures adapt to the requirements of tracking elderly subjects more efficiently. The development of mobile eye tracking systems that sample at a much higher rate than those presently available would help to account for problems encountered that result in data loss when eye tracking elderly subjects such as head and body movement in the laboratory environment. In particular, head-mounted mobile eye trackers would help to reduce data loss in elderly subjects.

A final caveat of this study relates to the sample used. Due to the technical constraints of eye tracking methodology, it was necessary to screen older adults very thoroughly. All adults with neurological, mental, cardiovascular, physical or visual problems (such as cataracts, double vision and colour blindness) were excluded. Further, subjects from both the younger, but particularly the older sample were obtained opportunistically. For the ageing subjects, the sample largely comprised mature PhD students, post-doctoral researchers and University lecturers and professors who were still taking part in teaching or active research after the age of 60. As such, this sample may not accurately represent the entire ageing population. Indeed, there is literature showing that the effect of level of education on executive functioning has interactive effects with age on performance in the Stroop task (Van der Elst, Boxtel, Breukelen, & Jolles, 2006). More financial and human resources would have allowed us to sample from a wider population, and future research addressing this caveat would help to strengthen our arguments made with respect to healthy ageing in general.

This study tested two main hypotheses relating to the effects of typical ageing on oculomotor behaviours during a symbolic learning spatial Stroop task. In support of the first hypothesis, accuracy during incongruent trials, but not control or congruent trials, reduced with age. Controversy remains in the field as to whether the Stroop effect reflects a general deterioration in executive processing or a highly automated semantic priming effect. This Chapter shows that even when the task does not involve linguistic cues, older subjects are less able to resist interference from task irrelevant symbolic information which automatically prime eye movements. In contradiction to our second hypothesis, eye movement parameters such as reaction time, saccade amplitude, and saccade direction for correctly executed trials did not differ depending on either age or degree of congruency between target and symbolic cue. These results are discussed in the context of disparate effects of ageing on cognitive and oculomotor processing, and in contradiction to speed of processing theory. Overall, this study suggests that even eye movements which are rapid, and can easily become learned, automatic behaviours are susceptible to interference from task-irrelevant information with

increasing age. This has important implications for understanding how ageing might affect every day behaviours which are important for elderly people, such as safe driving, which will be explored in Chapter 5 of this thesis, and also for investigating possible methods for training the ageing population to persist with their goals in the face of conflicting information.

Chapter 4: The Effects of Age on Eye Movements during the Useful Field of Vision task

4.1   Introduction

As discussed in Chapter 3 of this thesis, in previous years, research has focused on the effects of the ageing process on skilled cognitive processing outside the clinical domain. More recently, experiments have focused on the relationship between eye movements and cognition and how these are affected by the ageing process. It has been suggested that classical clinical tests of eyesight over-simplify the visual deficits experienced by the ageing population (Ball, 2003). This is because standardised tests analyse visual acuity as a standalone entity, in the absence of competing visual information. This is at odds with naturalistic environments, in which individuals must often be able to manipulate information with much more complexity, from multiple tasks or objects in multiple parts of the visual environment in parallel, in order to ensure successful behavioural performance (Richards, Bennett, & Sekuler, 2006). Scientists and policy makers are becoming increasingly aware that seeing objects is not enough for safe driving, we need to be able to process and manipulate this information to drive successfully. For this reason, the Useful Field of Vision test was developed.

In the Useful Field of Vision task, a central and a peripheral visual task must be performed simultaneously. The presence of an extra stimulus in the peripheral visual field during a task processed centrally in the visual field means attention must be divided between multiple tasks, so the task relies on both selective (completing the task in central vision) and divided (simultaneously completing the secondary task in peripheral vision) attention at once. Shiffrin & Schneider (1977) suggest that the time taken to elicit controlled processes in many divided attention tasks is the immediate cause of poor performance. Therefore, in the Useful Field of Vision task, poorer performance when both tasks must be completed at once is indicative of responses that are less automated. The further the peripheral target is away from central vision, the more difficult it becomes to divide attention across both tasks. This task has been widely used in the ergonomic and behavioural literature as it

combines both sensory and cognitive processes. The task aims to identify the area of the visual field from which an individual can meaningfully obtain information. Therefore, Useful Field of Vision is defined as the total area of the visual field from which useful information can be acquired within monocular – one eye –fixation, without eye or head movements (Sanders, 1970). The visual tasks used for the test include visual stimulus discrimination and stimulus localisation. Visual arrays in Useful Field of vision Experiments are presented rapidly, in an attempt to ensure simultaneous performance of the two tasks. However, an important caveat to the body of literature are the methods used. Traditionally, visual arrays are presented to subjects on a screen, but subjects respond using manual response button boxes. Therefore, no stringent controls exist to ensure the tasks are performed concurrently rather than consecutively. This is important because the concurrent, rather than serial, performance of the two tasks places demands on limited resources, and challenges automatic and controlled processing in ways that previous studies do not. This will be discussed in more detail later in this section. This has implications on how applicable the results of the task are to real-world situations. For example, during driving we are required to attend multiple sources of information at once, even if we are not directly looking at them such as hazards in wing and rear view mirrors.

It is well known that visual acuity decreases as the retinal eccentricity of visual stimuli increases (Aubert & Foerster, 1857). Many studies show that in younger populations, conducting both a central and peripheral visual field task in parallel negatively impacts performance more than conducting a peripheral visual field task alone (Abernethy & Leibowitz, 1971; Ikeda & Takeuchi, 1975). However, the concurrent performance of these two tasks has been shown to pose a particular problem for the ageing population. Ball, Beard, Roenker, Miller & Giggs (1988) used a classic Useful Field of Vision task on groups of young (age 22-33 years), middle-aged (age 40-49 years) and older (age 60-75 years) subjects. They used a central visual field task involving detecting whether a face was present or absent and a peripheral visual field task involving identifying whether faces that appeared in 24 peripheral locations ranging in eccentricities of 10° to 30° were smiling or

frowning. They found that at larger radial eccentricities, older adults made significantly more errors on both the central and peripheral tasks. Such evidence provides support for the notion that the area of the Useful Field of Vision reduces across the lifespan. This degree of visual field reduction has been found to be up to three times worse for healthy older adults than young adults (Ball et al, 1988). This conclusion is supported by a wide range of evidence within the literature assessing performance in the Useful Field of Vision task both across discrete age groups and continuously, across the lifespan (Ball, Owsley & Beard, 1990; Edwards et al, 2006; Sekuler, Bennett, & Mamelak, 2000).

The literature surrounding the Useful Field of Vision changes with age is of particular interest when looking at skilled performance across the lifespan. The study of both central and peripheral vision is reminiscent of many naturalistic settings, a prime example of which is driving. Safe driving requires vigilant attention to multiple areas of interest within the visual field in parallel for example being able to look at the road as well as being able to perceive objects in the wing mirrors is important for maintaining safe distances and safe driving behaviours. Indeed, it is not surprising then that there is a large body of literature showing that performance in the Useful Field of Vision test is related to driving performance. A population study investigating factors predicting vehicle crashes in older drivers (aged 55-90) found that Useful Field of Vision had high sensitivity and specificity, suggesting that it is high reliability, over and above other factors such as cognitive status and eye health, in predicting whether older drivers would have a recent history of motor vehicle accidents (Ball, Owsley, Sloane, Roenker & Bruni, 1993). Further, the authors found that substantial shrinkage of the Useful Field of Vision in older drivers made them six times more likely to have been involved in one or more motor vehicle crashes in the previous 5 years. A further study of older drivers aged between 55-87 years who held a current driving license found that out of a battery of eye health tests and visual processing tests, the only significant predictors of injurious motor vehicle crash involvement were reduced Useful Field of Vision and presence of glaucoma, an ophthalmological condition caused atrophy of the optic nerve, resulting in loss of peripheral visual field function (Owsley, McGwin,

& Ball, 1998; Quigley, 1993). Owsley & McGwin (1999) found that older drivers with a reduction in the Useful Field of Vision of over 40% were 2.2 times more likely to experience a crash in the 3 years after testing, even when other variables such as sex, age and health status were controlled for. Further, a meta-analysis of the literature combining Useful Field of Vision and driving measures, including simulated driving, on-road driving and state-recorded accidents was conducted by Clay, Wadley, Edwards, Roth, Roenker & Ball (2005). This study found that poor performance on the Useful Field of Vision task is a good predictor of poorer driving outcomes in ageing drivers. The meta-analysis showed a robust effect ranging across studies from various labs, employing various different methodologies.

It has also been shown that training can ameliorate the effects of ageing on Useful Field of Vision performance. Sekuler & Ball (1986) found four daily sessions of additional training on the task increased the performance of older subjects in all the conditions tested, with the greatest improvements seen in the most difficult task elements. However, these authors found training did not reliably improve performance at any one peripheral eccentricity over another, and they also found this level of additional training did not bring older subjects' performance to an equivalent level of the performance of younger subjects. In a similar study examining the effects of practice on young, middle-aged and older adults on the Useful Field of Vision task, Ball, Beard, Roenker, Miller & Giggs, 1988 found that 5 practice sessions in the task caused significant improvement at all age and eccentricity combinations except for the young participants at the smallest eccentricity, where performance was already at its highest. Results showed that these effects lasted during re-test periods up to six months and that with practice, performance of the older adults was at the level of middle-aged adults prior to practice and the performance of the middle-aged adults was at the level of the younger adults prior to practice, with both the older and the middle age groups expanding their UFOV by around 10º (Ball et al, 1988). Further, Rogé, Ndiaye & Vienne (2014) found that training elderly drivers aged 63-78 to increase their Useful Field of Vision led to increases in their ability to engage in safe driving behaviours in a simulated road environment such as pedestrian detection in both

central and peripheral vision, over and above a group of elderly drivers who received no training. Research in this area is particularly important for society given the rapidly growing elderly population and research suggesting that elderly drivers have more traffic convictions, more crashes and collisions and more fatalities per mile driven than any other age group (National Highway Traffic Safety Administration, 1989) and further evidence showing that older drivers are over-represented in accidents involving pedestrians (Bromberg, Oren-Gilad, Ronen, Borrowsky, & Parmet, 2012) and particular types of gap-acceptance crash, including when approaching turns and at T-junctions (Pai, Hwang, & Saleh, 2009).

Much like in Chapter 3 of this thesis, an obvious gap in the Useful Field of Vision literature is the lack of appropriate methods used to test this phenomenon. More recent literature makes use of eye movements to measure cognitive mechanisms as they provide a continuous overt indication of covert mental processes such as attention. It is now widely believed that as well as being influenced by perceptual mechanisms, attention also precedes eye movements, which in turn precede manual behaviours by up to 1 second (Land, Mennie, & Rustead, 1999; Orquin & Mueller Loose, 2013). Indeed, it is logical that if attention is not guided towards a location, no visual information will be computed from that area (Orquin & Mueller Loose, 2013). Studying eye movements is useful because eye tracking techniques allow to us to monitor cognitive processes much more continuously than other techniques which have lower sampling rates. Through this, we are able to get a more detailed picture of how cognitive processes progress and develop over time. That is, eye tracking methods allow us to look at the cognitive processes that precede responses, as well as the responses themselves (see Liversedge, Gilchrist & Everling, 2011 for a review of the literature).

As well as providing a novel insight into the cognitive processes that underpin the Useful Field of Vision task, using eye movements may help address a methodological problem in the field. Early findings suggested that the classic Useful Field of Vision task, which requires subjects to respond using a touch pad or other manual response method may mean that confounding or extraneous

variables such as body movements, head movement, instability of fixations or involuntary saccades make it difficult to interpret the way the task is performed (Sekuler & Ball, 1986; Ball et al, 1988). This is an issue because the presence of involuntary saccades towards the peripheral target affects how well we can interpret the data in terms of the actual definition of the Useful Field of Vision. That is, how much information can be meaningfully processed and retained from one fixation, without eye or head movements (Sanders, 1970). Whilst Sekuler & Ball (1986) argue that involuntary shifts in fixation cannot account for the effects seen in their study as performance between young and older participants in non-distractor conditions is equivalent, this is still a variable that is not experimentally controlled for in their study. Some have attempted to address this confound. Fujita, Mimura, & Iijima (2012) created a new version of the UFOV task with an inhibitory task designed to screen older participants for involuntary movements. The authors still found a high correlation between scores on the new test and driving performance in older drivers.

Therefore, it is surprising that very little previous research has used eye movements to investigate performance during the Useful Field of Vision task. A search of the literature revealed only one previous paper claiming to address this. Scialfia, Thomas & Joffe (1994) tested the ability of younger and older adults to detect the orientation of a line presented at eccentricities ranging from 4° to 14°, either with no distractors, homogenous distractors or heterogeneous distractors. They found that when targets were presented more peripherally, eye movements made towards the target were both more numerous, and slower. This effect was compounded when the target was presented within an array of homogenous distractors, and both effects increased with age, suggesting older adults have a more restricted field of vision than younger adults. However, this study had some important methodological oversights. The sample size was small - 6 older adults, the eye tracker used sampled at a very low rate of 30.3 Hz and whilst eye movements were recorded during the task, responses to the line orientation detection task were still manual, rather than oculomotor. Further, and most importantly, the study failed to replicate the classic Useful Field of Vision

paradigm, whereby a central and peripheral vision task are performed at the same time whilst gaze is maintained in central vision. No central visual field task was performed, and instead, eye movements were analysed as saccades were made towards the target which was presented at varying radial eccentricities. Therefore, the argument could be made that this task was not a Useful Field of Vision task, where multiple central and peripheral tasks much be completed at once, but instead a visual search task, where objects must be located in the presence or absence of distractors.

As such, this chapter aims to address two key, unanswered issues in this field. Firstly, do findings of a reduced Useful Field of Vision in older adults still hold true when stronger constraints are placed on methodology using eye-tracking techniques. Monitoring eye movements to ensure concurrent performance of a central and peripheral visual field task allows us to only analyse trials in which we are certain that no extraneous eye movements are made. The hypothesis here is that Useful Field of Vision is reduced in older adults. In keeping with the literature discussed above, performance on both tasks should still decrease in older adults as stimuli become more peripheral.

Secondly, the use of eye-tracking techniques allows us to explore further hypotheses in more detail. Expanding on Chapter 3, this Chapter also aimed to investigate the effect of the healthy ageing process on cognitive and motor systems separately. Therefore, a series of oculomotor measures were also examined to understand the changes to the kinematic properties of eye movements, in order to determine whether performance changes were cognitive or motor in nature. It was hypothesised that the metrics of eye movements such as reaction time, saccade duration and saccade amplitude would increase alongside increased task difficulty, and this increase would be more pronounced in older than younger subjects.

4.2 Methods

4.2.1 Subjects

Subjects were recruited from Royal Holloway, University of London and the surrounding residential area of Egham, Surrey. Subjects were divided into 2 groups, a young control and an ageing experimental group. 26 young participants were tested, but the data from 2 subjects were removed from the analysis stage for both direction and shape analysis leaving final n = 24 (mean = 18.83 years; range = 18 – 22 years; 21 females) for both shape and direction analyses. Data from one subject was removed prior to both direction and shape analyses due to a colour vision deficit. One further subject was excluded from both of the final analyses because over 30% of trials contained insufficient eye tracking data. 20 older subjects were tested. 3 were excluded from the direction analysis due to over 30% of trials containing insufficient eye tracking data (see Chapter 3, Section 3.2.1 for a fuller description and examples of insufficient or bad eye tracking data). This left final n = 17 (mean = 64.35 years; range = 59 – 76 years; 6 females) and 20 (mean = 65.85 years; range = 59 - 81 years; 7 females) for the direction and shape analyses, respectively.

Subjects used for this experiment also completed a spatial Stroop task (Chapter 3 of this thesis), which allowed the author to explore the relations between performance in this and the study in the previous chapter. As such, adherence to ethical protocols, recruitment, and reimbursement for participation is the same as reported in Chapter 3.

4.2.2 Apparatus

The experimental set-up for this study was the same as reported in the previous chapter. See Section 3.2.2 for more details.

4.2.3 Experimental design

This experiment aimed to compare two main hypotheses. Firstly, whether the previously reported decrease in Useful Field of Vision with increased age is still apparent when the experiment is placed under a higher degree of experimental control. Eye tracking methods were used to ensure concurrent performance of a selective attention task in the centre of the visual field and a divided attention task occurring in the peripheral visual field in parallel. In order to increase the distance required for attention to each task, the peripheral visual field task occurred in increasing radial eccentricities. This allowed analysis of the area of the visual field from which the individual can actively manipulate meaningful information. Secondly, this experiment also aimed to investigate whether the parameters of oculomotor behaviours also increase alongside increased task difficulty, and whether this effect is more significant in older than younger subjects.

Across both accuracy and eye movement analyses, performance on the central and peripheral visual field tasks was analysed separately. For all analyses there were two independent variables. Firstly, distance of the peripheral visual stimuli from central vision: 4°, 8° and 12°. Though previous tasks similar to this one used larger peripheral distances (generally ranging from 10° to 30°, see Ball et al, 1988), these distances were not possible in this study due to the technical constraints of the eye tracker, screen distance and screen size. However, the maximum visual distance achievable was used. Secondly, as in Chapter 3, two groups were used to test the independent variable of age: a young control group and an ageing experimental group.

Task:

Prior to the start of the experiment, subjects were familiarised with the paradigm using a guided PowerPoint presentation example of a series of trials covering each of the different experimental conditions. The subjects were given a chance to practice the task and to ask any questions prior to the start of the experiment. On-screen instructions were then given and the eye tracker was

calibrated and validated using a 5-point calibration when the subject was comfortable in the head rest.

Subjects were required to keep their gaze on a fixation cross in the centre of the screen, in order to keep this area in the centre of their visual field. The experimental array (see Figure 28) was presented in the centre of the screen at the beginning of each trial. The screen at the beginning of the trial also contained a background mask array of small grey triangles (see Figure 28) which were consistent in size, colour and shape and were consistent across all experimental conditions. This mask was a variable of no interest. However, it was used to create a more complex visual background than having the experimental array by itself, on a blank screen as there were multiple sources of visual information, which made the experimental set up more similar to the visual environments we experience during real-world driving. This was an important element of this task as it has been found that performance in visual tasks which rely on selective attention as they involve background visual clutter, rather than visual stimuli in isolation, is related to poorer driving performance (Avolio, Koroeck, & Panek, 1985).

A fixation cross was located in the centre of the screen and adjacent to the fixation cross, two shapes appeared – a square was placed to the left of the central fixation cross and a circle was placed equidistantly to the right of the centre fixation cross. The square and circle changed colour in between trials. They were always a variation of red, yellow, green or blue and the square was always a different colour to the circle. Subjects were prompted at the beginning of the experiment to remember the colour of both shapes whilst maintaining gaze on the central fixation cross.

As outlined in the introduction, subjects were required to maintain their gaze on the central fixation cross in order to reduce the confound of extraneous saccades or gaze shifts towards the peripheral visual stimuli when they appear, which affects how meaningfully data can be interpreted in relation to the definition of the Useful Field of Vision (see the Introduction of this Chapter). Trials in which subjects

shifted their gaze to the peripheral visual stimuli were categorised as 'failed to fixate' trials and were excluded from the Useful Field of Vision analysis. These trials were later used as a measure of response inhibition (see Section 4.2.4).

At the same time, an arrow appeared in one of twelve locations either towards the central cross or in increasing radial distances from the centre towards the four corners of the screen. The visual angles subtended for the arrows were 4°, 8° or 12° from the central fixation point. The arrow changed both its location and the direction in which it was pointing between each trial. Subjects were told at the beginning of the experiment that the arrow would be pointing either up, down, right or left and were verbally prompted prior to the to experiment and during calibration breaks to keep their eyes on the central fixation cross and try to identify which direction the arrow was pointing, regardless of where it appeared on the screen. This was monitored continuously by the experimenter.

Following presentation of the array, subjects were asked to use eye movements to answer two questions. Firstly, they were asked to identify which direction the arrow was pointing in by looking at the corresponding arrow. Secondly, they were presented with an array of colour patches and were asked to identify either the colour of the square or the colour of the circle by looking at the colour patch that was the same colour as the correct answer.
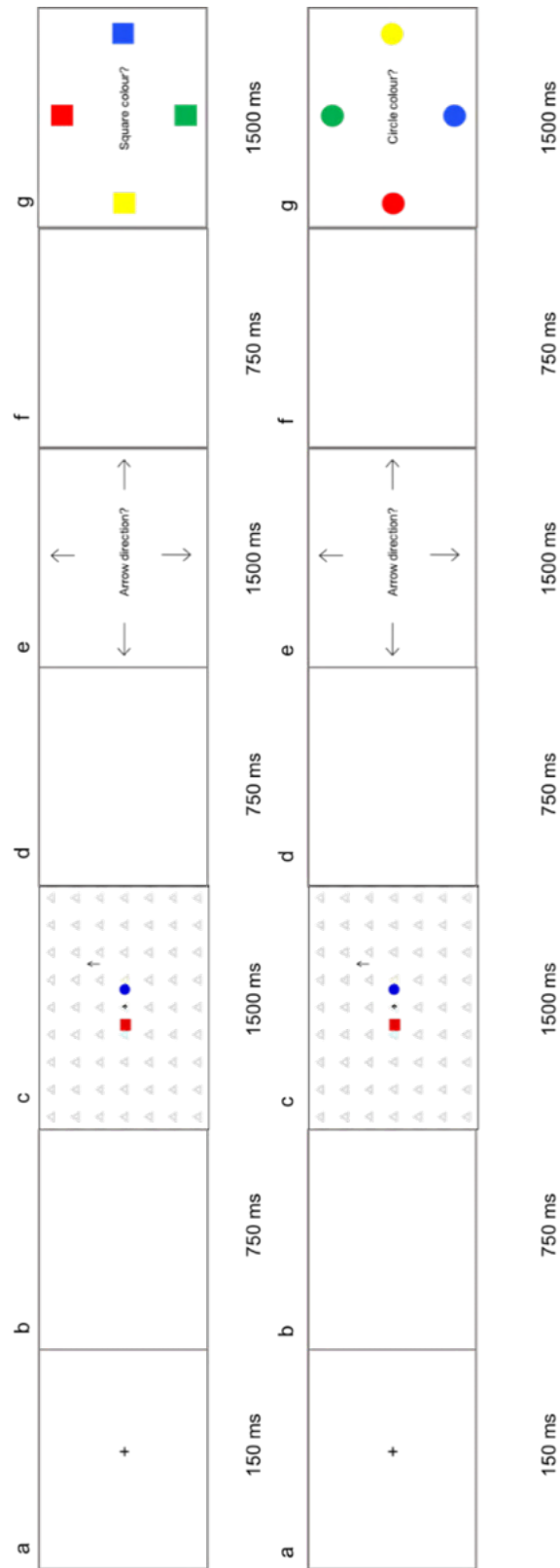
Figure 28: Experimental array for Useful Field of Vision task, involving the peripheral arrow detection task and the central shape-colour discrimination task. The colour discrimination task randomly varied between identifying the colour of the square (g, top) and the colour of the circle (g, bottom).

Experimental Sessions:

All experimental sessions for each subjects took place in the same behavioural set up during the same testing period to ensure consistent environments across conditions. The Useful Field of Vision session lasted roughly 15 minutes and contained 120 trials with each arrow location appearing in 10 different trials. This divided into blocks of 40 for each ascending distance – 40 trials for location 1 (4° from the central fixation point), 40 trials for location 2 (8° from the central fixation point) and 40 trials for location 3 (12° from the central fixation point). A break was given every 20 trials to prevent fatigue, particularly in the elderly subjects. Prior to the start of the experimental session and during each break after every 20 trials, the eye tracker was re-calibrated to allow for correction of gaze drift due to body of head movements. See Section 2.2.3 for full details on how calibration was achieved. Gaze drift and head movements were expected to be common in elderly subjects, so accounting for this using calibration breaks was very important.

Experimental Timings:

Experimental timings remained consistent across the two groups of participants to ensure that any differences in behaviour could be attributed to the experimental manipulation rather than to confounding differences due to differential presentation and response time windows. Due to the psychophysical aspects of this task, it was important that the presentation of stimuli and the collection of oculomotor responses was at a fairly rapid pace, in order to ensure that saccades were ballistic and natural and were not confounded by cognitive processes that were not of experimental interest such as the development of response patterns or strategies.

The experimental array (see Figure 28c) appeared at the beginning of the screen for 1500m/s followed by a blank screen lasting 750ms. This was followed by the direction identification question which lasted for 1500m/s and then a 750m/s blank screen and then following that, the shape colour identification question which

also lasted for 1500m/s followed by a 750m/s blank screen. The timings for the final experimental session were taken from initial piloting work on 4 young subjects and 7 ageing subjects suggesting that this was a sufficient speed to allow for the reduced speed of processing in the ageing population as well as not being too slow to cause confusion in the control group.

4.2.4   Preprocessing of oculomotor data

Accuracy: This study aimed to use a more stringent level of experimental control than has been using in previous useful field of vision tasks. Subjects were instructed to maintain gaze on the central fixation cross at all times during the presentation of the experimental array. The use of eye tracking methods allowed us to monitor eye movements during this period on a trial by trial basis. Trials were excluded if fixations were made in a 140-pixel radius of the arrow stimulus. These were defined as 'failed to fixate' trials and excluded from the accuracy analysis.

Reaction Time, Saccade Duration and Saccade Amplitude: In order to investigate where there were any psychophysical differences between responses in the different conditions, further analyses were undertaken looking at reaction time, saccade duration and saccade amplitude. For these trials, only correct trials were analysed. All trials where subjects failed to fixate centrally during the presentation period (see above) and incorrect trials were excluded from the analysis.

Response Inhibition: A further, exploratory analysis was conducted to investigate whether the frequency of excluded 'failed to fixate' trials (see above) differed with respect to experimental condition. For this analysis, only trials in which a fixation was made outside of central fixation were analysed.

4.2.5   Behavioural data analysis

A series of 3 (distance of arrow from central vision, 4°, 8° and 12°) x 2 (age group) mixed-measures ANOVAs were conducted to investigate the effect of peripheral arrow distance from central vision on the following dependent variables: accuracy, reaction time, saccade duration and saccade amplitude. Performance

during direction responses (See Figure 28e) and shape responses (see Figure 28g) was analysed separately. All ANOVA results are reported with Greenhouse-Geisser corrections where assumptions of sphericity are violated.

Data were checked for statistically significant outliers (3SD above or below the group mean). The number of outliers for each analysis can be found in Table 6.

An important assumption of the ANOVA is normal distribution of all variables. Where assumptions are violated in mixed-measures ANOVA, non-parametric tests cannot be applied, as they can with other forms of ANOVA, as no direct non-parametric equivalent of the mixed-measures ANOVA exists (Field, 2009). The tests for normality and the basis for transforming non-normal data is outlined in detail in Section 3.2.5. Where transformations are applied, a number of different transformations were tested, and the transformation that bought the data as close to normality as possible was applied. Therefore, some different data sets have been transformed using different transformations. Details of whether each separate set of analyses were transformed or not, which transformation was applied, and why are outlined below.

Table 6: Number of outliers deleted for accuracy, reaction time, saccade duration and saccade amplitude analyses for both shape and direction data, split by young subjects and ageing subjects.

	Young 1 Repetition	Young 2 Repetitions	Young 3 Repetitions	Ageing 1 Repetition	Ageing 2 Repetitions	Ageing 3 Repetitions
Accuracy (Shape)	0	0	0	0	0	0
Accuracy (Direction)	0	0	0	0	0	0
RT (Shape)	0	0	0	0	0	0
RT (Direction)	0	0	0	0	0	1
Duration (Shape)	1	1	1	0	0	0
Duration (Direction)	1	1	1	0	0	0
Amplitude (Shape)	0	0	0	0	0	0
Amplitude (Direction)	1	1	1	0	0	0

Accuracy (Direction): The data points with a non-normal distribution all showed a significant negative skew, however transforming the data made it difficult to interpret as it altered the relationship between the variables, so statistical analyses are reported using untransformed data.

Accuracy (Shape): Variables with a non-normal distribution showed a positive skew, so data for this analysis were adjusted using a base-10 logarithmic transformation. Statistical analyses are reported using transformed data.

Reaction Time (Direction): Ageing data showed a positive skew but base-10 logarithmic transformations made the previously normal young subject data skewed so no transformations were applied.

Reaction Time (Shape): All data were normally distributed.

Saccade Duration (Direction): Data for the closest distance for both young and ageing groups showed a significant positive skew. Base-10 logarithmic transformations did not correct for this so no transformations were applied.

Saccade Duration (Shape): Both young (closest distance) and ageing data (most peripheral distance) showed a significant positive skew. Applying base-10 logarithmic transformations made these variables normally distributed without causing a skew on any other variables, so statistical analyses are reported using transformed data.

Saccade Amplitude (Direction and Shape): All data were normally distributed.

Response inhibition: Data showed a non-normal distribution, so a non-parametric Kendall's tau correlation test was undertaken to investigate the relationship between age and response inhibition.

4.3   Results

4.3.1   Direction

In the excel data file, for each trial, co-ordinates for the arrow stimuli in all four directions were labelled with regards to their peripheral distance from the central fixation cross: 1 = 4° from the central fixation point, 2 = 8° from the central fixation point) and 3 = 12° from the central fixation point. Statistical tests were performed using these arbitrary values as a measure of peripheral distance of the arrow.

There was a significant main effect of distance from central vision on ability to detect the direction the arrow was pointing: $F_{(2, 78)}$ 138.179, $p < .001$, $\eta^2 = .780$, see Figure 29.
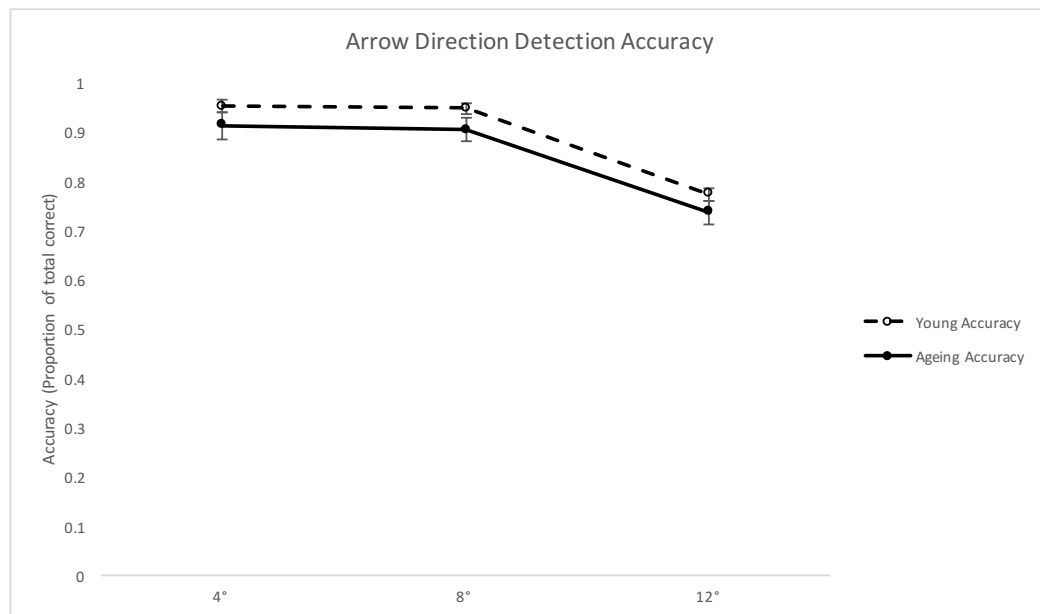
Figure 29: Peripheral arrow direction detection accuracy using raw, untransformed data for young and ageing subjects. Error bars: +/- 1 SEM.

Pairwise comparisons were performed, and adjusted with Bonferroni correction for the number of analyses conducted. These revealed that accuracy was not significantly different in the middle condition (mean = .930, SD = .079) than the closest condition (mean = .935, SD = .085; $p = 1.00$). However, accuracy was

significant lower in the most peripheral condition (mean = .761, SD = .080; p < .001) than both the closest and middle conditions.

The effect of age on ability to detect the direction the arrow was pointing was not significant: $F_{(1,39)}$ = 3.705, p = .062, η^2 = .087. There was also a non-significant interaction between distance and group: $F_{(2,78)}$ = .036, p = .964, η^2 = .001. Independent t-tests revealed no significant difference between the age groups at any of the distances (p > .05).

There was an insignificant main effect of peripheral arrow distance on reaction time during the direction response window ($F_{(2, 78)}$ = 1.240, p = .295, η^2 = .031). The effect of age on this variable was also non-significant ($F_{(1, 39)}$ = .048, p = .828, η^2 = .001), as was the interaction between distance and age ($F_{(2, 78)}$ = .871, p = .423, η^2 = .022).

The effect of peripheral arrow distance on saccade duration during the direction response window was not significant ($F_{(1.654, 62.836)}$ = 2.069, p = .133, η^2 = .052). However, saccade durations were significantly longer for older subjects (mean = 81.681s, SE = 6.895) than for younger subjects (mean = 61.818s, SE = 5.928; $F_{(1, 38)}$ = 4.71, p = .035, η^2 = .112). There was no significant interaction between age and peripheral arrow distance ($F_{(1.654, 62.836)}$ = .785, p = .438, η^2 = .020).

There was no significant effect of arrow distance ($F_{(2, 76)}$ = 2.200, p = .118, η^2 = .055) or age group ($F_{(1, 38)}$ = .028, p = .868, η^2 = .001) on saccade amplitude during the direction response window, nor was there a significant interaction between these variables ($F_{(2, 76)}$ = .137, p = .872, η^2 = .004).

4.3.2   Shape

There was a significant main effect of distance from central vision on ability to detect and maintain the colour of the shape stimuli in central vision: $F_{(2, 84)}$ = 5.864, p = .004, η^2 = .123. There was an insignificant overall main effect of age: F

$_{(1, 42)}$ = 2.337, p = .134, η^2 = .053. However, there was a significant interaction between distance and age group on the ability to perform the shape discrimination task in central vision: F $_{(2, 84)}$ = 3.725, p = .028, η^2 = .081 (see Figures 30 and 31). Independent t-tests revealed significant differences between young and ageing participants when the arrow was at the most peripheral distance (p = .017, equal variances assumed) but not at the middle or closest distance (p > .017, Bonferroni corrected for multiple comparisons).
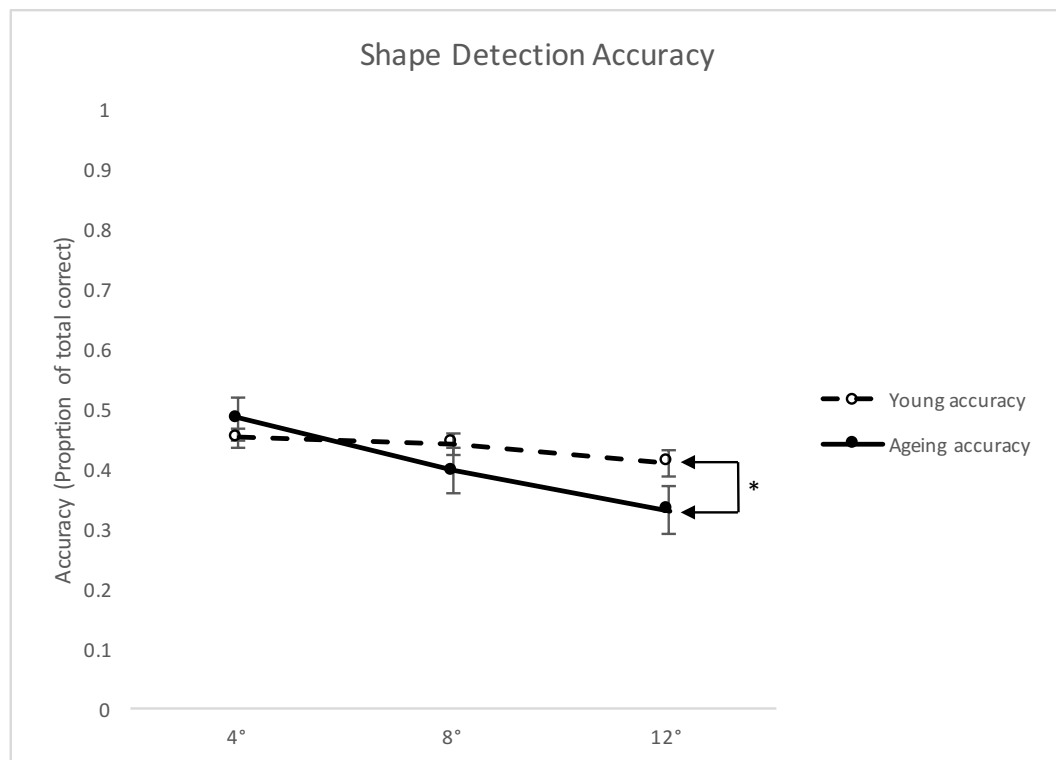
Figure 30: Shape colour detection accuracy using untransformed data for young and ageing subjects. * represents significant differences using independent measures t-tests between young and ageing subjects. Error bars: +/- 1 SEM.
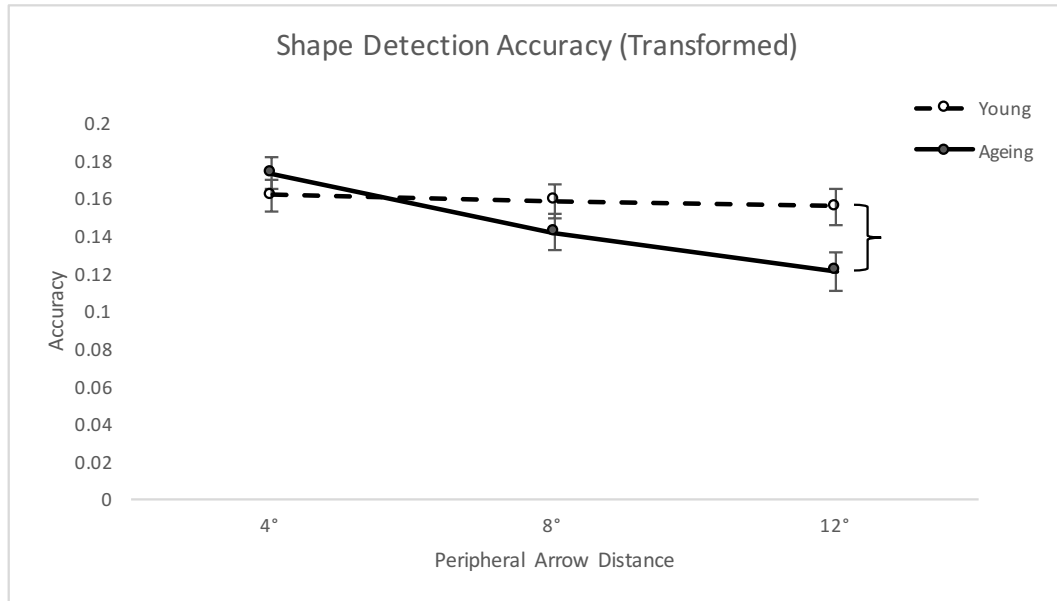
Figure 31: Shape colour detection accuracy using transformed data for young and ageing subjects. * represents significant differences using independent measures t-tests between young and ageing subjects. Error bars: +/- 1 SEM.

There was no significant effect of peripheral arrow distance on reaction time during the shape response window (F $_{(2, 76)}$ = 1.022, p = .365, η^2 = .026). However, reaction times were significantly longer for older subjects (mean = 1156.005, SE = 24.339) than younger subjects (mean = 1061.970, SE = 19.873, F $_{(1, 38)}$ = 8.990, p = .005, η^2 = .191). There was no significant interaction between these arrow distance and age group (F $_{(2, 76)}$ = .314, p = .731, η^2 = .008).

