Attentional refocusing between time and space in older adults: Investigation of neural mechanisms and relation to driving

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Older adults have a disproportionately high risk of causing collisions at intersections and causing collisions by failing to notice surrounding road signs or signals. Collisions caused by older drivers seem to result from attentional failures. There is limited research exploring the ability to refocus from orienting attention to events changing in time (i.e. temporal attention) to distributing attention spatially (i.e. spatial attention), a process that is particularly important while driving and, if impaired, could cause collisions. The aims of the project were firstly to assess whether the ability to refocus attention from time to space changes throughout the adult lifespan when assessed with a computer-based task and in an ecologically valid scenario during simulated driving, secondly, to use magnetoencephalography (MEG) to identify changes to neural mechanism that might explain difficulties in attentional refocusing, and finally, use mobile electroencephalography to explore the neural mechanisms involved in attentional refocusing while driving. Results demonstrated age-related declines in the ability to refocus attention from time to space both in a computer-based task and during simulated driving. MEG recorded in a computer-based attention refocusing task revealed that, compared to younger adults, older and middle-aged adults displayed task-related theta deficits in lower level visual processing areas, and instead, displayed compensatory increases in theta power and phase-related connectivity across frontal regions. Increased frontal lobe recruitment likely reflects enhanced top-down attention to cope with impaired lower level attention mechanisms, supporting compensatory recruitment models of ageing. During simulated driving, older participants displayed slower driving speeds and weaker beta desynchronization in preparation to read a road sign, instead displaying a stronger theta power increase in response to the road sign, further demonstrating neural and behavioural compensatory strategies that are only partially successful. Findings warrant the development of a training programme to improve attentional refocusing between time and space while driving.

Keywords: Visual spatial attention. Visual temporal attention. Ageing. Magnetoencephalography. Driving.

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Contents

List of abbreviations

ACC	Anterior cingulate cortex
ACE-3	Addenbrookes cognitive examination 3
ANOVA	Analysis of variance
ARCHA	Aston Research Centre for Healthy Ageing
AST	Attention switching task
CANTAB	Cambridge Neuropsychological Test Automated Battery
CRT	Choice response time
CRUNCH	Compensation-Related Utilization of Neural Circuits Hypothesis
d’	D prime
DBQ	Driving behaviour questionnaire
DICS	Dynamic imaging of coherent sources
EEG	Electrocencephalography
ELSA	Early to late shift in ageing
ERP	Event related potential
FFT	Fast Fourier Transform
fMRI	Functional magnetic resonance imaging
HAROLD	hemispheric asymmetry reduction in older adults
HPI	Head Position Indicator
ICA	Independent component analysis
IFG	Inferior frontal gyrus
IPL	Intraparietal lobule
IPS	Intraparietal sulcus
LCMV	Linearly constrained minimum variance
m	Meters
MCC	Median cingulate cortex
MEG	Magnetoencephalography
MFG	Middle frontal gyrus
mm	Millimetre
MNI	Montreal Neurological Institute
mph	Miles per hour
MRI	magnetic resonance imaging
ms	Milliseconds
MST	Minimum spanning tree
MTG	Middle temporal gyrus

NBS	Network based statistics
NTVA	Neural Theory of Visual Attention
PAC	Phase amplitude coupling
PASA	Posterior to anterior shift in ageing
PCA	Principal component analysis
PCC	Posterior cingulate cortex
PET	Positron emission tomography
PFC	Prefrontal cortex
PLI	Phase lag index
PLV	Phase locking value
RGB	Red-green-blue
RNG	Random number generation
RPM	Revolutions per minute
RSVP	Rapid serial visual presentation
RT	Response time
RVP	Rapid visual
s	Seconds
SD	Standard deviation
SE	Standard error
SFG	Superior frontal gyrus
SNR	Signal to noise
SPSS	Statistical Package for Social Sciences
SRT	Simple response time
STAC	scaffolding theory of aging and cognition
tDCS	Transcranial direct current stimulation
TFR	Time-frequency representation
TPJ	Transcranial magnetic stimulation
UFOV	Useful field of view
VS	Visual search
wPLI	Weighted phase lag index

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Chapter 1

Introduction

1.1 Introduction

1.1.1 Older drivers

Driving cessation can be detrimental to older adults' independence and has been shown to be a risk factor in developing depression (Marottoli et al., 1997; Ragland, Satariano, & MacLeod, 2005; Windsor, Anstey, Butterworth, Luszcz, & Andrews, 2007). Identifying age-related changes in cognition that contribute towards reduced driving performance is the first step in a trajectory of research towards developing an intervention to improve older adults' driving. This could lead to long-term advantages such as prolonging the time that people can continue to drive and help to preserve their independence.

At-fault collision statistics show that, while older adults have an overall reduced crash risk in comparison to young drivers, they present a disproportionate risk of at-fault collisions at intersections and collisions caused by a failure to give way, or to notice other objects, stop signs or signals (Arai & Arai, 2015; Guo, Brake, Edwards, Blythe, & Fairchild, 2010; Hakamies-Blomqvist, 1993; McGwin & Brown, 1999). Consistent with higher risks at intersections (Hakamies-Blomqvist, 1993), in their seminal work Parasuraman and Nestor (1991) concluded that older drivers' accidents were often due to failures in attention, particularly selective attention and switching. These findings are consistent with older drivers' own self-perceptions, who have reported an increased difficulty to read and process signs in time (Musselwhite & Haddad, 2010). It is therefore a viable hypothesis that changes in spatial attention and refocusing attention are having an impact on driving skills later in life.

Further support for age-related attentional impairments contributing to higher collision risks at intersections come from experimental driving simulator studies (Belanger, Gagnon, & Yamin, 2010; Cuenen et al., 2015; Dotzauer, Caljouw, de Waard, & Brouwer, 2013; Henderson, Gagnon, Collin, Tabone, & Stinchcombe, 2013; Henderson et al., 2015). For example, Belanger et al. (2010) found that older drivers reacted to events appropriately in the driving simulator when the event required only a single braking response and was predictable, which allowed them time to allocate attention to the event, however were more likely to crash when an event required multiple responses in parallel and was less predictable. These findings are reminiscent of dual-task driving simulator experiments, where older participants display reduced ability to complete dual-tasks in the driving simulator (Cantin, Lavalliere, Simoneau, & Teasdale, 2009). Age-related impairments in dual-task performance have important implications for on-road driving, which frequently requires processing and responding to multiple events in parallel, and results further emphasise the need to assess whether there is an age-related decline in the ability to refocus attention while driving.

1.1.2 Spatial attention

Spatial selective attention is often measured with visual search (VS) paradigms, where participants are presented with an array of visual stimuli and are required to make a speeded response to the detection of a predefined visual target stimulus (Bennett, Motes, Rao, & Rypma, 2012; Foster, Behrmann, & Stuss, 1995; Humphrey & Kramer, 1997; Li, Gratton, Fabiani, & Knight, 2013; Plude & Doussardroosevelt, 1989). There is extensive research demonstrating the relationship between spatial attention and driving performance and exploring how this changes with age (Ball et al., 2006; Cuenen et al., 2015; Hennessy, 1995; Hoffman, McDowd, Atchley, & Dubinsky, 2005; Leversen, Hopkins, & Sigmundsson, 2013; Richardson & Marottoli, 2003). However, poor spatial attention does not result in poor driving in all older individuals (Vaucher et al., 2014). These findings highlight the need to further investigate attentional deficits in older drivers and identify the factors that determine whether deficits in attention affect driving performance.

There is a consensus that there is no specific decline in VS performance with healthy aging when the target is distinct from the distractors and “pops out” of the display - i.e. a pop-out search - (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt, 1989). Although older adults show increased response times (RTs) to detect targets in pop-out searches in comparison to young adults, age group differences in RTs remain constant with increasing numbers of distractors (Plude & Doussardroosevelt, 1989) and have therefore been attributed to general slowing (Foster et al., 1995). In contrast, VS performance is thought to decline with age when the target is visually indistinct from distractors (i.e. in so-called “conjunction search”, where targets are defined as a combination of features shared with the distractors) and a serial search is required (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt, 1989). The increase in RTs with increasing numbers of distractors gets steeper with age, suggesting a specific deficit in serial VS rather than a general slowing of RTs.