Peripheral arrow distance had no significant effect on saccade duration during this period (F $_{(2, 76)}$ = .380, p = .685, η^2 = .010). There was a main effect of age group (F $_{(1, 38)}$ = 10.842, p = .002, η^2 = .222). Overall, saccade durations were significantly longer for older subjects (mean = 1.815, SE = .019) than younger subjects (mean = 1.734, SD = .016). However, there was no significant interaction between these variables (F $_{(2, 76)}$ = .133, p = .875, η^2 = .003).

There was no significant effect of peripheral arrow distance (F $_{(2, 78)}$ = 2.874, p = .062, η^2 = .069) or age group (F $_{(1, 39)}$ = .382, p = .540, η^2 = .010) on saccade amplitude during the shape response window, nor was there a significant interaction between these variables (F $_{(2, 78)}$ = .166, p = .847, η^2 = .004).

Response Inhibition

In order to ensure that central and peripheral space was present and distinct, whilst the experimental array of the useful field of vision task was on the screen, subjects were instructed to keep their eyes on a fixation cross in the centre of the screen and the stimuli were defined as distance peripheral to this point.

Due to non-normal distribution of the data, a non-parametric test was used for this analysis. Non-parametric correlation analysis (Kendall's tau) of the frequency of these trials showed a significant positive relationship between age (in years) and the total amount of trials in which a 'failed to fixate' saccade was made, revealing that the older the subjects were, the more inclined they were to look towards the peripheral stimulus and the less they were able to inhibit this response on the basis of explicit instruction, $r = .412$, $p < .001$.

The same relationship was found between the percentage of trials in which a 'failed to fixate' saccade was made and age, $r = .354$, $p = .001$ (see Figure 32).
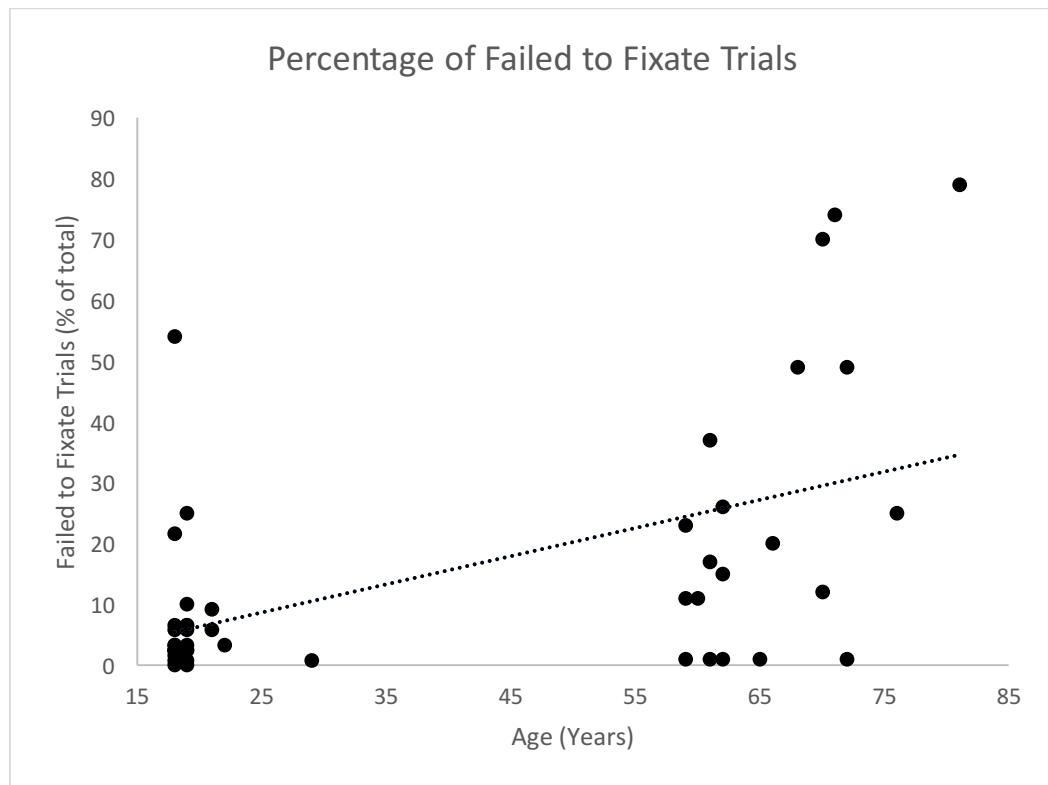
Figure 32: Relationship between failed to fixate trials (expressed as a percentage of the total amount of overall trials) and age (in years). A correlation was performed to investigate whether there were any age differences within the separate age groups themselves. During analysis, it was identified that within the older adults group, there was a positive trend between age and the amount of trials that were being removed prior to analysis. Therefore, a correlation was undertaken to explore this relationship. A within-groups ANOVA could not be undertaken due to the very small sample size. Such an analysis would have been significantly underpowered.

As the same subjects took part in the experiments in Chapters 3 and 4 of this study, the author was able to investigate whether reaction inhibition ability may have impacted performance on the Stroop task, in which subjects must also resist interference from task-irrelevant information in order to successfully complete the task. Interestingly, this measure of reaction inhibition also correlated highly with performance on the incongruent Stroop measure in the spatial Stroop task in Chapter 3 of this thesis. There was a negative correlation between the amount of 'failed to fixate' trials as a percentage of the total number of trials and ability to resist the direction-colour interference on the incongruent condition of the Stroop task ($r = -.355$, $p = .017$, see Figure 33) but not with the centre or congruent conditions, $p > .05$.
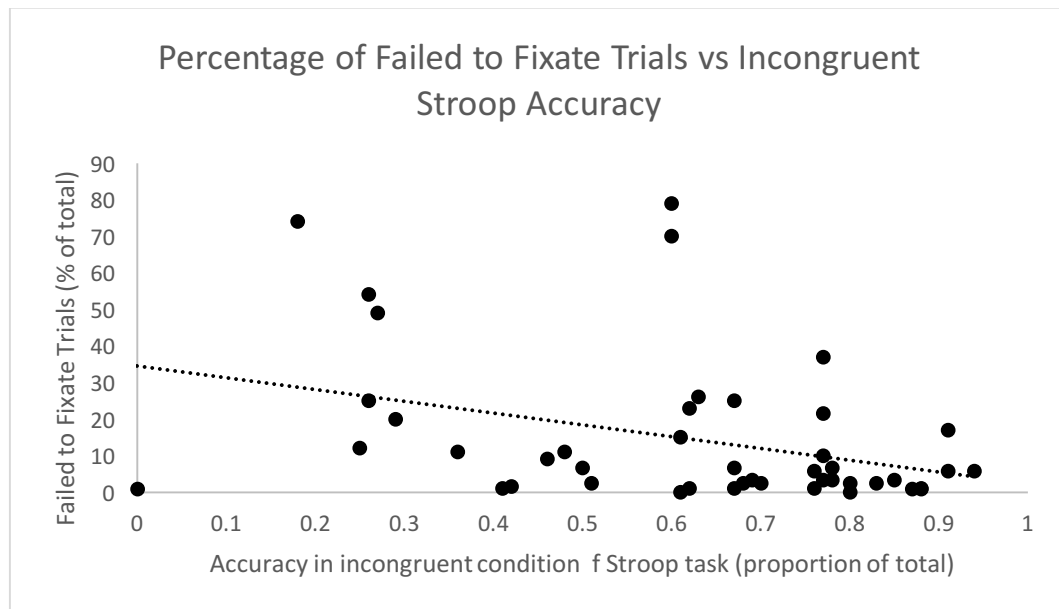
Figure 33: Relationship between failed to fixate trials on the Useful Field of Vision Task (expressed as a percentage of total trial number) and performance on incongruent trials of the Stroop task (see Chapter 3, both studies were carried out on the same subjects). See the paragraph above for a rationale for this correlation.

4.4   Discussion

The aim of this chapter was to investigate two main hypotheses. Firstly, do the classic findings of reduced Useful Field of Vision with increasing age still occur when eye tracking methods are used, which place higher levels of control on experimental testing? Secondly, as well as reduced accuracy when secondary visual information is located at higher radial eccentricities, do the metrics of eye movements such as response time, saccade duration and saccade amplitude increase, and is this increase more notable in older adults?

Previous studies testing the Useful Field of Vision have relied on manual response paradigms, in which a visual phenomenon is assessed and then examined using non-visual effector systems. As such, extraneous variables that cannot be controlled for in such paradigms such as head movements, body movements and involuntary saccades towards peripheral visual stimuli affect how we can interpret these results. As such, we sought to investigate all the above hypotheses using an adapted Useful Field of Vision task using eye tracking techniques.

It was expected that due to the well-documented decline in grey matter in the prefrontal cortices of older adults (Milham et al, 2002), tests placing a high demand on prefrontal mechanisms involving high attentional load, in this case the Useful Field of Vision task, would result in poorer performance for older than younger adults. Results did partially support this prediction, but were not entirely in line with previous findings. Accuracy on the central shape discrimination task and the radial arrow detection task did decrease as radial eccentricity of the simultaneously performed peripheral task increased. Further, a significant interaction revealed that performance in the central shape discrimination task did not differ between younger and older adults when the peripheral stimuli were at 4° or 8° but older adults had significantly lower accuracy when the peripheral visual stimuli were at 12°, the furthest distance.

Results showed that accuracy at identification of peripheral stimuli was not significantly poorer for older adults than younger adults. Many studies of ageing

and the Useful Field of Vision have shown that performance in both central and peripheral visual field tasks decreases with age (Ball et al, 1988; Ball, Owsley & Beard, 1990; Sekuler & Ball, 1986). This data somewhat supports this hypothesis, as we show that increasing radial eccentricity of a peripheral visual field task significantly impeded simultaneous performance of a central visual field task in ageing subjects, but not younger subjects. Sekuler et al (2000) have argued that a likely explanation for this is that both sets of information are processed in parallel, and both younger and older subjects have a field of vision that is the same in terms of visual extent but the information that can be extracted from the visual field decreases with age. That is, the total amount of meaningful information from both the central and peripheral visual fields that can be extracted and interpreted decreases with age. This helps to explain the results presented in this Chpater. When the peripheral arrow was at the largest distance, discrimination of the arrow did not significantly differ between younger and older subjects, but in this condition, older adults performed the shape discrimination task in the central visual field significantly more poorly. This suggests that when older adults are trying to divide attention at the largest distance, less information from the entire visual array is being extracted. This conclusion is also supported by Seiple, Szlyk, Yang & Holopigian (1996) who found that older adults did have decreased performance on a Useful Field of Vision task, but this did not vary with radial eccentricity of peripheral targets under conditions of divided attention, as was found in the direction analysis in this chapter.

This chapter also aimed to investigate whether the metrics of eye movements such as reaction time, saccade duration and saccade amplitude also indicate decreased performance when a secondary visual task places higher constraints on divided attention mechanisms. Reaction times were not significantly longer for older subjects, nor did these change with increased eccentricity during the peripheral arrow discrimination. However, reaction times for the shape discrimination task were longer for older subjects, but these did not differ depending on the eccentricity of the secondary peripheral task.

Chapter 3 of this thesis previously discussed the extent to which age differences found in cognitive task can be attributed to general slowing of speed of processing rather than changes in cognitive processes themselves. It has been argued that age-related variations in cognitive tasks such as the Stroop task in chapter 3 can be attributed to general slowing (Salthouse, 2001a; Verhaeghen & De Meersman, 1998). However, data from the spatial Stroop experiment presented in Chapter 3 contradicted this argument, as reaction times did not differ between younger and older subjects, suggested that older adults can perform tasks as quickly as younger subjects. As reaction times in this study were not consistently longer for older than younger subjects, it cannot be argued that there is a consistent slowing of responses and, consequently, speed of processing in older adults. The same argument has previously been advanced in the Useful Field of Vision Literature. Sekuler & Ball (1986) argued that equal performance by younger and older adults in a baseline condition of their Useful Field of Vision task when compared to experimental divided attention conditions refutes the idea that changes in performance can be explained by generalised reductions in speed of processing with increasing age. Instead, slower reaction times for older adults in correct trials during the shape discrimination task suggests that as well as less information being extracted, as discussed above, information cannot be usefully extracted as quickly by older adults under conditions of divided attention. Further, results showed no effect of age group or peripheral arrow distance on saccade amplitudes. However, saccade durations were longer for older than younger subjects during performance of both the central and peripheral tasks, but these were not affected by radial eccentricity of the peripheral visual field task. This suggests that older and younger adult take the same amount of time to begin executing a response, but once started, older adults take longer to complete the response.

A possible limitation to the results presented in this Chapter is sample size. Accuracy data generally showed middle to large effect sizes for main effects of age and repetition, as did the significant interaction analysis for the shape detection task. However, the interaction for peripheral arrow discrimination showed a very small effect size (a partial eta squared value of $< .01$). Previous studies that have found

effects of ageing on both tasks during the Useful Field of Vision task have had wide ranging sample sizes. The studies most similar to this chapter have used smaller sample sizes than ours, with groups of between 8 and 9 younger and older subjects and still found significant age differences on both tasks (Ball et al, 1988; Ball, Owsley, & Beard, 1990). Sekuler et al (2006) conducted a series of ANOVAs on age groups ranging from age 15 to 84 years, with between 20 and 33 subjects in each age group, which is not dissimilar to the sample sizes reported in this chapter. As discussed above, Sekuler et al (2006) found similar results to ours with respect to accuracy on the secondary peripheral visual field task. Comparisons with previous research therefore suggest three possible explanations. Firstly, previous studies have not had sufficient statistical power. Though this is not discussed explicitly in the literature, comparison with the partial eta squared values based on the sample sizes used in this study suggests these analyses were likely to have been underpowered in comparison with analyses in this chapter, which general showed medium to large effect sizes (with the exception of the interaction in the direction accuracy analysis, see above). Therefore, results in previous studies may have been susceptible to false positives. Secondly, that the argument made by Sekuler et al (2006) and supported by the data in this chapter is a more appropriate one. That is, the useful field of vision in younger and older subjects is the same in terms of visual extent but the information that can be meaningfully extracted from the visual field decreases with age. Or finally, that both previous studies and elements of current study (the direction analysis in particular) are underpowered. Future research replicating this study with larger sample sizes would help to elucidate which of these three explanations is most appropriate.

Previous research has suggested that training can ameliorate the effects of ageing on the Useful Field of Vision to some extent. Studies have shown that training sessions can improve the performance of older adults on Useful Field of Vision tasks to equivalent or nearly equivalent performance as younger subjects (Ball et al, 1988; Sekuler & Ball, 1986; Richards, Bennett, & Sekuler 2006). These studies show that with enough practice over a period of weeks, older adults can improve their divided attention skills, and these benefits can be retained for a period

of months (Ball et al, 1998; Richards et al, 2006). The current research could be used to develop eye movement based training packages to aid older subjects to attend and extract meaningful information from multiple sources in parallel and also to improve their oculomotor reaction times when attention must be divided across larger visual distances. This could improve the amount of meaningful information extracted during such conditions. Research also suggests that performance on the Useful Field of Vision task is reliably related to crash risk in elderly drivers (Ball, Owsley, Sloane, Roenker & Bruni, 1993; Clay et al, 2005; Mathias & Lucas, 2009; Owsley, McGwin, & Ball, 1998; Rogé, Ndiya, & Vienne, 2014; Stoneley et al, 2014). Eye movement training paradigms may be easy to develop and execute in the ageing population and this may help facilitate safe driving and reduce crash risk in older drivers.

Chapter 3 builds on previous research surrounding the effects of ageing on the Useful Field of Vision. Eye tracking methods were used to add an extra level of experimental control and to investigate whether previous findings surrounding the effects of ageing still hold true if eye movements cannot be made, and parallel processing of multiple visual stimuli is guaranteed. This hypothesis was partially supported. It was found that as radial eccentricity of the peripheral stimuli increased, discrimination of this task did not increase for older or younger subjects, but the simultaneous performance of a shape discrimination task in central vision did become less accurate in older subjects. This suggests that the extent of the visual field itself does not decrease with age, as previously suggested, but that the amount of meaningful information that can be extracted when attention must be divided across larger distances does decrease with increasing age. Further, we found that the metrics of eye movements made during the response window largely did not change with age. Response times did not significantly increase for older subjects across all conditions, suggesting that any changes in accuracy related to changes in cognitive processing rather than generalised changes in speed of processing. These findings are discussed with reference to possible benefits of oculomotor training in older adults, and how this may help to reduce crash risk in ageing drivers.

Chapter 5: The Effects of Age on Visual Learning and Hazard Perception in Simulated Driving

5.1   Introduction

With the rapidly growing elderly population, the ability to continue driving is becoming an ever more important area of research. The Older Driver's Task Force was developed by the United Kingdom's Government to establish how the older driving demographic in the UK is expected to change in upcoming years, and how support can help them continue driving safely. In the UK alone, the population aged over 70 grew by one million between the years 2000 and 2014, and the number of licensed drivers over the age of 85 is expected to double, reaching over a million people by 2025 (Older Driver's Task Force, http://www.roadsafetyfoundation.org/media/33073/modsfl-single-page-printable-version.pdf). In particular, the older driver population is higher in rural, low density areas, where drivers over 70 make up around 20% of the driving population, compared to high density urban areas where this population is only around 5%. In low density areas, public transport services are more limited, so helping older people remain licensed drivers in order to support their independence and retain their quality of life is very important (Ling & Mannion, 1995; Fonda, Wallace, & Herzog, 2001). The impact of ageing on driving affects women and men differently. Women are much more likely to relinquish their drivers' licenses. Analysis of driver data in Great Britain shows that between 2013 and 2014, the number of car drivers trips made by men changes little between the age of 50 and 70, whilst for women, this number falls by around 40% between the age of 50 and 70 (Department for Transport, 2014: https://www.gov.uk/government/statistics/national-travel-survey-2014).

Research shows that per total number of licensed drivers, drivers aged 60 and above show similar number of fatal injuries as drivers in their teens or twenties. However, when measured as a proportion of total distance driven, the amount of fatal casualties whilst driving increases steadily after the age of 55, with a sharp increase seen in drivers aged 75 and above (Reported Road Casualties Great Britain,

2014; National Travel Survey). Particular road environments, such as junctions, pose a particular problem for the ageing driver. Research suggests that crashes involving speed and alcohol, as well as crashes on straight and curved roads are equally as common in ageing as younger drivers (Clarke, Ward, Truman, & Bartle, 2007; Levin, Dukic, Henriksson, Mårdh, & Sagberg, 2009). However, the frequency of other types of crash does increase with age. In particular, research suggests that the percentage of fatal car crashes involving right of way violations increases most markedly between the ages of 55 and 75 (Clarke et al, 2007; Levin et al, 2009). Further, crashes that occur whilst turning across oncoming traffic increases by 10% between the ages of 50 and 75 (Department for Transport, 2014; Levin et al, 2009). Research from British driving statistics between 2012 and 2014 show that whilst the number of car crashes at, or near junctions does not significantly change with age, the percentage of these crashes that are fatal increases after the age of 60, reaching 50% for those aged over 75. A similar pattern is shown for fatal crashes at intersections, and crashes that involve fatalities or serious injury when turning across traffic. The percentage of crashes at crossroads, particularly where there are traffic signals, and roundabouts is low and is stable across the lifespan (Older Drivers Task Force).

A systematic review of papers addressing errors frequently made by older drivers aged 65 to 85 found that a number of common errors may explain this (Vichitvanichphong, Talaei-Khoei, Kerr, & Ghapanchi, 2015). The authors found that when coded by 5 experts in the field, decline in driving performance related to abilities that fall into three categories: physical abilities, cognitive impairment and visual abilities. Physical abilities include physical skills which are necessary to implement safe driving. The authors found that many physical abilities such as motor co-ordination, physical reaction time, and musculoskeletal problems such as neck rotation and limb and foot abnormalities are linked to increased driving errors in older age. Safe driving involves integrating multiple streams of information. The systematic review suggested that healthy older drivers suffer from decline in cognitive abilities such as attention, visual memory and speed of information processing, and this may contribute to the increase in accidents and collisions seen

in elderly drivers. It is accepted that the traditional test for eyesight does not sufficiently encompass the wide variety of visual impairments that may contribute to unsafe driving in older adults. Other factors such as the Useful Field of Vision, colour vision, speed of visual search, acuity and locus of eye movements are shown to correlate with older adults' driving abilities (Janke, 1994). Further, driving statistics show that older adults perceive driving in certain situations as more dangerous than others, including busy roads, multi-story car parks, urban environments, roads which involve roundabouts, right turns into and merging with oncoming traffic, weather, slippery roads, darkness, and unfamiliar routes, and the avoidance of these complex driving environments increases with age (Burns, 1999; Joly, Frigon, & Daigneault, 2002; Older Drivers Task Force).

As explored in Chapter 1 of this thesis, tasks such as driving, in which the same behaviours are repeatedly executed, may develop automaticity. The cognitive processes that underpin such behaviours, such as accessing previously learned memories and behaviours, are transformed from being effortful and consciously controlled, to becoming automatic processes which occur with little or no conscious awareness and require fewer attentional resources (Posner & Snyder, 1975; Shiffrin & Schneider, 1977). A natural hypothesis from this is that drivers in familiar locations should benefit from previous experience, and should have reached higher levels of automation in familiar than in unfamiliar locations. Due to this, they should be able drive more consistently and safely, and be able to allocate more attention to other tasks, such as hazard perception, more freely.

However, literature in this area is conflicted. Studies have shown that drivers more familiar with a route follow a pacer car more closely, are less able to notice salient events and changes in the environment, and have longer reaction times to hazards than drivers unfamiliar with the route (Charlton & Starkey, 2012; Yanko & Spalek, 2013). Further, research suggests that subjects are more likely to voluntarily increase their speed on routes as they become familiar with them (Initini, 2016; Colonna, Intini, Berloco, & Ranieri, 2016). In contrast with theories of automaticity, which would suggest drivers in familiar environments would be

able to allocate more attentional resources to detecting changes in the environment, these authors suggest that less safe driving occurs in familiar environments due to 'inattentional blindness'. That is, when a driver becomes familiar with a route, less attention is allocated to the driving task, and therefore their mind is more likely to wander and be distracted by task-irrelevant information, leaving the driver less able to respond to hazardous stimuli in the environment (Yanko & Spalek, 2013), an area that will be addressed in the latter part of this chapter. This may also be adequately explained by the Task Capability-Interface (TCI) model, proposed by Fuller (2005). This model suggests that task difficulty is inversely proportional to the difference between task demand and an individual's capability. That is, when there is a small difference between task demand and capability, task difficulty is low, but when this difference is large, task difficulty is high. In these situations, drivers compensate for high task difficulty by continuously adjusting their speed. However, in some situations drivers may overestimate their capability, such as when an environment is very familiar. In these situations, drivers may not calibrate their speed appropriately, leaving them vulnerable to risk of collision (Fuller, 2005; 2011). This may explain why epidemiological data shows crashes are more likely to happen in an environment near a driver's or passenger's home (Durand, 1980; Chen et al, 2005), though this may also be explained by the degree of exposure to roads near the home versus roads further away. That is, we are more likely to drive on roads near the home than roads further away.

However, this is not always the case. Read et al (2011) investigated the effects of familiarity on errors in a wayfinding driving task. Overall, the authors found that route familiarity increased performance on the task. Drivers that were more familiar with the environment committed fewer navigation errors and were less likely to get lost when following directions than drivers who self-reported being less familiar with the driven area used for the experiment. The authors also found that elderly drivers – aged 65 and above – were more likely to commit navigation and safety errors, and took longer to complete the route, even when familiar with the environment, although these were lessened by familiarity. Given that older drivers anecdotally claim they avoid unfamiliar situations (Burns, 1999), it seems

surprising that no other research, to the author's knowledge, has investigated changes in driving behaviour as an environment becomes more familiar.

This leaves two questions to be answered. Firstly, do drivers perform more skilfully in familiar than unfamiliar environments? Whilst some studies have investigated driving performance such as speed and change detection as environments became more familiar (e.g. Charlton & Starkey, 2012; Initini, 2016; Colonna, Intini, Berloco, & Ranieri, 2016), to our knowledge, no study to date has tested how familiarity affects performance of certain skilful driving techniques such as changing lanes, and navigating junctions, where crashes commonly occur. If behaviours become automated in the classic definition of the term, the hypothesis is that as behaviours become well learned, they can be automatically implemented when the same situation arises again, with no need for a conscious, controlled level of information processing. As such, in familiar situations, driver behaviours that indicate knowledge of an environment such as steering during manoeuvres should be performed more quickly and more readily than behaviours in novel environments. In novel environments, such behaviours are not able to be executed automatically, and will rely on a secondary level of controlled processing, so take longer to execute. However, if inattentional blindness is increased in familiar environments, this would not be the case. In the early stages of driving, such as driving in novel environments, a high level of attention is required. However, as environments become more familiar, and driving skills become more learned, the amount of attention required decreases, possibly due to a smaller disparity between task demand and capability (Charlton & Starkey, 2011; Fuller, 2005; Mader et al, 2009). In this case, when less attention is required, the mind might wander and be distracted by other elements of the environment. As such, driving performance would suffer.

Secondly, how do the cognitive changes that occur alongside healthy ageing affect this process in older drivers? Burns (1999) found that older drivers report driving in unfamiliar environments as more difficult, possibly due to the high attentional resources required. As a consequence, older drivers are more likely to

avoid such situations. However, to date, no one has investigated how performance in the older driver changes as environments become more familiar. This chapter seeks to bridge this gap in the literature.

Hazard perception is defined as the ability to predict dangerous situations on the road (Grayson & Sexton, 2002; McKenna & Crick, 1991; Quimby, Maycock, Carter, Dixon & Wall, 1986; Wetton et al, 2010). Hazard perception skill has been related to collision risk across a number of studies (Hull & Christie, 1993; McKenna & Crick, 1994; Wells, Tong, Sexton, Grayson, & Jones, 2008). Research suggests that experienced drivers have superior hazard perception skills than novice drivers, who typically have up to three years' experience, and this may be one reason why they are less likely to be involved in road traffic accidents (McKenna & Horswill, 1999; McKenna & Crick, 1994). Some studies have shown that poor hazard perception is associated with an increased risk of fatal or serious accidents but not total number of crashes or number of minor crashes (Drummond, 2000; Mayhew, Simpson, & Pak, 2003). Others show that hazard perception skill is related to accidents that result in damage but no injury (Wells et al., 2008). This is due to the source of the statistics. Studies that show a relationship between injury crashes and hazard perception skill rely on statistics from police records (Drummond, 2000; Mayhew et al, 2003). However, Wells et al (2008) included all accidents including injury-free crashes, which do not have to be reported to the police, so records are less likely to reflect these.

Research has shown that experienced drivers have more flexible visual search patterns, allowing them to scan more of the visual environment, which may in turn allow them to better anticipate hazardous situations (Grayson & Sexton, 2002; McKenna & Crick, 1991). Indeed, experienced drivers fixate on both hazards and information that precedes a hazard, known as 'hazard precursors', more often, and more rapidly than novice drivers (Crundall et al, 2012; Pradhan et al, 2005). Crundall (2016) investigated how the information extracted from hazard precursors differed between novice and experienced drivers. Crundall (2016) aimed to determine whether early fixation of hazard precursors in experienced drivers

actually provides any meaningful information, or whether it simply allows them to process hazard precursor information that has a later onset, more rapidly. Crundall (2016) found that early fixation of hazard precursors by experienced drivers did help them predict what would occur next, but experienced drivers were more accurate than novice drivers regardless of whether the hazard precursor had early, intermediate or late onset. However, novice drivers were more over-confident in their ratings of what would happen next as the hazard approaches across all onsets, but particularly over-confident when compared with experienced drivers in the early onset precursors. Further, Crundall (2016) found that novice drivers are significantly worse at detecting hazard on the basis of environmental cues than behavioural cues, but older drivers are equally good at both. Indeed, both types of cue of related to crash risk in newly qualified drivers (Maycock, Lockwood, & Lester, 1991). This suggests that familiarity with an environment benefits experienced drivers but not novice drivers, which helps to facilitate hazard prediction, and in turn, the benefits of experience will disappear in novel environments.

It is well known that with age, we experience decline in cognitive and visual abilities. In previous chapters of this thesis, it was argued that such decline affects the ability of older adults to automate new behaviours. However, there has been relatively little research surrounding how these changes affect the hazard perception abilities of older drivers. It is surprising that given the wealth of evidence suggesting differences between novice and experienced drivers, few have focused on how age and experience relate to this process. In this chapter, this hypothesis will be extended into the domain of driver performance. If older adults are less able to automate new skills, the implicit hypothesis here would be that with older age, reduced cognitive and visual abilities would impede hazard perception ability, particularly in unfamiliar environments (Horswill et al, 2008), but this does not seem to consistently be the case.

Previous studies provide conflicting evidence surrounding the hazard perception abilities of older drivers. Some previous studies have shown that older

drivers, typically aged over 65, do not have significantly different reaction times in hazard perception tasks than younger drivers (Olson & Sivak, 1986; Underwood, Phelps, Wring, van Loon, & Galpin, 2005; Borowsky, Shinar & Oron-Gilad, 2010). However, others suggest that in older drivers, hazard perception skills decline after age 55 (Quimby & Watts, 1981). The lack of consensus in this area may be due to methodological differences. For both Olson & Sivak (1986) and Underwood et al. (2005), the sample size of older drivers was 15 subjects or fewer, whereas Quimby & Watts (1981) used a much larger sample comparing across multiple age ranges. Horswill et al (2008) studied hazard perception in a large sample of community-dwelling older drivers and found a significant correlation between age and hazard perception response time using a simple response time measure. That is, they found that the older the drivers were, the slower they responded to the hazard. However, they found that age alone did not explain this variance, rather it correlated with the older drivers' contrast sensitivity, useful field of vision, simple reaction time and visual acuity. Further, the authors studied older drivers' hazard perception only for roads with which they were already familiar, which may have, to some extent, facilitated their performance. Indeed, Bolstad & Hess (2000) suggest that most of the problems older adults experience in attention relate to the presence of novel contexts. As far as we are aware, no studies to date have directly investigate the differences in hazard perception abilities of older drivers in novel and familiar contexts.

This chapter used a series of three experiments, all conducted on the same subjects, to broadly investigate how driver behaviour changes as it becomes more skilled. The three experiments aimed to answer three unanswered questions. The first two experiments aimed to investigate whether aspects of driver behaviour such as steering at junctions and during lane change manoeuvres improve with context familiarity in urban and motorway environments. Further, these two experiments aimed to investigate whether the effects of familiarity with a visual environment benefit experienced younger drivers more than experienced older drivers. Finally, a third experiment aimed to utilise the differential levels of familiarity developed in the first experiment to investigate whether familiarity with a visual environment

facilitates hazard perception skill. Hazard perception skill was measured using the onset of braking in anticipation of a hazard at junctions that had previously been seen a different number of times. It was predicted that in line with the idea of increased automation as behaviours become more skilled, increased familiarity with a visual environment would allow behaviour to become more optimal, and to be performed earlier, allowing drivers a higher degree of spare cognitive capacity, which would allow them to perceive hazards earlier. Further, it was predicted that the healthy ageing process would leave older adults less able to automate these behaviours, and less able to use previous learning to facilitate hazard perception.

5.2 Methods

5.2.1 General driving simulation methods

5.2.1.1 General experimental design

Each part of the experiment consisted of a number of 'drives'. Each drive was a single, distinct route which contained either a series of areas of interest in the urban drives or a single area of interest, as listed below:

- Urban drives: multiple areas of interest, made up of junctions and intersections, driven continuously.
- Motorway drives: one single area of interest, driven by itself.
- Hazard drives: one single area of interest, driven by itself.

These three experimental sessions will be discussed in more detail in the following sections along with schematic figures of the driving simulation scenarios but an outline of the general experimental design can be found below.

During these drives, subjects were instructed to drive as naturally as possible. They were instructed to drive at 30mph in the urban and hazard drives and 70mph in the motorway drives. For urban drives, subjects had to follow straight pieces of road and then when a turn or corner appeared, they had to follow instructions that appeared on the screen. For motorway drives, subjects had to drive forwards on long stretches of motorway and then when a gantry appeared, they were instructed to move left or right by one lane by instructions that also appeared on the screen. For hazard drives, subjects had to follow straight roads and then when a junction appeared, they had to follow auditory instructions that were played from speakers on the left and right side of the screens. Subjects were not informed that some areas of the driving simulation terrain would be repeated multiple times.

During urban and hazard drives, some corners contained an area of interest. These were novel visual stimuli that were designed to be easily discernible from other corners and were exactly the same every time that particular corner was

encountered across both experiments. Corners that did not contain an area of interest were left as they appeared in the driving simulation terrain. During motorway drives, each gantry contained a novel visual signpost that was discernible from the others. These visual stimuli were intended to be easily identifiable so that they could become familiar, or learned over time. Visual stimuli in areas of interest were seen 1, 2 or 3 times from the same angle so that they were more or less familiar, in a graded manner. Subjects were not informed that any visual scenes would be repeated so they could not anticipate this familiarity. These will be discussed in more detail in the following sections.

Across all sections of the experiment, the order of the drives was randomised for each subject using a random number generator. This randomisation was important as cognitive load at the beginning of drives is higher as subjects continue to get used to the controls of the simulated vehicle, and research has shown that visual stimuli at the beginning of simulated drives are not recognised as well as those which occur later, which might suggest subjects pay less attention to their visual environment early in the drives (Aginsky, Harris, Rensink, & Beusmans, 1997). Randomisation prevented the possibility that any learning effects may occur as a function of different levels of attention rather than the learning process itself. This also prevents any order or practice effects, which may affect the learning behaviour through either subjects learning order of presentation or through stereotyped patterns of fatigue.

One of the original aims of this set of experiments was to look at the patterns of eye movements that drivers make as visual environments became more familiar. In keeping with the findings of previous chapters of this thesis, it was hypothesised that eye movements would be made more rapidly and in a more predictable manner as visual environments became more familiar. Further, it was hypothesised that older subjects would be less able to benefit from this familiarity, and therefore their eye movements would be made more slowly, and less readily than those of younger subjects. Eye movement data was collected for all subjects used for the final

analysis (see below for eye tracking details) but this data was not used for the thesis due to time limitations and the complexity of data analysis.

5.2.1.2 Subjects

57 subjects in total took part in the experimental session. 27 subjects comprised an older driver group and 25 subjects formed a younger control group. 6 subjects did not complete the experimental session. All of these subjects belonged to the older experimental group. Five subjects could not complete the session due to simulation sickness. High levels of dropout due to simulator sickness is commonly reported in the literature, and this is more common in older individuals (Edwards, Creaser, Caird, Lamsdale, & Chisholm, 2003), so this was compensated for *a priori* by over-recruiting subjects. All subjects who experienced simulation sickness were female. Subjects who were unable to complete the full experiment were still paid £30 for their participation and time, but no data from these subjects were included in any of the final analyses within this chapter. One further subject did not complete the full experiment as we were unable to calibrate the eye tracking equipment. One subject from the younger, control group was unfamiliar with driving with manual gears so this subject's data was excluded from further analysis. This left 25 older (age range = 60-79 years, mean = 65.44 years, SD = 4.37, 7 females) and 25 younger drivers (age range = 22-33 years, mean = 26.81 years, SD = 2.87, 12 females) for the final analysis.

All subjects were recruited from the Transport Research Laboratory (TRL) subject database, TRL staff members and the surrounding local area. Staff members were compensated £20 for their time, and subjects who attended from the database and the local area were compensated £20 for their time and received a £10 attendance fee. All drivers were required to have a current, valid driving license and to have had this for a minimum of three years. All subjects had normal or corrected-to-normal vision. Subjects for whom corrective visual aids were needed were encouraged to use the appropriate correction for using a computer as opposed to driving, in order to minimise the risk of dropout due to simulator sickness.

The definition of the elderly driver is contested within the road safety literature, with different authors using the ages from 50-65 as the baseline cut-off of the elderly driver. However, Planek (1981) describes the age of 55 as being the starting point at which the ageing process beings to degrade the accuracy of driving performance. As such, and to fit in with previous work in this thesis, the age of 60 was used as the minimum cut-off point for the elderly driver.

All subjects gave written informed consent. The studies were approved by the Royal Holloway, University of London ethics committee and were in keeping with the Transport Research Laboratory ethical procedures. As the experiments in this chapter involved a level of deception, subjects were given a full verbal and written debrief following the experiment. Debriefing sheets are included in Appendix 15.

5.2.1.3 Apparatus

A 'MiniDigiSim' driving system developed by the Transport Research Laboratory (TRL) was used for collection of driving simulation data. Experiments were developed and data were collected using a bespoke Intel® Core ™ i7-5820k CPU running at 3.30GHz using Windows 7 (Ultimate) with 16 GB of RAM and a GTX 970 graphics card. The simulator used a three screens (see Figure 34 for arrangement) Each screen had a resolution of 1920 x 1080 pixels and a refresh rate of 60 Hz. A speedometer was placed in the middle of the lower half of the central screen (not pictured).
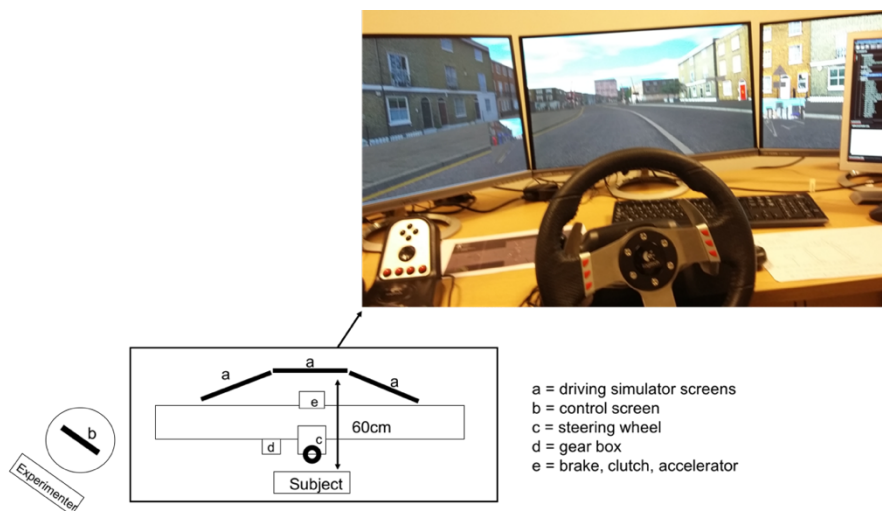
Figure 34: Experimental set up for the driving simulator.

Behavioural measures such as steering, braking, accelerating, lateral shift (deviation of the vehicle to the side), lane change, and speed were captured automatically by the machine using a Logitech G27 simulated driving set up including steering wheel, gear box (including a gear for reverse) and a pedal box with in-built clutch, brake and accelerator. There were no indicators or rear view mirror, but there were two wing mirrors at the furthest point away on the right and left peripheral screens. In order to prevent any unnecessary stress which might increase cognitive load during the drives which may be caused by the lack of rear view mirror, subjects were explicitly reminded that at no point would there be traffic behind the vehicle they were driving.

The simulator used SCANeR™ studio 1.4 simulation engine software which integrated all stimulus presentation and data collection at 20Hz, sampling every 0.05 seconds (20 samples per second). All output data was integrated using SCANeR™ studio and sampled at the same rate. Driving scenarios were developed using python and C++ programming and scripting tools. The control computer generated a low-frequency engine noise to provide auditory feedback to the driver. This was heard binaurally.

Eye movement data was collected using the Tobii X1 light camera system which was integrated with SCANeR software using a bespoke program written in C++. Although the eye-tracking system was able to sample at a maximum rate of 60 Hz, in order to synchronise with driving simulation data, eye movement data was collected at a frequency of 20Hz. The eye-tracker was attached to the central screen of the three screen set up using the mounted bracket on the reverse side of the screen. The eye tracker remained 60cm from the subjects' eyes at all times, but the angle of the centre screen was variable in order to prevent occlusion of the eye movement data from the steering wheel. A calibration method was developed using the Tobii X1 SDK and involved a 5-point calibration including the four corners and the centre point of the centre screen as eye movement data was collected solely from this visual region. Analysis of eye movement data was not practical for this

thesis, but the hypotheses in question can be analysed effectively using other behavioural measures.

Contributions

For all experiments in this Chapter, the author was involved in creating the experimental design, designing novel stimuli to be placed at junctions and at the locations of lane change manouevres and including them in driving simulation terrains, and adapting pre-existing driving simulation terrains to be appropriate to the drives used in these studies. The author was also responsible for adapting previously developed python code for the onsets and offsets of drives and visual and auditory direction stimuli. The author was solely responsible for all pilot work and all data collection in this Chapter (and the wider thesis). Within this Chapter, technical help was given by a computer technician at TRL for developing the original python code for adaptation, and for including the dynamic hazard stimuli for Experiment 3.

5.2.1.4 Familiarisation

Although most subjects used from the TRL database had been previously familiarised with driving simulation in general, only a small sample of subjects had been familiarised with the particular simulation system used for the experiments within this chapter. As such, prior to the experimental runs, subjects were familiarised with the simulator for around 5 minutes using a novel, rural scenario. Though practicing on the routes used during the experimental runs may have prevented any behavioural errors or attention effects at the start of these drives, it was imperative that we were able to precisely control the levels of visual and behavioural exposure to the areas of interest used during the experimental tasks. Therefore, the route used for familiarisation was different from those used during the experimental tasks. Subjects were encouraged to focus on practising with steering, braking and accelerating, as these differed most noticeably from on-road driving. Experimental testing did not begin until subjects reported feeling familiar and comfortable with the system when asked by the experimenter.

5.2.1.5 Simulation Analysis

Simulation data was imported from .txt files into excel. For the first two sections of the experiment where the same area of interest was repeated in separate drives, the repetition number could not be automatically generated because the order of the drives was randomised (see above). Therefore, the order of the drives for each subject, which had been noted during testing, was used to manually label the repetition number (1, 2 or 3) of each area of interest in the excel spreadsheets. Individual visual areas of interest were coded using alphabetic values for the urban drives (A-M) and numeric values for the motorway drives (1-9).

For all drives, behavioural data was extracted starting from 2 seconds prior to the onset of the visual or auditory sign which prompted the subjects which direction they should drive at the area of interest. This allowed us to time lock all behaviours of interest to the onset of the sign and to minimise the extraneous effects of behaviours prior to the event of interest. For urban drives, data until the offset of the sign was extracted, as the sign was programmed to disappear when a specific radius (marked using an X, Y co-ordinate) was reached, so we could be certain the manoeuvre had been fully completed. For motorway and hazard drives, data was extracted until the entire drive had been completed, as these were all short drives, including one singular area of interest. Any drives in which the visual or auditory sign did not appear – which was due to the subject not driving through the correct X, Y co-ordinate on approach to the area of interest – were removed prior to analysis.

All simulation data was then imported into IBM SPSS 21 and converted from long format into wide format using the SPSS restructure function. Data was then transferred back into excel and computed into chronological order. All further analysis (detailed below) was conducted using MATLAB R2017a and IBM SPSS 21.

5.2.2 Urban driving in novel and familiar environments

5.2.2.1 Experimental design

The first part of the experiment aimed to investigate two main hypotheses. Firstly, does familiarity with a visual environment enable drivers to anticipate cues and conduct manoeuvres in an urban environment more readily? Secondly, do younger drivers benefit from this learning process more than older drivers? There were two independent variables: the number of times a visual environment was encountered (1, 2 or 3) and driver age group (young or ageing).

In order to operationalise the variables in question in the simplest manner possible, performance at individual areas of interest was analysed using steering angle, which was measured in radians. This allowed assessment of four dependent variables:

- The time at which the onset of the manoeuvre occurred was used to measure when the 'decision' was made to start turning.
- The time of the first peak after the onset was used to measure when the first ballistic, most decisive part of the manoeuvre had occurred.
- The number of peaks in the steering behaviour was used to measure how many corrections were made whilst turning and thereby served as a proxy for how certain the driver was in the behaviour they were executing.
- The time taken to reach the peak after the onset was used to measure how long it took to reach the peak of the manoeuvre.

5.2.2.2 Procedure

Subjects took part in 8 short urban city drives, lasting between 2 and 4.5 minutes each. They were given a break between each drive, in order to minimise the chance of subjects experiencing simulator sickness.

Table 7: Areas of Interest and the amount of times they were seen, the number of cognitive operations (the amount of decisions to choose between) and the type of junction.

Area of Interest	Times Seen	Cognitive Operations	Type of Junction
A	1	2	Left
B	3	2	Left
C	2	2	Right
D	1	2	Right
E	1	2	Left
F	2	2	Forward
G	3	3	Left
H	3	3	Forward
I	1	2	Forward
J	2	2	Left
K	1	2	Left
L	2	3	Left
M	2	3	Forward

Subjects were guided around the short drives using visually presented instruction cues positioned at the top left, centre and top right of the central screen (see Figure 40 for the full range of instruction cues). These guides were consistent across all phases of the experiment, with the words 'Turn Left At Junction', 'Turn Right At Junction', 'Follow Road Ahead' or 'Go Around Roundabout'. At all roundabouts with multiple exits, subjects were instructed which exit to take with the words 'Take First Exit'. Subjects were instructed both verbally and using written instructions (see Appendix 12) to drive naturally at an average speed of 30mph, which could be gauged using a speedometer presented on the virtual dashboard at the bottom of the centre screen.

Subjects were instructed to drive in the right hand lane of two when driving on straight roads (see Figure 35), to follow the instructions when they appeared and to drive as naturally as possible when making manoeuvres. These manipulations allowed instructions to be given in as controlled a manner as possible. Directional cues (see Figure 36) were given to subjects at a distance equivalent to 80m before

the onset of an event of interest and remained on the screen whilst travelling a distance of 20m before disappearing when a trigger was reached.

Figure 35: A piece of straight road with no junctions. Subjects were instructed to drive in the right-hand lane so measurements such as steering angle during a manoeuvre could be measured from as controlled a baseline as possible.

A series of corners were deemed areas of interest and were seen a repeated number of times (see Table 7). At these corners, novel stimuli such as bike lanes, trees and advertisement boxes were placed in the driving simulation terrain to make them distinctive (see Figures 36-38).

Figure 36: A distinct area of interest that was seen from the same visual angle on multiple occasions. The directional cue can be seen in the top left-hand corner. A bike lane was used to make this junction distinguishable from the others.

Figure 37: A distinct area of interest that was seen from the same visual angle on multiple occasions. A series of advertisement boxes were used to make this junction distinguishable from the others.

Figure 38: An example of a roundabout that was seen multiple times from the same angle. A tree feature was used in the middle of the roundabout to make this junction distinguishable from the others.

These were interspersed with generic junctions which contained no areas of interest (see Figure 39).
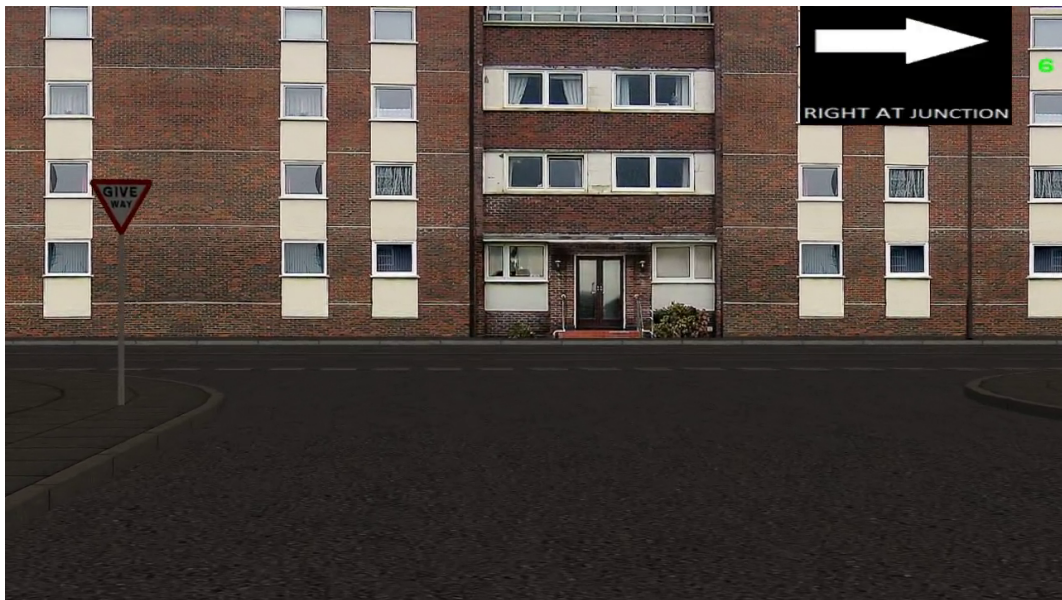
Figure 39: A junction during the urban drivers with no area of interest. The visually presented instruction cue can be seen in the top right-hand corner of the image.

Drives were both started and stopped when the vehicle came within a 5m radius of the pre-programmed start and end points. The start and end points were

the same for each subjects. Drives were conducted with no on-road traffic and, in these drives, subjects were instructed to treat the variable traffic lights as green in order to prevent long waiting times at traffic lights and to ensure, as far as possible, subjects were driving at the same speed when making manouevres so that speed did not act as a confounding variable. This abstracted the drives from reality further than in many other simulated driving environments, but provided a vital degree of experimental control.

The order of the drives was counter-balanced using a random number generator to minimise the risk of order effects. Across the 8 drives, there were 13 important events of interest, including simple and complex junctions and roundabouts. Five of these events were seen just once across the 8 drives, five of these events were seen twice across the 8 drives and 3 of the significant events were seen three times across the 8 drives (see Table 7). Events of interest in the routes featured differing amounts in order to manipulate exposure to visual stimuli in a meaningful way. Events of interest were counter-balanced so that there were equal numbers of events with the same degree of cognitive complexity with regards to the judgements required (events with two or three outcomes that require a judgement to be made), seen 1, 2 or 3 times (see Table 7). These areas of interest contained both passive junctions (junctions where choices were available but the route also continued forward so the subjects could follow the road ahead) and active junctions (junctions where subjects were forced to make a choice as the road did not continue on a natural forward route). Drives were programmed in such a manner so as to ensure that all events of interest were seen from the same angle with each additional exposure, and the layout of the drives ensured that these were never seen from any other direction or visual angle. This level of control was to make sure that visual exposure was completely experimentally manipulated.
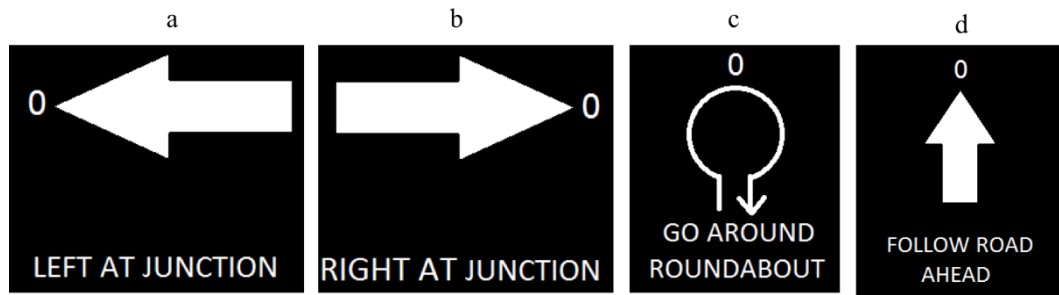
Figure 40: Visual instruction cues used for urban drives. Cues included a left turn (a), right turn (b), roundabout (c) and intersection (d).

5.2.2.3 Preprocessing of data

8 of the original 13 areas of interest were analysed (see Table 7). These were selected to avoid areas of interest that occurred on crossroads where possible, as previous research has shown navigation at crossroads is fairly stable across the lifespan (Older Drivers Task Force).

Table 8: Urban drive experimental conditions

Repetition #	One	Two	Three
Area Of Interest	A, D, E	C, J, M	B, G

Prior to statistical analysis, data were pre-processed in MATLAB, as the data sets were very large and had high variability. The main aim of preprocessing the data was to quickly and accurately separate reliable from unreliable trials, and to extract data that was meaningful and as consistent as possible for each subject and each trial, whilst removing any noise from the data set. A script was written to automate this as much as possible. A schematic of the pre-processing steps undertaken can be found in Figure 41.

Data restructured into matrices in excel
↓
Matrices imported into MATLAB
↓
Each row split by number of repetitions
↓
Data normalised to the first value(all values – first value)
↓
Absolute values taken
↓
Data smoothed
↓
Reject trials with high variability between 2s prior to onset of visual cue and 0.5s after cue
↓
Find all peaks
↓
Find total number of peaks
↓
Calculate rate of change
↓
Smooth rate of change
↓
Create onset threshold
↓
Identify point at which rate of change passes threshold, this is the onset of the response
↓
Find time of first peak after response onset
↓
Plot time of raw data, smoothed data and rate of change
↓
Identify time of visual cue, onset and first peak on graphs

Figure 41: Preprocessing steps for urban drive analysis. These were automated using MATLAB.

Steering data, which depicted the angle of the steering wheel at any one point in time, were restructured into matrices which were imported into MATLAB. These matrices contained one row for each subject which contained all the steering data for that area of interest, such that the time points of each trial were aligned in

the matrices. These rows of data were then split by the number of times that particular area of interest was seen – either 3, 2 or 1 to create comparable data sets for each repetition.

Each individual repetition was normalised by subtracting the first value from all values. This was so that each run started at a comparable point in time. Positive values in steering data indicated displacement of the steering wheel to the left and negative values indicated displacement to the right. All data points were converted to absolute values to allow for comparisons across areas of interest regardless of whether the manoeuvre was a left or right turn.

As the data were variable and noisy, it was difficult to find onset and peak values accurately in the raw data alone. Therefore, a temporal smoothing filter was applied which smoothed data using a running average across 12 data points. This helped identify patterns in the data whilst removing variations in the data that were not of experimental interest.

After the data had been smoothed, the standard deviation of the data was calculated from 2s before the onset of the visual cue and 0.5s after the onset of the cue. Trials with a standard deviation of higher than 0.2 between these time points were deemed bad trials and were rejected from any further analysis, as they had high variability.

The 'findpeaks' function in Signal Processing Toolbox was then used to identify the timing of all the peaks that occurred after the onset of the visual direction sign. The timing of the first peak and the total number of peaks that occurred was reported in the MATLAB output to use for statistical analysis.

The differential, or 'rate of change', from each data point to the next was then calculated using the 'diff' function. This allowed easy identification of when data significantly departed from the average. Another smoothing filter was applied to each 30 data points to further reduce any noise in the data set, and then the

amplitude of these differences was scaled up by a factor of 10 as the differentials were very small. This allowed large changes to be easily detected by eye on the plotted graphs.

An onset was then identified when the rate of change passed a threshold of either 15% or 20% of the range of that individual dataset. The threshold used was the same for all trials within a particular area of interest, but needed to be varied between different areas of interest depending on the general trajectory of the rate of change. If a smoother slope was generally shown in the data due to higher variability, a threshold of 20% was used. However, if a sharp slope was seen after a generally flat baseline prior to the onset of the slope, a threshold of 15% was used.

The script then reported five values for each subject and each repetition of the same area of interest:

- Time of onset
- Time of first peak
- Time to peak (calculated by subtracting time of onset from time of first peak)
- Number of peaks
- Reject the trial due to high variability: yes or no

Graphs were then plotted individually for each subject and for each repetition of the same drive, with the raw data, the smoothed data and the rate of change clearly identifiable. An example of a good trial where all there was not high variability and where both onsets and peaks were present were correct can be seen in Figures 42 and 43. If no onset or peak was detected using the automated script, the script was paused and these were manually identified using the Data Cursor tool in MATLAB. An example of this process can be seen in Figures 44. The time to peak was then manually recalculated for these trials using the new values. Trials were also deemed bad trials and rejected from statistical analysis if no peak was detected after manual inspection (see Figure 45a), or if a turn was made in the incorrect direction (see Figure 45b).
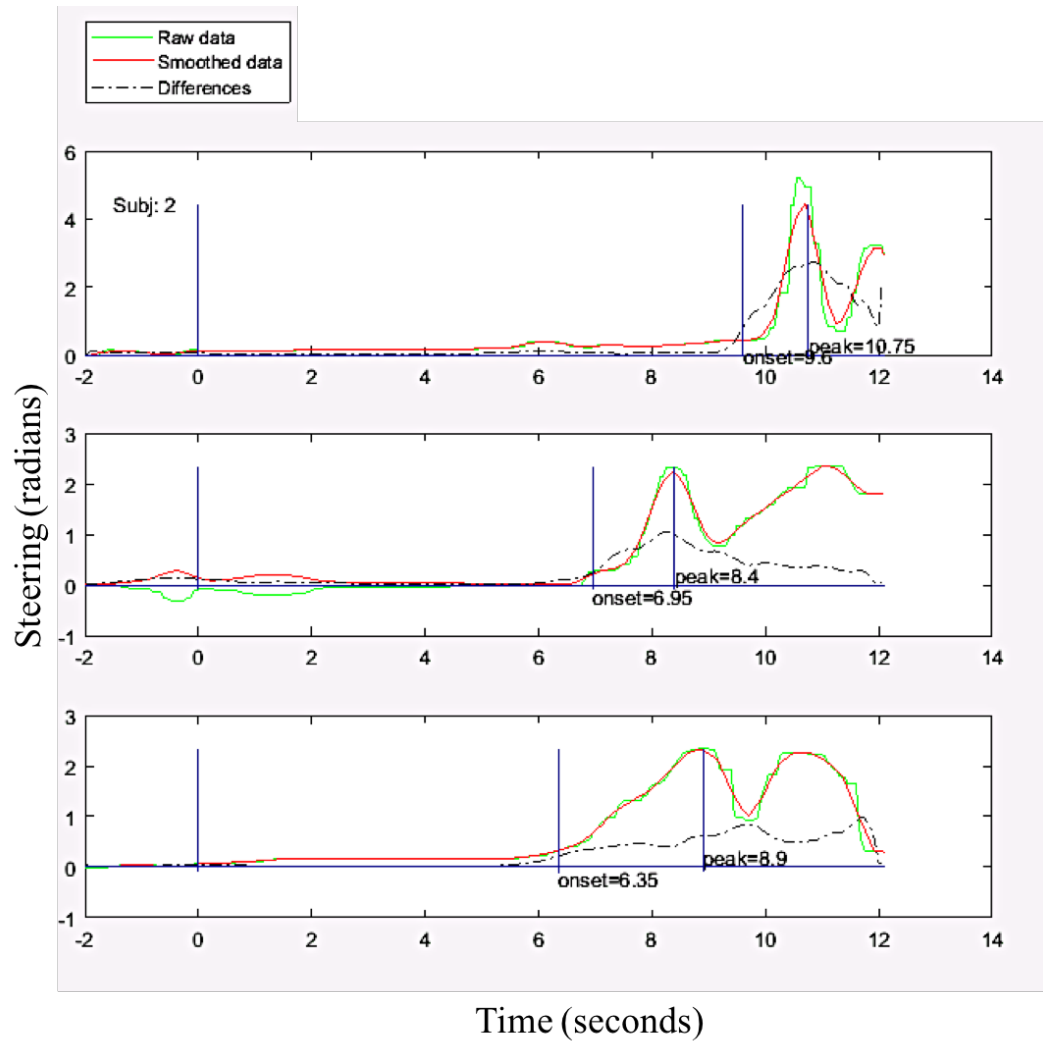
Figure 42: An example of a good trial from the urban drive three repetition analysis. Data from each subject, for each repetition of the same area of interest were plotted and inspected individually. Time 0 marks the onset of the visual direction cue.
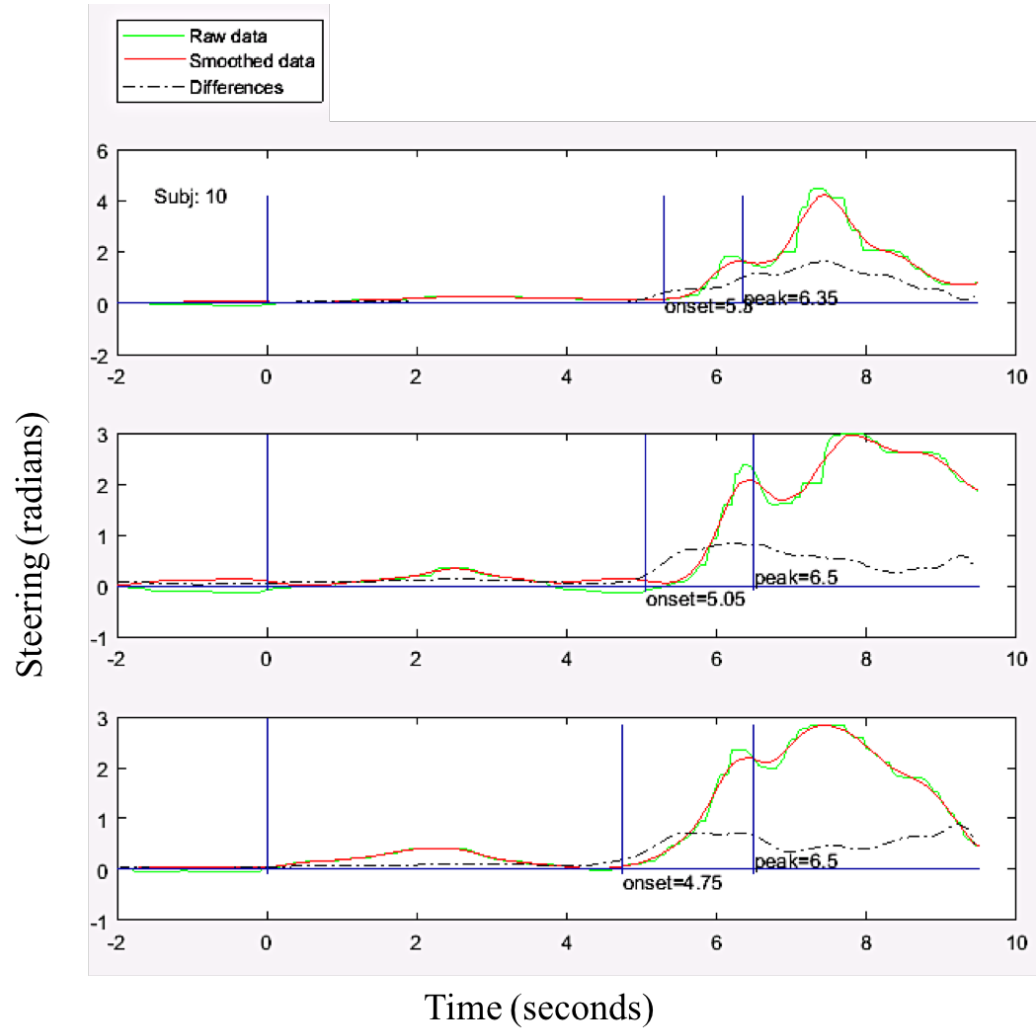
Figure 43: A second example of a good trial from the urban drive three repetition analysis. Data from each subject, for each repetition of the same area of interest were plotted and inspected individually. Time 0 marks the onset of the visual direction cue.
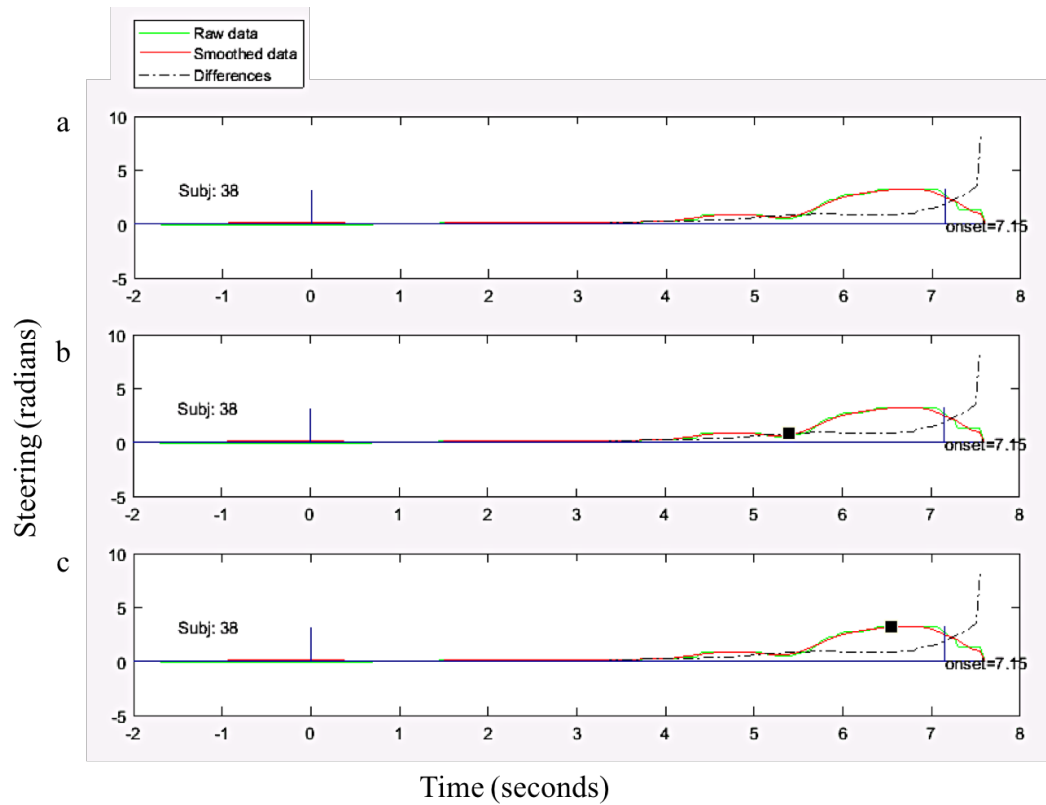
Figure 44: An example of a trial where the script detected no onset (a). The data cursor tool was used to manually identify the onset (b) and the peak (c). Time 0 marks the onset of the visual direction cue.
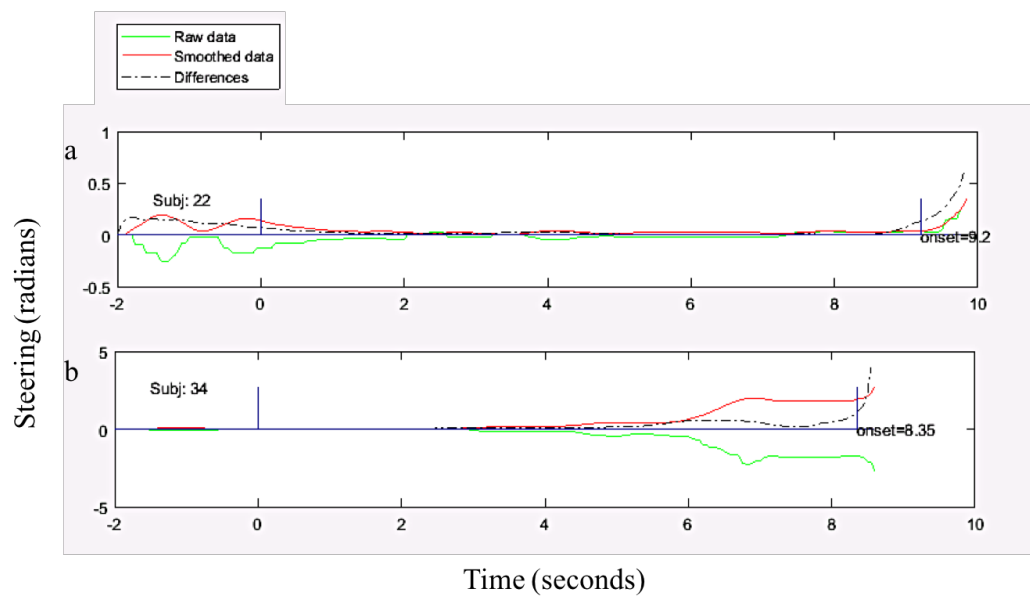
Figure 45: Examples of deleted trials with either no peak (a) or a turn in the wrong direction as detected by the raw data (b).

5.2.2.4 Statistical Analysis

In order to assess the effect of learning on driving behaviour, data for drives with 1, 2 and 3 repetitions in total were analysed separately. For example, in Table 9, the first repetition for areas of interest B, G and H were collapsed across, and merged into one data set, as were the second and third repetitions. The same was done across areas of interest repeated twice and once. This increased statistical power by increasing the amount of data points within each dataset and reducing variability.

It was not possible to collapse across all areas of interest, because if the first, second and third repetitions for all 9 areas of interest were merged, there would be three times as much data for the first repetition as the third. As unequal sample sizes can affect the homogeneity of variance assumption in ANOVA, this was the most appropriate analysis method.

Table 9: Experimental design for areas of interest in urban drives. The value in brackets shows the average position the area of interest occurred within the chronological order of the drives.

Area of Interest	Repetitions		
A	1 (4.1)		
D	1 (3.7)		
E	1 (4.7)		
C	1 (4.9)	2 (4.7)	
L	1 (4.7)	2 (4.2)	
M	1 (4.7)	2 (4.2)	
B	1 (4.9)	2 (4.7)	3 (4.5)
G	1 (4.5)	2 (3.7)	3 (4.9)
H	1 (4.5)	2 (3.7)	3 (4.9)

Dependent variables in areas of interest with only one repetition were analysed using a series of independent t-tests. For drives with two and three repetitions, a series of two-way (Repetition x Age Group) mixed-measures ANOVAs were used. All analyses are reported with Greenhouse-Geisser

corrections where the assumption of sphericity was violated, and corrected t-tests are reported where the assumption of equal variances was violated. All analyses are presented with *post-hoc* Bonferroni corrections where multiple comparisons are conducted.

All variables were assessed for normal distribution of the data. As data that showed non-normal distributions showed skew in both the positive and negative directions for different repetitions and different age groups, no transformations were applied to the data.

Data were checked for statistical outliers. Any data with a value 3 SD above or below the group mean for any variable were removed prior to analysis (see Table 10).

Table 10: Number of statistical outliers in urban drive data divided by age group. Number is shown as a proportion of group totals in brackets.

	Young N	Ageing N	Young N	Ageing N	Young N	Ageing N
Onset 1	0 (0%)	0 (0%)	1 (1.29%)	0 (0%)	0 (0%)	0 (0%)
Onset 2	_____	_____	0 (0%)	2 (2.86%)	0 (0%)	0 (0%)
Onset 3	_____	_____	_____	_____	0 (0%)	0 (0%)
Peak 1	0 (0%)	1 (1.38%)	1 (1.3%)	0 (0%)	0 (0%)	0 (0%)
Peak 2	_____	_____	0 (0%)	2 (2.86%)	0 (0%)	0 (0%)
Peak 3	_____	_____	_____	_____	0 (0%)	0 (0%)
# of peaks 1	1 (1.38%)	1 (1.37%)	0 (0%)	0 (0%)	1 (1.3%)	0 (0%)
# of peaks 2	_____	_____	0 (0%)	1 (1.35%)	0 (0%)	1 (1.37%)
# of peaks 3	_____	_____	_____	_____	0 (0%)	0 (0%)
Time to peak 1	0 (0%)	1 (1.38%)	1 (1.3%)	0 (0%)	0 (0%)	1 (2.22%)
Time to peak 2	_____	_____	1 (1.35%)	0 (0%)	0 (0%)	0 (0%)
Time to peak 3	_____	_____	_____	_____	0 (0%)	0 (0%)

5.2.3 Motorway driving in novel and familiar environments

5.2.3.1 Experimental design

The second part of the experiment aimed to investigate the same hypotheses seen in section 5.2.2 during motorway drives as distinct from the urban routes described arrive. The use of motorway drives in this part of the experiment allowed the hypotheses previously outlined to be investigated with a tighter degree of experimental control. As in section 5.2.2, there were two independent variables: the number of times a visual environment was encountered (1, 2 or 3) and driver age group (young or ageing). Performance at individual areas of interest was analysed using steering angle and the time of lane change, measured in seconds, which was automatically output by the driving simulator. The lane change value reflects the time point at which over half the car moves into the adjacent lane. Previous research has used the presence of lane change manoeuvres, and the time taken to change lanes to investigate response time to critical incidents (Merat, Jamson, Lai & Carsten, 2012), suggesting this a valid measure of response time to stimuli in the environment. This allowed assessment of three dependent variables:

- time of onset of the steering manoeuvre
- time of the lane change
- time taken to achieve the lane change from the onset of the manoeuvre.

5.2.3.2 Procedure

The second part of the experiment consisted of 9 short segments of straight-line motorway driving, with each motorway drive lasting roughly 20 seconds. There were 18 motorway trials in total, and each individual motorway drive was repeated one, two or three times (see Table 11), with all further aspects of the drive remaining the same for each additional exposure.

Table 11: Motorway drive experimental conditions.

Repetition #	One Repetition	Two Repetitions	Three Repetitions

Motorway Drive Name	3, 4, 9	1, 2, 5	6, 7, 8

Subjects were instructed very simply to stay in the central lane (see Figure 46) in which they began until prompted otherwise. Drives began 100m before the area of interest.

Figure 46: A section of free motorway driving prior to the area of interest appearing. Subjects were asked to continue driving in the middle lane at 70mph until prompted otherwise. Drives were started 100m before the area of interest to allow the subjects to reach the correct speed prior to making the manouevre

Visual prompts designed to function like a satellite navigation system prompted the subject to move either one lane to the left or one lane to the right. These prompts appeared 50m before the area of interest, and stayed on the screen for 30m of driving. Subjects were subsequently instructed using a visual prompt to move back into the starting lane 30m after the onset of the area of interest, and this visual prompt remained on the screen for 30m.

The purpose of this part of the experiment was to investigate whether skilled, automated behaviours are related to the complexity of the visual environment, and which driving behaviours comes routine and automated. All drives were randomised for each subjects using a random number generator in order

to prevent any order effects and to allow us to ensure that any changes in behaviour were due to the learning manipulation. Subjects were instructed to drive at 70mph using written instructions (see Appendix 14), which could be monitored using a speedometer on the dashboard of the simulated car in the bottom of the central screen.

Each route had an independent visual area of interest, either a bridge, a gantry, or a sign with specific, salient features which allowed it to be distinguished from those in other routes (see Figures 47 and 48).

Figure 47: An example of a gantry on a motorway drive that was designed to be distinct from other areas of interest and recognisable to the subject.

Figure 48: An example of a gantry with a sign on a motorway drive that was designed to be distinct from other areas of interest and recognisable to the subject.

5.2.3.3 Preprocessing of data

For the same reason outlined in Section 5.2.2.3, data were pre-processed in MATLAB prior to analysis. The pre-processing steps were slightly different from section 5.2.2.3 due to the presence of lane change data. This meant the timing of the peak did not need to be calculated, as the time of the line change was sufficient enough to indicate when the desired manoeuvre had been achieved. A schematic of the pre-processing steps undertaken for these data can be found in Figure 49.

Data restructured into matrices in excel

↓

Matrices imported into MATLAB

↓

Time of lane change converted into seconds

↓

Each row split by number of repetitions

↓

Data normalised to the first value (all values – first value)

↓

Data smoothed

↓

Create onset threshold

↓

Calculate rate of change of absolute values

↓

Identify point at which rate of change passes threshold, this is the onset of the response

↓

Plot time of raw data, smoothed data and rate of change

↓

Identify time of visual cue, onset and lane change on graphs

Figure 49: Preprocessing steps for motorway drive analysis. These were automated using MATLAB.

Steering data was manually extracted from the driving simulator output and converted into matrices using Excel. The time point at which the subject changed lanes, measured in number of data points from the onset of the directional sign was also manually extracted and added into the matrices for each subject and each repetition. Matrices were loaded into MATLAB. There was one matrix for each motorway drive, and each matrix contained a single row for each subject. All the data for each subject for a particular area of interest was contained in the same row, with the repetitions lined up chronologically.

First, the time of lane change was converted from number of time points to seconds by multiplying each value by the sampling rate.

Rows in the matrix were then split by the number of times that motorway drive was completed (either by 3, 2 or 1) to make comparable data sets. Data were then normalised to zero by subtracting the first value for each data set from all the values so that each data set began from a comparable starting point.

To remove noise, data were then smoothed using a running average across every 5 data points. A smaller smoothing filter was used than in Section 5.2.2.3 because each individual data was shorter and contained less data points. A smaller smoothing filter ensured no trends in the data sets were missed.

Data points were then converted to absolute values to allow for comparisons across motorway drives regardless of whether movements were made to the left or the right (see Section 5.2.2.3 for full details).

The rate of change was then calculated using the 'diff' function. An onset was then identified when the rate of change for each data set reached a threshold of 20% of the range. The timing of the onset in seconds was calculated relative to the onset of the visual sign.

The script then automatically reported three values for each subjects and each repetition of the same motorway drive:

- Time of onset
- Time of lane change
- Time taken to change (calculated by subtracting the time of onset to the time of lane change)

Graphs were then plotted individually for each subject and each repetition for the same motorway drive with the raw data, smoothed data and the rate of change plotted. An example of a good trial can be seen in Figure 50.
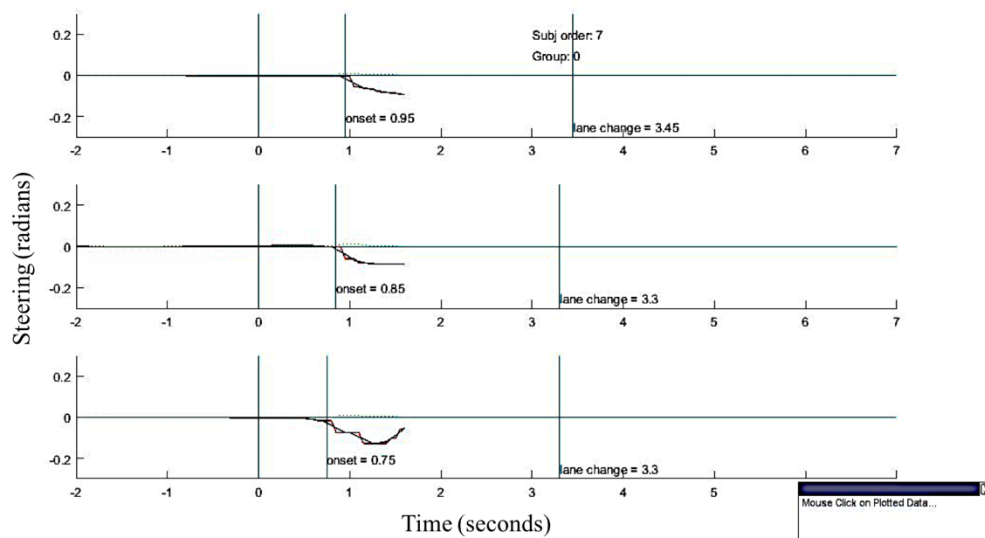
Figure 50: An example of a good trial from the motorway 3 repetition analysis. Time 0 marks the onset of the visual direction cue. Data for each subject and each repetition of the same drive was plotted and onsets were inspected manually to ensure they fitted the raw data properly. Due to the automatic analysis approach in each section of this chapter, each data set had to be an equal length. For each subject, the data had to be curtailed at the last point at which there was a valid data point for all repetitions. A gap can be seen between the end of the plot and the lane change value as the lane change data was automatically generated by the simulation software so this could be extracted even if it lay beyond this point.