It is often argued that older adults have deficits in inhibiting irrelevant visual information (Adamo, Westerfield, Haist, & Townsend, 2003; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig, Hasher, & Zacks, 2007; Maciokas & Crognale, 2003). It may be that poor selective attention is caused by deficits in inhibitory mechanisms. Competition models of visual selective attention (Beck & Kastner, 2009; Bundesen, Habekost, & Kyllingsbæk, 2005; Desimone, 1998; Scalf, Torralbo, Tapia, & Beck, 2013; Treisman & Gormican, 1988) and evidence from single cell recordings (Reynolds, Chelazzi, & Desimone, 1999) suggest that multiple stimuli are processed in parallel but in separate cell groups (Luck, Girelli, McDermott, & Ford, 1997). Visual stimuli compete for processing resources and attention is implemented to bias excitation in favour of salient and task relevant stimuli. The Neural Theory of Visual Attention (NTVA; Bundesen et al., 2005) proposes that attention works to increase or decrease the number of cells involved in processing each object and alters the firing rate of neurons coding for certain features. Impairments in these excitatory-inhibitory attentional mechanisms may lead to difficulties in inhibiting irrelevant visual information and exciting target stimuli in older adults. This hypothesis would explain older participants' disproportionately increased number and duration of saccadic eye movements on serial searches (Porter et al., 2010). In contrast, Lien, Gemperle, and Ruthruff (2011) demonstrated that older and younger participants were equally able to attend to task-relevant stimuli and inhibit salient but irrelevant stimuli. However, it may be that the salience of the distractors aided inhibition due to the distinct visual features prompting a strong inhibitory response. Thus, deficits in excitatory-inhibitory mechanisms could lead to difficulties in selective attention.

There is evidence to suggest that older adults compensate for excitatory-inhibitory deficits with top-down control of attention. Neider and Kramer (2011) found that older participants not only benefited more than younger participants from using contextual information in a VS within a realistic scene, but also displayed greater costs to their performance when the location of the VS target was incongruent with its contextual information. Furthermore, McLaughlin and Murtha (2010) found that older adults utilized cues more than younger people in a VS task. Similarly, Watson and Maylor (2002) demonstrated that the benefits of visual marking were preserved in adults aged 65-80 years. Visual marking is where a proportion of distractors within a VS task is shown before the onset of the remaining distractor stimuli and the target stimulus, enabling top-down driven inhibition of the distractors that were presented first. However, the benefits of visual marking were not preserved in older adults when VS items were moving. Previous research has demonstrated that older participants have higher motion detection thresholds (Conlon & Herkes, 2008; Henderson, Gagnon, Belanger, Tabone, & Collin, 2010) and find it more difficult to judge the speed of moving stimuli and vehicles (Norman, Ross, Hawkes, & Long, 2003; Schiff, Oldak, & Shah, 1992; Scialfa, Ference, Boone, Tay, & Hudson, 2010; Snowden & Kavanagh, 2006). The absence of visual marking of moving stimuli in older adults could therefore be due to difficulties in processing moving stimuli. Together findings suggest that older participants may rely more on top-down processes to compensate for declines in excitatory-inhibitory mechanisms in attention.

1.1.3 Temporal attention

In addition to the importance of spatial attention in driving, the allocation of attention to events changing in time, i.e. temporal attention, is important to be able to attend, process and respond to rapidly changing visual stimuli in a dynamic environment such as driving. It is well established that older adults require longer to process visual stimuli - i.e. have slower processing speeds (Ball et al., 2006; Rubin et al., 2007) - and display an increased magnitude of the so-called "attentional blink" (Lahar, Isaak, & McArthur, 2001; Lee & Hsieh, 2009; Maciokas & Crognale, 2003; Shih, 2009; van

Leeuwen, Müller, & Melloni, 2009). The attentional blink is the reduced ability to detect a second target (T2) in a rapidly changing stream of stimuli - i.e. a rapid serial visual presentation (RSVP) stream - up to 500ms after detecting a first target (T1) in the stream (Raymond, Shapiro, & Arnell, 1992). This effect is inflated and lasts for an increasing length of time with increased age. There is evidence to suggest that, whereas individuals in their 60s have no difficulties in temporal attention (Lee & Hsieh, 2009; Quigley, Andersen, & Mueller, 2012), difficulties may begin to develop between the ages of 70-80 years (Conlon & Herkes, 2008; Shih, 2009). Conlon and Herkes (2008) concluded that impairments were due to slowed processing speed. However, age-related deficits observed in other temporal attention tasks have been demonstrated not to be due to general slowing (Lee & Hsieh, 2009; Maciokas & Crognale, 2003). Difficulties in temporal attention in those aged over 70 years could therefore be due to a specific decline in selective attentional mechanisms and could share the same underlying cause as difficulties in spatial selective attention, i.e. in excitatory-inhibitory selective attention processes, where excitatory mechanisms fail to respond to the target and inhibitory mechanisms fail to mitigate interference from the distractors in the RSVP stream.

1.1.4 Switching attention between time and space

Equally vital to safe driving, particularly at intersections, is the ability to switch between temporal and spatial attention. For example, when driving, one must switch from attending to fast moving and changing cars on the road ahead, to distributing attention across space to attend to road signs and surrounding hazards.

Although there has been very little research on switching between different modalities of attention in any age group, there is a vast literature demonstrating inflated switch-costs with increased age in task switching paradigms (Cepeda, Kramer, & de Sather, 2001; Gamboz, Borella, & Brandimonte, 2009; Gold, Powell, Xuan, Jicha, & Smith, 2010). Information about older adults' attentional flexibility also comes from dual-task paradigms, which have demonstrated that older participants are poorer at efficiently dividing attentional resources compared to younger adults, even when tasks seem to depend on different cognitive processes (Hawkes, Siu, Silsupadol, & Woollacott, 2012; Liston, Bergmann, Keating, Green, & Pavlou, 2014; Maki, Zecevic, Bateni, Kirshenbaum, & McIlroy, 2001). For example, Hawkes et al. (2012) found that older adults displayed impaired balance when switching their attention between a motor task and a cognitive task. Impairments in the ability of middle and older age groups to distribute attentional resources was also presented by Tsang (2013) in a dual-task paradigm. Participants were presented with a single picture of an aeroplane, and had to make two judgements about the stimulus. Firstly, whether the left or right wing engine was the same colour as a central fixation cross, and secondly whether the plane had been presented in a previously memorised array of images (i.e. the Sternberg task; Sternberg, 1969). Participants were either instructed to complete the tasks in parallel, or were instructed to prioritise one or the other. The authors found the older and middle-aged groups were poorer at prioritising the visual discrimination task over the Sternberg task, an effect that was further inflated in the oldest group. Together these findings suggest that older participants are impaired at dual-task performance compared to younger adults and may be less able to prioritise which tasks to perform first, a deficit that appears to start in middle-age (50-59 years).

Despite the extensive research investigating dual-task and task switching performance in older age, there is limited research into age-related changes in the ability to switch between temporal and spatial attention. Jefferies et al. (2015) demonstrated that younger adults require less time than older adults to narrow their focus of attention from two RSVP streams to one, indicating that there may be an age-related decline in the redistribution of attention spatially from a single location. However, both RSVP streams remained on the screen. Rather than a deficit in switching to distribute attention spatially, increased times taken to divert attention may be due to an age-related impairment in disengaging from task irrelevant stimuli (Greenwood & Parasuraman, 1994). In a separate study by Lee and Hsieh (2009), participants switched from attending to an RSVP stream to identify a target, to allocating their attention in space to identify and point to a masked peripheral target in varying locations. Although the older age group displayed lower performance when the peripheral target was presented at 100, 300 and 700ms after the RSVP target onset, lower performance was exaggerated at 100 and 300ms. These findings show that older participants had greater difficulties in switching from temporal to spatial attention when there was 300ms or less between target onsets. Russell, Malhotra, Deidda, and Husain (2013) has since replicated these findings, further demonstrating that the impairment lasted for 450ms. However, Lee and Hsieh's (2009) aim was to investigate the attentional blink in older adults, and failed to distinguish between impaired task performance resulting from an increased attentional blink after processing the RSVP target, or due to increased switch-costs between temporal and spatial attention. Poorer performance at 100 and 300ms, but not 700ms, could equally be due to requiring longer to switch between temporal and spatial attention, or an extended attentional blink. A comparison of the relevant attentional blink and attention switching literature is presented in Table 1.1. The table compares the duration of the attentional blink in older age groups in addition to the duration of impairment from attention switching.