If no onset was detected by the script, this was manually detected from the graph using the Data Cursor tool in MATLAB (see Figure 51). Only onsets which occurred after the onset of the sign were included as any variability prior to this was considered not of experimental interest. Trials in which no lane changes occurred were removed from analysis completely (see Figure 52), and for trials where no onsets were detected, only lane change data was used for analysis if it was present.
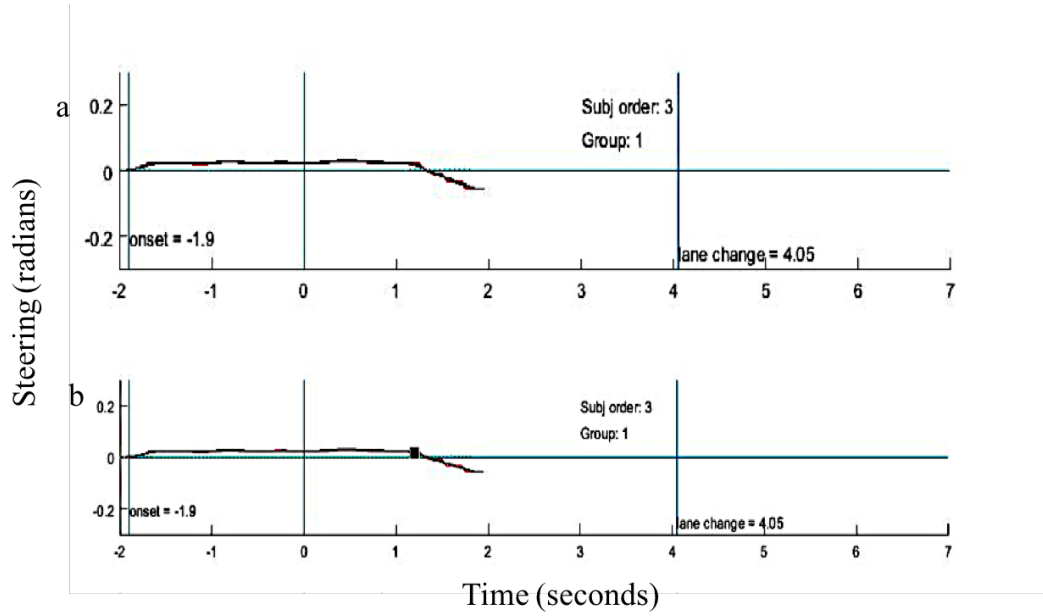
Figure 51: An example of a trial where a spurious onset was detected before the sign (a), which was manually edited to include only the onsets in the correct direction after the onset of the visual sign, marked at 0 (b).
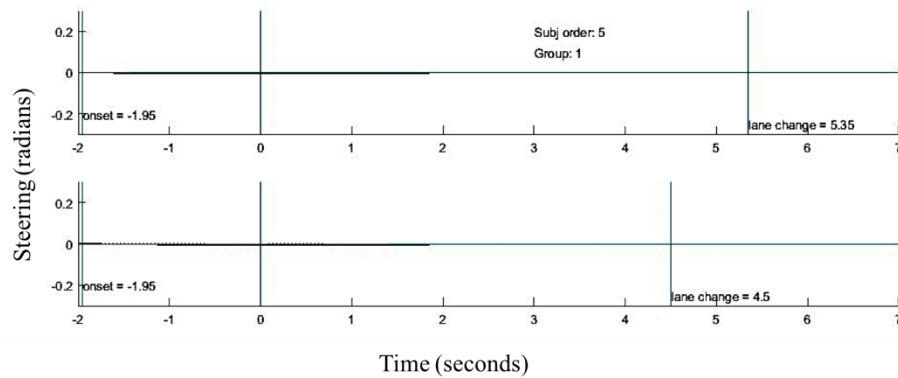
F**igure 52**: A series of examples of deleted trials, where no lane change and no onset was detected. Time 0 marks the onset of the visual direction cue.

5.2.3.4 Statistical Analysis

Data for all drives with 1, 2 and 3 total repetitions were analysed separately. Within drives that were repeated multiple times, data was collapsed across repetitions in order to increase statistical power, see section 5.2.2.4 for a fuller explanation of this approach. For example, for the motorway drives with three

repetitions (drives 6, 7 and 8), all of the first repetitions were grouped together, as were the second and the third. Motorway drives with only one repetition were analysed using an independent t-test. For drives with two and three repetitions, a series of two-way (repetition x age group) mixed-measures ANOVAs were used. All analyses are reported with Greenhouse-Geisser corrections where the assumption of sphericity was violated and corrected t-tests are reported where the assumption of equal variances was violated.

All variables were assessed for normal distribution of the data (the reasoning and methods behind this are outlined in detail in Chapter 2 Methods). Where variables reported positive skew, data were transformed using a logarithmic base-10 transformation prior to statistical to analysis. Where variables reported negative skew, variables were reverse scored and transformed using a logarithmic base-10 transformations. As in previous chapters, where the application of transformations created a skew in variables that were previously normally distributed, no transformations were applied.

Data were checked for statistical outliers. Any data with a value 3 SD above or below the group mean for any variable were removed prior to analysis. The amount of outliers for each variable can be seen in Table 12.

Table 12: Number of statistical outliers in all motorway drive data divided by age group. Proportion of group totals is shown in brackets.

	Young N	Ageing N	Young N	Ageing N	Young N	Ageing N
Onset 1	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Onset 2	_____	_____	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Onset 3	_____	_____	_____	_____	0 (0%)	1 (1.92%)
Lane Change 1	0 (0%)	3 (4%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Lane Change 2	_____	_____	0 (0%)	1 (1.45%)	0 (0%)	1 (1.45%)
Lane Change 3	_____	_____	_____	_____	0 (0%)	0 (0%)
Time to change 1	0 (0%)	1 (2.63%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Time to change 2	_____	_____	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Time to change 3	_____	_____	_____	_____	0 (0%)	1 (1.92%)

5.2.4 Hazard perception in novel and familiar environments

5.2.4.1 Experimental design

The third part of the experiment aimed to investigate two main hypotheses: does the automation of driver behaviour due to previous familiarity with a visual environment enable drivers to perceive hazards earlier than in novel environments. Further, are older drivers, who reach a lesser state of automation, less able to benefit from this than younger drivers. There were three independent variables: the number of times a visual environment had been previously seen in Section 5.2.2 (1, 2 or 3), the presence of a hazard (absent or present) and driver age group (young or ageing). Performance at individual areas of interest was analysed using braking behaviour. This allowed assessment of one independent variable: the time of braking onset, measured from the onset of the auditory cue.

5.2.4.2 Procedure

The third part of the study utilised areas from within the 8 urban city environments seen in Section 5.2.2 of this chapter. Small sections including manoeuvres in the areas of interest mentioned in Section 5.2.2 were re-formulated to create short drives lasting roughly 30 seconds. There were 19 drives in total, the order of which was randomised for each subject. As before, each area of interest was seen only from the same direction and visual angle as in Section 5.2. Across this section, there were manoeuvres involving areas of interest seen one, two and three times in Section 5.2.2 and also novel areas not seen before.

These drives contained either a novel hazard (see Figure 53), a typical pedestrian hazard (see Figures 54 and 55) or no hazard. During novel hazards, a range of vehicles and cyclists either emerged from the pavement, from another road at the junction or roundabout, pulled out in front of the subject or braked in front of the subjects as they approached the junction.

Figure 53: A non-pedestrian hazard of bikes crossing a left-hand junction where the subjects were required to turn left. Auditory cues were used to instruct the subjects to turn a corner so as not to visually clutter the screen further.

In pedestrian hazards, a single pedestrian or group of pedestrians emerged from the left hand side of the pavement and walked in front of the subject as they approached the junction. Pedestrian hazards were added as they were much less variable than the novel vehicle hazards, and so added an extra level of control.

Figure 54: A pedestrian hazard on the pavement as the car approaches the junction.

Figure 55: The same pedestrian hazard seen in Figure 54 as it emerges onto the road.

In order to prevent predictability of the hazards, a series of drives were also included in this section with no hazards. This provided a control condition. These were counter-balanced across the drives so that equal numbers of hazards appeared in areas of interest that had previously been seen one, two and three times, see Table 7. The hazards included in this section included a variety of scenarios including cars pulling out at junctions, buses pulling out from bus stops, improper braking and indicating and cyclists or pedestrians crossing at junctions (see Figures 53-55). Hazards were triggered when the vehicle came within reasonable viewing distance of the area of interest.

Subjects were asked by the experimenter to reach 30 mph as quickly as possible and to remain at this speed until making the manoeuvre. Subjects were prompted to drive in the right hand lane until necessary to make a manoeuvre. At each area of interest, subjects were instructed to manoeuvre by way of automatically generated spoken word instructions which played when the subject passed a particular X, Y co-ordinate in the road. These differed from the visual instructions used in Sections 5.2.2 and 5.2.3 of this chapter in order to decrease cognitive load and to ensure that any changes in behavioural and data was due to the experimental manipulation of the presence of the hazards. This also prevented the visual signs

from interfering with the eye tracking data (this was collected but not used for final analysis).

5.2.4.3 Preprocessing of data

9 drives, covering 6 of the areas of interests seen in Section 5.2.2 of this chapter were analysed. Braking data was manually extracted, transposed and made into matrices. These matrices were then imported into MATLAB. Each string contained the data from one subject, for one drive. These strings were analysed one by one using MATLAB. Data were normalised to the onset of the auditory signal (see Figure 56). Absolute values of the data were taken to ensure that all manoeuvres could be compared across. The rate of change was then calculated using the 'diff' function, and the onset was identified as the first point after the onset of the sign when the rate of change was above a value of zero. The script returned the time of the onset, and these were used for further statistical analysis.

Graphs were plotted individually for each subject and for each repetition of the same drive, with the raw data and rate of change clearly identifiable. This allowed visual spot checking of every trial to ensure the values being returned by the script reflected the changes in the raw data properly. An example of a good trial can be seen in Figure 56. If no braking behaviour was detected (see Figure 57), a null value was returned, and these trials were removed from further analysis.
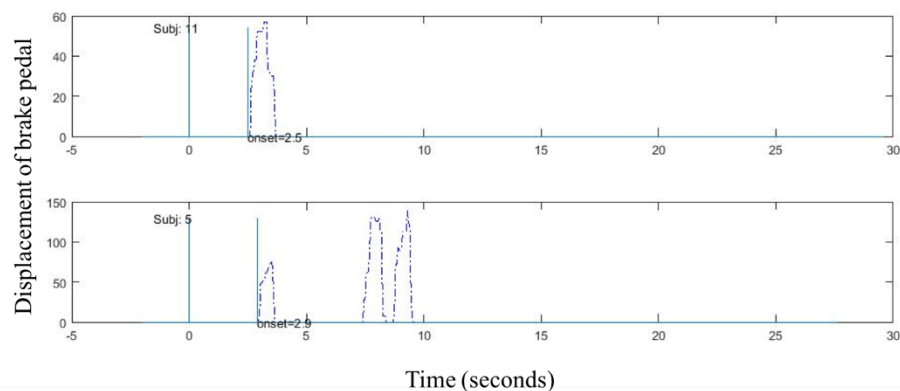
Figure 56: A series of examples of a hazard trials where the onset of the braking behaviour was correctly identified. Time 0 marks the onset of the auditory direction cue.
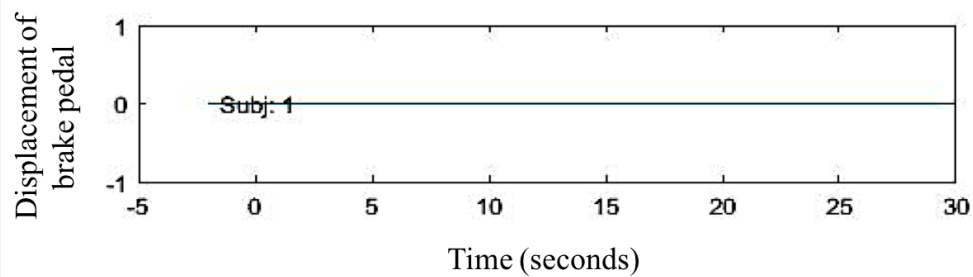
Figure 57: An example of a hazard perception trial where no braking behaviour occurred. These trials were removed from analysis. Time 0 marks the onset of the auditory direction cue.

5.2.4.4 Statistical Analysis

In order to assess the effect of previous learning on hazard perception, two separate analyses were undertaken. A 2 (age group) x 3 (previous repetition number in area of interest) mixed-measures ANOVA was undertaken to investigate whether vehicle hazard perception was improved in areas of interest that were more familiar to the subject. A further 3 (previous repetition number) x 2 (age group) x 2 (pedestrian hazard present or absent) mixed-measures ANOVA was also undertaken with a higher level of control. For this analysis, three of the previous areas of interest from Section 5.2.2 were used, and these were driven both with and without an added pedestrian hazard. All analyses are reported with Greenhouse-Geisser corrections where the assumption of sphericity was violated and corrected t-tests are reported where the assumption of equal variances was violated.

Data was checked for normal distribution. For the vehicle hazard analysis, data for the ageing group on the third repetition showed a positive skew. Log transformations were tested to correct for this, but they caused a negative skew in the young driver group on this variable, so no transformations were applied to the analysis. All variables in the pedestrian analyses showed normal distributions.

Data were checked for statistical outliers (see Table 13). Any data with a value of 3 SD above or below the group mean were removed from the analysis.

Table 13: Number of statistical outliers in all hazard drive data divided by age group. Proportion of group totals is shown in brackets.

	Young N	Ageing N
Vehicle Onset 1	0 (0%)	1 (3.45%)
Vehicle Onset 2	0 (0%)	0 (0%)
Vehicle Onset 3	0 (0%)	0 (0%)
Pedestrian Onset 1	1 (4%)	1 (4.76%)
Pedestrian Onset 2	0 (0%)	0 (0%)
Pedestrian Onset 3	0 (0%)	0 (0%)
No Pedestrian Onset 1	0 (0%)	0 (0%)
No Pedestrian Onset 2	0 (0%)	0 (0%)
No Pedestrian Onset 3	1 (5.88%)	0 (0%)

5.3   Results

5.3.1   Urban driving in novel and familiar environments

Data for urban drives with one, two and three repetitions were analysed separately. See Section 5.2.2.4 for the rationale behind this approach. As absolute values were taken, we collapsed across trials and analysed all left and right turns for each repetition together. Where transformations are applied, these are reflected in the in-text descriptive statistics.

Drives with One Repetition

A significant difference was found between young and older drivers for time of onset for turns with one repetition ($t_{(112.098)} = -4.492$, $p < .001$, $d = .74$), time at which the first peak was reached ($t_{(119.960)} = -3.774$, $p < .001$, $d = .62$), the number of peaks ($t_{(148)} = -5.906$, $p < .001$, $d = .91$), and also the time taken to for the peak of the manoeuvre to be reached ($t_{(148)} = 3.177$, $p = .002$. $d = .52$). As shown in Figure 58, the time of onset of the manoeuvre and the time of the first peak of the manoeuvre was earlier in younger than older subjects. Further, younger subjects made significantly fewer adjustments, as shown by the total number of peaks. Older drivers took significantly less time to reach the first peak than younger drivers.

Table 14: Number of data points (N), raw means and raw standard errors of the mean (SEM) for urban drives with one repetition, split by age group. The significance of these measures are outlined in Section 5.2.2.1.

	N (Young)	Mean (Young)	SEM (Young)	N (Ageing)	Mean (Ageing)	SEM (Ageing)
Onset	78	7.165	.266	73	9.661	.487
Peak	78	8.871	.284	72	10.909	.459
# of Peaks	77	4.520	.177	73	6.945	.364
Time to peak	78	1.705	.069	72	1.394	.069
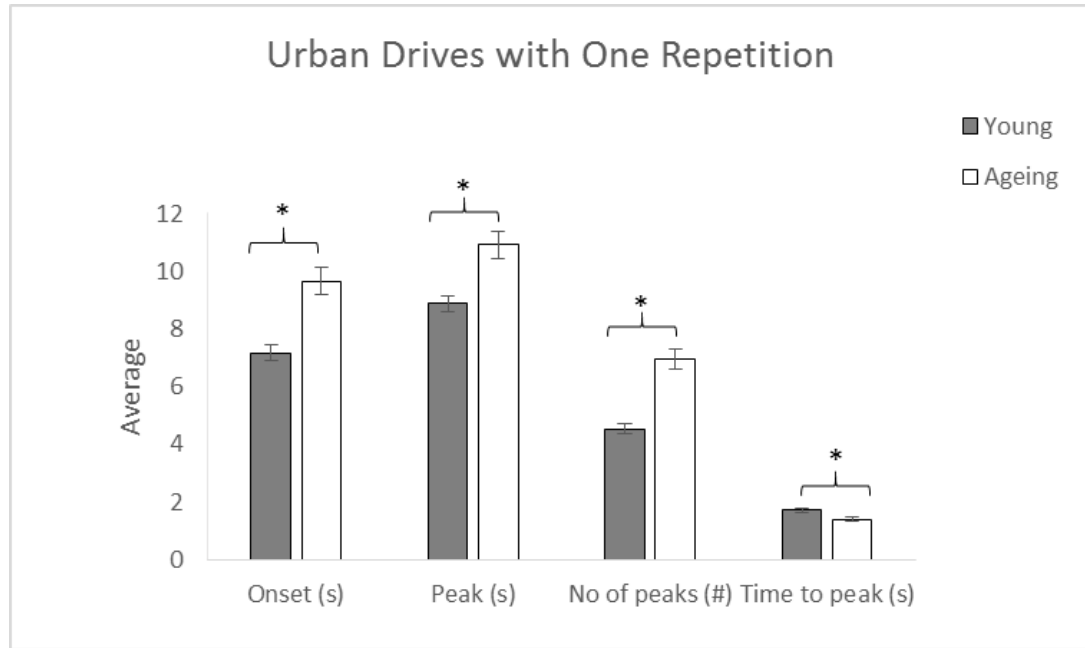
Figure 58: Raw data for time of onset of the movement after the appearance of the visual signal, time of the first peak of the movement after the appearance of the visual signal, overall number of peaks and the time to peak from urban drives with one repetition. Non-transformed means are plotted. Error bars: +/- 1 SEM. * denotes significant differences.

Drives with Two Repetitions

There was a significant main effect of repetition ($F_{(1, 143)}$ = 11.069, p = .001, η^2 = .072 and age ($F_{(1, 143)}$ = 31.320, p < .001, η^2 = .180) on time of onset. Pairwise comparisons revealed onsets were significantly earlier for the second repetition (mean = 8.332s, SE = .203) than the first repetition (mean = 8.878s, SE = .206). Onsets were significantly earlier for younger drivers (mean = 7/594, SE = .260) than for older drivers (mean = 9.689, SE = .269). However, there was no significant interaction between these two variables ($F_{(1, 143)}$ = .304, p = .582, η^2 = .002).
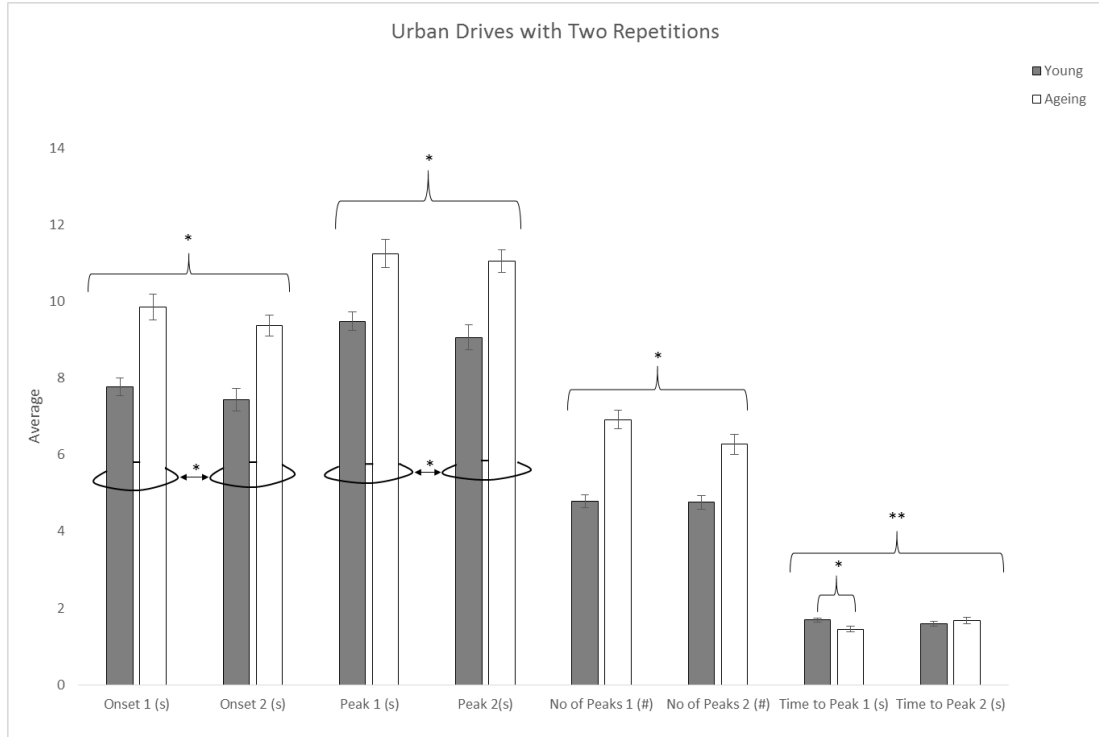
Figure 59: Raw data for onsets, peaks, number of peaks and time to peak from urban drives with two repetitions. Non-transformed means are plotted. Error bars: +/- 1 SEM. Brackets with a * indicate a significant main effect of age. Lasso with a * denotes a significant main effect of repetition number. Brackets with a ** denotes a significant interaction.

There was a significant main effect of repetition ($F_{(1, 141)} = 7.438$, $p = .007$, $\eta^2 = .050$) and age group ($F_{(1, 141)} = 23.673$, $p < .001$, $\eta^2 = .144$) on time at which the first peak of the manoeuvre was made. Overall, the first peak during the second repetition (mean = 10.034s, SE = .221) was significantly earlier than the first peak during the first repetition (mean = 10.506s, SE = .218). Younger drivers (mean = 9.288, SE = .280) also reached the peak significantly more early than older drivers (mean = 11.252, SE = .290). However, we found no significant interaction between these two variables ($F_{(1, 141)} = .308$, $p = .580$, $\eta^2 = .002$).

There was a significant main effect of age on the number of peaks ($F_{(1, 150)} = 47.485$, $p < .001$, $\eta^2 = .240$). Younger drivers (mean = .653, SE = .014) made significantly fewer peaks than older drivers (mean .793, SE = .015). However, there was an insignificant main effect of repetition on number of peaks ($F_{(1, 150)} = 3.466$, $p = .065$, $\eta^2 = .023$) and a non-significant interaction between these variables ($F_{(1, 150)} = 2.652$, $p = .106$, $\eta^2 = .017$).

There was a non-significant main effect of repetition ($F_{(1, 142)}$ = 1.000, p = .319, η^2 = .007) and age group ($F_{(1, 142)}$ = .564, p .454, η^2 = .004) on the time taken to make the manoeuvre. However, there was a significant interaction between the two variables ($F_{(1, 142)}$ = 5.683, p = .018, η^2 = .038). Independent t-tests revealed that the time taken was significant longer for younger than older drivers on the first repetition ($t_{(149)}$ = 2.632, p = .009) but there were no significant differences between the age groups on the second repetition ($t_{(144)}$ = -.670, p = .504).

Table 15: Number of data points (N), raw means and raw standard errors of the mean (SEM) for urban drives with two repetitions, split by age group.

	N (Young)	Mean (Young)	SEM (Young)	N (Ageing)	Mean (Ageing)	SEM (Ageing)
Onset 1	77	7.765	.232	75	9.846	.336
Onset 2	76	7.428	.294	70	9.368	.281
Peak 1	77	9.484	.245	74	11.251	.360
Peak 2	75	9.064	.325	70	11.057	.293
# of peaks 1	78	4.782	.174	75	6.920	.241
# of peaks 2	78	4.756	.182	74	6.270	.254
Time to peak 1	77	1.684	.057	74	1.445	.071
Time to peak 2	74	1.596	.062	72	1.666	.083

Drives with Three Repetitions

Data showed significant main effects of repetition ($F_{(1.278, 103.510)}$ = 22.980, p < .001, η^2 = .221) and age group ($F_{(1, 81)}$ = 5.102, p = .027, η^2 = .59) on the time at which the onset of the turn occurred. Bonferroni-corrected pairwise comparisons indicated onsets were significantly earlier on the third repetition (mean = 2.682s, SE = .285) than the first repetition (mean = 4.035s, SE = .336), and significantly earlier on the second repetition (mean = 2.912s, SE = .303) than the first repetition, but there were no significant differences between the second and third repetitions (p = .107). Onsets were significantly earlier for younger drivers (mean = 2.532, SE = .412) than older drivers (mean = 3.810, SE = .388). The interaction between these two variables was not significant ($F_{(1.278, 103.510)}$ = .103, p = .810, η^2 = .001).
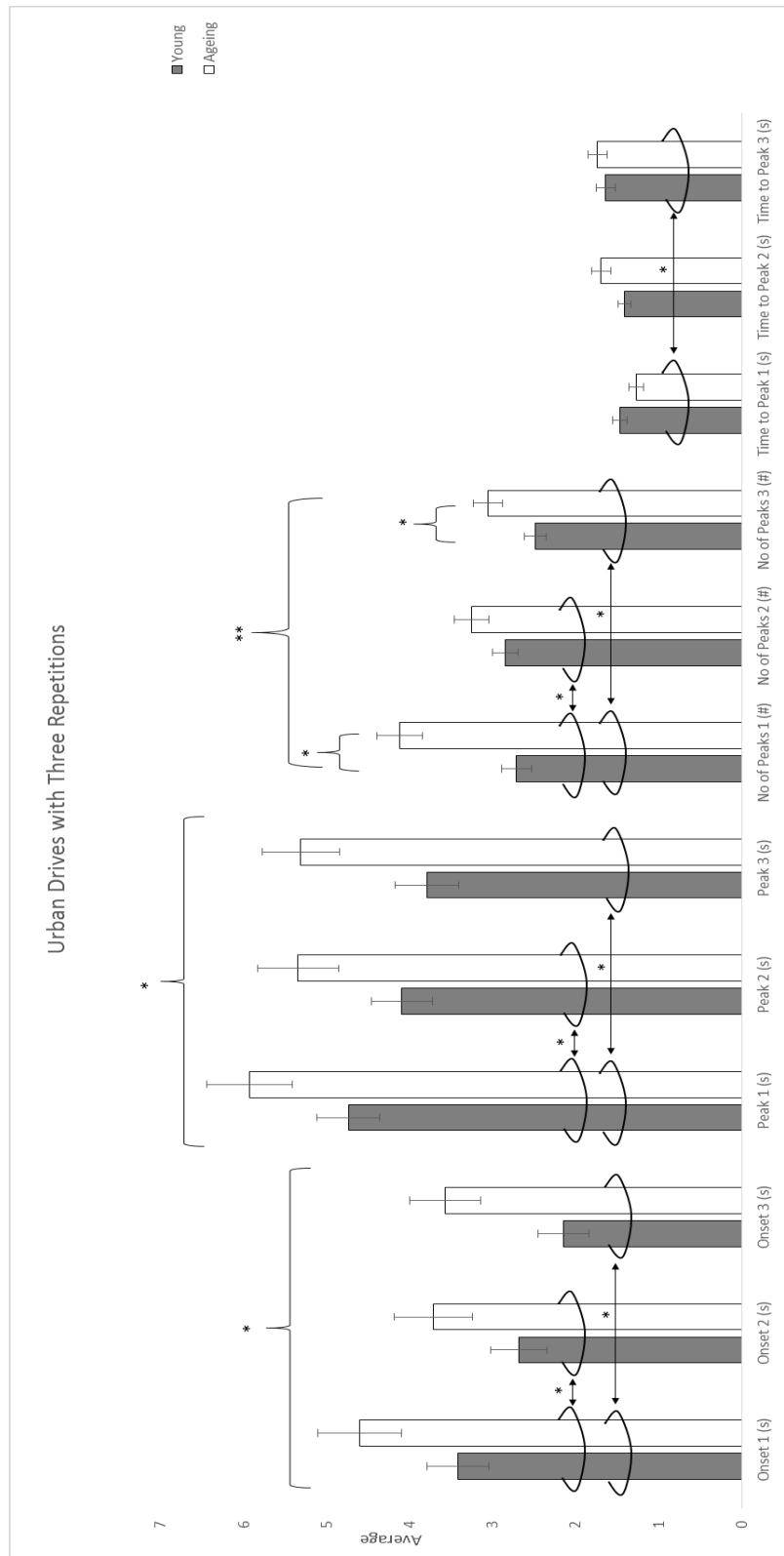
Figure 60: Raw data for onsets, peaks, number of peaks and time to peak for urban drives with three repetitions Non-transformed means are plotted. Error bars: +/1 SEM. Brackets with a * indicate a significant main effect of age. Lasso with a * denotes a significant difference.

There was a significant main effect of repetition (F $_{(1.483, 117.119)}$ = 13.180, p < .001, η^2 = .143) and age group (F $_{(1, 79)}$ = 5.183, p = .026, η^2 = .62) on the time at which the first peak occurred (see Figure 60). Pairwise comparisons indicated that overall, steering behaviour during the third (mean = 4.313s, SE = .325) and second repetitions (mean = 4.402s, SE = .324) peaked earlier than during the first repetition (mean = 5.307s, SE = .344). However, there was no significant difference between the second and third repetitions (p = 1.000). Overall, younger drivers (mean = 3.932, .447) peaked significantly earlier than older drivers (mean = 5.330, SE = .421). Despite the effects of repetition and age group, the interaction between these two variables was not significant (F $_{(1.483, 117.119)}$ = .153, p = .793, η^2 = .002).

There was a significant main effect of repetition on the number of peaks made during the response window (F $_{(2, 294)}$ = 11.680, p < .001, η^2 = .074). Pairwise comparisons indicated that there were significantly fewer peaks in the third repetition (mean = 2.758, SE = .110) than the first repetition (3.389, SE = .163), and significantly fewer peaks in the second repetition (mean = 3.034, SE = .128) than the first repetition. There were no significant differences between the amount of peaks made during responses in the second and third repetitions. There was a significant main effect of age on this variable (F $_{(1, 147)}$ = 12.899, p < .001, η^2 = .081) and a significant interaction between these variables (F $_{(2, 294)}$ = 7.697, p = .001, η^2 = .050). *Post-hoc* independent t-tests indicated young drivers made significantly fewer peaks than older drivers in the first repetition (t (125.305) = -4.315, p < .001, Bonferroni corrected alpha level = .025) and the third repetition (t (149) = -2.612, = .010), though the significance levels decreased.

There was a significant main effect of repetition number on the time taken to complete the turn (F $_{(2, 156)}$ = 6.637, p = .002, η^2 = .078). Pairwise comparisons showed that time to peak was significantly shorter on the first repetition (mean = 1.334s, SE = .061) than the third (mean = 1.641s, SE = .083), but there were no significant differences between the first and second repetitions (mean = 1.482s, SE =.086, p = .250) or the second and third repetitions (p = .124). The effect of age

group on this variable was not significant ($F_{(1, 78)} = .742$, $p = .392$, $\eta^2 = .009$) and the interaction between these variables did not reach significance ($F_{(2, 156)} = 2.870$, $p = .060$, $\eta^2 = .035$).

Table 16: Number of data points (N), raw means and raw standard errors of the mean (SEM) for onsets, time of first peak, total number of peaks and time to peak for urban drives with three repetitions, split by age group.

	N (Young)	*Mean (Young)*	*SEM (Young)*	*N (Ageing)*	*Mean (Ageing)*	*SEM (Ageing)*
Onset 1	48	3.418	.374	46	4.600	.504
Onset 2	48	2.683	.338	48	3.716	.468
Onset 3	43	2.147	.308	49	3.574	.429
Peak 1	47	4.738	.382	46	5.927	.513
Peak 2	48	4.095	.367	47	5.345	.488
Peak 3	43	3.787	.384	49	5.310	.467
# of peaks 1	77	2.714	.179	73	4.123	.273
# of peaks 2	78	2.846	.150	72	3.250	.208
# of peaks 3	78	2.487	.135	73	3.055	.172
Time to peak 1	47	1.464	.086	45	1.270	.085
Time to Peak 2	48	1.411	.074	47	1.696	.115
Time to Peak 3	43	1.641	.113	49	1.737	.115

Table 17: Summary table of main effects of repetition and age group and significant interactions in onsets, time of first peak, number of peaks and time to peak for urban drives with one, two and three repetitions.

	Repetition Number	Main Effect of Repetition	Main Effect of Age Group	Significant Interaction
Onset	One	_____	Yes	_____
Peak	One	_____	Yes	_____
# of Peaks	One	_____	Yes	_____
Time to Peak	One	_____	Yes	_____
Onset	Two	Yes	Yes	No
Peak	Two	Yes	Yes	No
# of Peaks	Two	No	Yes	No
Time to Peak	Two	No	No	Yes
Onset	Three	Yes	Yes	No
Peak	Three	Yes	Yes	No
# of Peaks	Three	Yes	Yes	Yes
Time To Peak	Three	Yes	No	No

Urban Drives with One Repetition vs Third Repetition of Drives with Three Repetitions

A further analysis was undertaken comparing areas of interest that were seen once with the third repetition of areas of interest that were seen three times.

There was a significant effect of repetition ($F_{(1, 90)} = 123.391$, $p < .001$, $\eta^2 = .578$) and age group ($F_{(1, 90)} = 49.925$, $p < .001$, $\eta^2 = .343$) on the time of onset of the manoeuvre. Pairwise comparisons revealed that the onset of the manoeuvre was significantly earlier in the third repetition (mean = 2.86s, SE = .27) than the first (mean = 8.81s, SE = .34). Younger drivers had significantly earlier onsets

(mean = 4.87s, SE = .22) than older drivers (mean = 6.81s, SE = .20). However, there was not a significant interaction between these two variables ($F_{(1, 90)}$ = .908, p = .343, η^2 = .010).

There was a significant effect of repetition ($F_{(1, 89)}$ = 112.097, p < .001, η^2 = .557) and age group ($F_{(1, 89)}$ = 37.191, p < .001, η^2 = .295) on the time of the peak of the manoeuvre. Pairwise comparisons revealed that the peak of the manoeuvre was significantly earlier in the third repetition (mean = 4.58s, SE = .31) than the first repetition (mean = 10.29s, SE = .31). Further, younger drivers had significantly earlier peaks (mean = 6.55s, SE = .21) than older drivers (mean = 8.33s, SE = .20). There was a non-significant interaction between these variables ($F_{(1, 89)}$ = .117, p < .733, η^2 = .001).

There was a non-significant effect of repetition ($F_{(1, 89)}$ = 1.128, p = .291, η^2 = .013) and age ($F_{(1, 89)}$ = .617, p = .434, η^2 = .007) on the time taken to complete the manouevre. However, there was a significant interaction between these variables ($F_{(1, 89)}$ = 4.005, p < .048, η^2 = .043). Post-hoc independent t-tests revealed that there was a significant difference in the time taken for younger and older drivers to complete the manouevre in the areas of interest with only one repetition ($t_{(148)}$ = 3.177, p = .002, Bonferroni corrected alpha level = .025) but no significant difference in the third repetition of areas of interest that were seen three times ($t_{(90)}$ = -.590, p = .557, Bonferroni corrected alpha level = .025).

5.3.2   Motorway driving in novel and familiar environments

Data was analysed for motorway drives with one, two and three repetitions separately. Time of the onset of the steering response, time to lane change and time to change were measured in seconds. Where transformations are applied to the data, these are reflected in the in-text statistics.

Motorway Drives with One Repetition

Onsets were significantly earlier in young drivers (mean = 0.279s, SE = .006) than ageing drivers (mean = 0.230s, SE = .014) in motorway drives with one repetition, t $_{(49.59)}$ = 3.21, p = .002, d = .70. The time of lane change was also significant earlier in young drivers (mean = 2.88s SE = .579, d = .95) than ageing drivers (mean = 3.54s, SE = .790, t $_{(146)}$ = -5.807, p = < .001, d = .05).
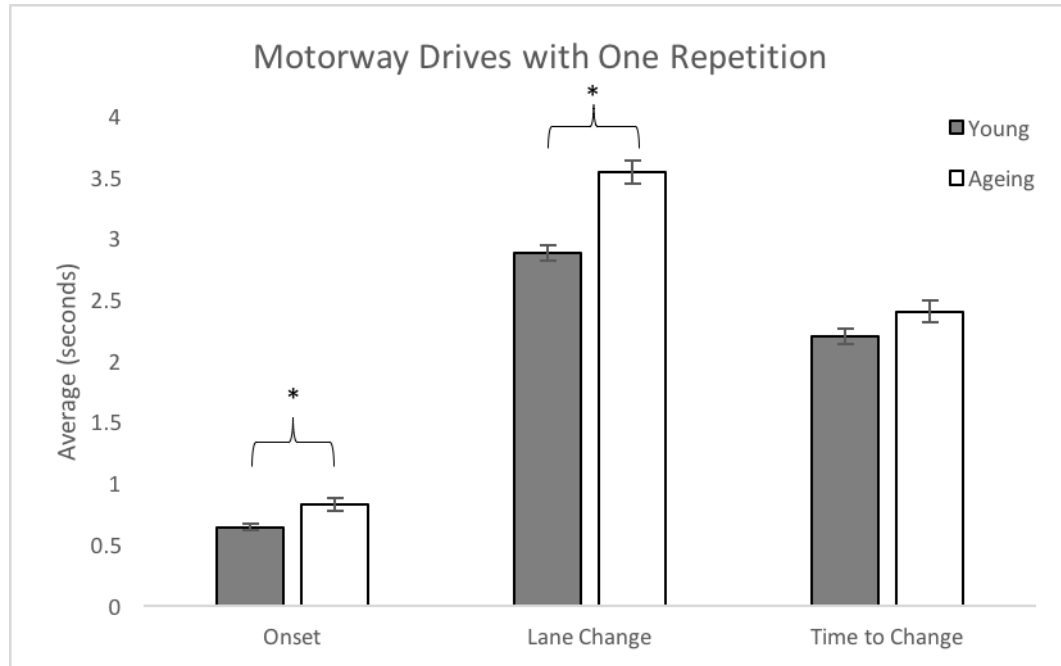
Figure 61: Raw data for onset, lane change and time to change from motorway drives with one repetition. Error bars: +/- 1 SEM. * denotes significant differences.

However, no significant differences were shown between young drivers (mean = 2.20s, SE = .062) and ageing drivers (mean = 2.46s, SE = .109) in the time taken to complete the lane change manoeuvre, t $_{(98)}$ = -1.755, p = .082.

Table 18: Number of data points (N), raw means and raw standard errors of the mean (SEM) for onsets, time of lane change and time to complete the lane change for motorway drives with one repetition, split by age group.

	N (Young)	Mean (Young)	SEM (Young)	N (Ageing)	Mean (Ageing)	SEM (Ageing)
Onset	64	.636	.025	37	.820	.051
Lane change	77	2.877	.066	71	3.535	.094
Time to change	65	2.196	.062	37	2.397	.089

Motorway Drives with Two Repetitions

There was a significant main effect of repetition on latency to onset. Overall, latencies to onset were shorter in the second repetition (mean = -.221s, SE = .020) than the first repetition (mean = -.132s, SE = .015) $F_{(1, 67)}$ = 17.266, p < .001, η^2 = .205. There was also a main effect of age group. Overall, older drivers (mean = -.142, SE = .023) had later onsets than younger drivers (mean = -.210, SE = .015), $F_{(1, 67)}$ = 159.691, p = .017, η^2 = .003. There was also an insignificant interaction between age and repetition, $F_{(1, 67)}$ = .206, p = .651, η^2 = .082. *Post-hoc* independent t-tests showed that the time of onset was significantly earlier for young drivers than ageing drivers for the first repetition ($t_{(78)}$ = -.2656, p = .010, Bonferroni corrected alpha level = 0.025) but not the second repetition of the same motorway drives ($t_{(95)}$ = -1.632, p = .106).
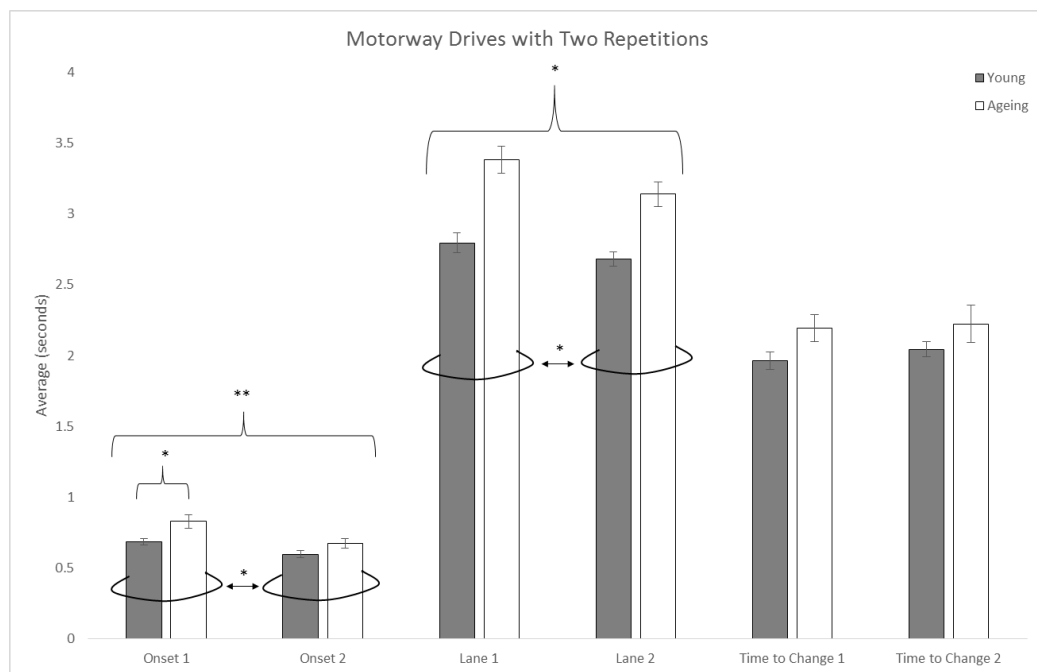
Figure 62: Raw onset, lane change and time to complete the lane change data from motorway drives with two repetitions. Error bars: +/- 1 SEM. Brackets with a * indicate a significant main effect of age. Lasso with a * denotes a significant main effect of repetition number. Brackets with a ** denotes a significant interaction.

There was also a significant main effect of repetition number of time at which the lane change manoeuvre was made. Overall, lane changes were made later in the first repetition (mean = .474s, SE = .008) than the second repetition (mean =

.451s, SE = .008), $F_{(1, 133)}$ = 9.886, p = .002, η^2 = .069. There was also a main effect of age. Older drivers (mean = .502, SE = .010) generally made lane changes later than younger drivers (mean = .429, SE = .009), $F_{(1, 133)}$, = 28.730, p = < .001, η^2 = .178. However, the interaction between age and repetition number was not significant, $F (1, 133) = 1.323$, p = .252, η^2 = .010.

There were insignificant main effects of repetition number and age group on time to change, as well as an insignificant interaction between these variables, p > .05.

Table 19: Number of data points (N), raw means and raw standard errors of the mean (SEM) for motorway drives with two repetitions, split by age group.

	N (Young)	Mean (Young)	SEM (Young)	N (Ageing)	Mean (Ageing)	SEM (Ageing)
Onset 1	52	.686	.020	28	.829	.048
Onset 2	59	.598	.025	38	.676	.034
Lane change 1	74	2.795	.069	66	3.383	.093
Lane change 2	77	2.681	.052	68	3.138	.089
Time to change 1	52	1.964	.064	28	2.193	.095
Time to change 2	59	2.044	.054	37	2.224	.130

Motorway Drives with Three Repetitions

There was a significant overall main effect of number of repetitions on time of onset, $F_{(1.847, 151.447)}$ = 20.176, p < .001, η^2 = .197. Onsets were earlier in the second (mean = .764, SE = .034) and third repetitions (mean = .626, SE = .039) than the first (mean = .870, SE = .046). Onsets were also significantly earlier in the third repetition than the second. There was an insignificant main effect of age. Overall, older drivers did not have significantly different latencies than younger drivers, $F (1, 82) = 1.043$, p = .310, η^2 = .013. However, there was a significant interaction between age and repetition, $F (1.847, 151.887) = 7.374$, p = .001, η^2 = .083. *Post-hoc* independent t-tests showed that there was a significant difference between latency to onset for young and ageing drivers for the first

repetition (t (102) = -3.525, p = .001, Bonferroni corrected alpha level = 0.025) but not the third repetition of the same motorway drives (t (116) = 0.727, p = .469).

There was a significant overall main effect of number of repetitions on time at which the lane change manoeuvre was made (F (1.512, 185.930) = 33.027, p < .001, η^2 = .212). Lane changes were made earlier in the second repetition (mean = 3.31, SE = .063) than the first (mean = 3.654, SE = .077), and also earlier in the third repetition (mean = 3.279, SE = .063) than the first. There were no significant differences between the second and third repetitions (p = .420). There was a significant main effect of age. Overall, older drivers made lane change manoeuvres later than younger drivers, F (1, 123) = 13.557, p < .001, η^2 = .099. There was also a significant interaction between age and repetition number (F (1.512, 185.930) = 8.653, p = .001, η^2 = .066). Independent t-tests indicated that the time of the lane change was significantly earlier for younger drivers than older drivers on both the first repetition (t (136) = -4.877, p < .001, Bonferroni corrected alpha level = 0.025) and the third repetition of same drive (t (140) = -2.761, p = .007) although again, the significance levels decreased.

There was no significant main effect of repetition number or age group on time taken to complete the overall manoeuvre, nor was there a significant interaction between these variables, p > .05.
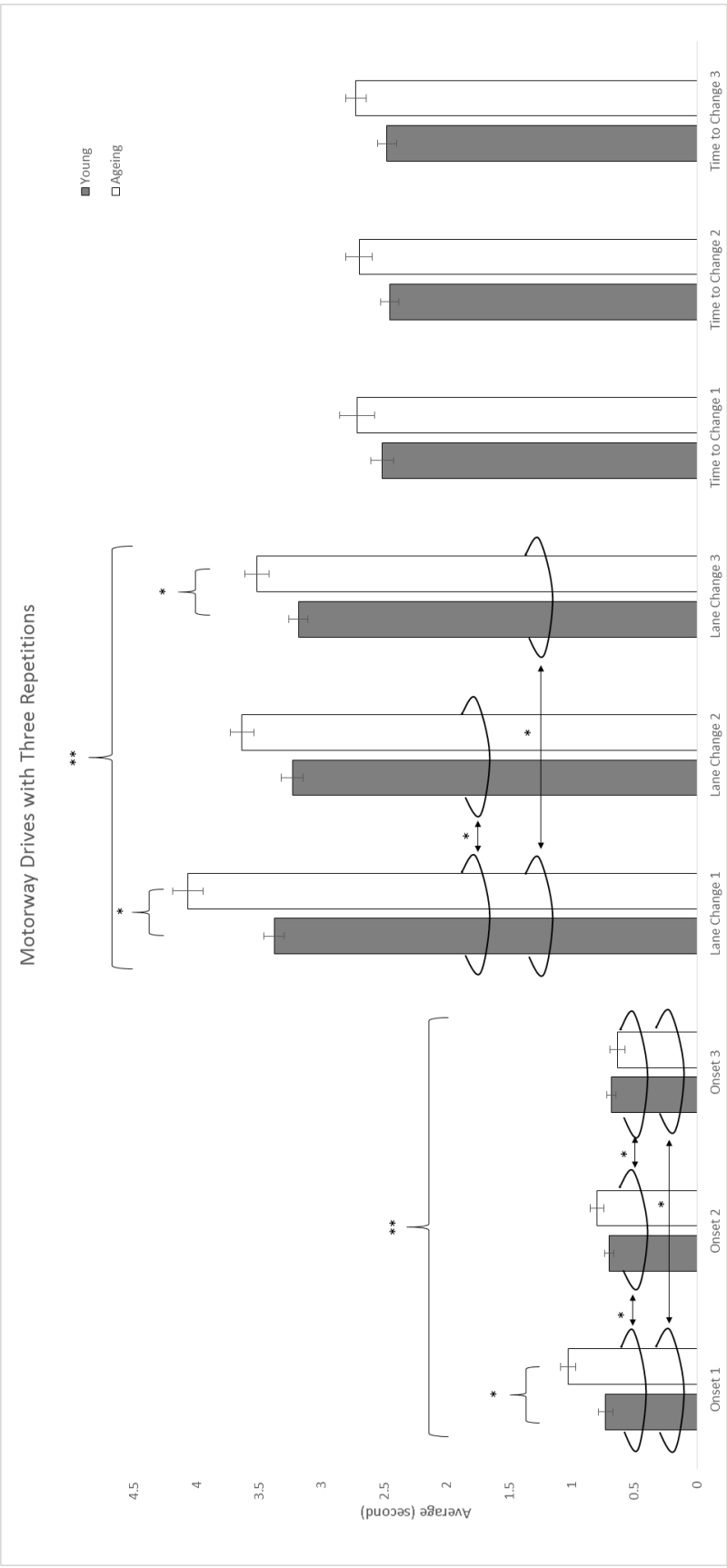
Figure 63: Raw onset, lane change and time to change data from motorway drives with three repetitions. Error bars: +/- 1 SEM. Brackets with a * indicate a significant main effect of age. Lasso with a * denotes a significant main effect of age. Lasso with a * denotes a significant main effect of repetition number. Brackets with a ** denotes a significant interaction.

Table 20: Number of data points (N), raw means and raw standard errors of the mean (SEM) for motorway drives with three repetitions, split by age group.

	N (Young)	Mean (Young)	SEM (Young)	N (Ageing)	Mean (Ageing)	SEM (Ageing)
Onset 1	65	.730	.056	39	1.031	.058
Onset 2	64	.705	.036	50	.799	.057
Onset 3	67	.684	.035	51	.636	.059
Lane change 1	75	3.381	.080	63	4.071	.120
Lane change 2	73	3.236	.088	68	3.638	.093
Lane change 3	76	3.186	.076	66	3.520	.096
Time to change 1	60	2.517	.091	38	2.717	.137
Time to change 2	64	2.456	.075	50	2.702	.105
Time to change 3	67	2.478	.077	51	2.727	.080

Table 21: Summary table of main effects of repetition and age group and significant interactions in onsets, time of lane change, and time to change for motorway drives with one, two and three repetitions.

	Repetition Number	Main Effect of Repetition	Main Effect of Age Group	Significant Interaction
Onset	One	_____	Yes	_____
Lane Change	One	_____	Yes	_____
Time to Change	One	_____	No	_____
Onset	Two	Yes	Yes	No
Lane Change	Two	Yes	Yes	No
Time to Change	Two	No	No	No
Onset	Three	Yes	No	Yes
Lane Change	Three	Yes	Yes	Yes
Time to Change	Three	No	No	No

5.3.3 Hazard perception in novel and familiar environments

The onset of the first braking point was measured in seconds from the onset of the auditory signal. Vehicle and pedestrian hazards were analysed separately.

Vehicle Hazards

There was a significant main effect of previous repetition number on the time of braking (F $_{(1.454, 49.443)}$ = 11.957, p < .001, η^2 = .260). The onset of the braking movement was earlier for the first repetition (mean = 4.713, SE = .096) than the third (mean = 6.810, SE = .535, p = .002, Bonferroni corrected alpha level .025) and the onset of the braking movement was made significantly earlier on the second repetition (mean = 4.722, SE = .288) than the third (p = .002). However, there was no significant difference between the first and second repetitions (p = 1.000).
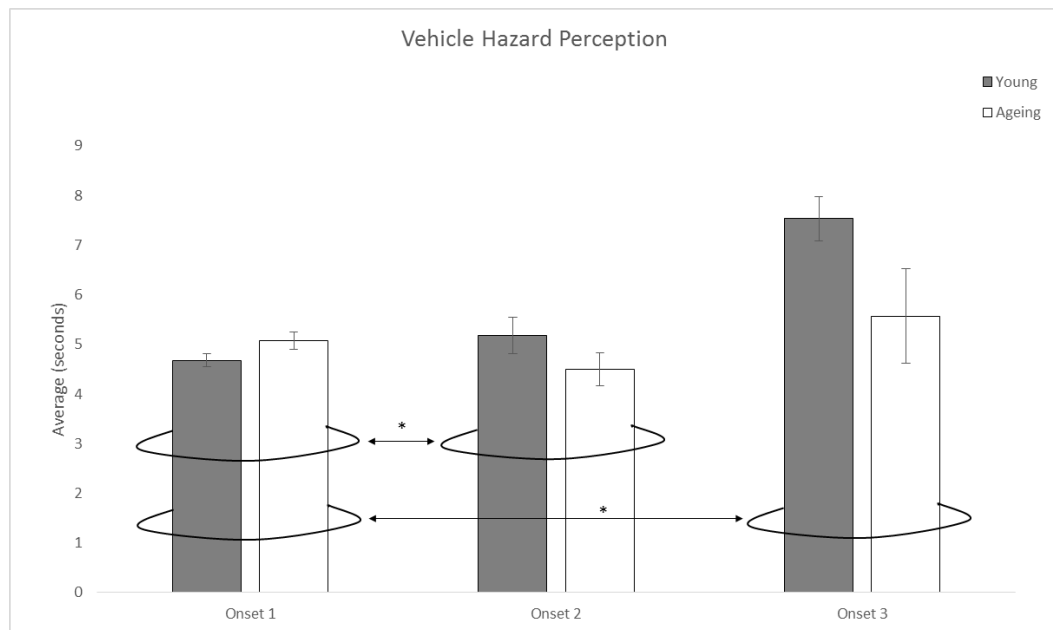
Figure 64: Average braking onsets for drives previously seen one, two or three times with added hazards (see section 2.2). Error bars: +/- 1 SEM. * denotes significant differences.

There was no significant main effect of age group (F $_{(1, 34)}$ = 2.526, p = .121, η^2 = .069), nor was there a significant interaction between the two variables (F $_{(1.454, 49.443)}$ = 11.959, p = .162, η^2 = .054).

3 drives were driven both with a pedestrian hazard and without a hazard, which acted as the control condition. There was an insignificant overall main effect of repetition number (F $_{(2, 34)}$ = 2.004, p = .150, η^2 = .055) and age group (F $_{(1, 17)}$ = .545, p = .470, η^2 = .031) on the time of first braking. There was also an insignificant interaction between these variables, F $_{(2, 34)}$ = .983, p = .384, η^2 = .055).

There was a significant effect of whether the pedestrian hazard was present or not on time of first braking (F $_{(1, 17)}$ = 22.417, p < .001, η^2 = .569). The time of the braking onset was significantly earlier when a hazard was present (mean = 2.870, SE = 250) than when there was no hazard present (mean = 4.278, SE = .206, p < .001). There was an insignificant interaction between this variable and age group (F $_{(1, 17)}$ = 2. 337, p = .145, η^2 = .121).

There was a significant interaction between the presence of the pedestrian hazard and previous repetition number (F $_{(2, 34)}$ = 7.667, p = .002, η^2 = .311.) *Post-hoc* paired t-tests indicated that the difference braking behaviour the hazard between the hazard present and hazard absent conditions on the first repetition was non-significant (t $_{(38)}$ = -1.656, p = .106) but on the third repetition, braking occurred significantly earlier in the hazard present than hazard absent condition (t $_{(30)}$ = -2.379, p = .024, Bonferroni corrected alpha level = .025).
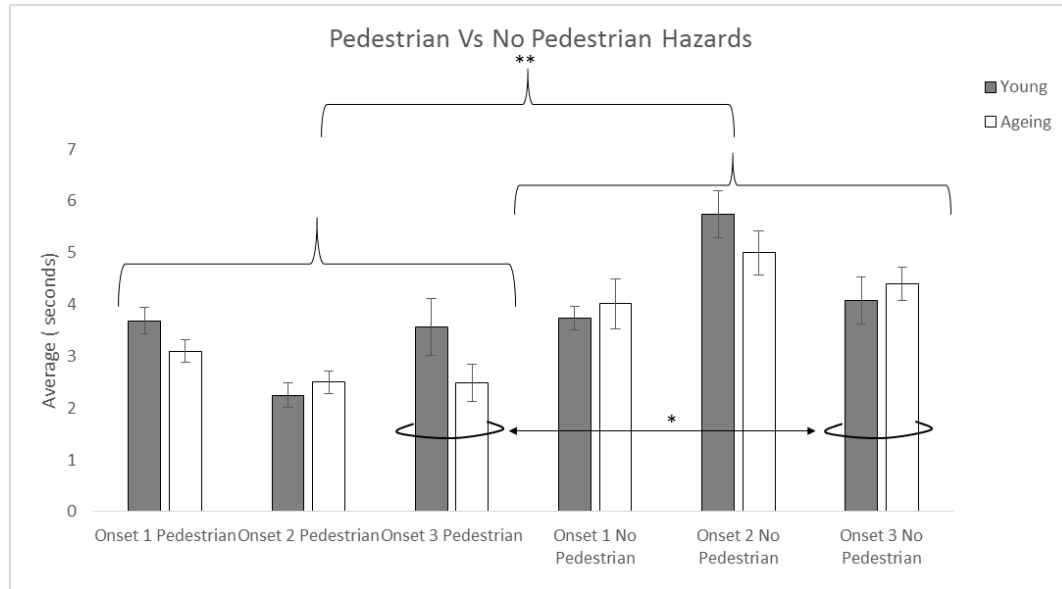
Figure 65: Average braking onsets for drives seen previously one, two or three times (see section 2.2) driven either with (L) or without (R) a pedestrian hazard. Error bars: +/- 1 SEM. * denotes significant differences, ** denotes a significant interaction.

There was no significant three-way interaction between the presence of the hazard, previous repetition number and age group on time at which braking occurred ($F_{(2, 34)} = 2.562$, $p = .092$, $\eta^2 = .131$).

Table 22: Number of data points (N), raw means and raw standard errors of the mean (SEM) for hazard drives with vehicle hazards, pedestrian hazards, and no hazards.

	N (Young)	*Mean (Young)*	*SEM (Young)*	*N (Ageing)*	*Mean (Ageing)*	*SEM (Ageing)*
Vehicle Onset 1	25	4.678	.127	28	5.072	.176
Vehicle Onset 2	23	5.174	.366	21	4.495	.336
Vehicle Onset 3	26	7.537	.445	18	5.569	.947
Pedestrian Onset 1	24	3.688	.262	20	3.098	.215
Pedestrian Onset 2	24	2.246	.236	21	2.498	.217
Pedestrian Onset 3	20	3.565	.541	22	2.480	.360
No Pedestrian Onset 1	23	3.735	.227	20	4.013	.483
No Pedestrian Onset 2	18	5.744	.457	19	4.997	.422
No Pedestrian Onset 3	16	4.078	.460	19	4.392	.320

5.4   Discussion

The series of studies presented in this chapter aimed to address four main hypotheses: Firstly, does familiarity with a route facilitate the automatic performance of driving performance such as steering at junctions and making lane changes in motorway environments? Secondly, does familiarity with a visual environments benefit young drivers more than elderly drivers? Thirdly, does familiarity with a visual environment facilitate the onset of braking during hazard perception? Finally, if older drivers are less able to familiarise themselves with visual environments, does this impede their hazard perception abilities more than younger drivers?

5.4.1   Hypothesis 1 and 2

During driving, the same behaviours may be executed multiple times. As they become familiar, they make take on the qualities of automatic behaviours (discussed in detail during Chapter 1). Previous chapters in this thesis have shown that as visual behaviours are repeated, they are executed earlier, and more accurately. This chapter aimed to investigate this process during driving. Consistent with our hypotheses, results from the first two experiments in this chapter showed that as both urban and motorway environments became more familiar, driving behaviour was executed earlier, suggestive of the behaviours becoming more automatic. Whilst navigating junctions and intersections during urban drives, the onset of manoeuvres and the peak of the manoeuvres occurred significantly earlier with each additional repetition Further, the number of adjustments made during navigating these environments decreased significantly as exposure to the environment increased. Interestingly, Figure 60 shows that significant differences exist between the first and second repetitions of manoeuvres that are performed twice in total. However, pairwise comparisons also showed that across all variables measured there were no significant differences between the second and third repetitions (see Figure 60). This suggests that the benefits of learning largely come from the first additional repetition. In a motorway environment, similar results were shown. Subjects were instructed to change lanes in visually distinct locations. As

these locations were encountered more times, the onset of steering to begin changing lanes was significantly earlier, and the time at which the lane change occurred was also significantly earlier.

Previous work has investigated the effects of route familiarity on driver behaviour, but results have been inconsistent. Consistent with our research, some studies have shown that familiarity with a route benefits driver behaviour such as route navigation (Read et al, 2011). However, numerous studies have shown that as familiarity with an environment increases, so does unsafe or risky driver behaviour such as smaller following distances, longer reaction times to stimuli in the environment and higher voluntary speed increases (Charlton & Starkey, 2012, Colonna et al, 2016; Initini, 2016; Yanko & Spalek, 2013). The authors of these studies suggest that poorer performance in familiar locations is due to lowered attention, which may lead to 'mind wandering' or 'inattentional blindness'. However, these results dispute this hypothesis. Instead, and in agreement with classic ideas about the cognitive processes that underpin automatic behaviours, our results show that familiarity facilitates stereotyped driver behaviours which may become anticipatory over time. It must be noted that the degree to which driving terrains are familiar vary across experiments. For example, in the study by Yanko & Spalek (2013), subject drove the same route 4 times to reach a point of familiarity. However, subjects in Initini (2016)'s study drove the same road 24 times over a 5-day period and Charlton & Starkey (2012) used the same stretch of road, driven in either a north or south direction, in 20 sessions across a three-month period of time so it could be argued, relatively, that these routes were much more familiar than those used by Yanko & Spalek (2013) and, further, that these are all much less familiar than the environments we encounter on a regular basis in the real world.

Chapters 3 and 4 of this thesis explored the hypothesis that older adults are less able to automate new behaviours. This chapter also explored the hypothesis. Consistent with this prediction, results from urban drive data showed that older drives had later onsets, later peaks and a higher number of adjustments whilst

making manoeuvres than younger drivers. Further, during motorway drives, the onset of steering to change lanes and the time of the lane change were significantly earlier in younger than older drivers. The one exception to this were onsets during motorway drives with three repetitions. In this condition, there were no overall effects of age group but a significant interaction between repetition number (outlined in the previous paragraph) and age group showed that onsets were later when an environment was first seen and was completely novel, but by the third repetition, these significant age differences disappeared. A similar result is shown in the time of lane change analysis in motorway drives with three repetitions. Exploration of a significant interaction showed that the difference between young and older drivers decreased in significance as exposure increased. This suggests that overall, older drivers take longer to automate new behaviours, but with a degree of training, they are able to perform at equivalent, or nearly equivalent levels as younger experienced drivers. Previous research in this area is very limited. The one study to address this to date found that drivers aged 65 and over were more likely to get lost and commit safety errors than younger drivers during an on-road wayfinding task (Read et al, 2011). The authors also found that these differences were smaller in routes that the older drivers self-reported being very familiar with. Broadly, the results from these experiments agree with the findings of Read et al (2011), but we have added a critical level of experimental control by investigating the performance of driving behaviours as they become more familiar, rather than than relying on self-reported familiarity with a location, which could be open to differential interpretation.

Research suggests that older drivers tend to avoid driving in unfamiliar situations as they age (Burns, 1999; Joly, Frigon, & Daigneault, 2002; Older Drivers Task Force). Therefore, it could be argued that increased performance in younger drivers in the tasks presented in this chapter may reflect more experience with unfamiliar environments than in older drivers. On the other hand, it may also be argued that older drivers have cumulatively much more driving experience than younger drivers, which may equip them with more cognitive resources to manage unfamiliar situations. Better performance on the task in younger drivers suggest that

the latter argument is unlikely to explain the results found in this chapter. However, these results cannot be taken in evidence in favour of the former argument as we did not record driving patterns of the subjects. Future research which controls for the driving experience of both age groups would help to elucidate this argument.

5.4.2   Hypothesis 3 and 4

As behaviours become more skilled, it is suggested they require less attention, and are less susceptible to the interfering effects of a secondary task (Posner & Snyder, 1975; Shiffrin & Schneider, 1977). As such, in environments that are highly familiar, we hypothesised that drivers would have more spare attentional capacity and they should therefore be more readily able to detect hazards earlier than in novel environments. The onset of braking behaviour in anticipation of a variety of hazards was used to assess this. Hazards involving cars and pedestrians were analysed separately.

Data broadly supported this hypothesis. In line with this with hypothesis, investigation of a significant interaction between the presence of a pedestrian hazard and familiarity showed that there was no difference between braking onsets in the hazard present and hazard absent conditions in environments that had only been seen once before, but in environments that had been seen three times previously in Experiment 1 – and were therefore much more familiar – braking onsets were significantly earlier in the hazard present than the hazard absent condition. However, contrary to predictions, for non-pedestrian hazards, braking onsets were significantly later in environments that were more familiar than less familiar. For pedestrian hazards, there was no overall effect of familiarity on braking onsets. Much of the research surrounding hazard perception focuses on novice and experienced drivers. Many studies show hazard perception skill is related to crash risk (Hull & Christie, 1993; McKenna & Crick, 1994; Wells, Tong, Sexton, Grayson, & Jones, 2008). Some studies have shown that experienced drivers are more able to use environmental cues in general to predict hazards (Crundall, 2016), but no studies have attempted to explain how familiarity with a particular environment benefits hazard perception. Our studies do contribute

somewhat to bridging the gaps in this field. The results of our pedestrian hazard data did show that familiarity with a visual environment did facilitate earlier braking onset when compared with the same routes when driven with no hazards, but these results were not consistent across all the data sets. This may be due to methodological caveats in the comparisons made. These will be discussed later.

It was also hypothesised that older adults would not reach equivalent levels of automation as younger drivers. This would leave them with less spare attentional capacity to process secondary information, and the hypothesis that older drivers would take longer to respond to hazards was also explored. This hypothesis was not supported. Braking onsets did not significantly differ between older and younger drivers in either vehicle or pedestrian hazard conditions. Previous research provides a conflicting view on the hazard perception abilities of older drivers. Some studies have shown that the hazard perception abilities of older drivers do not significantly differ from younger drivers (Olson & Sivak, 1986; Underwood, Phelps, Wring, van Loon, & Galpin, 2005; Borowsky, Shinar & Oron-Gilad, 2010). However, a large-scale population study by Quimby & Watts (1981) compared hazard perception skills across multiple age ranges and found hazard perception abilities decline sharply after the age of 55. The lack of significant differences between older and younger drivers in experiment three of this chapter largely agree with the former studies, suggesting that hazard perception does not differ between older and younger drivers, nor is this affected by how familiar the drivers were with the routes tested.

An interesting observation may refute this. Hazard perception was tested in urban environments that had previously been seen 1, 2 or 3 times (see section 5.2.2 of this chapter for a full explanation of the methods for the previous experiment using the same environments). Therefore, in actual terms, no routes were completely novel when experienced in the hazard perception section of this series of experiments. In Section 4.1 it was argued the benefits of increased familiarity on driver behaviour come largely from the first additional repetitions. Indeed, though not directly related to this section, it was previously discussed that during motorway

drives, age differences were seen in onsets and time of lane change in the first repetition, but not the third repetition, and it was argued that age differences may be eliminated by increased exposure. If these were the case, equivalent levels of automation may have been reached by the second repetition in both younger and older drivers, and this may explain why hazard perception did not differ in this data set. Future research using this paradigm but including completely novel areas of interest may help to answer this question.

5.4.3 Limitations and conclusions

Statistical power should be discussed at this point. A criticism of previous research surrounding ageing and driver behaviour has been small sample sizes. As previously discussed, research surrounding the effects of ageing on hazard perception has been criticised due to small samples, generally 15 subjects or less, of older drivers (see Olson & Sivak, 1986l Underwood et al, 2005). For urban and motorway drive analysis, data sets were merged in order to increase statistical power as much as possible (see Section 5.2.2.4 for a full explanation of how this was achieved). Consequently, main effect analyses for these two experiments had middle or large effect sizes. However, interactions in these analyses had small effect sizes. As drives during the third, hazard perception experiment of this chapter relied on the number of times routes were driven in the previous experiment, the same approach of merging data sets as not possible. However, across hazard data sets, partial eta squared values showed generally middle to large effect sizes, so these analyses are unlikely to have been under-powered.

Some suggest behaviour during driving simulation differs to on-road driving behaviour as it lacks the same idiothetic (self-motion) cues (Aginsky et al, 1997). The authors suggest the lack of feedback from elements of a driving simulator such as brakes and steering wheel make driving simulation a perceptually different experience from on road driving. However, many have argued that even a video-based test of hazard perception skill can distinguish novice from experienced drivers, and can successfully discriminate between accident-involved and accident-

free drivers (McKenna & Crick, 1991; McKenna & Horswill, 1999). Indeed, an important aspect of hazard perception tests is that they are able to discriminate between high and low crash risk groups such as novice and experienced drivers (McKenna & Crick, 1991). Whilst this was not achieved in this chapter, as performance between young and older drivers did not differ in our hazard perception tasks, future research repeating these experiments using on-road driving performance would help show the reliability of the methods and expand the conclusions that can be made from this body of research.

A further limitation concerns the types of junction and used across the urban driving and hazard perception experiments. Previous research suggests older drivers have particular problems with turning across traffic at junctions and navigating intersections, as these place a higher load on attentional capacity (Burns, 1999; Dotzauer et al, 2013; Dukic & Broberg, 2012; Joly et al, 2002; Older Drivers Task Force). For the urban drive analysis, we collapsed across both left and right turns in order to increase statistical power. Separate analyses of left and right turns may have yielded more significant interaction effects but for this chapter, it would have further reduced the statistical power of the analyses. Future research should investigate the effects of familiarity on driver behaviour during left and right turns at junctions and intersections separately to investigate whether the cognitive demands of the manoeuvre have an extraneous effect on the automation of driver behaviour in general, and in older drivers.

It was previously discussed that the lack of effects of familiarity on hazard perception skill may be due to methodological caveats. The third, hazard perception experiment contained a mixture of left turns, right turns and 'straight ahead' drives at intersections. Results showed the braking onsets during vehicle hazards were longer in locations that were more familiar than those in locations that were less familiar. Further, pedestrian hazard data showed no overall significant main effect of familiarity on time of braking onset. Within this data set, drives that had been seen one and three times previously were straight ahead drives and the drive that had been seen previously was left-hand turn. Due to this, the types of drives across

the repetitions may not be comparable, and this may be why no overall familiarity effects are seen. The generation of new driving simulation terrains which allow different types of junction to be investigated separately was beyond the scope of this thesis, but future work addressing this systematically may help investigate these hypotheses more appropriately.

Previous research suggests older adults prefer to drive more slowly than younger drivers (Hakamies-Blomqvist, 1999). It could be argued that earlier onsets of manouevres in younger than older drivers may just reflect slower average speeds. However, a number of methods were put in place to control for this. Firstly, there was a speedometer on the dashboard and the required speed was highlighted to subjects across the experimental period using written and verbal instructions. Secondly, the time period used for analysis was minimised to reduce the overall impact of speed as an extraneous variable. Further, the time between the onsets and peak of manouevres in both urban and motorway drives (named time to peak and time to change) was analysed for age differences. If the older drivers had a slower average speed, it would be expected that the time taken between these two points would be larger for older than younger drivers. Results showed no significant age differences on 5 of 6 of these analyses, suggesting that this is an unlikely explanation for age differences in the results presented in this chapter. Though speed data was collected, the degree of manual coding required made analysis of this data beyond the scope of this thesis. Future work should consider running analyses like those presented in this Chapter that control for overall speed.

Finally, the hazards used in the hazard perception section of the experiment may have impacted the results. Firstly, this may have been due to the types of hazard used. The pedestrian hazards were very stereotypical and very salient to the driver. Although they both require additional attention to the driver, drivers may prioritise their attention to more salient, meaningful events in the environment and this may explain why familiarity effects were seen in drives with pedestrian hazards but not with vehicle hazards. Further, it could be argued that younger drivers are more familiar with hazard perception tasks like this than older drivers as the hazard

perception test was introduced in the UK in 2002, so the younger drivers but not the older drivers would have undertaken training and testing in this. However, the lack of significant differences between the performance of drivers of different age groups (see earlier) refutes this argument.

Taken together, the results presented in this Chapter demonstrate that familiarity with an environment does facilitate the automatic execution of driver behaviours. Behaviours that become skilled, and thereby develop automaticity, are performed quicker, and more accurately than those which remain unskilled, and highly controlled. In line with this, results from Experiments 1 and 2 showed that with increased familiarity, steering behaviours at junctions in urban environments and during lane changes in motorway environments can be implemented earlier, with less hesitation and uncertainty than those in novel environments. Further, and in line with eye movement data in Chapters 3 and 4 of this thesis, results showed for the first time that older subjects were less able to benefit from increases in familiarity, suggesting they take longer to automate new behaviours than younger subjects. Tentative results suggested that over time, however, older adults are able to reach the same levels of skill as younger adults. Further, the results from these studies provide provisional evidence that hazard perception skill is facilitated by familiarity with an environment. When a high level of experimental control was placed on hazards (in this case, pedestrian hazards), allowing easy comparison across each, results showed that the onset of braking behaviour in anticipation of the hazard was earlier in environments that were more familiar than those which were less familiar. However, this was not consistent across all data sets. When hazards had a higher degree of variability, these results were not found. Possibly methodological explanations for this, and avenues for clarification in future research are discussed. Hazard perception skill in both younger and older experienced drivers were able to benefit from increased familiarity with an environment. Together, these results may provide a new basis for training older drivers to extract meaningful information from their environment to more rapidly automate driver behaviour and thereby improve hazard perception skill in such conditions.

Chapter 6: General Discussion

6.1   Overview

The main aim of this thesis was to explore the process by which human behaviours become skilled and the effects of ageing on this process. This included investigating the neural basis of visual behaviours as they become skilled, how these change with age during cognitive tasks, and how the ageing process affects skilled behaviour in applied human performance.

As behaviours become more skilled, they develop automaticity (Ashby et al, 2010). Early research in cognitive psychology focused on the fundamental characteristics of automatic and controlled processing. The properties of these processes can be found in Table 22. Theoretical models widely agree that as behaviours are repeated, they reach a point of automaticity. That is, they can be implemented without the need for conscious processing. On the other hand, novel behaviours require high levels of attention (Shiffrin & Schneider, 1977).

Table 23: Properties of automatic and controlled processes (adapted from Kahneman, 2011; Ramnani 2014; Shiffrin & Schneider, 1977).

Automatic	Controlled
Fast	Slow
More Accurate	Less Accurate
Require less effort	Effortful
Less sensitive to feedback	Reliant on feedback
Require less attention	Highly reliant on attention
Difficult to suppress or alter	Flexible
Subconscious	Conscious

The application of these theoretical models in some areas of human behaviour remains somewhat limited. This thesis aims to bridge gaps present in the literature. Chapter 2 sought to investigate the neural basis of automaticity in visual

sequence learning. Chapters 3 and 4 then sought to investigate the effects of ageing on learning and implementing new skilled visual behaviours. Chapter 3 focused on the effects of ageing on resisting cognitive interference during a spatial Stroop task and Chapter 4 investigates the effect of ageing on selective and divided attention during a Useful Field of Vision task. Finally, Chapter 5 focused on similar questions in the real world. This chapter sought to elucidate the effects of increased route familiarity and age the development of skilled driver behaviours in urban and motorway environments, and how the increased automation of driver behaviours facilitates hazard perception skill.

6.2   Chapter Summaries

6.2.1   Memory-guided oculomotor sequences: prefrontal and cerebellar working memory mechanisms

Chapter 2 of this thesis aimed to explore prefrontal and cerebellar contributions to oculomotor sequence learning. Based on its connections with distinct areas of the motor and prefrontal cortices, previous studies have identified the role of the cerebellum in the control of skilled motor and cognitive operations such as sequences of movements. Rule-related activity used to control manual operations has been found, independent of activity related to motor control itself in Lobule HVIIA of the cerebellum (Balsters & Ramnani, 2008; 2011). In keeping with computational models of cerebellar learning, such activity has been shown to decline as behaviours become more familiar (Albus, 1971; Balsters & Ramnani, 2011). Further, previous research suggests the cerebellum plays a pivotal role in motor sequence learning. Many suggest the early stages of motor sequence learning rely on cortico-cerebellar loops (Bernard & Seidler, 2013; Doyon et al, 2003; Doyon & Benali, 2005; Tsvi, Munter, & Kramer, 2014). Such activity declines as motor sequences become more familiar (Grafton et al, 2002; Toni et al, 1994; Tzvi et al, 2014). Previous sequence learning literature largely relies on learning motor sequences using button press responses (Seidler, 2006). Only one study has addressed visual contributions to learning a sequence of eye movements (Albouy et al, 2008), and this focused on implicit sequence learning. This chapter aimed, for

the first time, to investigate changes in the control of eye movements during explicit visual sequence learning.

The role of some areas of the cerebellum in the control of eye movements is well-documented. Previous research suggests that the cerebellar vermis is involved in oculomotor control (Batini et al, 1978; Thier et al, 2002). The role of the cerebellar hemispheres in this process remains somewhat elusive. Anatomical literature suggests that there are neural connections between the frontal eye fields, located in the prefrontal cortex, and Lobule HVII, suggesting that the cerebellar hemispheres may play a role in the cognitive control of eye movements (Xiong et al, 2002). This chapter aimed to investigate whether activity in Lobule HVII of the cerebellar hemispheres contributes to explicit sequence learning, and whether this activity decreases as oculomotor sequences *become* more familiar, and are executed from memory, in the absence of visual guidance.

In line with predictions, activity was found in Crus I and Crus II in Lobule HVIIa of the cerebellum. Further, this activity decreased as visual sequences became more familiar, suggesting this activity could be explained in terms of differential learning levels and differing working memory demands. These results suggest that activity in Lobule HVIIa does not relate to the kinematic control of eye movements, as has been argued previously (Doron et al, 2010; Glickstein & Doron, 2008), but to the cognitive control of eye movements as they become more skilled.

6.2.2 Conflict resolution during a spatial Stroop task in young and ageing populations

Chapter 2 explored whether the neural properties of eye movements changed as they became executed more skilfully. Chapter 3 then aimed to explore the effect of ageing on this process. Previous research provides conflicting evidence surrounding the effects of ageing on the Stroop task. Whilst some show that the healthy ageing process is accompanied by increased error rates in incongruent trials of a Stroop task (Adólfsdóttir, Wollschlaeger, Wehling, & Lundervold, 2017; Andrés, Guerrini, Phillips, & Perfect, 2008; Aschenbrenner & Balota, 2015; Bugg,

DeLosh, Davalos, & Davis, 2007; West & Baylis, 1998; West & Alain, 2000), others suggest this is not the case, and other explanations such as generalised slowing in speed of processing with increased age may explain age-related changes in Stroop tasks more appropriately (Verhaegen & De Meersman, 1998; Verhaegen, 1999; 2011; Williams et al, 2007). No previous studies have investigated the effects of ageing on the automatic execution of eye movements during the Stroop task, nor have they investigated whether non-linguistic cues that may automatically capture visual attention can cause the same Stroop effect.

Results showed that overall, across both younger and ageing subjects, accuracy on incongruent Stroop trials was not significantly different from congruent trials. In line with predictions, ageing had no effect on the accuracy of eye movements during control trials, or congruent trials where responses were made on the basis of directional cues alone. However, during incongruent trials, where eye movements had to be made in the face of conflicting colour-location mappings, older subjects performed less accurately than younger subjects. It was also predicted that the kinematics of eye movements themselves would be susceptible to the Stroop effect, and this effect would be more significant in ageing subjects than younger subjects. Contrary to these hypotheses, reaction times, saccade durations and saccade amplitudes did not differ between incongruent trials and congruent trials, nor did they differ between older and younger subjects.