Table 1.1. Comparison of results from previous studies

	Author	Mean age (years)	Method	Duration of impairment
Attentional blink				
	Lahar et al. (2001)	68.70	Attentional blink	520ms
	Lee & Hsieh (2009)	59.30	Attentional blink	300ms. None at 700ms
	Maciokas & Crognale (2003)	64-79	Attentional blink	824ms
Switching				
	Jefferies et al. (2015)	66.40	Time taken to narrow focus from two to one RSVP stream	266ms
	Lee and Hsieh (2009)	55-62	Attention switch from temporal to spatial attention	300ms. None at 700ms
	Russel et al. (2013)	66.00	Attention switch from temporal to spatial attention	450ms

1.1.5 Neural mechanisms

Overlapping networks across occipital, frontal, parietal and motor regions have been implicated in both directing attention in time and space (Coull & Nobre, 1998; Fu, Greenwood, & Parasuraman, 2005; Gross et al., 2004; Li et al., 2013; Madden, Spaniol, Whiting, et al., 2007; Shapiro, Hillstrom, & Husain, 2002). Although Coull and Nobre (1998) found overlapping activation for both temporal and spatial attention in a functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) study, they found patterns of activation for the two types of attention were distinct. PET revealed that spatial orienting involved more activity in the inferior parietal lobule (IPL) and the left cerebellum, whereas temporal orienting triggered more activity in the left intraparietal sulcus (IPS) and left ventral premotor cortex, the latter of which was exclusive to temporal attention. The authors’ fMRI results displayed right IPS and temporo-parietal junction (TPJ) activity only in spatial orienting. Imaruoka, Yanagida, and Miyauchi (2003) found the right IPS was more involved in pop-out than serial search, implicating an involvement in bottom-up attention, while prefrontal regions have been implicated more generally in top-down executive control of attention (Badre & Wagner, 2004; Baluch & Itti, 2011; Bouvier, 2009; Kastner & Ungerleider, 2000; Kerns et al., 2004). In particular, the anterior cingulate cortex (ACC) has been shown to be involved in selective attention in more demanding tasks that require resolving conflict between incongruent or ambiguous information (Badre & Wagner, 2004; Kerns et al., 2004).

To reiterate, competition models of visual selective attention (Beck & Kastner, 2009; Bundesen et al., 2005; Desimone, 1998; Scalf et al., 2013; Treisman, 1985; Treisman & Gormican, 1988) and evidence from single cell recordings (Reynolds et al., 1999) suggest that multiple stimuli can be processed in parallel by separate cell groups (Luck et al., 1997) up to a certain stage of processing, but compete for resources at the level of access to processing in working memory, as proposed by Dehaene, Changeux, Naccache, Sackur, and Sergent (2006). Attention can therefore be conceived as a set of mechanisms that bias processing in favour of salient and task relevant stimuli through bottom-up as well as top-down signal enhancement (Dehaene et al., 2006). Similar to the notion proposed by Dehaene and colleagues (1998; 2006), the NTVA (Bundesen et al., 2005) suggests that attention works to increase or decrease the number of cells involved in processing each object and alters the firing rate of neurons coding for certain features. In an extension of the NTVA, it has been proposed that as temporal expectation increases, temporal attention works to increase the firing rate of neuronal populations that represent certain features. In contrast, one would expect spatial attention to alter the number of cell assemblies allocated to processing objects in the visual field (Bundesen et al., 2005; Vangkilde, Coull, & Bundesen, 2012; Vangkilde, Petersen, & Bundesen, 2013). Thus, it may be expected that switching between temporal and spatial attention would require the efficient re-allocation of cell assemblies to receptive fields, as well as changes to the firing rates of feature-coding neuronal populations. Based on Dehaene et al.'s (2006) framework, frontoparietal networks would be crucially involved in such top-down changes in selective enhancement, reflecting dynamic adjustments of expectations in space and time, by modulating the temporal and spatial dynamics of firing rates in posterior neuronal populations.

Accounts of ageing brain function

The literature has frequently demonstrated more widely distributed cortical responses in older compared to younger adults, particularly in frontal regions (Adamo et al., 2003; Lague-Beauvais, Brunet, Gagnon, Lesage, & Bherer, 2013; Li et al., 2013; Madden, Spaniol, Whiting, et al., 2007). It has been debated as to whether this increase in activity reflects increased neural noise (Welford, 1981) or compensatory recruitment (Fabiani, Low, Wee, Sable, & Gratton, 2006; Madden, Spaniol, Whiting, et al., 2007). Numerous hypotheses of neural ageing have been put forward to explain age group differences in neural signatures. The key principles of some of the primary models are outlined below.

Cabeza (2002) proposed a dedifferentiation hypothesis, where ageing results in a decreased specialisation of cortical processing. Dedifferentiation is consistent with a neural noise hypotheses of neural ageing. For example, Shih (2009) proposed that age-related declines in neural processing are a result of increased neural noise or impaired inhibition. Both increased neural noise and impaired inhibition could result in increased activation thresholds to select visual stimuli, resulting in difficulties in reaching activation thresholds, and would explain impaired inhibitory and/or excitatory mechanisms in older adults (Adamo et al., 2003; Aydin, Strang, & Manahilov, 2013; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig et al., 2007; Maciokas & Crognale, 2003). Increased neural noise is supported by the reduced amplitudes that are observed in event related potentials as a result of increased age-related variability (Polich, Howard, & Starr, 1985) and increased variability and higher noise levels found with fMRI in older age groups (Huettel, Singerman, & McCarthy, 2001). As previously argued in the current chapter, difficulties in temporal and spatial attention may therefore be due to a decline in selective attentional mechanisms, possibly in the form of impaired excitatory-inhibitory selective attention processes, where excitatory mechanisms fail to reach activation thresholds and inhibitory mechanisms fail to suppress interference from visual distractors (Shih, 2009). Thus, deficits in mechanisms sustaining a balance between excitation and inhibition could lead to a decline of selective attention efficiency.

Both Braver, Paxton, Locke, and Barch (2009) and the early-to-late shift in ageing (ELSA) model (Dew, Buchler, Dobbins, & Cabeza, 2012) propose an alternative framework of neural ageing that posits that older adults move away from "proactive control" and move towards "reactive control", where proactive control utilises top-down information such as cues to prepare for a response, reactive control is a response to an event. This proposal is consistent with neural findings of impaired anticipatory attention (Deiber, Ibanez, Missonnier, Rodriguez, & Giannakopoulos, 2013; Gamboz, Zamarian, & Cavallero, 2010; Zanto et al., 2011) and evidence that older adults are impaired at utilising temporal cues (Zanto et al., 2011), however it is inconsistent with the wealth of literature presenting that older adults rely on top-down attentional guidance more than younger adults in order to compensate for impaired lower level attentional mechanisms (McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002). Furthermore, there is evidence contradicting an age-related impairment in utilising temporal cues (Chauvin, Gillebert, Rohenkohl, Humphreys, & Nobre, 2016). It could be that a shift from a proactive to a reactive control strategy is task dependent. For example, it may be that older participants move towards a more reactive strategy when there is more demand on cognitive resources, such as in more realistic scenarios. Further investigation is required to develop our understanding of the situations that such a change in strategy is apparent in.

An alternative explanation of increased cortical activity with increased age is the "posterior to anterior shift in ageing hypothesis" (PASA; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008), which proposes that there is a compensatory shift in activity towards frontal regions in conjunction with declines in occipital sensory processing. Studies across multiple cognitive paradigms have seen decreases in posterior occipital activity (Buckner, Snyder, Sanders, Raichle, & Morris, 2000; Cabeza et al., 2004; Davis et al., 2008; Huettel et al., 2001; Madden et al., 2002; Ross, et al., 1997) and increases in more anterior regions, including the pre-frontal cortex (PFC) and parietal regions (Cabeza et al., 2004; Grady, 2000; Madden, 2007). Note that while parietal regions are typically considered as posterior, increases in parietal activity have been observed in conjunction with occipital declines, and thus the shift in cortical activity is in a posterior to anterior direction (Davis et al., 2008). While controlling for task difficulty, Davis et al. (2008) found age-related decreases in occipital activity coupled with age-related increases in PFC activity. Furthermore, cognitive performance positively correlated with increased PFC response, supporting a compensatory role of increased PFC recruitment. The widely acknowledged decline in the structure of frontal regions with increased age makes the proposal that the PFC is implemented in compensation, as is proposed by the PASA hypothesis, counterintuitive (Colcombe, Kramer, Erickson, & Scalf, 2005; Daigneault, Braun, & Whitaker, 1992; West, 1996; 2000). However, in addition to the vast literature supporting a deteriorating frontal lobe hypothesis of ageing (Colcombe et al., 2005; Daigneault et al., 1992; West, 1996; 2000), there is equally vast evidence demonstrating increased activity in the frontal lobe (Cabeza et al., 2004; Grady, 2000; Madden, 2007) as well as a reduced magnitude and spatial extent of visual cortex response during visual processing (Buckner et al., 2000; Huettel et al., 2001; Ross et al., 1997). Furthermore, Colcombe et al. (2005) found that areas with the largest grey matter reductions e.g. middle frontal gyrus (MFG) and superior frontal gyrus (SFG), also show greatest increases in activity.

Consistent with the compensatory focus of PASA (Davis et al., 2008) is the Compensation-Related Utilization of Neural Circuits Hypothesis (CRUNCH; Reuter-Lorenz & Cappell, 2008), which states that older adults recruit more resources than younger adults to accomplish low level cognitive tasks. The authors of the CRUNCH model later proposed the scaffolding theory of aging and cognition (STAC; Park & Reuter-Lorenz, 2009), which is consistent with the CRUNCH model and provides an explanation for the discrepancy between evidence towards a PASA hypothesis (Cabeza et al., 2004; Davis et al., 2008) and evidence of frontal lobe atrophy (Colcombe et al., 2005; Daigneault et al., 1992; West, 1996; 2000). The STAC proposes that age-related neurophysiological deterioration - for example atrophy, white matter degradation and dopamine receptor depletion - is accompanied by functional degradations which are compensated for with the implementation of additional neural mechanisms such as additional activation across the cortex. The authors term this compensation “scaffolding”. The scaffolding applied is dependent on the individual’s experience, for example their level of education, new learning experiences, engagement in mentally stimulating activities and their physiological health. Cognitive function is predicted by the neural degradation combined with the amount of scaffolding applied.

An advantage of the STAC framework is that it is consistent with other compensation models of ageing that focus on specific patterns of compensatory activity, for example the PASA, which is outlined above, and the hemispheric asymmetry reduction in older adults (HAROLD; Cabeza, 2002) theory. The HAROLD framework is based on evidence of a reduction in lateralisation of activity with increased age (Deiber, Sallard, Ibañez, Ludwig, & Barral, 2014; Hong, Sun, Bengson, Mangun, & Tong, 2015). It is thought that, as the hemisphere that is typically recruited during a cognitive process deteriorates, the opposite hemisphere supports processing. Although a HAROLD model is well supported in the literature (Deiber et al., 2014; Hong et al., 2015), it does not provide a model that can be easily applied to processes that typically do not have a clear lateralisation. Instead, the phenomena explained in the HAROLD model is better explained in an all-encompassing STAC framework.

Cabeza and Dennis (2012) outlined a simplified model of compensation mechanisms in the ageing brain that have important implications for current and future research. They suggested that certain neural resources are utilised during cognitive processing, but as task demands increase reserve neural resources are recruited to meet these demands. Ageing results in a reduction in neural resources which leads to difficulties in coping with task demands. Older individuals must recruit "reserve resources" to attempt to meet increased task demands, for example, through stronger and more widely distributed recruitment of neural sources or increased functional connectivity between regions. This "attempted compensation" can either be successful or unsuccessful. The authors suggested that in order to conclude that patterns of altered cortical activity reflect compensation experimental findings must meet four criteria. Firstly, increased activity should be correlated with increased performance. Secondly, disrupting processing in regions where increased activity is observed - for example through brain stimulation techniques or in lesion studies - should interfere with cognitive performance. Thirdly, as illustrated in Cabeza and Dennis's (2012) Figure 37-3 (A), attempted compensation should have an inverted "U" relationship with brain decline. As age-related decline progresses, compensatory mechanisms increase. However, once reserve resources decline, compensation decreases. This pattern has been observed in the progression of neural signatures in memory encoding from healthy ageing to mild cognitive impairments to Alzheimer's dementia (Dickerson et al., 2005; Wierenga & Bondi, 2007). Finally, as illustrated in Cabeza and Dennis's (2012) Figure 37-3 (B), attempted compensation should have an inverted "U" relationship with task demands, which has been observed in younger adults when manipulating task demands (D'Esposito, 2001). Ageing shifts this U function to the left, as older participants start to recruit reserve resources at lower levels of task demand and therefore reach a peak and begin to decline at lower levels of task demands (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Mattay et al., 2006). Cabeza and Dennis (2012) illustrate that instead of neural activity plateauing once a peak is reached, activity begins to decline. The authors proposed that this decline could either function to avoid interference with other cognitive processes, or may reflect that participants reach a point where they no longer attempt to perform the task. The four criteria proposed by Cabeza and Dennis (2012) provide a framework for future research trajectories to follow to confirm or disconfirm whether observed increases in neural activity are indeed due to compensation or are due to neural noise.

Theta oscillations

In addition to age-related increases in the distribution of neural activity, a reduction in the power of theta oscillations (3-7Hz) has been observed with increased age in both resting state and task related conditions, and particularly along the frontal midline (Cummins & Finnigan, 2007; Finnigan, O'Connell, Cummins, Broughton, & Robertson, 2011; Reichert, Kober, Witte, Neuper, & Wood, 2016; van de Vijver, Cohen, & Ridderinkhof, 2014). Theta is associated with a broad array of task processes including pre-stimulus top-down control (Cavanagh, Cohen, & Allen, 2009; Cavanagh & Frank, 2014; Min & Park, 2010), target processing (Demiralp & Başar, 1992), working memory (Sauseng, Griesmayr, Freunberger, & Klimesch, 2010) and selective attention (Green & McDonald, 2008). Frontal midline theta is thought to reflect medial PFC and ACC activity (e.g. Asada, Fukuda, Tsunoda, Yamaguchi, & Tonoike, 1999) which play an important role in attentional control (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Konishi et al., 1999; Pollmann, 2004). Functional connectivity of theta has also been shown to play an important role in attention and cognitive control (Cavanagh et al., 2009; Schack, Klimesch, & Sauseng, 2005; Voloh, Valiante, Everling, & Womelsdorf, 2015; Wang, Viswanathan, Lee, & Grafton, 2016). For example, Voloh et al. (2015) found increases in phase amplitude coupling (PAC) between ACC and PFC in theta-gamma frequencies before successful attentional shifts but not unsuccessful ones in non-human primates.

Decreases in frontal-midline theta with increased age are inconsistent with the simple formulation of the PASA hypothesis of ageing (Davis et al., 2008). Age-related reductions in frontal midline theta have most commonly been observed in memory recall tasks and during resting state and mostly recorded with electroencephalography (EEG; Cummins & Finnigan, 2007; Finnigan et al., 2011; Reichert et al., 2016; van de Vijver et al., 2014). Although there is an overall reduction in frontal midline theta power with increased age, there could be an increase in compensatory lateral PFC activation, which may not be reflected in theta power modulation (but in alpha, for instance) or may actually include theta power increases that have not been picked up by previous EEG studies due to poor spatial resolution. However, weaker theta network connectivity has been observed in EEG recordings in older adults during VS (Li & Zhao, 2015). To continue to develop our understanding of age-related declines in visual attention it could be advantageous to further investigate changes in theta modulation with increased age, and our understanding of changes in theta modulation across different areas of the network could particularly benefit from the spatial resolution of MEG compared to EEG.