The implications of this study will be discussed in Section 6.3 of this Chapter, but broadly, results from Chapter 2 suggested that even during a novel spatial Stroop paradigm that did not rely on linguistic cues, older subjects are less able to resist interference from task-irrelevant symbolic cues that prime eye movements. Further, the supplementary investigation of the kinematics of eye movements suggest that a domain-general decrease in speed of processing during cognitive tasks with increased age cannot adequately explain the results shown in the Stroop task, as have been previously argued (Salthouse, 1996; Verhaegen & De Meersman, 1998; Verhaegen, 1999; 2011; Williams et al, 2007).

6.2.3 The effects of age on eye movements during useful field of vision

One of the most reliable predictors of crash risk in elderly drivers is the Useful Field of Vision. Many studies assessing visual performance examine eye movements in isolation. However, this is inconsistent with eye movements in the real world, where we must extract and integrate meaningful information from multiple sources of visual stimuli. For this reason, the Useful Field of Vision task was generated. The Useful Field of Vision itself is defined as the total area of the visual field from which meaningful information can be acquired in the absence of head or eye movements (Sanders, 1970). The task used to examine this requires completing both a selective attention task in central vision and, in parallel, another task in the peripheral visual field, thereby relying on divided attention mechanisms simultaneously. The parallel nature of this task is of experimental interest as it allows the findings of laboratory tasks to be extrapolated onto real-world behaviours such as driving. In Chapter 3, it was found that older adults are less able to execute eye movements in the face of multiple streams of information. In this Chapter, this was extended into the Useful Field of Vision paradigm. Previous research suggests that older subjects, even in the absence of clinical visual problems, are less able to accurately perform both central and peripheral visual tasks in parallel than younger subjects, particularly as the cognitive load on divided attention mechanisms increase, suggesting a decrease in Useful Field of Vision with increasing age (Ball et al, 1988; Ball et al, 1990; Edwards et al, 2006; Sekuler et al, 2000). Further, research suggests that performance in Useful Field of Vision tests is related to driving performance and crash risk in older adults (Ball et al, 1993; Clay et al, 2005; Owsley et al, 1998; Owsley & McGwin, 1999; Quigley, 1993).

Few previous studies have investigated eye movements during the Useful Field of Vision task. Not only do eye tracking methods provide us with a more continuous and rapid view of the development and implementation of the cognitive processes that underpin behaviour, the use of these methods may help to address a caveat in the literature. The fundamental definition of Useful Field of Vision is the amount of meaningful information that can be extracted from the visual field in the absence of eye or head movements (Sanders, 1970). However, due to the lack of

eye tracking methods used in previous studies, they have not been able to control for the possibility that extraneous eye movements may occur during presentation of the visual stimuli, and this may affect interpretation of the data in light of this definition (Ball et al, 1988; Sekuler & Ball, 1986). An adapted version of the Useful Field of Vision was used to test whether previous findings of a reduced field of view in ageing subjects still holds true when eye tracking methodologies are used.

In this version of the task, subjects were instructed to fixate at a point in the centre of the screen whilst extracting information from the visual array containing both central and peripheral stimuli. This method allowed any trials in which saccades were made towards the peripheral stimuli (thereby indicating serial processing of the two sets of information) to be deleted prior to statistical analysis. It was predicted that when performed in parallel, performance on both central and peripheral visual tasks would decrease as the task difficulty increased, as indicated by increased radial eccentricity of peripheral visual stimuli, which places a higher load on divided attention mechanisms. Further, it was predicted that this decrease in performance would be more substantial in older than younger adults, given previous research suggesting the concurrent performance of these two tasks poses a particular problem for the ageing population (see Ball et al, 1998). The use of eye tracking methods also allowed two further predictions to be tested: do eye movements parameters such as reaction time, saccade duration and saccade amplitude increase alongside task difficulty? Further, is this increase more pronounced in older than younger subjects?

In line with the first hypothesis, accuracy during both a shape discrimination task performed in central vision and an arrow detection task performed at increasing radial eccentricities decreased as the radial eccentricity of a simultaneously performed peripheral visual field task increased. Further, older adults were significantly less accurate at the task in central vision than younger subjects when the peripheral stimuli were at the most peripheral distance, but not at any other distances. Contrary to these predictions, there was no difference between performance in older and younger adults at the peripheral arrow detection task at

any radial distance. These results contradict previous research suggesting performance on both tasks decreases as radial eccentricity increases, and this effect is more pronounced in older adults (Ball et al, 1998). Contrary to the final two hypotheses, eye movement reaction times during the peripheral arrow discrimination task did not differ based on age group or task difficulty, and in the central shape discrimination task, reaction times were generally longer for older subjects but these did not differ based on task difficulty. No effects of age or task difficulty were seen in saccade amplitudes. Saccade durations were longer for older subjects on both central and peripheral visual tasks, but these were not affected by radial eccentricity of the divided attention task.

In sum, the research in this Chapter suggests that older adults are not limited in terms of their overall visual acuity in the central or peripheral visual fields, but they are less able to learn to divide attention across two tasks, and therefore the amount of meaningful information they can extract from the visual scene without any eye or head movements does decrease (Sekuler et al, 2000; Seiple et al, 1996). As discussed in light of Chapter 3, the investigation of the kinematics of eye movements in this Chapter also suggest that older adults do not show a domain-general slowing of reaction time. Reaction times after the go signal were equivalent in older and younger adults. This suggests that the effects of the task that cause age-related deterioration prior to the implementation of the response rather than during the eye movement response itself. This suggests that changes in performance on the task in older adults is related to planning of the response, which is cognitive in nature, rather than motor or oculomotor implementation of the response itself.

6.2.4 The effects of age on visual learning and hazard perception in simulated driving

In Chapters 3 and 4, the ability of older adults to skilfully execute new behaviours was explored. These studies showed that the healthy ageing process prevents older adults from transferring information to an automated state, and instead they rely more on controlled processes. One of the main aims of this thesis was to investigate this process in real world situations, such as in driver behaviour.

This Chapter originally intended to explore this using eye movements. Although eye movement data were collected, assessing this data was beyond the scope of this thesis. The eye movement data had a large degree of dropout due to the lack of head restraint, particularly in the older adults and the low sampling rate of the eye tracker used. Therefore, the eye movement data would have required a large amount of manual coding and the analysis would have been complex and this was not possible due to the time constraints to finish this thesis. However, driver behaviour can be used to effectively assess processes such as skill learning and automaticity, and these processes are comparable with those discussed in the previous experimental chapters.

A candidate variable for testing automaticity during driving is route familiarity. Two experiments were used to test the effects of route familiarity in younger and older adults, in both urban and motorway environments. It was predicted that as visual environments such as junctions were encountered multiple times, driver behaviours such as steering during manoeuvres and lane changes would be conducted earlier and with less hesitation than in novel environments. Further, it was predicted that older drivers would be less able to learn these behaviours than younger drivers. In line with these predictions, the onset of steering behaviours and the peak of the steering during manoeuvres at junctions were performed earlier as visual environments became more familiar, and were performed earlier in younger than older subjects. Further, fewer adjustments were made during turns as they became more familiar, and fewer adjustments were made for younger than older drivers. In motorway environments, similar results supported this hypothesis. The onset of the steering manoeuvre to change lanes, and the time at which the lane change manoevure was performed occurred earlier as routes became more familiar. These also generally occurred earlier in younger than older subjects for all conditions except onsets of steering manoeuvres in the most familiar environments. In this condition, a significant interaction revealed that younger subjects started steering earlier than older drivers on the first repetition, but by the third repetition of the same visual environments, older drivers had reached

equivalence with younger drivers. These interactions effects were not found for other analyses, this is discussed with reference to possible sample size limitations.

The differential levels of familiarity with urban environments achieved in the first part of this chapter allowed the exploration of a further hypothesis: does reaching higher levels of automation through familiarity with a given environment facilitate hazard perception skill? It was predicted that braking onsets in response to vehicle and pedestrian hazards would occur earlier in environments that were more familiar, and earlier in younger than older subjects. This prediction was partially supported. When highly controlled pedestrian hazards were compared with no hazard control conditions, braking was significantly earlier in the most familiar environment, but not less familiar environments. No effect of previous familiarity was seen in more variable, novel vehicle hazards, nor did braking onsets differ between older and younger drivers in either set of analyses.

Taken together, data presented in this Chapter suggest increased familiarity with a visual environment facilitates the development of skilled driver behaviours. In familiar environments, driver behaviours can be performed earlier and with more certainty than in novel environments. Further, older drivers take longer to reach the same level of skill as younger (but experienced) drivers, but tentative findings show that with enough exposure, they can eventually reach equivalent performance. Further, these results show that to some extent, increased familiarity does facilitate increased hazard perception skill in both younger experienced and older experienced drivers, but these results were not consistent. Suggestions for future research to help elucidate the mechanisms that underlie hazard perception skill are discussed in Chapter 5 itself.

6.3   Implications of Findings

6.3.1   Automaticity and ageing

One of the main aims of this thesis was to investigate the implication of models of automatic and controlled processing in human behaviour, and how these are affected by the non-clinical ageing process. Many theoretical models of

information processing suggest that as behaviours become skilled, they transfer from being controlled to automatic processes. Both Neisser (1967) and LeBerge (1973; 1975) described a pre-attentive stage early in the encoding process and Kahneman (2011) outlines two systems of information processing, with System 1 being a rapid, automatic, subconscious system and System 2 being a slow, effortful system, which is sensitive to feedback and requires conscious input. In combination with Shiffrin & Schneider's (1977) dual-process, these models broadly agree on the characteristics of automatic and controlled processes, some of which are outlined in Table 22. Across all experiments in this thesis, automatic processing was investigated with a focus on skilled visual behaviours in the laboratory, and driver behaviours in a real-world setting.

Previous research has shown that as the rules that guide motor behaviours become well-learned, activity in Lobule HVIIa of the cerebellum declines to background levels, and this decline happens faster when higher levels of feedback facilitate more rapid learning (Balsters & Ramnani, 2008; 2011). It is suggested, therefore, that the cerebellum is a candidate area for the automation of behaviours through the acquisition and storage of forward models. These are representations of previously learned behaviours which allow the same behaviours to be executed when the same situation arises in the future, requiring fewer attentional resources (Albus, 1971; Marr, 1969; Thach, 1998; Wolpert, Miall & Kawato, 1998). The results of this thesis further support accounts of the role of the cerebellum in the automatic execution of human behaviours by extending this research into the oculomotor domain. Much like in the motor domain, early accounts of cerebellar involvement in eye movements focused on motor control (Batini et al, 1978; Their et al, 2002). However, here, results show that areas of the human cerebellum, in particular Lobule HVIIA of the cerebellar hemispheres, also plays a role in the cognitive control of eye movements as they become automated, and this activity is dissociable from activity that underpins controlled processing of novel information. Further, consistent with computational models of cerebellar plasticity, this activity decreases as behaviours become more automatic in a graded manner. Further, the use of eye tracking methods in this study allowed the author to show that a higher

frequency of anticipatory eye movements, suggestive of automatic implementation of previously learned behaviours, can be made during the execution of a highly familiar sequence than during the execution of novel sequences. On the contrary, the execution of novel sequences of eye movements relies much more heavily on reflexive eye movements than familiar sequences.

Two important characteristics of automatic behaviours are that they are almost always elicited by the same sensory cues, and they can be successfully performed without interference from a secondary task (Poldrack et al, 2005; Shiffrin & Schneider, 1977). The Stroop task is commonly used to test these characteristics. It has been suggested that the classic Stroop effect, whereby subjects respond to the semantic content of colour words rather than the colour itself, as they are instructed to, may be caused by an inability to resist interference from automatic processes. For most, reading is a well-practiced procedural skill and can be implemented rapidly. During the Stroop task, this automatic process will interfere with controlled processing of other information about the word (Anderson, 1990).

In Chapter 2, it was found that eye movements that become well-learned can be executed more accurately than those which are novel. Some studies have investigated the automatic priming of eye movements based on linguistic cues during the Stroop task. Such studies have found higher error rates and longer saccade latencies during incongruent trials than congruent trials (Hermens & Walks, 2012; Hodgson, Parris, Gregory, & Jarvis, 2009). These studies suggest that as well as manual responses, eye movements can be primed on the basis of previously learned linguistic cues, but this has never been tested using non-linguistic but still informative cues. As previously summarised, Chapter 3 found no overall Stroop effect in accuracy data. However, during incongruent trials but not during congruent or control trials, older adults performed significantly less accurately than younger subjects. This evidence suggests that as hypothesised, even when a task does not involve linguistic cues, older but not younger adults are less able to resist interference from symbolic information that primes eye movements. Though this study was not a classic dual-task paradigm, it was still comprised of

two tasks. Firstly, subjects had to learn and implement new colour-direction mappings and secondly, subjects were required to implement these in the face of conflicting information. That the first task was more inhibited by the second task in older adults could be argued to reflect lower levels of automation on the newly acquired stimulus-response mappings in older adults.

Eye tracking methods also allowed the concurrent exploration of the hypothesis that the psychophysical parameters of eye movements would be susceptible to the Stroop effect. However, this was not the case. None of the psychophysical parameters tested – reaction time, saccade duration or saccade amplitude – differed between correctly executed incongruent and congruent trials, nor did they differ between older and younger subjects. Whilst these results are in contrast with previous research suggesting that in younger subjects, reaction times and saccade latencies increase during incongruent trials of a Stroop task (Hermens & Walker, 2012; Hodgson et al, 2009), no previous studies have investigated this in the ageing population. These findings demonstrated that the effects of ageing on accuracy during Stroop performance is most likely to be due to a decreased ability to execute automatic behaviours in the face of multiple sources of information, and cannot be attributed to generalised slowing of cognitive processing in the ageing population, as has been previously suggested in the literature (Bugg et al., 2007; Graf, Uttl, & Tuokko, 1995; Müller et al., 2016; Verhaeghen & De Meersman, 1998).

The Useful Field of Vision paradigm relies on both selective and divided attention in parallel. As such, it has been suggested that poorer performance on divided attention tasks reflects an increased reliance on controlled processes (Shiffrin & Schneider, 1977). In Chapter 3, it was discussed that older adults may be less able to rely on automatic processes to execute previously learned eye movements in the face of a secondary, conflicting information. Chapter 4 aimed to investigate whether this may explain reductions in the Useful Field of Vision with increased age. Results showed that during the task, older adults were not limited in terms of the amount of information they could discriminate in any extent of their visual field, up to 12°, which was the maximum distance tested in the laboratory

setting. However, when attention was divided across the maximum distance tested, concurrent performance on a central vision task decreased in older but not younger adults. This suggests when a task requires higher levels of divided attention, older but not younger adults are more reliant on controlled processes. As in Chapter 3, the parameters of eye movements such as reaction time, saccade duration and saccade amplitude were also tested. Saccade durations were significantly longer for older than younger subjects, but reaction times were not consistently longer for older subjects. This suggests that one initiated, motor responses are slower in older adults but in line with results in Chapter 3, the speed of processing does not differ between younger and older adults.

Overall, these studies show that automated and controlled oculomotor behaviours have different characteristics. As expected, familiar behaviours that may be argued to have become automatic behaviours can be executed more accurately and in some cases more rapidly than novel, unfamiliar behaviours. Further, this transition relies on plastic mechanisms in brain circuits that are likely to include the cerebellum. These studies also show that in line with previous research suggesting ageing is related to deterioration in the neural mechanisms that underpin cognitive processes, older adults are less able to acquire and implement automatic behaviours, relying more heavily on controlled process. This has important implications for the ageing population when considering their continued ability to take part in behaviours that rely on integrating multiple sources of information to succeed, such as during driving.

6.3.2   Driver behaviour

During driving, the same behaviours may be repeated over many occasions. Due to this, automaticity can be studied effectively in driver behaviour. The studies presented in this thesis focused on the effects of increased route familiarity on skilled driver behaviour When the same route is driven the same way on a daily basis, such as driving to work or to the local shop, many people report not remembering how they got to their final destination. This suggests that when routes become well known, driving moves from being controlled, effortful and requiring

high levels of attention, to being automatic, requiring fewer attentional resources. When driving reaches automaticity, the same sensory stimuli in the environment should evoke the same stereotyped patterns of behaviours, and these behaviours should be performed with much more certainty than behaviours in novel environments.

This thesis aimed to expand the hypotheses explored in Chapters 3 and 4 regarding the effects of ageing on automatic behaviours into the driving field by investigating how route familiarity facilitates automaticity in driver behaviour. Previous research on the effects of route familiarity on driving are mixed. Some argue that increased familiarity with a route facilitates driving performance (Read et al, 2011), but many others argue that familiarity with a route can lead to attentional blindness, whereby driver behaviour becomes more variable and less safe (Charlton & Starkey, 2012; Yanko & Spalek, 2013). These authors have suggested that in highly familiar driving situations, 'mind wandering' may occur, which leaves drivers less about to respond to stimuli in the environment (Yanko & Spalek, 2013). Research suggests as they age, older drivers avoid certain situations that they perceive as more dangerous such as driving on unfamiliar roads (Burns, 1999; Henriksson, Levin, Willstrand, & Peters, 2014). However, very little research has investigated how older drivers' performance changes as a function of route familiarity. Importantly, this was investigated with a higher degree of experimental control than previous studies. Previous studies largely rely investigate route familiarity using self-report measures of drivers in their local areas (see Read et al, 2011). However, in the studies presented in Chapter 5, visual environments were always seen from the same visual angle and the order of the drives was randomised to ensure the effect of familiarity could be separated from overall changes in driving simulation ability. Further, using design elements similar to those presented in the fMRI experiment in Chapter 2 of this thesis, specific visual environments were repeated either once, twice, or three times in order to investigate performance changes that became apparent with an increase in repetition number.

The first two experiments focused on steering during manoeuvres at junctions in urban environments and during lane changes in motorway environments. Steering was the primary behaviour used for analysis during these two experiments as it allowed for the clear definition of a number of variables in environments where a turn must be made in order to complete the task at hand (i.e. turning a corner or changing lane). As summarised above, results showed that increased familiarity with a visual environment did facilitate the automation of driver behaviour. In both urban and motorway environments, behaviours were performed earlier as familiarity increased, and in urban environments, data showed manouevres in more familiar environments were performed with more certainty than those made in novel environments. These results show that route familiaity does facilitate the automation of driver behaviours. Results also showed that older drivers generally performed maneouvres later than younger drivers, suggesting they take longer to reach the same levels of automaticity when performing manoevures at junctions and on motorways. This may explain why although older drivers are not generally over-represented in crash statistics, the frequency of fatal crashes that occur at or near junctions increases after the age of 60 (Older Drivers Task Force Appendix A.4.).

Finally, this thesis aimed to address whether increased automation of driver behaviour allowed drivers to better manage the impact of a secondary task which places high cognitive load on the driver. The cognitive control hypothesis argues that situations with a high cognitive load should selectively impede controlled but not automatic processes (Engström et al, 2017). As such, when unanticipated actions occur on the road, increased automation of driver behaviour should facilitate hazard perception. In Chapter 5, this was tested using braking response times in anticipation of hazards in novel and familiar environments. It was predicted that braking onsets would occur earlier in familiar environments, due to the higher amount of attentional resources that can be allocated to tasks with high cognitive load (Engström et al, 2017; Shiffrin & Schneider, 1977). Data broadly supported this hypothesis. When compared to the same routes driven with no hazards, routes driven with standardised hazards where a pedestrian walked out in front of the car

at a junction, braking onsets were significantly earlier in environments that were more familiar than in those that were novel. However, this pattern of results was not shown during more variable novel vehicle hazards. It was further predicted that if older drivers take longer to achieve equivalent levels of automation than younger drivers, they would benefit less from increased familiarity during hazard perception. Data did not support this hypothesis, as no significant differences were found in the onsets of braking behaviour in any of the data sets. Although these results were not consistent, this provides tentative evidence in favour of the cognitive control hypothesis in terms of hazard perception.

6.4   Limitations and Future Directions

Limitations for individual experiments are discussed in the relevant chapters throughout this thesis. However, a number of more broad limitations will be discussed here, as well as ideas for future experimental work to resolve these issues.

One primary issue is the gaps in the literature in a number of chapters in this thesis. In Chapter 2, evidence is presented supporting the role of the prefrontal cortex and the cerebellum in the automation of visual skills. Further, in this chapter, the possibility of a series of distinct reciprocal oculomotor cerebro-cerebellar loops underpinning the motor and cognitive control of eye movements separately is discussed. Within these, a cognitive oculomotor loop would comprise connections between the frontal eye fields and Lobule HVII of the cerebellar hemispheres. Though these have been shown in non-human primates (Middleton & Strick, 2000; Xiong et al, 2002), point to point anatomical evidence has not been shown in humans. Anatomical connectivity data in human would help to support the conclusions made in this chapter. Further, Chapters 3 through to 5 discussed the effects of ageing on automaticity. Previous studies have documented neural decline in both the prefrontal cortex and the cerebellum with increased age (Cabeza et al, 1997; Hall et al, 1975; Raz et al, 1997; Raz, 2000). However, no studies to date have investigated how neural deterioration in healthy ageing affects activity in the cerebellum as rule-based eye movements become more automatic, and whether this activity can be distinguished from the activity that underpins rule-based manual

responses. A further study was developed to investigate the role of the cerebellum during a symbolic first order rule-learning paradigm using both manual and oculomotor responses, and the effect of ageing on this activity. Such a study would have provided evidence on how the circuitry discussed in Chapter 2 of this thesis changes with the healthy ageing process. Data collection for this study was beyond the resources of this thesis, but future research addressing this gap in the literature would help our understanding of the neural basis of automatic visual behaviours and how these change across the lifespan.

A further limitation considers the methods used. Across all chapters, bespoke experimental paradigms were modified to test the hypotheses in question. This is a particularly prudent issue for the Stroop and UFOV chapters. These were both loosely based on previously tested experimental paradigms but a lot of elements of these experimental paradigms were changed. Whilst this means that the paradigms used for all the experiments in this thesis were novel and allowed us to explore a more specific set of questions, this limits the comparisons that can be drawn against previous literature. For example, although the Stroop task is very well known and has been reliably tested in the literature, a completely novel spatial Stroop task using colour-location rather than colour-word mappings was developed to test the Stroop effect using non-linguistic cues. In this study, no colour words were used in the experimental array nor as a comparison task which is commonly used as a baseline in the Stroop literature, as the mechanisms which underpin this process both behaviourally and neutrally are well known (see Brink & McDowd, 1999). Further, oculomotor responses were used rather than hand movement responses. This is still relatively new in the literature and no studies have used an oculomotor Stroop paradigm in the ageing population, so comparisons with measurements such as the kinematics of eye movements are very limited. In the UFOV task, similar issues arise. For example, an eye-tracking adaptation of the well-known UFOV task was used which meant that the radial eccentricities that could be used in the periphery of the screen were much more limited than in previous versions of the task which were tested behaviourally. In this study, a maximum radial eccentricity of 12° could be used but in the previous behavioural

literature, the maximum radial eccentricity is usually 30°. This limits the conclusions that can be made about the acuity of peripheral vision in the subjects tested and the extent of the useful field of vision in these subjects. The use of eye tracking methods to test the hypotheses in question, particularly in the Stroop and UFOV studies is still relatively novel, and led to relatively high amounts of data exclusion. These two factors made it hard to calculate appropriate sample sizes to compare the studies in this chapter with the previous literature. This has been addressed in individual Chapters – in particular with regards to the Useful Field of Vision paradigm where sample sizes were generally larger than previous studies but effect sizes quite low – but future research would benefit from repeating these experiments with large sample sizes to account for data dropout and to add power and reliability to the conclusions drawn in this thesis.

The use of ageing subjects in Chapter 3 through to 5 in this thesis opens up a further limitation. The comparison between young and ageing subjects made the experiments cross-sectional and prevented any analysis of changes within these groups. This is particularly important for the ageing subject groups. Chapters 3 through to 5 used subjects ranging from 59 to 79 years old, and this group could not be divided into smaller age ranges as this would have reduced sample sizes even further. Previous studies have shown that even within ageing subjects, there is a progressive trajectory of cognitive and behavioural decline. For example, research has shown that performance on incongruent trials in the classic colour-word Stroop task declines progressively across the lifespan, with sharp declines seen between the ages of 60 and 80 (Bugg et al., 2007). Further, Sekuler et al. (2000) showed error rates on a central vision task during both focused and divided attention conditions during the Useful Field of Vision increased steadily after the age of 60. These changes are also of importance when looking at crash risk and hazard perception in older drivers. Number of casualties per mile driven, percentage of casualties caused by right of way violations, and percentage of injury crashes caused by turning across traffic all increase steadily with age after the age of 60 (Clarke et al, 2007; DfT, 2014). Future research using larger sample sizes that can use longitudinal methods or investigate the ageing process using smaller age ranges

would help us to understand exactly how and when the ageing process affects automatic execution of behaviours across the lifespan, which could provide vital information regarding the time point at which training interventions may be useful to maintain safe driving.

Studies in this thesis have shown that older adults are less able to execute automatic oculomotor behaviours, particularly in the face of multiple, competing sources of information. These results have been shown both in the laboratory and during real-world driving simulation. Previous training studies have shown that in older adults, dual-task performance and attentional control in the face of distracting information can be improved through training (Bherer, Kramer, Peterson, Colcombe, Erickson & Becic, 2005; 2008; Mozolic, 2009). Mozolic (2009) also found that such training in older adults can facilitate further improvements in speed of processing, dual-task performance, and working memory, showing that attentional control training programs may also show transfer effects due to improved suppression of irrelevant stimuli. Further, training has been shown to ameliorate the issues highlighted by the Useful Field of Vision test. Roenker, Cissell, Ball, Wadley & Edwards (2003) found that speed of processing training, but not generic driver training improved abilities as measured by the traditional Useful Field of Vision task. These improvements translated to improved real-world driving performance measures within the simulator including fewer dangerous manoeuvres. The performance effects were sustained 18 months post-training, showing that training in speed of processing and measures could provide lasting behavioural effects which assist and improved older adults' abilities to continue to engage in their daily activities such as driving without risk of harm or danger (Roenker et al, 2003).

The results of the studies presented in this thesis could contribute to this research. Across this thesis, studies have shown that increased familiarity with a task can facilitate performance. This has been shown with eye movements in the laboratory, and with driver behaviour during driving simulation. The studies presented across the thesis have also shown that older adults are less able to benefit

from increased exposure but over time, they can reach skill levels that are equivalent with younger subjects (this is discussed earlier in this Chapter). The literature surrounding how much exposure is enough to make an environment familiar, or well-learning is variable. Previous studies testing the effects of familiarity on driver behaviour have shown that as few as 4 repetitions and as many as 24 repetitions are sufficient to have a significant effect on driver behaviour (see Charlton & Starkey, 2012; Initini, 2016; Yanko & Spalek, 2013), and chapters 2 and 5 of this thesis show that as little as 3 repetitions are sufficient to advantage behaviour both in the laboratory and during driving simulation. Whilst it could be argued that such exposure is far less than we would experience in everyday life, these studies show that even a small amount of learning can benefit behaviour and this may have important implications for road safety. Studies have shown that eye movements in older adults are more impaired by conflicting information and situations that required divided attention than those in younger subjects. Training studies using a combination of eye tracking and driving simulation methods could help older adults to learn to ignore task-irrelevant information and to pay particular attention to salient elements in the environment which may help them to execute automatic eye movements more accurately and more rapidly, particularly in the face of competing information. This may help to increase the amount of information they can meaningfully extract from the visual environment. Such training may help facilitate automatic driver performance in familiar environments and improve hazard perception, which could in turn decrease crash risk at junctions and intersections.

6.5   Conclusions

Many theoretical models have discussed the differences between automatic and controlled information processing in human cognition, but many questions about the applications of these models remain unanswered. Studies in this thesis aimed to answer three broad questions: what is the neural basis of skilled visual behaviours? How do skilled visual behaviours change with age? And finally, how does this apply to driver behaviour?

This thesis shows that activity in an interconnected set of areas in the prefrontal cortex and the cerebellar hemispheres underpins the acquisition of automatic visual behaviours, and this activity is separable from that which guides motor responses. In line with research suggesting these areas are prone to neural degeneration with healthy ageing, two studies using eye tracking techniques have shown that ageing subjects are less able to implement automatic visual behaviours and rely more on controlled processing to complete visual tasks which rely on the implementation of cognitive rules. Contrary to previous studies, data from these tasks provide evidence that changes in performance with increased age relate to declines in cognitive but not motor or oculomotor processing.

These findings were then developed to look at changes in skilled oculomotor behaviours with increased age. Results showed that in older adults, visual skills acquired through trial-and-error instrumental learning during a spatial Stroop task were performed less accurately than in younger subjects in the face of competing symbolic visual cues that primed eye movements. This was also investigated during a Useful Field of Vision task, when a central visual field task and a peripheral visual field task had to be performed in parallel. Performance on the task in central vision decreases as the concurrently performed peripheral task task was performed at higher radial eccentricities. Performance was significantly poorer for older than younger adults at the highest radial eccentricity, but not at lower eccentricities. However, it was found that older subjects were no less accurate than young, control subjects in detecting visual information in the peripheral visual field at any of the radial distances tested. Further analysis revealed a significant age-related reduction in the ability to inhibit learned saccadic responses.

This thesis moved into investigating automatic processes during real-world driver behaviour. The findings of the previous studies were used to investigate the automatic performance of driver behaviours as visual environments became more familiar. Increased familiarity with both urban and motorway environments facilitated automatic driver behaviour including earlier, more certain manoeuvres at junctions and lane changes. Older drivers did benefit from increased familiarity,

but they took longer to reach equivalent levels of automation as younger drivers. Further, the effect of increased familiarity was used to investigate hazard perception skill. Increased familiarity did facilitate hazard perception to some extent in both older and younger drivers, but this effect was not consistent across all analyses.

To conclude, this thesis has added to the literature suggesting that automatic processes have different characteristics to controlled processes both in laboratory and real-world settings, and these are significantly affected by the healthy ageing process. These findings may help to develop training programmes to facilitate safe driving in the rapidly increasing ageing population.

References

Abernethy, C. N., & Leibowitz, H. W. (1971). The effect of feedback on luminance thresholds for peripherally presented stimuli. *Perception & Psychophysics, 10*(3), 172–174. http://doi.org/10.3758/BF03205781

Adólfsdóttir, S., Wollschlaeger, D., Wehling, E., & Lundervold, A. J. (2017). Inhibition and Switching in Healthy Aging: A Longitudinal Study. *Journal of the International Neuropsychological Society, 23*(1), 90–97. http://doi.org/10.1017/S1355617716000898

Adrian, J., Postal, V., Moessinger, M., Rascle, N., & Charles, A. (2011). Personality traits and executive functions related to on-road driving performance among older drivers. *Accident Analysis & Prevention, 43*(5), 1652–1659. http://doi.org/10.1016/j.aap.2011.03.023

Aginsky, V., Harris, C., Rensink, R., & Beusmans, J. (1997). Two strategies for learning a route in a driving simulator. *Journal of Environmental Psychology, 17*(4), 317–331. http://doi.org/10.1006/jevp.1997.0070

Albus, J. S. (1971). A theory of cerebellar function. *Mathematical Biosciences, 10*(1), 25–61. http://doi.org/10.1016/0025-5564(71)90051-4

Allen, G. I., & Tsukahara, N. (1974). Cerebrocerebellar communication systems. *Physiological Reviews, 54*(4), 957-1006.

Amiez, C., & Petrides, M. (2009). Anatomical organization of the eye fields in the human and non-human primate frontal cortex. *Progress in Neurobiology, 89*(2), 220–230. http://doi.org/10.1016/j.pneurobio.2009.07.010

Anderson, J. (1990). *Cognitive psychology and its implications.* New York: W.H. Freeman and Company.

Andrés, P., Guerrini, C., Phillips, L. H., & Perfect, T. J. (2008). Differential Effects of Aging on Executive and Automatic Inhibition. *Developmental Neuropsychology, 33*(2), 101–123. http://doi.org/10.1080/87565640701884212

Apps, R., & Garwicz, M. (2005). Anatomical and physiological foundations of cerebellar information processing. *Nature Reviews Neuroscience, 6*(4), 297–311. http://doi.org/10.1038/nrn1646

Aschenbrenner, A. J., & Balota, D. A. (2015). Interactive effects of working memory and trial history on Stroop interference in cognitively healthy aging. *Psychology and Aging, 30*(1), 1–8. http://doi.org/10.1037/pag0000012

Ashby, F. G., Turner, B. O., & Horvitz, J. C. (2010). Cortical and basal ganglia contributions to habit learning and automaticity The Classical View of Automaticity. *Trends in Cognitive Sciences, 14*(5), 208–215. http://doi.org/10.1016/j.tics.2010.02.001

Attebo, K., Mitchell, P., & Smith, W. (1996). Visual Acuity and the Causes of Visual Loss in Australia. *Ophthalmology, 103*(3), 357–364. http://doi.org/10.1016/S0161-6420(96)30684-2

Aubert, H. R., & Foerster, C. F. R. (1857). Beitrage zur Kenntnisse der indirecten Sehens. *Graefes Archiv fur Ophthalmologie, 3*, 1-37.

Avolio, B. J., Kroeck, K. G., & Panek, P. E. (1985). Individual Differences in Information-Processing Ability as a Predictor of Motor Vehicle Accidents. *Human Factors: The Journal of the Human Factors and Ergonomics Society, 27*(5), 577–587. http://doi.org/10.1177/001872088502700506

Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence a tool for studying human eye movements. Mathematical Biosciences, 24(3-4), 191-204. http://doi: 10.1016/0025-5564(75)90075-9

Ball, K. (2003). Real-world evaluation of visual function. *Opthalmology Clinics Of North America, 16*, 289–298.

Ball, K. K., Beard, B. L., Roenker, D. L., Miller, R. L., & Griggs, D. S. (1988). Age and visual search: expanding the useful field of view. *Journal of the Optical Society of America A, 5(*12), 2210. http://doi.org/10.1364/JOSAA.5.002210

Ball, K., & Owsley, C. (1993). The useful field of view test: a new technique for evaluating age-related declines in visual function. *Journal of the American Optometric Association, 64*(1), 71–9. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8454831

Ball, K., Owsley, C., & Beard, B. (1990). Clinical visual perimetry underestimates peripheral field problems in older adults. *Clinical Vision Sciences, 5*(2), 113-125.

Ball, K., Owsley, C., Sloane, M. E., Roenker, D. L., & Bruni, J. R. (1993). Visual attention problems as a predictor of vehicle crashes in older drivers. *Investigative Ophthalmology and Visual Science, 34*(11), 3110–3123.

Balsters, J. H., & Ramnani, N. (2008). Symbolic representations of action in the human cerebellum. *NeuroImage, 43*(2), 388–398. http://doi.org/10.1016/j.neuroimage.2008.07.010

Balsters, J. H., & Ramnani, N. (2011). Cerebellar Plasticity and the Automation of First-Order Rules. *Journal of Neuroscience, 31*(6), 2305-2312.

Balsters, J. H., Whelan, C. D., Robertson, I. H., & Ramnani, N. (2013). Cerebellum and Cognition: Evidence for the Encoding of Higher Order Rules. *Cerebral Cortex, 23*(6), 1433–1443. http://doi.org/10.1093/cercor/bhs127

Barbas, H., & Mesulam, M.-M. (1981). Organization of afferent input to subdivisions of area 8 in the rhesus monkey. Journal of Comparative *Neurology, 200*(3), 407–431. http://doi.org/10.1002/cne.902000309

Batini, C., Buisseret-Delmas, C., Corvisier, J., Hardy, O., & Jassik-Gerschenfeld, D. (1978). Brain stem nuclei giving fibers to lobules VI and VII of the cerebellar vermis. *Brain Research, 153*(2), 241–261. http://doi.org/10.1016/0006-8993(78)90405-5

Berger, A., Henik, A., & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology. General, 134*(2), 207–221. http://doi.org/10.1037/0096-3445.134.2.207

Bernard, J. A., & Seidler, R. D. (2013). Relationships between regional cerebellar volume and sensorimotor and cognitive function in young and older adults. *Cerebellum, 12*(5), 721–37. http://doi.org/10.1007/s12311-013-0481-z

Bherer, L., Kramer, A. F., Peterson, M. S., Colcombe, S., Erickson, K., & Becic, E. (2005). Training effects on dual-task performance: Are there age-related differences in plasticity of attention control. *Psychology and Aging, 20*(4), 695-709.

Bherer, L., Kramer, A. F., Peterson, M. S., Colcombe, S., Erickson, K., & Becic, E. (2008). Transfer effects in task-set cost and dual-task cost after dual-task training in older and younger adults: further evidence for cognitive plasticity

in attentional control in late adulthood. *Experimental Aging Research, 34*(3), 188-219.

Blanke, O., Spinelli, L., Thut, G., Michel, C. M., Perrig, S., Landis, T., & Seeck, M. (2000). Location of the human frontal eye field as defined by electrical cortical stimulation. *Neuroreport, 11*(9), 1907–1913.

Bludau, S., Eickhoff, S. B., Mohlberg, H., Caspers, S., Laird, A. R., Fox, P. T., Schleicher, A., Zilles, K., & Amunts, K. (2014). Cytoarchitecture, probability maps and functions of the human frontal pole. *NeuroImage, 93,* 260–275. http://doi.org/10.1016/j.neuroimage.2013.05.052

Bohensky, M., Charlton, J., Odell, M., & Keeffe, J. (2008). Implications of Vision Testing for Older Driver Licensing. *Traffic Injury Prevention, 9*(4), 304– 313. http://doi.org/10.1080/15389580801895277

Borowsky, A., Shinar, D., & Oron-Gilad, T. (2010). Age, skill, and hazard perception in driving. *Accident Analysis and Prevention, 42*(4), 1240–9. http://doi.org/10.1016/j.aap.2010.02.001

Bourne, V. (2017). *Starting Out in Methods and Statistics for Psychology: a Hands-on Guide to Doing Research*. Oxford: Oxford University Press.

Braitenberg, V., & Atwood, R. P. (1958). Morphological observations on the cerebellar cortex. *Journal of Comparative Neurology, 109*(1), 1-33.

Braitman, K. A., Kirley, B. B., Ferguson, S., & Chaudhary, N. K. (2007). Factors leading to older drivers' intersection crashes. *Traffic Injury Prevention, 8,* 267–274. http://doi.org/10.1080/15389580701272346

Brink, J. M., & McDowd, J. M. (1999). Aging and selective attention: an issue of complexity or multiple mechanisms? *The Journals of Gerontology. Series B, Psychological Sciences and Social Sciences, 54*(1), P30-3. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9934393

Brodmann, K. (1908) Beiträge zur histologischen Lokalisation der Großhirnrinde. VI. Mitteilung. Die Cortexgliederung des Menschen. *Journal of Psychology and Neurology, 10*, 231–246.

Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Großhirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues.* Leipzig: Barth 1909

Bromberg, S., Oron-Gilad, T., Ronen, A., Borowsky, A., & Parmet, Y. (2012). The perception of pedestrians from the perspective of elderly experienced and experienced drivers. *Accident Analysis and Prevention, 44*(1), 48–55. http://doi.org/10.1016/j.aap.2010.12.028

Brooks, N. and Hawley, C. A. (2005). Return to driving after traumatic brain injury: a British perspective. *Brain Injury, 19,* 165–175.

Brouwer, W. H. (2002). Attention and driving: a cognitive neuropsychological approach. *Applied neuropsychology of attention: Theory, diagnosis and rehabilitation*, 230-254.

Brown, I. D. (1982). Exposure and experience are a confounded nuisance in research on driver behaviour. Accident Analysis & Prevention, 14(5), 345–352. http://doi.org/10.1016/0001-4575(82)90012-4

Brown, M. R. G., DeSouza, J. F. X., Goltz, H. C., Ford, K., Menon, R. S., Goodale, M. A., & Everling, S. (2004). Comparison of Memory- and Visually Guided Saccades Using Event-Related fMRI. *Journal of Neurophysiology, 91*(2), 873-889.