Alpha oscillations

As mentioned above, there is a decline in the ability to inhibit irrelevant visual information with increased age (Adamo et al., 2003; Aydin et al., 2013; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig et al., 2007; Maciokas & Crognale, 2003). There is a consensus that stimulus inhibition is at least partly achieved through increased alpha (8-12Hz) amplitudes (or frequency power), whereas an alpha decrease reflects enhanced attention to a stimulus (Capotosto, Babiloni, Romani, & Corbetta, 2009; Hanslmayr et al., 2007; Hanslmayr et al., 2005; Klimesch, Sauseng, & Hanslmayr, 2007; Sauseng et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Yamagishi et al., 2003). In addition to inhibition of irrelevant sensory information, alpha increases are also typically present during sustained attention (Dockree, Kelly, Foxe, Reilly, & Robertson, 2007; Rihs, Michel, & Thut, 2007, 2009), likely inhibiting unattended locations and irrelevant sensory information (Rihs et al., 2007). Successful visual target discrimination can be predicted by the amount of pre-stimulus alpha suppression (Hanslmayr et al., 2007; Hanslmayr et al., 2005) and by the instantaneous phase of the alpha cycle during stimulus presentation (Busch, Dubois, & VanRullen, 2009; Busch & VanRullen, 2010; Dugué, Marque, & VanRullen, 2011; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). It has therefore been proposed that alpha oscillations suppress processing through sensory gating, where the processing of a stimulus is modulated by the phase of the alpha cycle (Bonnefond & Jensen, 2015; Busch et al., 2009; Dugué et al., 2011; Jensen & Mazaheri, 2010; Mathewson et al., 2009). The direct relationship between increased alpha power and suppression of processing has been corroborated by the manipulation of alpha oscillations through TMS (Gooding-Williams, Wang, & Kessler, 2016; Herring, Thut, Jensen, & Bergmann, 2015). Entraining cortical rhythms to alpha frequency inhibited processing in the TPJ in a spatial perspective taking task, whereas theta entrainment enhanced task performance (Gooding-Williams et al., 2016). Overall, there is therefore extensive evidence demonstrating that inhibition is partly achieved through increased alpha power, whereas an alpha decrease reflects enhanced attention.

Evidence suggests that older adults display deficits in both alpha synchronisation and alpha desynchronization (Deiber et al., 2013; Hong et al., 2015; Pagano, Fait, Monti, Brignani, & Mazza, 2015; Vaden, Hutcheson, McCollum, Kentros, & Visscher, 2012) and consistently display slowed alpha frequency when measuring individual alpha peak frequencies (Pons, Cantero, Atienza, & Garcia-Ojalvo, 2010). In particular, older participants have been shown to fail to modulate alpha in anticipation of a visual target (Deiber et al., 2013; Zanto, Hennigan, Ostberg, Clapp, & Gazzaley,

2010) and to inhibit irrelevant visual distractors (Vaden et al., 2012). It could be that impaired alpha modulation reflects impaired attentional mechanisms, as typical enhancement and inhibition of external stimuli is diminished. However, failure to modulate alpha oscillations does not seem to consistently impair performance. Older individuals have been found to successfully inhibit visual information despite a failure to modulate alpha (Vaden et al., 2012), possibly indicating the implementation of alternative compensatory neural mechanisms. Similarly, in a visual spatial attention task, Hong et al. (2015) found that age-related decreased alpha lateralisation did not impair behaviour. Vaden et al. (2012) therefore proposed that age-related changes in alpha band power and frequency could render alpha modulations redundant. This raises the question of what mechanisms could be available to the ageing brain that could compensate for decreased flexibility in the alpha range. One visual attention study by Deiber et al. (2013) found that rather than a posterior alpha modulation, the older group displayed a low beta frequency response to cues and targets (conforming to Gross et al., 2004). It could be that older adults were engaging alternative mechanisms that implement different frequencies to compensate for impaired alpha modulation, a notion that requires further investigation.

Beta oscillations

Beta frequency has been implicated in visual attention and perception (Gola, Kaminski, Brzezicka, & Wrobel, 2012; Gola, Magnuski, Szumska, & Wrobel, 2013; Gross et al., 2006; Kamiński, Brzezicka, Gola, & Wróbel, 2012; Park et al., 2016), motor preparation, and motor response (Donoghue, Sanes, Hatsopoulos, & Gaál, 1998; Farmer, 1998; Kühn et al., 2004; Park, Kim & Chung, 2013). Contrasting with the thorough understanding of alpha oscillations, as outlined above, the role of beta modulations is less clear. Where some studies have observed a beta decrease prior to and during enhanced attention or during motor preparation (Park et al., 2013; Park et al., 2016; Kühn et al., 2004; Zaepffel, Trachel, Kilavik, & Brochier, 2013) other studies have observed increased beta power in anticipation of a target stimulus (Basile et al., 2007) and high beta power during alertness (Kamiński et al., 2012). There is evidence to imply that this discrepancy may depend on task demands. For example, higher beta synchronisation is observed during cognitively demanding tasks, when further stimulus evaluation is required, and greater beta desynchronization occurs when task demands are reduced (Park et al., 2013; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010). Increased alpha power is observed during periods of sustained attention (Dockree et al., 2007; Rihs et al., 2007, 2009) and working memory maintenance (Palva, Monto, Kulashekhar, & Palva, 2010), as one inhibits irrelevant spatial locations and sensory information (Rihs et al., 2007). Similarly, increased beta synchronisation during anticipation of a target or during the evaluation of stimuli could reflect inhibition of prepared motor responses and attention to sustain the current attention and motor state (Engel & Fries, 2010; Gross et al., 2006).

Changes in the modulation of beta frequency has been found with increased age (Christov & Dushanova, 2016; Gola et al., 2012; Gola et al., 2013; Kamiński et al., 2012). Christov and Dushanova (2016) found that, in comparison to younger adults, older adults demonstrated a weaker beta increase during sensory processing of an auditory target (50-250ms) and a greater beta decrease during cognitive processing of the same target (400-600ms). Similarly, in a visual attention task where participants signified whether a target was present in a visual array or not, Gola et al. (2013) found that, in contrast to younger adults and high performing older adults, low performing older adults displayed occipital beta desynchronization instead of beta synchronisation during the presentation of a cue that preceded target onset. Greater beta desynchronization in older age has also been found in motor preparation tasks (Rossiter, Davis, Clark, Boudrias, & Ward, 2014) and in a haptic memory task (Sebastian, Reales, & Ballesteros, 2011). Furthermore, older participants have been shown to display wider distribution and decreased lateralisation of beta oscillations compared to younger adults when preparing for voluntary actions (Deiber et al., 2013; Deiber et al., 2014; Quandt et al., 2016) an effect that has been shown previously to correlate with slow RTs (Deiber et al., 2014).

Age-related changes in the modulation of theta, alpha and beta oscillations can therefore be informative by helping to uncover why cognitive task performance deteriorates and what alternative mechanisms might be in place to cope with this deterioration. Note that while gamma oscillations have been shown to be involved in visual processing and are therefore important in visual attention tasks (Cabral-Calderin, Schmidt-Samoa, & Wilke, 2015; Gruber, Muller, Keil, & Elbert, 1999; Womelsdorf, Fries, Mitra, & Desimone, 2006), it has been suggested that higher level cognitive control guides lower level visual processing though a mechanism where gamma oscillations are modulated by long-range synchronisation with lower frequency oscillations such as theta and alpha oscillations (Canolty et al., 2006; Canolty & Knight, 2010; Doesburg, Green, McDonald, & Ward, 2009b; Doesburg, Ward, & Ribary, 2015; Osipova, Hermes, & Jensen, 2008; Voytek et al., 2010). As the current thesis focuses on age-related changes in flexible attentional control of visual processing, the current focus remains on the lower frequency oscillations of theta, alpha and beta frequencies and does not explore gamma oscillations. However, future work could benefit from additionally investigating how age-related changes in theta, alpha and beta frequencies interact with gamma oscillations.

Functional connectivity

Vital for the functioning of attention networks is the communication between different regions across the network, which is thought to partly occur through the synchronisation of oscillations across those regions (Gray, König, Engel, & Singer, 1989; Singer, 1999). Functional connectivity has therefore been quantified through oscillations by measuring the phase relationship between two signals of the same frequency (e.g. imaginary coherence; Nolte et al., 2004; phase lag index, PLI, Stam, Nolte, & Daffertshofer 2007; phase locking value, PLV, Lachaux et al., 1999), cross frequency coupling, which measures the phase relationship between two signals of different frequencies (Hyafil, Giraud, Fontolan, & Gutkin, 2015; Jensen, Kaiser, & Lachaux, 2007) and PAC (Canolty et al., 2006; Canolty & Knight, 2010), which measures the relationship between the phase of one signal and the amplitude of a second signal. Many measures of connectivity indicate only the strength of communication between two regions but provide no information about the direction of connectivity (e.g. PLI; coherence). Granger-causality on the other hand indicates the direction of connectivity and can provide important information about the feedback and feedforward trajectories of information (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Plomp, Hervais-Adelman, Astolfi, & Michel, 2015). Phase coupling, cross frequency coupling and PAC across the cortex have each been found to be related to behavioural performance across a range of cognitive tasks (Friese et al., 2013; Gross et al., 2004, 2006; Sauseng, Klimesch, Gruber, & Birbaumer, 2008; Seymour, Rippon, & Kessler, 2017; Voloh et al., 2015).