Bruce, C. J., & Goldberg, M. E. (1985). Primate Frontal Eye Fields. I. Single Neurons Discharging Before Saccades. *Journal Of Neurophysiology, 53*(3), 603-635.

Bugg, J. M., DeLosh, E. L., Davalos, D. B., & Davis, H. P. (2007). Age Differences in Stroop Interference: Contributions of General Slowing and Task-Specific Deficits. *Aging, Neuropsychology, and Cognition, 14*(2), 155–167. http://doi.org/10.1080/138255891007065

Burg, A. (1967). *The Relationship Between Test Scores and Driving Record: General Findings.* Report 67-24. Los Angeles: University of California-Los Angles, Department of Engineering.

Burg, A. (1968). *Vision test scores and driving record: Additional findings.* (Report No. 68-27). Los Angeles: Department of Engineering, University of California.

Burke, D. M., & Osborne, G. (2007). Aging and inhibition deficits: Where are the effects? In D. S. Gorfein & C. M. MacLeod (Eds.), *Inhibition in cognition* (pp. 163-183). Washington, DC: American Psychological Association.

Burns, P. C. (1999). *Navigation and the mobility of older drivers.* The Journals of Gerontology: Series B, 54(1), S49.

Cabeza, R., McIntosh, A. R., Tulving, E., Nyberg, L., & Grady, C. L. (1997). Age-related differences in effective neural connectivity during encoding and recall. *Neuroreport, 8*(16), 3479-3483.

Charlton, S. G., & Starkey, N. J. (2012). *Does familiarity breed inattention? Why drivers crash on the roads they know best.* Australasian Road Safety Research, Policing and Education Conference, (October), 1–10.

Chen, I. G., Durbin, D. R., Elliott, M. R., Kallan, M. J., & Winston, F. K. (2005). Trip characteristics of vehicle crashes involving child passengers. *Injury Prevention, 11*, 219–224

Clarke, D. D., Ward, P., Truman, W., & Bartle, C. (2007). *Fatal Vehicle-occupant Collisions: An In-depth Study.* Road Safety Research Report No. 75, (75), 1–44.

Clay, O. J., Wadley, V. G., Edwards, J. D., Roth, D. L., Roenker, D. L., & Ball, K. K. (2005). Cumulative meta-analysis of the relationship between useful field of view and driving performance in older adults: current and future implications. *Optometry and Vision Science: Official Publication of the American Academy of Optometry, 82*(8), 724–731. http://doi.org/10.1097/01.opx.0000175009.08626.65

Colonna, P., Intini, P., Berloco, N., & Ranieri, V. (2016). The influence of memory on driving behavior: How route familiarity is related to speed choice. An on-road study. *Safety Science, 82,* 456–468. http://doi.org/10.1016/j.ssci.2015.10.012

Constantinidis, C; Franowicz, M. N., & Goldman-Rakic, P. S. (2001). The sensory nature of mnemonic representation in the primate prefrontal cortex. *Nature Neuroscience, 4*(3), 311–316.

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex, 6*(1), 39–49. http://doi.org/10.1093/CERCOR/6.1.39

Courville, J., & Otabe, S. (1974). The rubro-olivary projection in the macaque: An experimental study with silver impregnation methods. *The Journal of Comparative Neurology, 158*(4), 479–491. http://doi.org/10.1002/cne.901580407

Crepel, F., Mariani, J., & Delhaye-bouchaud, N. (1976). Evidence for a Multiple Innervation of Purkinje Cells by Climbing Fibers in the Immature Rat Cerebellum. *Journal of Neurobiology, 7*(6), 567–578.

Crundall, D. (2016). Hazard prediction discriminates between novice and experienced drivers. *Accident Analysis and Prevention, 86*, 47–58. http://doi.org/10.1016/j.aap.2015.10.006

Crundall, D., Chapman, P., Trawley, S., Collins, L., Van Loon, E., Andrews, B., & Underwood, G. (2012). Some hazards are more attractive than others: Drivers of varying experience respond differently to different types of hazard. *Accident Analysis & Prevention, 45,* 600-609.

Dash, S. & P, Thier. (2014). Cerebellum-Dependent Motor Learning: Lessons from Adaptation of Eye Movements in Primates. In Ramnani, N (Ed), *Cerebellar Learning* (pp 121-149). Oxford: Elsevier.

d'angelo, E. (2014). The organization of plasticity in the cerebellar cortex: from synapses to control. *Progress In Brain Research, 210*, 31-58.

De Raedt, R., & Ponjaert-Kristoffersen, I. (2001). Short Cognitive/Neuropsychological Test Battery for First-Tier Fitness-To-Drive Assessment of Older Adults. *The Clinical Neuropsychologist (Neuropsychology, Development and Cognition: Section D), 15*(3), 329–336. http://doi.org/10.1076/clin.15.3.329.10277

Desimone, R. & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Reviews Neuroscience, 18*, 193-222.

Desmond, J. E., Gabrieli, J. D. E., Wagner, A. D., Ginier, B. L., & Glover, G. H. (1997). Lobular Patterns of Cerebellar Activation in Verbal Working-Memory and Finger-Tapping Tasks as Revealed by Functional MRI. *Journal of Neuroscience, 17*(24), 9675–9685.

Deutsch, J. A., & Deutsch, D. (1963). Attention: Some Theoretical Considerations. *Psychological Review, 70*(1), 80–90. http://doi.org/10.1037/h0039515

DfT (2014). *Reported road casualties in Great Britain*. London: Department for Transport. Retrieved from: https://www.gov.uk/government/statistics/reported-road-casualties-in-great-britain-main-results-2014

Department for Transport National Travel Survey (special tabulation) https://www.gov.uk/government/collections/ national-travel-survey-statistics

Dias, E. C., & Segraves, M. A. (1999). Muscimol-Induced Inactivation of Monkey Frontal Eye Field: Effects on Visually and Memory-Guided Saccades. *Journal of Neurophysiology, 81*(5), 2191-2214.

Diedrichsen, J. (2006). A spatially unbiased atlas template of the human cerebellum. *Neuroimage, 33*(1), 127-138.

Diedrichsen, J., Balsters, J. H., Flavell, J., Cussans, E., & Ramnani, N. (2009). A probabilistic MR atlas of the human cerebellum. *Neuroimage, 46*(1), 39-46.

Diedrichsen, J., Maderwald, S., Küper, M., Thürling, M., Rabe, K., Gizewski, E. R., ... & Timmann, D. (2011). Imaging the deep cerebellar nuclei: a probabilistic atlas and normalization procedure. *Neuroimage, 54*(3), 1786-1794.

Diedrichsen, J., & Zotow, E. (2015). Surface-based display of volume-averaged cerebellar imaging data. *PloS one, 10*(7), e0133402.

Dirnberger, G., Novak, J., & Nasel, C. (2013). Perceptual sequence learning is more severely impaired than motor sequence learning in patients with chronic cerebellar stroke. *Journal of Cognitive Neuroscience, 25*(12), 2207–15. http://doi.org/10.1162/jocn_a_00444

Doron, K.W., Funk, C.M., & Glickstein, M. (2010). Fronto-cerebellar circuits and eye movemenet control: a diffusion imaging tractography study of human cortico- pontine projections. *Brain Research, 1307*, 63-71.

Dotzauer, M., Caljouw, S. R., De Waard, D., & Brouwer, W. H. (2013). Intersection assistance: A safe solution for older drivers? *Accident Analysis and Prevention, 59,* 522–528. http://doi.org/10.1016/j.aap.2013.07.024

Dow, R. S. (1949). Action potentials of cerebellar cortex in response to local electrical stimulation. *Journal of Neurophysiology, 12,* 245–256.

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology, 15*(2), 161–167. http://doi.org/10.1016/j.conb.2005.03.004

Doyon, J., Penhune, V., Ungerleider, L.G., 2003. Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia, 41,* 252–262

Drummond, A.E. (2000). *Paradigm lost! Paradise gained? An Australian's perspective on the novice driver problem.* In: Proceedings of the Novice Driver Conference, Bristol.

Dukic, T., & Broberg, T. (2012). Older drivers' visual search behaviour at intersections. *Transportation Research Part F: Traffic Psychology and Behaviour, 15*(4), 462–470. http://doi.org/10.1016/j.trf.2011.10.001

Durand, A. (1980). *An Analysis of Accident Location in Relation to Area of Residence.* Research Report A80-4, Oak Brook, IL: All-Industry Research Advisory Council

Duvernoy H.M., & Bourgouin, P. (1999). *The human brain: surface, three-dimensional sectional anatomy and MRI.* Vienna: Springer.

Ebner, T. J., Johsnon, M. T. V., Roitman, A., & Fu, Q. (2002). What Do Complex Spikes Signal about Limb Movements? *Annals of the New York Academy of Sciences, 978 (The Cerebellum: Recent Developments in Cerebellar Research),* 205–218. http://doi.org/10.1111/j.1749-6632.2002.tb07568.x

Edwards, C. J., Creaser, J. I., Caird, J. K., Lamsdale, A. M., & Chisholm, S. L. (2003). Older and younger driver performance at complex intersections: Implications for using perception-response time and driving simulation. Paper presented at the Second International Symposium on Human Factors in Driver Assessment, Training, and Vehicle Design, Park City, UT.

Edwards, J. D., Ross, L. A., Wadley, V. G., Clay, O. J., Crowe, M., Roenker, D. L., & Ball, K. K. (2006). The useful field of view test: Normative data for older adults. *Archives of Clinical Neuropsychology, 21,* 275–286. http://doi.org/10.1016/j.acn.2006.03.001

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic

cytoarchitectonic maps and functional imaging data. *Neuroimage, 25,* 1325–1335.

Engström, J., Markkula, G., Victor, T., & Merat, N. (2017). Effects of cognitive load on driving performance: The cognitive control hypothesis. *Human factors*, *30*(6), 734-764.

Evans, J. S. B. (2008). Dual-processing accounts of reasoning, judgment, and social cognition. *Annu. Rev. Psychol.*, *59*, 255-278. http://doi.org/10.1146/annurev.psych.59.103006.093629

Ferrera, V. P., Yanike, M., & Cassanello, C. (2009). Frontal eye field neurons signal changes in decision criteria. *Nature Neuroscience, 12*(11), 1458–1462. http://doi.org/10.1038/nn.2434

Field, A. (2009). *Discovering statistics using SPSS*. Sage publications.

Fitts, P. M. (1964). Perceptual-motor skill learning. In Melton, A. W. (Ed.), *Categories of Human Learning*. New York: Academic Press, 1964, p. 243-285.

Fitts, P. M., & Posner, M. I. (1967). *Human performance.* Brooks-Cole, Belmont, CA.

Fonda SJ, Wallace RB, Herzog AR. (2001). Changes in driving patterns and worsening depressive symptoms among older adults. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 56,* 343–351.

Fox, C. A., & Barnard, J. W. (1957). A quantitative study of the Purkinje cell dendritic branchlets and their relationship to afferent fibres. *Journal of Anatomy, 91*(3), 299–313. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/13448989

Friston, K. J., Ungerleider, L. G., Jezzard, P., & Turner, R. (1995a). Characterizing modulatory interactions between areas V1 and V1 in human cortex: A new treatment of functional MRI data. *Human Brain Mapping, 2,* 211–224.

Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-B., Frith, C. D., & Frackowiak, R. S. J. (1995b). Statistical parametric maps in 228 FRISTON ET AL. functional imaging: A general linear approach. *Human Brain Mapping, 2,* 189–210.

Friston, K. J., Holmes, A. P., Poline, J.-B., Grasby, P. J., Williams, S. C. R., Frackowiak, R. S. J., & Turner, R. (1995c). Analysis of fMRI time-series revisited. *NeuroImage, 2*, 45–53.

Fujita, Y., Mimura, M., & Iijima, S. (2012). Correlating driving fitness and functional visual field in the elderly. *Sagyou Ryouhou, 31,* 233-44.

Fuller, R. (2005). Towards a general theory of driver behaviour. *Accident Analysis & Prevention, 37*(3), 461-472)

Fuller, R. (2011). *Driver Control Theory–From Task Difficulty Homeostasis to Risk Allostasis.* Handbook of Traffic Psychology.

Gilbert, P. F. C., & Thach, W. T. (1977). Purkinje cell activity during motor learning. *Brain Research, 128*(2), 309–328. http://doi.org/10.1016/0006-8993(77)90997-0

Gilhotra, J. S., Mitchell, P., Ivers, R., & Cumming, R. G. (2001). Impaired vision and other factors associated with driving cessation in the elderly: the Blue Mountains Eye Study. *Clinical and Experimental Ophthalmology, 29*(3), 104–107. http://doi.org/10.1046/j.1442-9071.2001.00411.x

Gitelman, D. R., Parrish, T. B., LaBar, K. S., & Mesulam, M.-M. (2000). Real-Time Monitoring of Eye Movements Using Infrared Video-oculography during Functional Magnetic Resonance Imaging of the Frontal Eye Fields. *NeuroImage, 11*(1), 58-65.

Glass, G. V., Peckham, P. D., & Sanders, J. R. (1972). Consequences of failure to meet assumptions underlying the fixed effects analyses of variance and covariance. Review of Educational Research, 42(3), 237–288.

Glickstein, M. & Doron, K. (2008). Cerebellum: connections and functions. *Cerebellum, 7,* 589-594.

Grady, C. L. (2008). Cognitive neuroscience of aging. *Ann. N. Y. Acad. Sci. 1124,* 127–144.

Graf, P., Uttl, B., & Tuokko, H. (1995). Color- and picture-word stroop tests: Performance changes in old age. Journal of Clinical and Experimental *Neuropsychology, 17*(3), 390–415. http://doi.org/10.1080/01688639508405132

Grafton, S. T., Hazeltine, E., & Ivry, R. B. (2002). Motor sequence learning with the nondominant left hand. *Experimental Brain Research, 146*(3), 369–378. http://doi.org/10.1007/s00221-002-1181-y

Grayson, G. B. & Sexton, B. (2002). *The development of hazard perception testing.* TRL report. TRL 558. Crowthorne: Transport Research Laboratory (TRL).

Griffin, L. I. (2004). *Older driver involvement in injury crashes in Texas 1975– 1999.* AAA Foundation for Traffic Safety, Texas Transportation Institute, Arlington, TX.

Grosbras, M.-H., Lobel, E., Moortele, P.-F. Van de, LeBihan, D., & Berthoz, A. (1999). An Anatomical Landmark for the Supplementary Eye Fields in Human Revealed with Functional Magnetic Resonance Imaging. *Cerebral Cortex, 9*(7), 705–711. http://doi.org/10.1093/CERCOR/9.7.705

Hakamies-Blomqvist, L. (1994). Compensation in older drivers as reflected in their fatal accidents. *Accident Analysis & Prevention, 26*(1), 107–112. http://doi.org/10.1016/0001-4575(94)90073-6

Hakamies-Blomqvist, L. (1999). *Safety of Older Persons in Traffic Paper to a TRB Conference on Transportation in an Aging Society: A Decade of Experience, held in November 1999;* published in Transportation in an Aging Society - A Decade of Experience TRB Conference Proceedings 27, Transportation Research Board, Washington DC

Hakamies-Blomqvist, L., Sirén, A., & Davidse, R. (2004). *Older drivers-a review.* Statens väg-och transportforskningsinstitut., VTI rapport 497A.

Hall, T. C., Miller, A. K. H., & Corsellis, J. A. N. (1975). Variations in the human purkinje cell population according to age and sex. *Neuropathology and Applied Neurobiology, 1*(3), 267–292. http://doi.org/10.1111/j.1365-2990.1975.tb00652.x

Harré, N., & Sibley, C. G. (2007). Explicit and implicit self-enhancement biases in drivers and their relationship to driving violations and crash-risk optimism. *Accident Analysis & Prevention, 39*(6), 1155–1161. http://doi.org/10.1016/j.aap.2007.03.001

Hasher, L., & Zacks, R. T. (1988). Working Memory, Comprehension, and Aging: A Review and a New View. *Psychology of Learning and Motivation -*

Advances in Research and Theory, 22(C), 193–225. http://doi.org/10.1016/S0079-7421(08)60041-9

Haworth, N., Symmons, M., Kowadlo, N. (2001). *Hazard Perception by Inexperienced Motorcyclists, Report No. 179*. Monash University Accident Research Centre.

Henssen, A., Zilles, K., Palomero-Gallagher, N., Schleicher, A., Mohlberg, H., Gerboga, F., Eickhoff, S. B., Bludau, S., & Amunts, K. (2016). Cytoarchitecture and probability maps of the human medial orbitofrontal cortex. *Cortex, 75,* 87–112. http://doi.org/10.1016/j.cortex.2015.11.006

Hermens, F., & Walker, R. (2012). The site of interference in the saccadic Stroop effect. *Vision Research, 73,* 10–22. http://doi.org/10.1016/j.visres.2012.09.017

Hikosaka, O., Nakamura, K., Sakai, K., & Nakahara, H. (2002). Central mechanisms of motor skill learning. *Current Opinion in Neurobiology, 12*(2), 217–222. http://doi.org/10.1016/S0959-4388(02)00307-0

Hills, B. L. (1980). Vision, Visibility, and Perception in Driving. *Perception, 9*(2), 183–216. http://doi.org/10.1068/p090183

Hodgson, T. L., Parris, B. A., Gregory, N. J., & Jarvis, T. (2009). The saccadic Stroop effect: Evidence for involuntary programming of eye movements by linguistic cues. *Vision Research, 49*(5), 569–574. http://doi.org/10.1016/j.visres.2009.01.001

Hofstetter, H. W. (1976). Visual acuity and highway accidents. *Journal of the American Optometric Association, 47*(7), 887–93. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1030715

Holmes, G. (1939). The cerebellum of man. *Brain, 62*(1), 1–30. http://doi.org/10.1093/brain/62.1.1

Hommel, B., Pratt, J., Colzato, L., Godijn, R., & Godijn3, R. (2001). Symbolic Control of Visual Attention. *Psychological Science, 12*(5), 360–365.

Horn, K. M., Pong, M., & Gibson, A. R. (2004). Discharge of inferior olive cells during reaching errors and perturbations. *Brain Research, 996*(2), 148–158. http://doi.org/10.1016/j.brainres.2003.10.021

Horswill, M. S., Marrington, S. A., McCullough, C. M., Wood, J., Pachana, N. A., McWilliam, J., & Raikos, M. K. (2008). The hazard perception ability of older drivers. *The Journals of Gerontology. Series B, Psychological Sciences and Social Sciences, 63*(4), P212–P218.

Hull, M. A. & Christie, R. J. (1993). *The hazard perception test: the Geelong trial and future developments.* VicRoads Report GR 93-13

Ikeda, M., & Takeuchi, T. (1975). Influence of foveal load on the functional visual field. *Perception & Psychophysics, 18*(4), 255–260. http://doi.org/10.3758/BF03199371

Intini, P. (2016). *The Impact of Route Familiarity on Drivers' Speeds, Trajectories and Risk Perception.* 17th International Conference Road Safety On Five Continents (RS5C 2016), 12.

Ito, M. (1982). Cerebellar Control of the Vestibulo-Ocular Reflex--Around the Flocculus Hypothesis. *Annual Review of Neuroscience, 5*(1), 275–297. http://doi.org/10.1146/annurev.ne.05.030182.001423

Ito, M. (2001). Cerebellar Long-Term Depression: Characterization, Signal Transduction, and Functional Roles. *Physiological Reviews, 81*(3).

Jacob, R.J.K. & Karn, K.S. (2003). Eye tracking in human-computer interaction and usability research: Ready to deliver the promises. In: Hyona, J, Radach, R, & Deubel, H (Eds.), *The mind's eye: cognitive and applied aspects of eye movement research* (pp 573-603). Elsevier Science, Oxford, UK.

James, W. (1890). *Principles of psychology.* New York: Holt. Jeannerod.

Janke, M. K. (1994). *Age related disabilities that may impair driving and their assessment.* (No. CAL-DMV-RSS-94-156). Sacramento, California: California State Department of Motor Vehicles.

Jirenhed, D.-A., Bengtsson, F., & Hesslow, G. (2007). Acquisition, extinction, and reacquisition of a cerebellar cortical memory trace. Journal of Neuroscience: *The Official Journal of the Society for Neuroscience, 27*(10), 2493–502. http://doi.org/10.1523/JNEUROSCI.4202-06.2007

Joly, P., Frigon, J.-Y., & Daigneault, G. (2002). Executive Functions in the Evaluation of Accident Risk of Older Drivers. *Journal of Clinical and Experimental Neuropsychology (Neuropsychology, Development and*

Cognition: Section A), 24(2), 221–238. http://doi.org/10.1076/jcen.24.2.221.993

Kahneman, D. (2011). *Thinking fast and slow*. New York: Farrar, Straus and Giroux.

Keele, S. W. (1973). *Attention and human performance*. Goodyear Publishing Company.

Kelly, R. M., & Strick, P. L. (2003). Cerebellar Loops with Motor Cortex and Prefrontal Cortex of a Nonhuman Primate. *Journal of Neuroscience, 23*(23), 8432-8444.

Kline, D. W., Kline, T. J., Fozard, J. L., Kosnik, W., Schieber, F., & Sekuler, R. (1992). Vision, aging, and driving: the problems of older drivers. *Journal of Gerontology, 47*(1), P27-34. http://doi.org/10.1093/GERONJ/47.1.P27

Krupa, D. J., Thompson, J. K., & Thompson, R. F. (1993). Localization of a memory trace in the mammalian brain. *SCIENCE-NEW YORK THEN WASHINGTON-, 260*, 989-989.

Küper, M., Kaschani, P., Thürling, M., Stefanescu, M. R., Burciu, R. G., Göricke, S., Maderwald, S., Ladd, M.E., Hautzel, H., & Timmann, D. (2016). Cerebellar fMRI Activation Increases with Increasing Working Memory Demands. *The Cerebellum, 15*(3), 322–335. http://doi.org/10.1007/s12311-015-0703-7

LaBerge, D. (1973). Attention and the measurement of perceptual learning. *Memory & Cognition, 1*(3), 268–276. http://doi.org/10.3758/BF03198108

LaBerge, D. (1975). Acquisition of automatic processing in perceptual and associative learning. In P. M. A. Rabbit & S. Dornic (Eds.), *Attention and performance V*. New York: Academic Press.

Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception, 28*(11), 1311–1328. http://doi.org/10.1068/p2935

Lang, C. E., & Bastian, A. M. Y. J. (2002). Cerebellar Damage Impairs Automaticity of a Recently Practiced Movement. *Journal of Neurophysiology, 87*(3), 1336–1347.

Larsell, O., & Jansen, O. (1972). *The comparative anatomy and histology of the cerebellum: the human cerebellum, cerebellar connections and cerebellar cortex.* Minneapolis, MN: University of Minnesota.

Leiner, H. C., Leiner, A. L., & Dow, R. S. (1986). Does the cerebellum contribute to mental skills? *Behavioural Neuroscience, 100* (4), 443–454.

Lehéricy, S., Benali, H., Van de Moortele, P.-F., Pélégrini-Issac, M., Waechter, T., Ugurbil, K., & Doyon, J. (2005). Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. *Proceedings of the National Academy of Sciences of the United States of America, 102*(35), 12566–71. http://doi.org/10.1073/pnas.0502762102

Levin, L., Dukic, T., Henriksson, P., Mårdh, S., & Sagberg, F. (2009). *Older car drivers in Norway and Sweden Studies of accident involvement, visual search behaviour, attention and hazard perception.* VTI Rapport 656A, 1–80.

Li, G., Braver, E. R., & Chen, L. H. (2003). Fragility versus excessive crash involvement as determinants of high death rates per vehicle-mile of travel among older drivers. *Accident Analysis and Prevention, 35,* 227–235. http://doi.org/10.1016/S0001-4575(01)00107-5

Ling, D. J. & Mannion, R. (1995). *Enhanced Mobility and Quality of Life of Older People: Assessment of Economic and Social Benefits of Dial-a- Ride Services,* in Proceedings of the Seventh International Conference on Transport and Mobility for Older and Disabled People, Vol. 1, DETR, United Kingdom.

Liversedge, S. P., & Findlay, J. M. (2000). Saccadic eye movements and cognition. *Trends in cognitive sciences*, *4*(1), 6-14.

Liversedge, S., Gilchrist, I., & Everling, S. (Eds.). (2011). *The Oxford handbook of eye movements*. Oxford University Press.

Logan, G. D., & Zbrodoff, N. J. (1998). Stroop-Type Interference: Congruity Effects in Color Naming With Typewritten Responses. *Journal of Experimental Psychology: General, 24*(3), 978–992.

Lyman, S., Ferguson, S. A., Braver, E. R., & Williams, A. F. (2002). Older driver involvements in police reported crashes and fatal crashes: trends and projections. *Injury Prevention: Journal of the International Society for*

Child and Adolescent Injury Prevention, 8, 116–120. http://doi.org/10.1136/ip.8.2.116

Mader, M., Bresges, A., Topal, R., Busse, A., Forsting, M., & Gizewski, E. R. (2009). Simulated car driving in fMRI—Cerebral activation patterns driving an unfamiliar and a familiar route. *Neuroscience Letters 464*(3), 222-227.

Mano, N., Ito, Y., & Shibutani, H. (1991). Saccade-related Purkinje cells in the cerebellar hemispheres of the monkey. *Experimental Brain Research, 84*(3), 465–470. http://doi.org/10.1007/BF00230957

Marple-Horvat, D. E., & Stein, J. F. (1990). Neuronal activity in the lateral cerebellum of trained monkeys, related to visual stimuli or to eye movements. *Journal of Physiology, 428,* 595–614.

Marr, D. (1969). A theory of cerebellar cortex. *The Journal of Physiology, 202*(2), 437–70. http://doi.org/10.1113/JPHYSIOL.1969.SP008820

Mathias, J. L., & Lucas, L. K. (2009). Cognitive predictors of unsafe driving in older drivers: a meta-analysis. *International Psychogeriatrics, 21*(4), 637–653. http://doi.org/10.1017/S1041610209009119

Maycock, G., Lockwood, C. R. & Lester, J. (1991). *The accident liability of car drivers*. TRRL Report RR315. Crowthorne: Transport and Road Research Laboratory.

Mayhew, D. R., Simpson, H. M., & Pak, A. (2003). Changes in collision rates among novice drivers during the first months of driving. *Accident Analysis & Prevention, 35*(5), 683–691. http://doi.org/10.1016/S0001-4575(02)00047-7

McCartt, A. T., Shabanova, V. I., & Leaf, W. A. (2003). Driving experience, crashes and traffic citations of teenage beginning drivers. *Accident Analysis & Prevention*, *35*(3), 311-320.

McGwin, G., Sarrels, S. A., Griffin, R., Owsley, C., & Rue, L. W. (2008). The impact of a vision screening law on older driver fatality rates. *Archives of ophthalmology*, *126*(11), 1544-1547.

McGwin, G., Khoury, R., Cross, J., & Owsley, C. (2010). Vision Impairment and Eye Care Utilization among Americans 50 and Older. *Current Eye Research, 35*(6), 451–458. http://doi.org/10.3109/02713681003664931

McKenna, F. P. & Crick, J. L. (1994). *Hazard perception in drivers: a methodology for testing and training.* TRRL Report CR313. Crowthorne: Transport and Road Research Laboratory.

McKenna, F. P. & Horswill, M. S. (1999). *Hazard perception and its relevance for driver licensing.* IATSS Research, 23, 36–41.

McKenna, F. P. & Crick, J. L. (1991) Experience and expertise in hazard perception. In G. B. Grayson and J. F. Lester (Eds.) *Behavioural Research in Road Safety.* Crowthorne: Transport and Road Research Laboratory.

Mele, M. L., & Federici, S. (2012). Gaze and eye-tracking solutions for psychological research. *Cognitive Processing, 13*(1), 261-265 http://doi.org/10.1007/s10339-012-0499-z

Merat, N., Jamson, A. H., Lai, F. C., & Carsten, O. (2012). Highly automated driving, secondary task performance, and driver state. *Human factors*, *54*(5), 762-771.

Miall, R. C., & Wolpert, D. M. (1996). Forward Models for Physiological Motor Control. *Neural Networks, 9*(8), 1265–1279. http://doi.org/10.1016/S0893-6080(96)00035-4

Michon, J. (1985). A critical view of driver behavior models: what do we know, what should we do? *Human Behavior and Traffic Safety,* 485–520. http://doi.org/10.1007/978-1-4613-2173-6

Middleton, F., & Strick, P. (2000). Basal ganglia and cerebellar loops: motor and cognitive circuits. *Brain Research Reviews, 31*(2–3), 236–250. http://doi.org/10.1016/S0165-0173(99)00040-5

Milham, M. P., Erickson, K. I., Banich, M. T., Kramer, A. F., Webb, A., Wszalek, T., & Cohen, N. J. (2002). Attentional Control in the Aging Brain: Insights from an fMRI Study of the Stroop Task. *Brain and Cognition, 49*(3), 277–296. http://doi.org/10.1006/brcg.2001.1501

Mitchell, C. G. B. (2013). The licensing and safety of older drivers in Britain. *Accident Analysis and Prevention, 50,* 732–741. http://doi.org/10.1016/j.aap.2012.06.027

Miyachi, S., Hikosaka, O., & Lu, X. (2002). Differential activation of monkey striatal neurons in the early and late stages of procedural learning. *Experimental Brain Research, 146*(1), 122–126. http://doi.org/10.1007/s00221-002-1213-7

Miyashita, K., R., M. K., Miyachi, S., & Hikosaka, O. (1996). Anticipatory saccades in sequential procedural learning in monkeys. *Journal of Neurophysiology, 76*(2). 1361-1366.

Mozolic, J. (2009). *Reducing distractibility in healthy older adults.* (Doctoral Dissertation). Retrieved from http://oatd.org/oatd/record?record=handle%5C:10339%5C%2F14730)

Müller, N. C. J., Genzel, L., Konrad, B. N., Pawlowski, M., Neville, D., Fernández, G., … Stickgold, R. (2016). Motor Skills Enhance Procedural Memory Formation and Protect against Age-Related Decline. *PLOS ONE, 11*(6), e0157770. http://doi.org/10.1371/journal.pone.0157770

National Highway Traffic Safety Administration (1989). Retrieved from https://www.congress.gov/bill/101st-congress/senate-bill/673

Neisser, U. (1967). *Cognitive psychology*. New York: Appleton-Century-Crofts.

Noda, H., Sugita, S., & Ikeda, Y. (1990). Afferent and efferent connections of the oculomotor region of the fastigial nucleus in the macaque monkey. *Journal of Comparative Neurology, 302*(2), 330–348.

Norman, D. A. (1969). Memory while shadowing. *Quarterly Journal of Experimental Psychology, 21*(1), 85–93. http://doi.org/10.1080/14640746908400200

Norman, D. A., & A., D. (1968). Toward a theory of memory and attention. *Psychological Review, 75*(6), 522–536. http://doi.org/10.1037/h0026699

Norman, D. A., & Shallice, T. (1986). Attention to Action. *Consciousness & Self-Regulation, 4,* 1–18. http://doi.org/10.1007/978-1-4757-0629-1_1

Oguro, H., Okada, K., Yamaguchi, S., & Kobayashi, S. (1998). Sex differences in morphology of the brain stem and cerebellum with normal ageing. *Neuroradiology, 40*(12), 788–792. http://doi.org/10.1007/s002340050685

Ohki, M., Kitazawa, H., Hiramatsu, T., Kaga, K., Kitamura, T., Yamada, J., & Nagao, S. (2009). Role of Primate Cerebellar Hemisphere in Voluntary Eye Movement Control Revealed by Lesion Effects. *Journal of Neurophysiology, 101*(2), 934-947.

Older Drivers Task Force. Retrieved from: http://www.roadsafetyfoundation.org/media/33073/modsfl-single-page-printable-version.pdf

Older Driver Task Force Research Report Appendix A.3 Casualties and Accidents Source of statistics: Department for Transport (annual) Reported Road Casualties Great Britain https://www.gov.uk/government/collections/road-accidents-and-safety-statistics

Olson, P. L., & Sivak, M. (1986). Perception-response time to unexpected roadway hazards. *Human Factors, 28,* 91-96.

Öngür, D., Ferry, A. T., & Price, J. L. (2003). Architectonic subdivision of the human orbital and medial prefrontal cortex. *Journal of Comparative Neurology, 460*(3), 425–449. http://doi.org/10.1002/cne.10609

Orquin, J. L., & Mueller Loose, S. (2013). Attention and choice: A review on eye movements in decision making. *Acta Psychologica, 144*(1), 190–206. http://doi.org/10.1016/j.actpsy.2013.06.003

Owsley, C; Ball, K; McGwin, G; Sloane, M. E.; Roenker, D. L; White, M. F.; & Overley, E. T. (1998). Visual Processing Impairment and Risk of Motor Vehicle Crash Among Older Adults. *JAMA, 279*(14), 1083. http://doi.org/10.1001/jama.279.14.1083

Owsley, C., & McGwin, G. (2010). Vision and driving. *Vision Research, 50*(23), 2348–2361. http://doi.org/10.1016/j.visres.2010.05.021

Owsley, C., McGwin, G., & Ball, K. (1998). Visual impairment, eye disease and injurious motor vehicle crashes in the elderly. *Opthalmic Epidemiology, 5*(2), 101–113.

Pai, C.-W., Hwang, K. P., & Saleh, W. (2009). A mixed logit analysis of motorists' right-of-way violation in motorcycle accidents at priority T-junctions. *Accident Analysis & Prevention, 41*(3), 565–573. http://doi.org/10.1016/j.aap.2009.02.007

Paus, T. (1996). Location and function of the human frontal eye-field: A selective review. *Neuropsychologia, 34*(6), 475–483. http://doi.org/10.1016/0028-3932(95)00134-4

Paterson, K. B., McGowan, V. A., & Jordan, T. R. (2013). Effects of adult aging on reading filtered text: evidence from eye movements. *PeerJ, 1*, e63.

Percheron, G., François, C., & Pouget, P. (2015). What makes a frontal area of primate brain the frontal eye field? *Frontiers in integrative neuroscience, 9.* http://doi.org/10.3389/fnint.2015.00033

Peterburs, J., Cheng, D. T., & Desmond, J. E. (2015). The Association Between Eye Movements and Cerebellar Activation in a Verbal Working Memory Task. *Cerebral Cortex, 26*(9), 3802-3813. http://doi.org/10.1093/cercor/bhv187

Petrides, M. (2000). The role of the mid-dorsolateral prefrontal cortex in working memory. *Experimental brain research, 133*(1), 44-54.

Petrides, M., & Pandya, D. N. (1999). Dorsolateral prefrontal cortex: comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *European Journal of Neuroscience, 11*(3), 1011–1036. http://doi.org/10.1046/j.1460-9568.1999.00518.x

Planek, T. W. (1981). The Effects of Ageing on Driver Abilities, Accident Experience, and Licensing. *Road Safety. Research and Practice*, 171-179.

Poldrack, R. A., Sabb, F. W., Foerde, K., Tom, S. M., Asarnow, R. F., Bookheimer, S. Y., & Knowlton, B. J. (2005). The Neural Correlates of Motor Skill Automaticity. *Journal of Neuroscience, 25*(22), 5356-5364. http://www.jneurosci.org/content/25/22/5356.long

Posner, M., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review Neuroscience, 13*, 25–42.

Posner, M. I., & Snyder, C. R. R. (1975). *Facilitation and inhibition in the processing of signals*. Attention and Performance V, (JULY 1975), 669–682.

Pradhan, A. K., Hammel, K. R., DeRamus, R., Pollatsek, A., Noyce, D. A., & Fisher, D. L. (2005). Using eye movements to evaluate effects of driver age on risk perception in a driving simulator. *Human factors, 47*(4), 840-852.

Prevosto, V., Graf, W., & Ugolini, G. (2010). Cerebellar Inputs to Intraparietal Cortex Areas LIP and MIP: Functional Frameworks for Adaptive Control of Eye Movements, Reaching, and Arm/Eye/Head Movement Coordination. *Cerebral Cortex, 20(*1), 214–228. http://doi.org/10.1093/cercor/bhp091

Purves, D., Augustine, G. J., Fitzpatrick, D., Katz, L. C., LaMantia, A. S., McNamara, J. O., & Williams, S. M. (2001). Neuroscience. Sunderland. *MA: Sinauer Associates*.

Quigley, H. A. (1993). Open-Angle Glaucoma. *New England Journal of Medicine, 328*(15), 1097–1106. http://doi.org/10.1056/NEJM199304153281507

Quimby, A. R., & Watts, G. R. (1981). *Human factors and driving performance (Laboratory Report 1004)*. Crowthorne, England: Trans- port and Road Research Laboratory.

Quimby, A. R., Maycock, G., Carter, L. D., Dixon, R. & Wall, J. G. (1986). *Perceptual abilities of accident involved drivers*. TRRL Report RR27. Crowthorne: Transport and Road Research Laboratory.

Rajkowska, G., & Goldman-Rakic, P. S. (1995). Cytoarchitectonic definition of prefrontal areas in the normal human cortex: II. Variability in locations of areas 9 and 46 and relationship to the Talairach Coordinate System. *Cerebral Cortex, 5*(4), 323–37. http://doi.org/10.1093/CERCOR/5.4.323

Ralston, D. D. (1994). Cerebellar Terminations in the Red Nucleus of Macaca fascicularis : An Electron-Microscopic Study Utilizing the Anterograde Transport of WGA:HRP. *Somatosensory & Motor Research, 11*(2), 101– 107. http://doi.org/10.3109/08990229409028863

Ramnani, N. (2006). The primate cortico-cerebellar system: anatomy and function. *Nature Reviews Neuroscience, 7*(7), 511–522. http://doi.org/10.1038/nrn1953

Ramnani, N. (2014). Automatic and Controlled Processing in the Corticocerebellar System. *Progress in Brain Research, 210,* 255-285. http://doi.org/10.1016/B978-0-444-63356-9.00010-8

Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience, 5*(3), 184–194. http://doi.org/10.1038/nrn1343

Rasmussen, J. (1983). Skills, Rules, and Knowledge: Signals, Sights and Symbols, and Other Distinctions in Human Performance Models. *IEEE Transactions on Systems, Man, and Cybernetics, 13*(3), 257–266.

Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Integration of structural and functional findings. In F. I. M. Craik & Salthouse, T. A. (Eds.), *Handbook of aging and cognition* (Vol. II). Mahwah, NJ: Erlbaum.

Raz, N., Gunning, F. M., Head, D., Dupuis, J. H., McQuain, J., Briggs, S. D., Loken, W. J., Thornton, A. E., & Acker, J. D. (1997). Selective aging of the human cerebral cortex observed in vivo: Differential vulnerability of the prefrontal gray matter. *Cerebral Cortex, 7*(3), 268-282.

Read, K., Yu, L., Emerson, J., Dawson, J., Aksan, N., & Rizzo, M. (2011). Effects of familiarity and age on driver safety errors during wayfinding. *International Driving Symposium on Human Factors in Driver Assessment, Training, and Vehicle Design,* 569–575.

Richards, E., Bennett, P. J., & Sekuler, A. B. (2006). Age related differences in learning with the useful field of view. *Vision Research, 46,* 4217–4231. http://doi.org/10.1016/j.visres.2006.08.011

Richardson, D. C., & Johnson, S. P. (2008). Eye tracking research in infants and adults. 30th Annual Meeting of the Cognitive Science Society: *CogSci,* 23–26.

Roenker, D. L., Cissell, G. M., Ball, K. K., Wadley, V. G., & Edwards, J. D. (2003). Speed-of-processing and driving simulator training result in improved driving performance. *Human Factors: The Journal of Human Factors and Ergonomics Society, 45*(2), 218-233.

Rogé, J., Ndiaye, D., & Vienne, F. (2014). Useful visual field training: A way to improve elderly car drivers' ability to detect vulnerable road users. *Transportation Research Part F: Traffic Psychology and Behaviour, 26,* 246–257. http://doi.org/10.1016/j.trf.2014.08.005

Rogers, W. A., & Fisk, A. D. (1991). Age-Related Differences in the Maintenance and Modification of Automatic Processes: Arithmetic Stroop Interference. *Human Factors: The Journal of the Human Factors and Ergonomics Society, 33*(1), 45–56. http://doi.org/10.1177/001872089103300104

Rolison, J. J., Hewson, P. J., Hellier, E., & Husband, P. (2012). Risk of fatal injury in older adult drivers, passengers, and pedestrians. *Journal of the American Geriatrics Society, 60*, 1504–1508. http://doi.org/10.1111/j.1532-5415.2012.04059.x

Rorden, C., Karnath, H.-O., & Bonilha, L. (2007). Improving Lesion-Symptom Mapping. *Journal of Cognitive Neuroscience, 19*(7), 1081–1088. http://doi.org/10.1162/jocn.2007.19.7.1081

Ross, L. A., Browning, C., Luszcz, M. A., Mitchell, P., & Anstey, K. J. (2011). Age-Based Testing for Driver's License Renewal: Potential Implications for Older Australians. *Journal of the American Geriatrics Society, 59*(2), 281–285. http://doi.org/10.1111/j.1532-5415.2010.03241.x

Ruigrok, T. J. (1997). Cerebellar nuclei: the olivary connection. *Progress in brain research, 114*, 167-192.

Sakai, K., Rowe, J. B., & Passingham, R. E. (2002). Active maintenance in prefrontal area 46 creates distractor-resistant memory. *Nature Neuroscience, 5*(5), 479–84. http://doi.org/10.1038/nn846

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review, 103*(3), 403–428. http://doi.org/10.1037/0033-295X.103.3.403

Salthouse, T. A. (2001). Structural models of the relations between age and measures of cognitive functioning. *Intelligence, 29*(2), 93–115. http://doi.org/10.1016/S0160-2896(00)00040-4

Salthouse, T. A., & Meinz, E. J. (1995). Aging, Inhibition, Working Memory, and Speed. *Journal of Gerontology: Psychological sciences, 50*(6), 297–3.

Sanders, A. F. (1970). Some Aspects of the Selective Process in the Functional Visual Field. *Ergonomics, 13*(1), 101–117. http://doi.org/10.1080/00140137008931124

Schall, J. D. (2004). On the role of frontal eye field in guiding attention and saccades. *Vision Research, 44*(12), 1453–1467. http://doi.org/10.1016/j.visres.2003.10.025

Schall, J. D., Stuphorn, V., & Brown, J. W. (2002). Monitoring and Control of Action by the Frontal Lobes. *Neuron, 36*(2), 309–322. http://doi.org/10.1016/S0896-6273(02)00964-9

Schanke, A.-K., & Sundet, K. (2000). Comprehensive Driving Assessment: Neuropsychological Testing and On-road Evaluation of Brain Injured Patients. *Scandinavian Journal of Psychology, 41*(2), 113–121. http://doi.org/10.1111/1467-9450.00179

Schmahmann, J. D., & Pandya, D. N. (1997). Anatomic Organization of the Basilar Pontine Projections from Prefrontal Cortices in Rhesus Monkey. *Journal of Neuroscience, 17*(1), 438-458.

Scialfa, C. T., Thomas, D. M., & Joffe, K. M. (1994). Age differences in the useful field of view: an eye movement analysis. *Optometry & Vision Science, 71*(12), 736-742. http://doi.org/10.1097/00006324-199412000-00003

Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Research Bulletin, 70*(4), 337–346. http://doi.org/10.1016/j.brainresbull.2006.06.008

Seidler, R. D., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., … Lipps, D. B. (2010). Motor control and aging: Links to age-related brain structural, functional, and biochemical effects. *Neuroscience & Biobehavioral Reviews, 34*(5), 721–733. http://doi.org/10.1016/j.neubiorev.2009.10.005

Seiple, W., Szlyk, J. P., Yang, S., & Holopigian, K. (1996). Age-related functional field losses are not eccentricity dependent. *Vision Research, 36*(12), 1859–1866. http://doi.org/10.1016/0042-6989(95)00288-X

Sekuler, R., & Ball, K. (1986). Visual localization: age and practice. *The Journal of the Optical Society of America A, 3*(6), 864–867.

Sekuler, A. B., Bennett, P. J., & Mamelak, M. (2000). Effects of Aging on the Useful Field of View. *Experimental Aging Research, 26*(2), 103–120. http://doi.org/10.1080/036107300243588

Shallice, T. (1982). Specific impairments of planning. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *298*(1089), 199-209. http://rstb.royalsocietypublishing.org/content/298/1089/199

Sherrington, C. (1906). *The integrative action of the nervous system.* Yale: New Haven.

Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychological Review, 84*(2), 127–190. http://doi.org/10.1037/0033-295X.84.2.127

Siren, A., Heikkinen, S., & Hakamies-Blomqvist, L. (2001). *Older female road users: A review.* (VTI report 467A). Linkoping: VTI.

Sivak, M., & Schoettle, B. (2012). Recent changes in the age composition of drivers in 15 countries. *Traffic injury prevention*, *13*(2), 126-132.

Sommer, S. M., Falkmer, T., Bekiaris, E., & Panou, M. (2004). Toward a client-centred approach to fitness-to-drive assessment of elderly drivers. *Scandinavian Journal of Occupational Therapy, 11*(2), 62–69. http://doi.org/10.1080/11038120410020539

Spencer, R. M., & Ivry, R. B. (2009). Sequence learning is preserved in individuals with cerebellar degeneration when the movements are directly cued. *Journal of cognitive neuroscience*, *21*(7), 1302-1310. http://doi.org/10.1162/jocn.2009.21102.Sequence

Spieler, D. H., Balota, D. A., & Faust, M. E. (1996). Stroop Performance in Healthy Younger and Older Adults and in Individuals With Dementia of the Alzheimer's Type. *Journal of Experimental Psychology: Human Perception and Performance, 22*(2), 461–479. http://doi.org/10.1037/0096-1523.22.2.461

Spivey, M.J., Richardson, D. & Dale, R. (2009). The movement of eye and hand as a window into language and cognition. In E. Morsella, J. Bargh, and P.M. Gollwitzer (eds.). *The Psychology of Action* (Vol. 2) (pp. 225-249). New York: Oxford University Press.

Staplin, L., Lococo, K., & Byington, S. (1998). *Older driver highway design handbook* (No. FHWA-RD-97-135).

Stein, J. F., & Glickstein, M. (1992). Role of the cerebellum in visual guidance of movement. *Physiological Reviews, 72*(4), 967-1017.

Stoneley, S., Harrison, J., Manning, L., & Haunton, V. (2014). A review of current guidance and evidence on driving in older age. *J Geriatr Med*, *15*(1), 31-40.

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology, 18*(6), 643–662. http://doi.org/10.1037/h0054651

Tehovnik, E. J., Sommer, M. A., Chou, I. H., Slocum, W. M., & Schiller, P. H. (2000). Eye fields in the frontal lobes of primates. *Brain Research Reviews*, *32*(2), 413-448.

Thier, P., Dicke, P. W., Haas, R., Thielert, C.-D., & Catz, N. (2002). The Role of the Oculomotor Vermis in the Control of Saccadic Eye Movements. *Annals of the New York Academy of Sciences, 978(1 The Cerebellum),* 50–62. http://doi.org/10.1111/j.1749-6632.2002.tb07555.x

Thürling, M., Hautzel, H., Küper, M., Stefanescu, M. R., Maderwald, S., Ladd, M. E., & Timmann, D. (2012). Involvement of the cerebellar cortex and nuclei in verbal and visuospatial working memory: A 7T fMRI study. *NeuroImage, 62*(3), 1537–1550.

Troyer, A. K., Leach, L., & Strauss, E. (2006). Aging and Response Inhibition: Normative Data for the Victoria Stroop Test. *Aging, Neuropsychology, and Cognition, 13*(1), 20–35. http://doi.org/10.1080/138255890968187

Tzvi, E., Münte, T. F., & Krämer, U. M. (2014). Delineating the cortico-striatal-cerebellar network in implicit motor sequence learning. *NeuroImage, 94,* 222–230. http://doi.org/10.1016/j.neuroimage.2014.03.004

Ugolini, G., & Kuypers, H. G. J. M. (1986). Collaterals of corticospinal and pyramidal fibres to the pontine grey demonstrated by a new application of the fluorescent fibre labelling technique. *Brain Research, 365*(2), 211–227. http://doi.org/10.1016/0006-8993(86)91632-X

Underwood, G., Phelps, N., Wright, C., van Loon, E., & Galpin, A. (2005). Eye fixation scanpaths of younger and older drivers in a hazard perception task. *Ophthalmic & Physiological Optics, 25,* 346–356.

Van der Elst, W., Boxtel, M. P. J. Van, Breukelen, G. J. P. Van, & Jolles, J. (2006). The Stroop Color-Word Test: Influence of Age, Sex, and Education; and Normative Data for a Large Sample Across the Adult Age Range. *Assessment, 13*(1), 62–79. http://doi.org/10.1177/1073191105283427

Verhaeghen, P. (1999). The effects of age-related slowing and working memory on asymptotic recognition performance. *Aging, Neuropsychology and Cognition, 6*(3), 201–213.

Verhaeghen, P. (2011). Aging and Executive Control: Reports of a Demise Greatly Exaggerated. *Current Directions in Psychological Science, 20*(3), 174–180. http://doi.org/10.1177/0963721411408772

Verhaeghen, P., & De Meersman, L. (1998). Aging and the Stroop effect: a meta-analysis. *Psychology and Aging, 13*(1), 120–6. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9533194

Vichitvanichphong, S., Talaei-Khoei, A., Kerr, D., & Ghapanchi, A. H. (2015). What Does Happen to Our Driving When We Get Older? *Transport Reviews, 35*(1), 56–81. http://doi.org/10.1080/01441647.2014.997819

Vilberg, K. L., & Rugg, M. D. (2012). The Neural Correlates of Recollection: Transient Versus Sustained fMRI Effects. *Journal of Neuroscience, 32*(45), 15679–15687. http://doi.org/10.1523/JNEUROSCI.3065-12.2012

Visscher, K. M., Miezin, F. M., Kelly, J. E., Buckner, R. L., Donaldson, D. I., Mcavoy, M. P., … Petersen, S. E. (2003). Mixed blocked/event-related designs separate transient and sustained activity in fMRI. *NeuroImage, 19*(4), 1694-1708. http://doi.org/10.1016/S1053-8119(03)00178-2

Voogd, J., & Glickstein, M. (1998). The anatomy of the cerebellum. *Trends in Cognitive Sciences, 2*(9), 307–313. http://doi.org/10.1016/S1364-6613(98)01210-8

Voogd, J., Schraa-Tam, C. K. L., van der Geest, J. N., & De Zeeuw, C. I. (2012). Visuomotor Cerebellum in Human and Nonhuman Primates. *The Cerebellum, 11*(2), 392–410. http://doi.org/10.1007/s12311-010-0204-7

Wells, P., Tong, S., Sexton, B., Grayson, G., Jones, E., 2008. *Cohort II: A Study of Learner and New Drivers.* Department for Transport, London.

West, R., & Alain, C. (2000). Age-related decline in inhibitory control contributes to the increased Stroop effect observed in older adults. *Psychophysiology, 37*(2), 179–189. http://doi.org/10.1111/1469-8986.3720179

West, R., & Baylis, G. C. (1998). Effects of increased response dominance and contextual disintegration on the Stroop interference effect in older adults. *Psychology and Aging, 13*(2), 206–217. http://doi.org/10.1037/0882-7974.13.2.206

West, R., & Bell, M. A. (1997). Stroop color--word interference and electroencephalogram activation: Evidence for age-related decline of the anterior attention system. *Neuropsychology, 11*(3), 421–427. http://doi.org/10.1037//0894-4105.11.3.421

Wetton, M. A., Horswill, M. S., Hatherly, C., Wood, J. M., Pachana, N. A., & Anstey, K. J. (2010). The development and validation of two complementary measures of drivers' hazard perception ability. *Accident Analysis & Prevention*, *42*(4), 1232-1239.

Williams, B. R., Strauss, E. H., Hultsch, D. F., Michael, A., Williams, B. R., Strauss, E. H., … Michael, A. (2007). Reaction Time Inconsistency in a Spatial Stroop Task: Age-Related Differences Through Childhood and Adulthood Reaction Time Inconsistency in a Spatial Stroop Task: Age-Related Differences Through Childhood and Adulthood. *Aging, Neuropsychology, and Cognition, 14*(4), 417–439. http://doi.org/10.1080/13825580600584590

Willingham, D. B. (1998). A neuropsychological theory of motor skill learning. *Psychological Review, 105*(3), 558–584. http://doi.org/10.1037/0033-295X.105.3.558

Wise, S. P., & Murray, E. A. (2000). Arbitrary associations between antecedents and actions. *Trends in Neurosciences, 23*(6), 271–276. http://doi.org/10.1016/S0166-2236(00)01570-8

Withaar, F. K., Brouwer, W. H., & van Zomeren, A. H. (2000). Fitness to drive in older drivers with cognitive impairment. *Journal of the International Neuropsychological Society, 6*(4), 480-490.

Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences, 2*(9), 338–347. http://doi.org/10.1016/S1364-6613(98)01221-2

Wood, J. M. (2002). Aging, driving and vision. *Clinical and Experimental Optometry, 85*(4), 214–220. http://doi.org/10.1111/j.1444-0938.2002.tb03040.x

Xiong, G., Hiramatsu, T., & Nagao, S. (2002). Corticopontocerebellar pathway from the prearcuate region to hemispheric lobule VII of the cerebellum: an anterograde and retrograde tracing study in the monkey. Neuroscience Letters *322*(3), 173-176.

Yamada, J., & Noda, H. (1987). Afferent and efferent connections of the oculomotor cerebellar vermis in the macaque monkey. *Journal of Comparative Neurology, 265*(2), 224–241. http://doi.org/10.1002/cne.902650207

Yanko, M. R., & Spalek, T. M. (2013). Route familiarity breeds inattention: A driving simulator study. *Accident Analysis and Prevention, 57,* 80–86. http://doi.org/10.1016/j.aap.2013.04.003

Yarbus, & L., A. (1965). *Role of eye movements in the visual process.* Oxford, England: Nauka. Retrieved from http://psycnet.apa.org/psycinfo/1970-15810-000

Zagon, I. S., McLaughlin, P. J., & Smith, S. (1977). Neural populations in the human cerebellum: estimations from isolated cell nuclei. *Brain Research, 127*(2), 279-282.

Appendices

Appendix 1: Study 1 Information Sheet and Consent Form

Department of Psychology
Egham, Surrey TW20 0EX, UK

Participant Information Sheet
Learning Oculomotor Behaviours: Sequence Learning and Eye-Tracking
Information specific to the study

This study is being conducted by the following researchers at Royal Holloway, University of London:

Ms. Jennifer Mills	Jennifer.Mills.2009@live.rhul.ac.uk	+44 (0) 1784 443703
Prof. Narender Ramnani	n.ramnani@rhul.ac.uk	+44 (0) 1784 443519
Dr. Georgios P. Argyropoulos	Georgios.Argyropoulos@rhul.ac.uk	+44 (0) 1784 443705

You are being invited to take part in a research study. Before you decide, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully to decide whether or not you wish to take part. Please ask if there is anything that is not clear or if you would like more information.

Purpose of the study

We are studying the brain processes that underlie sequence learning and automatic, rule-based eye movements. The results of this study are intended to be used for my PhD thesis with the further intention of preparation for publication in scientific journals.

Who is organizing this study?

Prof. Ramnani, Dr. Argyropoulos, and Ms. Mills have organized this study and will be very happy to answer any questions you may have concerning the procedures you will be asked to undertake. They may be contacted at the address shown at the top of this sheet.

What the study involves

This study involves learning a number of 5-point pattern sequences presented on a 3 x 3 grid by monitoring these patterns with your eyes, and then engaging in rhythmically paced, memory-guided rehearsal of these patterns. We will use eye-tracking methods to monitor your eye movements during this task. We will spend about 10-15 minutes explaining things to you before you begin and filling out some paperwork with you, and a few minutes settling you into the scanner and adjusting the eyetracker to see your eyes. The experiment will then run for about 40 minutes. After the experiment we will spend a few minutes explaining the experiment to you

in more detail for your information, and asking you a few questions about your experience.

Eye tracking

While you are making those responses, your eye movements will be monitored using a camera and the data will be recorded by the eye tracking device and its software. Only data about the movements themselves will be recorded. We will not store images of your eye, and no images of your face will be taken or recorded.

What are the potential benefits of taking part?

Please note that this study is for research purposes and there are no direct benefits to subjects. However, it is hoped that your participation will help researchers learn more about how the brain learns and controls rule-based eye movements.

Confidentiality- who will have access to the data?

All information that will be collected about you during the course of the research will be kept strictly confidential. Any information about you will have your name and address removed so that you cannot be recognized from it. Only Ms. Mills, Prof. Ramnani, and Dr. Argyropoulos will have access to your raw data.

Your rights

You do not have to take part in this study if you don't want to. If you decide to take part, then you may withdraw at any time without having to give a reason. If you are a student at Royal Holloway, your decision whether or not to take part will not affect your education in any way. You are free not to answer any question if you prefer not to. Please keep this part of the sheet for reference and contact us with any queries. Please also feel free to ask any questions before you complete the consent form below, then hand the completed consent form to the researcher. It will be stored separately from the anonymous information you provide for the research project. This study has been reviewed and approved by the Psychology Department's internal ethical procedure at Royal Holloway.

Thank you for considering taking part in this study

Appendix 2: Study 1 Behavioural Consent Form

Consent form

ID number……………….

Learning Oculomotor Behaviours: Sequence Learning and Eye-Tracking

You have been asked to participate in a study about the brain processes that underlie eye movements, which is being carried out by Ms. Mills, Prof. Ramnani, and Dr. Argyropoulos.
 Have you (please circle yes or no):

- Read the information sheet about the study?   yes   no
- Understood that the study is solely for scientific research purposes?   yes   no
- Had an opportunity to ask questions?   yes   no
- Got satisfactory answers to your questions?   yes   no
- Understood that all data collected will be kept strictly confidential   yes   no
  and that any published findings will retain your anonymity?
- Understood that any personal information (such as your age   yes   no
  or occupation) will be used only for creating general statistics?
- Understood that the study will involve recording of what you   yes   no
  will be looking at, but not showing pictures of you.
- Understood that you're free to withdraw from the study   yes   no
  at any time, without giving a reason (and without it
  affecting your education if applicable)?
- Do you agree to take part in the study ?   yes   no

Signature_____

Name in block letters _____

Date_____ Date of Birth_____; Sex (M/F):_____

NB: This consent form will be stored separately from the anonymous information you provide.

Appendix 3: fMRI Consent Form

INFORMATION FORM

These notes give some information about an fMRI study in which you are invited to take part.

FMRI is a method for producing images of the activity in the brain as people carry out various mental tasks. It involves placing the participant inside a large, powerful magnet which forms part of the brain scanner. When particular regions of the brain are active, they require more oxygen, which comes from red corpuscles in the blood. As a result, the flow of blood increases. This can be detected as changes in the echoes from brief pulses of radio waves. These changes can then be converted by a computer into 3D images. This enables us to determine which parts of the brain are active during different tasks.

As far as we know, this procedure poses no direct health risks. However, the Department of Health advises that certain people should NOT be scanned. Because the scanner magnet is very powerful, it can interfere with heart pacemakers and clips or other metal items which have been implanted into the body by a surgeon, or with body-piercing items. If you have had surgery which may have involved the use of metal items you should NOT take part. Note that only ferro-magnetic materials (e.g. steel) are likely to cause significant problems. Thus normal dental amalgam fillings do not prohibit you from being scanned, though a dental plate which contained metal would do so, and you would be asked to remove it. You will be asked to remove metal from your pockets (coins, keys), remove articles of clothing which have metal fasteners (belts, bras, etc), as well as most jewellery. Alternative clothing will be provided as necessary. Watches and credit cards should not be taken into the scanner since it can interfere with their operation. You will be asked to complete a questionnaire (the Initial Screening Form) which asks about these and other matters to determine whether it is safe for you to be scanned. In addition, you are asked to give the name and address of your Family Doctor. This is because there is a very small chance that the scan could reveal something which required investigation by a doctor. If that happened, we would contact your doctor directly. By signing the consent form, you authorise us to do this. You will also be asked to complete a second, shorter, screening form immediately before the scan.

To be scanned, you would lie on your back on a narrow bed on runners, on which you would be moved until your head was inside the magnet. This is rather like having your head put inside the drum of a very large front-loading washing machine. The scanning process itself creates intermittent loud noises, and you would wear ear-plugs or sound-attenuating headphones. We would be able to talk to you while you are in the scanner through an intercom. If you are likely to become very uneasy in this relatively confined space (suffer from claustrophobia), you should NOT take part in the study. If you do take part and this happens, you will be able to alert the experimenters by activating an alarm and will then be removed from the scanner quickly. It is important that you keep your head as still as possible during the scan, and to help you with this, your head will be partially restrained with padded headrests. We shall ask you to relax your head and keep it still for a period that depends on the experiment but may be more than one hour, which may require some effort on your part. If this becomes unacceptably difficult or uncomfortable, you may demand to be removed from the scanner.

You may be asked to look at a screen through a small mirror (or other optical device) placed just above your eyes and/or be asked to listen to sounds through headphones. You may be asked to make judgements about what you see or asked to perform some other kind of mental task. Details of the specific experiment in which you are invited to participate will either be appended to this sheet or else given to you verbally by the experimenter. Detailed instructions will be given just before the scan, and from time to time during it.

The whole procedure will typically take about 1 hour, plus another 15 minutes to discuss with you the purposes of the study and answer any questions about it which you may raise. You will be able to say that you wish to stop the testing and leave at any time, without giving a reason. This would not affect your relationship with the experimenters in any way. The study will not benefit you directly, and does not form part of any medical diagnosis or treatment. If you agree to participate you will be asked to sign the initial screening form that accompanies this information sheet, in the presence of the experimenter (or other witness, who should countersign the form giving their name and address, if this is not practical). It is perfectly in order for you to take time to consider whether to participate, or discuss the study with other people, before signing. After signing, you will still have the right to withdraw at any time before or during the experiment, without giving a reason.

The images of your brain will be held securely and you will not be identified by name in any publications that might arise from the study. The information in the two screening forms will also be treated as strictly confidential and the forms will be held securely until eventually destroyed.

Further information about the specific study in which you are invited to participate may have been appended overleaf, if the experimenter has felt that this would be helpful. Otherwise, he/she will already have told you about the study and will give full instructions prior to the scan. Please feel free to ask any questions about any aspect of the study or the scanning procedure before completing the initial screening form.

ROYAL HOLLOWAY, UNIVERSITY OF LONDON - MAGNETIC RESONANCE IMAGING UNIT

INITIAL SCREENING FORM

NAME OF PARTICIPANT ………………………………………………… Sex: M / F

Date of birth……………………… Approximate weight in kg………… (one stone is about 6.3 kg)

Please read the following questions CAREFULLY and provide answers. For a very small number of individuals, being scanned can endanger comfort, health or even life. The purpose of these questions is to make sure that you are not such a person.

You have the right to withdraw from the screening and subsequent scanning if you find the questions unacceptably intrusive. The information you provide will be treated as strictly confidential and will be held in secure conditions.

Delete as appropriate

1. Have you been fitted with a pacemaker or artificial heart valve?	YES/NO
2. Have you any aneurysm clips, shunts or stents in your body or a cochlear implant?	YES/NO
3. Have you ever had any metal fragments in your eyes?	YES/NO
4. Have you ever had any metal fragments, e.g. shrapnel in any other part of your body?	YES/NO
5. Have you any surgically implanted metal in any part of your body, other than dental fillings and crowns (e.g. joint replacement or bone reconstruction)	YES/NO
6. Have you ever had any surgery that might have involved metal implants of which you are not aware?	YES/NO
7. Do you wear a denture plate or brace with metal in it?	YES/NO
8. Do you wear a hearing aid?	YES/NO
9. Have you ever suffered from any of: epilepsy, diabetes or thermoregulatory problems?	YES/NO
10. Have you ever suffered from any heart disease?	YES/NO
11. Is there any possibility that you might be pregnant?	YES/NO
12. Have you been sterilised using clips?	YES/NO
13. Do you have a contraceptive coil (IUD) installed?	YES/NO
14. Are you currently breast-feeding an infant?	YES/NO

I have read and understood the questions above and have answered them correctly.

SIGNED……………………………… DATE…………………………

In the presence of ……………………………….. (name) ………………………………..(signature)

Address of witness, if not the experimenter:

Please enter below the name and address of your doctor (general practitioner).
(Not required for persons entering the controlled area but not being scanned.)

Appendix 4: Study 1 Demographic Questionnaire

1) Are you left or right handed?

2) What is your age (in years?)

3) What is your weight?

4) Do you wear contact lenses or glasses, or have any vision difficulties?

5) What colour are your eyes?

6) Do you have an difficulties with colour vision?

7) Have you ever had any kind of surgery? If so, what kind and how long ago?

8) Do you have any metal implants or non-removable piercings?

9) Do you have any dental fillings or crowns?

10) Do wear a permanent denture plate or brace with metal in it?

11) Do you have a pacemaker or artificial heart valve?

12) Do you have any aneurysm clips or shunts in your body?

13) Do have a cochlear implant?

14) Is it possible that any metal fragments e.g. shrapnel may have accidentally entered your body?

15) Is there a possibility that you may be pregnant?

16) Have you had a contraceptive coil installed?

17) Do you use a hearing aid?

18) Do you have any tattoos?

19) Do you, or have you ever suffered from claustrophobia?

20) Do you, or have you ever suffered from any psychiatric or neurological disorders?

21) Do you, or have you ever suffered from epilepsy, diabetes, or thermoregulatory problems?

22) Have you ever suffered from any heart disease?

23) Are you currently taking any medication? If so, what kind?

Appendix 5: Studies 2 and 3 Information Sheet

Department of Psychology
Egham, Surrey TW20 0EX, UK

Participant Information Sheet
Eye Movements and Useful Field of Vision Across The Lifespan
Information specific to the study

This study is being conducted by the following researchers at Royal Holloway, University of London:

Ms. Jennifer Mills Jennifer.Mills.2009@live.rhul.ac.uk   +44 (0) 1784 443703
Prof. Narender Ramnani N.Ramnani@rhul.ac.uk   +44 (0) 1784 443519
Dr. Georgios P. Argyropoulos Georgios.Argyropoulos@rhul.ac.uk +44(0) 1784 443 519

You are being invited to take part in a research study. Before you decide, it is important for you to understand why the research is being done and what it will involve. Please take the time to read the following information carefully to decide whether or not you wish to take part. Please ask if there is anything that is not clear or if you would like more information.

Purpose of the study

We are studying how rule-based eye movements are learned, how they adapt to conflicting information, and how this skilled learning relates to acuity in the visual field. The results of this study are intended to be used for my PhD thesis with the further intention of preparation for publication in scientific journals.

Who is organising this study?

Prof. Ramnani and Ms. Mills have organised this study and will be very happy to answer any questions you may have concerning the procedures you will be asked to undertake. They may be contacted at the address shown at the top of this sheet.

What the study involves

This study involves two separate tasks:

(1): Identifying the characteristics of a number of varied shapes which are presented at different locations on the screen, all whilst looking at the centre of the screen.

(2): Learning the associations between colours and where to move your eyes on the screen. The colours used to guide these eye movements will be presented in different areas of a shape in the centre of a screen.

We will use eye-tracking methods to monitor your eye movements during this task. We will spend about 10 minutes explaining things before you begin and filling out some paperwork with you, and a few minute adjusting the eyetracker to see your eyes. The experiment will run for around 45 minutes. After the experiment, we will spend a few minutes explaining the experiment to you in more detail for your information, and asking you a few questions about your experience

Eye tracking

While you are making those responses, your eye movements will be monitored using a camera and the data will be recorded by the eye tracking device and its software. Only data about the movements themselves will be recorded. We will not store images of your eye, and no images of your face will be taken or recorded.

What are the potential benefits of taking part?

Please note that this study is for research purposes and there are no direct benefits to subjects. However, it is hoped that your participation will help researchers learn more about how the brain learns and controls rule-based eye movements.

Confidentiality- who will have access to the data?

All information that will be collected about you during the course of the research will be kept strictly confidential. Any information about you will have your name and address removed so that you cannot be recognized from it. Only Ms. Mills and Professpr Ramnani will have access to your raw data.

Your rights

You do not have to take part in this study if you don't want to. If you decide to take part, then you may withdraw at any time without having to give a reason. If you are a student at Royal Holloway, your decision whether or not to take part will not affect your education in any way. You are free not to answer any question if you prefer not to. Please keep this part of the sheet for reference and contact us with any queries. Please also feel free to ask any questions before you complete the consent form below, then hand the completed consent form to the researcher. It will be stored separately from the anonymous information you provide for the research project. This study has been reviewed and approved by the Psychology Department's internal ethical procedure at Royal Holloway.

Thank you for considering taking part in this study

Appendix 6: Studies 2 and 3 Consent Form

Consent form

Learning Oculomotor Behaviours: Sequence Learning and Eye-Tracking

You have been asked to participate in a study about the brain processes that underlie eye movements, which is being carried out by Ms. Mills, Prof. Ramnani, and Dr. Argyropoulos.

Have you (please circle yes or no):

- Read the information sheet about the study?   yes   no
- Understood that the study is solely for scientific research purposes?yes no
- Had an opportunity to ask questions?   yes   no
- Got satisfactory answers to your questions?   yes   no

- Understood that all data collected will be kept strictly confidential   yes   no
  and that any published findings will retain your anonymity?

- Understood that any personal information (such as your age   yes   no
- or occupation) will be used only for creating general statistics?

- Understood that the study will involve recording of what you   yes   no
  will be looking at, but not showing pictures of you.

- Understood that you're free to withdraw from the study   yes   no
  at any time, without giving a reason (and without it
  affecting your education if applicable)?

- Do you agree to take part in the study ?   yes   no

Signature_____

Name in block letters_____

Date_____ Date of Birth_____; Sex (M/F):_____

NB: This consent form will be stored separately from the anonymous information you provide.

Appendix 7: Studies 2 and 3 Participant Questionnaire

Participant Questionnaire:

1. What is your age? _____

2. What is your sex (M/F)? _____

3. Are you able to drive? _____ If so, for how many years have you been driving? _____

4. Do you engage in any sports/exercise? _____ If so, what type (e.g. swimming)

   _____

5. How many hours per week do you engage in sports/exercise?

   _____

6. What is your eyesight/prescription? _____

7. If needed, at what age did you start wearing glasses? _____

8. Have you noticed any other issues with your eyesight? If so, please list here:

   _____

9. Do you have any history of neurological disorders?

   _____

10. Do you have any history of psychiatric disorders?

    _____

11. Do you have any history of cerebrovascular disorder (e.g. stroke)?

    _____

Appendix 8: Study 5 Recruitment Letter

«ADDRESS1»
«ADDRESS2»
«POSTALTOWN»
«COUNTY»
«POSTCODE»

01 February 2018

Dear «FORENAME»,

As discussed on the telephone, we are currently undertaking studies at the Transport Research Laboratory (TRL) as part of the behaviour research programme within the Psychology Department at Royal Holloway University of London. We are interested in eye movements during route learning in drivers. Our interests are focused on the types of eye movements made during driving in different environments, and how this may differ with age. The results will help inform us about how safe driving behaviours may be aided by skilled visual techniques.

I am writing to confirm your agreement to participate in our research at «TTIME1» on «TDAY1», «TDATE1» at the Transport Research Laboratory (Crowthorne House, Nine Mile Ride, Wokingham, Berkshire, RG40 3GA. Tel: 01344 773131). The study involves various computer-based driving simulation tasks and will typically take between 1.5 to 2 hours to complete. During these tasks, the movements of your eyes will be monitored. No images or recordings of your eyes will be captured or stored – we will simply store a plot of where you look when driving in various situations. A payment of £30 will be made as compensation for your time and reimbursement of your travelling expenses.

In preparation for the study, we would be very grateful if you could complete the enclosed consent form and participant questionnaire. Please remember to bring this along to TRL on the day of the study.

If you have any queries you may contact us by email Jennifer.Mills.2009@live.rhul.ac.uk or shelman@trl.co.uk We greatly appreciate your participation in this research programme, which has been funded by Royal Holloway University and the Transport Research Laboratory. I have also attached an information sheet for your convenience.

Yours sincerely

Jennifer Mills,
PhD Student

Appendix 9: Study 5 Information Sheet

Department of Psychology

Royal Holloway, University of London
Egham, Surrey TW20 0EX, UK
www.rhul.ac.uk

Information Sheet

Project title - Skill Learning: Brain Systems, Eye Movements and Driver Behaviour

My name is Jennifer Mills and I am a PhD researcher at Royal Holloway, University of London. I am carrying out a study with Dr Shaun Helman (TRL) and Dr Narender Ramnani (Royal Holloway) on the types of eye movements and driver behaviours made when navigating simulated driving routes in different types of environment. We would be very grateful for your participation with this study, as we are aiming to determine which different types of eye movements underpin the navigation of different driving routes.

If you decide to take part, I will ask you to conduct a series of short simulated driving routes on a mini (desktop) driving simulator. There will be regular breaks and you will be able to opt out for any reason at any point during the course of the experiment. During the study, I will monitor your eye movements using an eye-tracker. This will analyse the location of your pupils and will at no point record or store any images or videos of your eyes – it will simply tell me where you looked during the drive. The study will take place at the Transport Research Laboratory (TRL) and will typically take between 1.5 to 2 hours to complete. Nobody except myself and the immediate research team will be allowed to see your data, and your information will be stored securely and confidentially.

Your participation in this experiment is entirely voluntary. You do not have to take part in this study if you do not want to, and you are free to withdraw at any time without having to give a reason. You will receive £30 for your participation.

Please keep this part of the sheet yourself for reference. Please feel free to ask any questions before you complete the consent form below, then hand the completed consent form to the researcher on the day of the study. It will be stored separately from the anonymous information you provide for the research project. This study has been reviewed and approved by the Psychology Department internal ethical procedure at Royal Holloway, University of London, and is also cleared by a TRL research ethics panel.

If you would like to ask further questions or discuss any aspect of the research with me please feel free to email (jennifer.mills.2009@live.rhul.ac.uk). Alternatively, you can contact Shaun Helman directly (shelman@trl.co.uk).

Appendix 10: Study 5 Consent Form

Eye Movements and Driver Behaviour Consent Form   ID:

You have been asked to participate in a study about eye movements and simulated driving behaviour being carried out by Jennifer Mills. Have you (please circle yes or no):

- Read the information sheet about the study?   yes   no
- Had an opportunity to ask questions?   yes   no
- Got satisfactory answers to your questions?   yes   no
- Understood that you're free to withdraw from the study
  at any time, without giving a reason   yes   no

    Do you agree to take part in the study ?   yes   no

Signature   _____

Name in block letters   _____

Date   _____

NB: **Please remember to bring this form with you when you attend the session at TRL.** This consent form will be stored separately from the anonymous information you provide elsewhere.

Appendix 11: Study 5 Participant Questionnaire

Participant Questionnaire

- Name _____

- Age   _____

- Sex (Please Circle)   Male   /   Female

- Date of Birth _____

- How many years have you been driving?   _____

- Do you have from any vision problems? If so, please give details

  _____

- Do you wear glasses? _____

- Are you short or long sighted? _____

- Do you have a history of neurological disorder? If so, please give

  details _____

- Do you have a history of psychological disorder? If so, please give

  details _____

- Do you have a history of cardiovascular disorder? If so, please give

  details _____

- What is your highest level of education? _____

- Do you hold any advance driving qualifications e.g. Police, IAN,

  RoSPA? If so, please give details _____

  _____

Appendix 12: Study 5a Participant Information Sheet

Participant Information Sheet – Section 1

- You will be asked to complete 8 short city drives
- This section will last 30 minutes in total
- Please drive in the 2nd lane from the left during long stretches and make junction manoeuvres as you naturally would
- You will see direction cues on the screen prompting you when to make manoeuvres, please continue forward otherwise
- At the end of the direction signs, there will be a small number. Please read these out loud when they appear
- Please drive at 30 mph, you will see the speed on the virtual dashboard
- Please keep the car in neutral in between drives
- There will be no other traffic in these drives
- Ignore the stop signs and traffic lights if they are red, continue driving
- Feel free to drive over small roundabouts in order to ensure smooth manoeuvres
- Please try to keep your hands at 10 to 2 on the steering wheel and move your head and body as little as possible, this will help the eye tracker to detect your eyes
- Please ask for a break in between drives whenever you feel you need it
- Please ask any questions before we begin

Appendix 13: Study 5b Participant Information Sheet

Participant Information Sheet – Section 2

- You will be asked to complete 19 short city drives
- This section will last 30 minutes in total
- There will be traffic during these drives, please interact with the traffic in the way you normally would
- You will hear auditory cues prompting you when to make manoeuvres, please continue forward otherwise
- Please drive at 30 mph, you will see the speed on the virtual dashboard
- Please keep the car in neutral between drives
- Please adhere to the traffic lights
- Please try to keep your hands at 10 to 2 on the steering wheel and move your head and body as little as possible, this will help the eye tracker to detect your eyes
- Please ask for a break in between drives whenever you feel you need it
- Please ask any questions before we begin

Appendix 14: Study 5c Participant Information Sheet

Participant Information Sheet – Section 3

- You will be asked to complete 18 short motorway drives
- This section will last 30 minutes in total
- You will see directions on the screen prompting you when to change lanes, please stay in the middle lane otherwise
- At the end of the direction signs, there will be a small number. Please read these out loud when they appear
- Please drive as you usually would in a motorway environment
- Please keep the car in neutral in between drives
- There will be no other traffic in these drives
- Please try to keep your hands at 10 to 2 on the steering wheel and move your head and body as little as possible, this will help the eye tracker to detect your eyes
- Please ask for a break in between drives whenever you feel you need it
- Please ask any questions before we begin

Appendix 15: Study 5 Debriefing Statement

Department of Psychology
Royal Holloway, University of London
Egham, Surrey, TW20 0EX
www.rhul.ac.uk

Debriefing Statement

Eye movements, skill learning and driver behaviour

The aim of this research was to understand the types of eye movements and driving behaviours made during navigating routes which are more or less familiar to a driver. Specifically, we were examining whether eye movements are made in anticipation of stimuli in familiar visual environments, and the way in which this may help us to automate routine safe driver behaviours, as well as enable us to navigate potentially hazardous road situations. We are also attempting to understand if the types of eye movements in which we are interested vary with the age of the driver. Thus, in this study there were two groups of participants; one group comprised individuals over 60, and the other comprised individuals aged up to 30.

In order to ensure we saw learning effects, you were not made aware that there would be different amounts of exposure to different routes. This manipulation was for experimental purposes and has been deemed to cause no risk of psychological distress or discomfort by the ethics panel of Royal Holloway, University of London.

The results of this study will be stored anonymously and will be kept confidential. Any data used for consequent publication in academic journals will not permit identification of any individuals in the study.

Please keep a copy of this debriefing summary for your reference. If you have any further questions please contact myself, Jennifer Mills, at jennifer.mills.2009@live.rhul.ac.uk or Dr Shaun Helman at shelman@trl.co.uk.

If you have questions about your rights as a participant in this research, or if you feel that you have been placed at risk, you may contact the Chair of the Ethics Committee, School of Psychology, Royal Holloway, University of London, Egham, Surrey, TW20 0EX.
Phone: (+44) 01784 443715. Email: Hanna.Zagefka@rhul.ac.uk

Thank you for your participation with this research.