While the aforementioned measures of connectivity based on oscillations can provide information about the strength of connectivity across regions of the network, graph theoretical approaches are often applied to whole-brain functional connectivity analysis to better describe the topology of a network. In graph theoretical analysis, certain connections (i.e. edges) between pairs of brain regions (i.e. nodes) remain in the network for further analysis. Graph theoretical metrics can then be extracted from the network to provide information about the connectedness of each node. For example, a measure of “degree” provides an index of how many other brain regions a particular node is connected to. Similarly, “clustering coefficient” is a measure of both the degree of the node in addition to the degree of the adjoining nodes. Both degree and clustering coefficient quantify the extent that certain nodes are “hubs” in the network. One problem with applying a graph theoretical approach to neural connectivity is that it is necessary to apply an arbitrary threshold to define which connected pairs remain in the network for further analysis. For example, a threshold could be selected based on the strength of connections (e.g. PLI or coherence values), discarding any connections that do not exceed the set threshold, or alternatively a predefined number of the strongest connections could be entered into the network, regardless of their actual connectivity values. The first example results in an arbitrary number of connections being entered into the network, making it difficult to fairly compare networks across groups or conditions, and the latter example is vulnerable to entering weak or spurious connections into the network. Networks that contain different numbers of nodes and/or edges bias graph theoretical metrics such as degree and path length. One way to overcome these difficulties is by constructing and analysing a Minimum Spanning Tree (MST; Otte et al., 2015; Tewarie et al., 2014; Tewarie, van Dellen, Hillebrand, & Stam, 2015). The MST is a graph theoretical approach that enables the comparison of network topologies while controlling for the number of nodes and edges in a network while avoiding the requirement to select an arbitrary threshold (Tewarie et al., 2014). A more detailed discussion of MST analysis can be found in Tewarie et al. (2014). MST metrics have been shown to be sensitive to differences in network topology and correspond well to conventional graph theoretical metrics, while providing the added advantage of controlling for the number of edges and nodes in the network (Boersma et al., 2012; Tewarie et al., 2015).

Although there is extensive literature demonstrating an age-related decline in structural connectivity - i.e. white matter integrity (Bennett et al., 2012; Daselaar et al., 2015; Davis et al., 2009; Madden et al., 2012; Madden, Spaniol, Whiting, et al., 2007) - and in functional connectivity through fMRI (Geerligs, Saliasi, Renken, Maurits, & Lorist, 2014; Mary et al., 2017), the development of techniques to measure functional connectivity through brain oscillations is comparatively recent, leaving a scarcity of literature exploring oscillatory connectivity in healthy ageing. Measuring functional connectivity through fMRI has two major limitations. Firstly, estimating functional connectivity in fMRI data is an indirect measure of connectivity that assesses the relationship between the changes in the haemodynamic response across two regions. Secondly, the haemodynamic response across brain regions is susceptible to age-related changes in vascular functioning (D'Esposito, Deouell, & Gazzaley, 2003; Liu, 2013). It is therefore unclear whether estimated connectivity reflects the communication between cortical regions or whether it reflects the effects of neurovascular ageing on haemodynamic response.

Age group differences in resting state functional connectivity through oscillations have been explored, where older adults display weaker connectivity (Knyazev, Volf, & Belousova, 2015; Zhu et al., 2011), although Coquelet et al. (2017) found no age group differences. Age group differences in network topology at resting state have also been demonstrated, between young and middle-aged groups (Petti et al., 2016; Petti et al., 2013) and between younger and older age groups (Gaal, Boha, Stam, & Mark, 2010; Schlee et al., 2012). However, the literature investigating age-related changes in network connectivity during task modulation is limited in regards to both the strength of connectivity across regions of the network and the topology of functional networks. In contrast to much of the resting state literature (Knyazev et al., 2015; Zhu et al., 2011), in a go/no-go task, Hong, Liu, Sun, and Tong (2016) found that older adults exhibited equal or stronger connectivity in comparison to younger adults. Estimating functional connectivity with dynamic causal modelling in a visual evoked response paradigm, Gilbert and Moran (2016) found that, whereas younger adults presented early EEG signal in visual areas which drove frontal, temporal and parietal activity, older adults presented early visual and frontal activity. An early frontal recruitment in the older age group but not the younger group is consistent with an aforementioned tendency for older adults to rely more on top-down attentional control compared to younger adults (McLaughlin & Murtha, 2010; Neider, Boot, & Kramer, 2010; Watson & Maylor, 2002). Furthermore Gilbert and Moran’s (2016) findings illustrate how assessing age-related changes in task-related functional connectivity can provide rich information about age group differences in the processes involved in achieving task goals. Considering the dearth of research into age-related changes in task-related connectivity using direct measures of connectivity, combined with the evidence outlined above of compensatory recruitment in older age, age differences in task-related connectivity might be expected in both strength and network topology. Further investigation into how task-related connectivity changes with age is therefore warranted.

Neural mechanisms during driving

Recording neural activity in more ecologically valid settings could be informative regarding the neural processes that are involved during tasks such as driving. For example, exploring the neural mechanisms involved in driving could address important questions about how the brain works in more realistic environments when sensory information is much richer than in laboratory based tasks. Although previous literature has successfully recorded EEG in driving simulator environments (Campagne, Pebayle, & Muzet, 2004; Lowden, Anund, Kecklund, Peters, & Akerstedt, 2009; Ross et al., 2018), many studies looked at the effects of fatigue on EEG (Ahn, Nguyen, Jang, Kim, & Jun, 2016; Hsu & Jung, 2017; Lowden et al., 2009; Perrier et al., 2016) rather than looking at task-related modulations of oscillatory signatures. However, there have been some exceptions (Huang, Jung, & Makeig, 2009; Lin, Chen, Chiu, Lin, & Ko, 2011; Vossen, Ross, Jongen, Ruiter, & Smulders, 2016). Huang et al. (2009) found that gradual increases in alpha power in occipital and parietal sensors were associated with slower RTs in a sustained attention driving simulator task. Secondly, in a dual-task driving simulator paradigm in which participants were asked to maintain lane centrality while completing a maths sum, Lin et al. (2011) found task-related increases in frontal theta and beta power and decreases in motor cortex alpha and beta power in reaction to a distraction event, where the vehicle drifted to the adjacent lane. Interestingly, Sakihara et al. (2014) recorded MEG during simulated driving. They found that active driving relative to passive viewing resulted in theta increases in SFG and decreases in alpha and beta and lower gamma bands in the right IPL, left post central gyrus, middle temporal gyrus and posterior cingulate gyrus. They concluded that frontal theta reflected attention, IPL reflected selectively divided attention and visuospatial processing, postcentral gyrus activity reflected sensorimotor processing, and posterior cingulate and MTG power decreases could be associated with object recognition. While the outlined literature has been informative, further investigating the neural mechanisms that are engaged in more ecologically valid settings could progress our understanding of how the brain works in more realistic environments.

1.1.6 Project aims and overview

From the literature outlined above multiple issues have arisen. Firstly, older participants have a disproportionately higher risk of being involved in at-fault collisions at intersections and in collisions that seem to been caused by impaired attentional mechanisms (Arai & Arai, 2015; Guo et al., 2010; Hakamies-Blomqvist, 1993; McGwin & Brown, 1999). While there is a vast literature assessing changes in spatial and temporal attention with increased age and how changes effect driving performance (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Lahar et al., 2001; Lee & Hsieh, 2009; Li et al., 2013; Maciokas & Crognale, 2003; Plude & Doussardroosevelt, 1989) there has been very little research into the refocusing of attention between temporal and spatial attention in any age group. Secondly, the literature suggests that healthy ageing is associated with more widely distributed cortical activity (Adamo et al., 2003; Lague-Beauvais et al., 2013; Li et al., 2013; Madden, Spaniol, Whiting, et al., 2007), which could either be due to neural noise (Shih, 2009; Welford, 1981) or compensatory functioning (Fabiani et al., 2006; Madden, Spaniol, Whiting, et al., 2007), in addition to age-related changes in theta, alpha and beta modulations (Christov & Dushanova, 2016; Cummins & Finnigan, 2007; Deiber et al., 2013; Deiber et al., 2014; Finnigan et al., 2011; Gola et al., 2012; Gola et al., 2013; Reichert et al., 2016; Vaden et al., 2012; van de Vijver et al., 2014). The aim of the current project was therefore to investigate whether there is an age-related decline in the ability to refocus attention between temporal and spatial attention, and if so, firstly to explore the neural mechanisms that might help to explain this difficulty in attentional refocusing, and secondly to explore whether such a decline is present during simulated driving.

Chapter 2 aims

Firstly, the aim of Chapter 2 was to explore whether there are age-related changes in the ability to switch between temporal and spatial attention and to explore the cognitive mechanisms that might underpin these changes. In Experiments 1 and 2 of Chapter 2, a paradigm was developed to compare age groups on their ability to switch from allocating attention in time, in order to identify a single target in an RSVP stream, to allocating attention spatially, in order to identify a VS target. An example of the stimuli are presented in Figure 1.1. In the version of the paradigm that we chose to take forward, to manipulate the cost of switching (of attentional focus) from the RSVP stream to the VS display, the position of the target in the RSVP stream was either the first item in the stream, towards the end of the stream, or absent from the stream. When the target was the first item in the stream participants were no longer required to attend to the stream, and thus no cost of switching was expected (No-Switch condition). On the contrary, when the target was near the end of the stream or the stream consisted of only distractor items, participants needed to attend to the stream until towards the end of the stream, inducing a cost of switching (Target Switch condition/No-Target Switch condition).

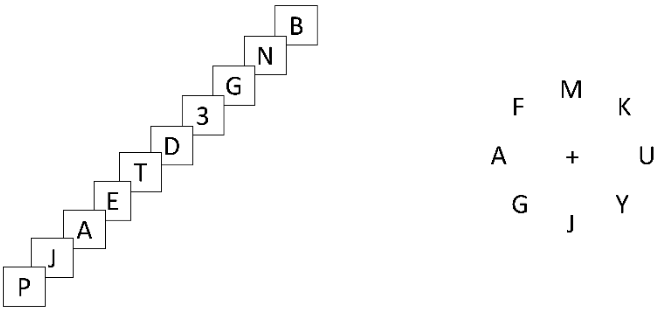

Figure 1.1. Illustration of examples of the experiment set up. The RSVP stream illustration (left) displays a Target Switch RSVP stream (digit = target), and the VS display illustration (right) displays a serial VS display (‘K’ = target). Each trial consisted of a fixation cross (2000ms) followed by an RSVP stream immediately followed by a VS display.

In Experiment 3 of Chapter 2 (published in Callaghan, Holland, & Kessler, 2017), we compared five age groups (21-30, 40-49, 50-59, 60-69, and 70+ years) on their ability to refocus from temporal to spatial attention by assessing their performance on the attention switching task developed in Experiments 1 and 2. To explore the cognitive mechanisms that might underpin age-related changes in refocusing attention from time to space the Random Number Generation task (RNG) and the useful field of view task (UFOV; Ball, Beard, Roenker, Miller, & Griggs, 1988) were implemented. The RNG was applied to measure executive functions of updating and inhibition (Miyake et al., 2000) in order to examine the effect of executive function on task performance. Performance on random generation tasks has previously been found to decline with age (Van der Linden, Beerten, & Pesenti, 1998). The UFOV task was implemented to measure visual processing speed, divided attention and selective attention. Performance on the UFOV tasks have been found to decline with age (Ball et al., 2006; Edwards et al., 2006; Rubin et al., 2007).

It could be argued that any age differences in Experiment 3, described in the previous paragraph, were due to age-related differences in switching from a challenging task (i.e. the RSVP stream) to a less challenging task (i.e. the VS task). The RSVP stream was presented at a presentation rate of 10Hz rendering target detection challenging, possibly more so for older adults considering evidence of impaired temporal attention in the literature (Conlon & Herkes, 2008; Shih, 2009). In Experiment 4 of Chapter 2, we therefore aimed to assess whether age-related changes in refocusing attention from temporal to spatial attention were present when switching from the RSVP task to the VS task when the two tasks were more equally matched in difficulty. This was achieved by presenting the RSVP target digit in the colour red (among the black distractor letters) to enhance bottom-up attentional processing of the target (Lien et al., 2011; Theeuwes, 1994, 2004). Two age groups were compared (18-25 and 60+ years).

The attention switching task implemented in Experiments 1-4 involved switching from identifying a number in the RSVP stream to identifying a letter in the VS display. It could be argued that age differences observed in Experiment 3, described above, were due to age-related differences in switching between different target types. Experiment 5 of Chapter 2 therefore aimed to investigate this argument by comparing age groups (18-30 and 60+ years) on the ability to identify a target digit in the RSVP stream and identify a second target digit in the VS display.

Experiment 6 in Chapter 2 compared age groups on the ability to refocus attention from identifying a target digit in an RSVP stream to detecting a target letter in the VS display, but aimed to better mirror aspects of attention implemented while driving, i.e. by attending to events changing in time and responding to them (temporal attention), followed by distributing attention spatially and making decisions about information in the environment (spatial attention). In Experiment 6 participants were required to respond to the detection of the RSVP target digit with a speeded spacebar response, similar to a driver braking in response to identifying an event on the road ahead. Participants were then required to make a two choice left-right response to the VS display to signify whether the target was in the left or right visual hemifield, similar to a driver signalling left or right with their indicators after reading a road sign. An example of the stimuli is presented in Figure 1.2.

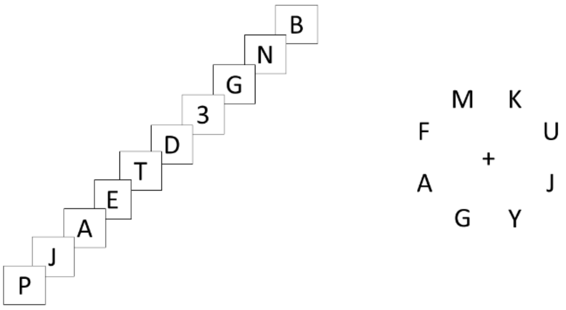

Figure 1.2. Illustration of examples of the stimuli set up in Experiment 6. The RSVP stream illustration (left) displays a Target Switch RSVP stream (digit = target). Each trial consisted of a fixation cross (2000ms) followed by an RSVP stream immediately followed by a blank grey screen (until the participant responds to the RSVP target), followed by a serial VS display (right; ‘K’ = target).

Chapter 3 aims

Chapter 3 aimed to explore age-related changes in the neural mechanisms that underpin difficulties in refocusing from temporal to spatial attention. MEG was recorded while participants completed the attention switching task implemented in Experiments 2 and 3. A focus on oscillatory analysis and network connectivity was pursued. MEG helped to define the oscillatory mechanisms that may differ in older age that could explain difficulties in refocusing attention between time and space. There is limited research investigating network connectivity in older age. Previous studies have often looked at age-related changes in functional connectivity during resting state, which can produce contradictory findings when compared to changes in task-related functional connectivity (Hong et al., 2016). Chapter 3 therefore presents novel research of age-related changes in oscillatory mechanisms, including in functional connectivity, that underlie difficulties in switching between temporal and spatial attention. MEG provided better spatial resolution compared to EEG and the necessary temporal resolution to investigate the transient nature of refocusing attention, as well as enabling the measurement of neural oscillations and direct phase-based functional connectivity, which are two advantages over fMRI.

Chapter 4 aims

Chapter 4 aimed to assess whether age-related changes in refocusing attention from a temporal attention task to a spatial attention task were present during simulated driving. It may be that difficulties in switching between temporal and spatial attention cause difficulties in switching from attending to traffic on the road ahead to attending to road signs and other surrounding objects. Findings of an association between impaired driving performance and difficulties in switching would emphasise the importance of developing an intervention to improve switching between modalities of attention to help improve driver performance and safety. This would have the long-term benefit of prolonging the time that older drivers can continue to drive and help to preserve their independence. Age groups were compared on their ability to switch from allocating attention in time, where participants attended to the fast changing traffic in front of them, to allocating attention spatially, in order to complete a VS of a road sign. On “Dual-Task” trials the road sign VS task was preceded by a “braking event” task, where participants were required to brake in response to a car suddenly pulling in front of them from the over-taking lane and braking. In “Single-Task” trials the road sign VS task was carried out without a preceding braking event task.

Chapter 5 aims

Chapter 5 discusses the aims and key findings of the current research together with its theoretical implications, in addition to outlining limitations and future directions.

Chapter 2

Behavioural Experiments

2.1 Chapter aims

Despite the extensive literature investigating spatial attention and temporal attention and how these change with age (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Lahar et al., 2001; Lee & Hsieh, 2009; Li et al., 2013; Maciokas & Crognale, 2003; Plude & Doussardroosevelt, 1989), there has been very little research looking at our ability to switch between these two types of attention within any age group. The ability to efficiently refocus attention between temporal events and spatial locations is likely to be important for driving. For example, it is often necessary refocus attention from attending to the fast changing traffic on the road ahead, to distributing attention spatially to attend to road signs, pedestrians and other hazards in the surroundings. Older adults have been shown to have disproportionality increased risks of having collisions at intersections, as well as collisions caused by a failure to give way, or to notice other objects, stop signs or signals (Arai & Arai, 2015; Guo et al., 2010; Hakamies-Blomqvist, 1993; McGwin & Brown, 1999; Musselwhite & Haddad, 2010; Raja Parasuraman & Nestor, 1991). These findings are consistent with Parasuraman and Nestor's (1991) conclusions that older drivers' accidents were often due to failures in attention, particularly selective attention and switching. The aim of the current chapter was therefore to identify whether there are age-related changes in the ability to refocus attention from temporal to spatial attention and to understand the cognitive mechanisms that might influence these changes.

Spatial selective attention is often measured with VS paradigms, where participants are presented with an array of visual stimuli and are required to make a speeded response to the detection of a predefined visual target stimulus (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt, 1989). As outlined in Chapter 1, visual spatial attention deteriorates with increased age in serial but not "pop-out" VS (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt, 1989). Furthermore, selectively attending to temporal events becomes more difficult over the age of 70 years (Conlon & Herkes, 2008; Shih, 2009) but is preserved in those aged 60-70 years (Lee & Hsieh, 2009; Quigley et al., 2012).

The literature investigating the ability to switch between temporal and spatial attention is limited across all age groups. There is some evidence to suggest that, compared to younger adults, older adults take longer to narrow their attentional focus from spatial to temporal attention (Jefferies et al., 2015) and are impaired for at least 450ms after switching from orienting attention in time (to identify a central target) to distributing attention in space (to detect a peripheral target), reflected in both lower accuracy and increased RTs (Lee & Hsieh, 2009; Russell et al., 2013). As discussed in Chapter 1, it is unclear whether the findings of Russell et al. (2013) and Lee and Hsieh (2009) are due to the well documented increased magnitude of the attentional blink with increased age (Lahar et al., 2001;

Maciokas & Crognale, 2003; Shih, 2009; van Leeuwen et al., 2009) or due to deficits in the ability to switch from orienting attention in time to distributing attention spatially. Given the importance of switching attention between time and space for safe driving (Parasuraman & Nestor, 1991), further research is warranted to investigate whether the refocusing of attention between different modalities deteriorates with increased age.

To measure participants' ability to switch from temporal to spatial attention, a task was developed in which participants refocused from orienting attention in time, in order to identify a single target in an RSVP stream, to allocating attention spatially, in order to identify a VS target.

2.2 Experiment 1: Pilot with Choice Response Time

2.2.1 Aims

Experiment 1 was carried out to pilot the paradigm that would later be used to compare age groups on their abilities to switch between temporally focused attention and spatially distributed attention. Participants switched from allocating attention in time, in order to identify a target digit in an RSVP stream, to allocating attention spatially, in order to identify a VS target. An example of the stimuli is illustrated in Figure 2.1.

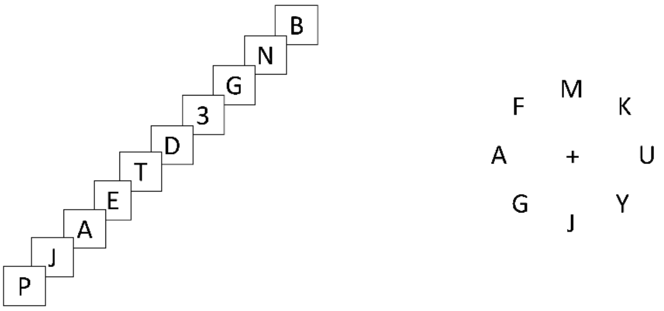

Figure 2.1. Illustration of examples of the experiment set up. The RSVP stream illustration (left) displays a Target Switch RSVP stream, and the VS display illustration (right) displays a serial VS display. Each trial consisted of a fixation cross (2000ms) followed by an RSVP stream immediately followed by a VS display. Note that the current figure was presented previously in Chapter 1 (Figure1.2).

To manipulate the cost of switching, the target digit was either 1) the only item in the RSVP stream as a single static digit, 2) the first item in the stream, 3) towards the end of the stream, or 4) absent from the stream. When the target was the only item in the stream (Target Only No-Switch condition) or the first item in the stream (Target 1st No-Switch condition), participants were no longer required to attend to the RSVP stream after target identification, and thus no cost of switching was expected on VS RTs. On the contrary, when the target was near the end of the stream (Target Switch condition) or the stream consisted of only distractor items (No-Target Switch condition), participants needed to attend to the stream until towards the end of the stream, inducing a cost of switching. Longer VS RTs were therefore expected when switching from the RSVP task to the VS in both the Target Switch and No-Target Switch conditions compared to Target Only No-Switch and Target 1st No-Switch conditions. Based on previous literature (Treisman, 1985; Wolfe, 1998), it was also expected that serial search RTs would be significantly slower than pop-out search RTs.

2.2.2 Methods

Participants

Twenty participants (8 males, 12 females) age 21-30 years (mean=25.10 years, SD=2.57) were recruited from Aston University staff and students and the community. Participants with photosensitive epilepsy or visual impairments were excluded.

Materials and procedures

Attention switching task version 1

In the attention switching task, participants alternated between attending to an RSVP stream and attending to a VS display. Each trial consisted of a fixation cross, presented for 2000ms, followed by the RSVP stream, which was immediately followed by the VS display. Illustrations of the RSVP stream and of the VS display are presented above in Figure 2.1. Stimuli were presented on stimulus presentation software E-Prime 2.0 Professional (Psychology Software Tool. Inc.) on a windows computer, on a 22inch monitor (1280×1050 resolution) which was approximately 55cm in front of the participant. All stimuli were presented in black (RGB 0-0-0) on a grey background (RGB 192-192-192).

The RSVP stream consisted of a rapidly changing stream of letters in the centre of the display. There were ten items in each RSVP stream, each presented for 100ms with no inter-stimulus interval. Stimuli were presented in font size 30pt (0.75×0.75cm, 0.78°). On three quarters of the trials, one of the items in the stream was a target digit ranging from 1-9. The participant's task was to remember the digit. The remaining quarter of trials contained no target. Based on their visual similarity to certain numbers, letters I, O, and S were excluded from the stream, as well as VS targets K and Z. It should be noted that the current RSVP task differs from the attentional blink paradigm as the RSVP stream contains only a single target.

The VS display consisted of eight letters presented in a circle around a fixation cross in the centre of the screen, including seven distractors and one target. The target letter was always either a ‘K’ or a ‘Z’. Stimuli were presented in font size 20pt (0.50×0.50cm, 0.52°) and the centre of each stimulus was 2.3cm (2.40°) from the centre of the fixation cross. Participants responded to the VS by pressing the ‘K’ key if the target was a ‘K’ and the ‘Z’ key if the target was a ‘Z’. Participants were instructed to keep their eyes fixed on the cross while they completed the VS and to respond as quickly and accurately as possible. Participants then indicated whether they had seen a target digit in the RSVP stream by typing in the number that they had seen if they had, or ‘N’ if they had not. Participants’ RTs on the VS, and accuracy throughout the task was recorded.

On 50% of the trials the VS display was a ‘pop-out’ VS, in which the distractors were all the letter ‘P’, allowing the target to ‘pop-out’ to the participant. On 50% of the trials the VS display was a ‘serial’ VS, in which all distractor letters were unique prompting a serial search.

To manipulate the cost of switching, there were four different conditions of the RSVP stream that preceded the VS, including two ‘No-Switch’ conditions and two ‘Switch’ conditions. In the No-Switch conditions, the RSVP stream either consisted of a single static target digit (Target Only No-Switch) or the position of the target digit in the RSVP stream was the first item in the stream (Target 1st No-Switch). In the switch conditions the target digit was either the fourth, fifth, sixth or seventh item in the stream (Target Switch) or absent from the stream (No-Target Switch).

There were 20 trials of each of the eight conditions (pop-out search: Target Only No-Switch/Target 1st No-Switch/Target Switch/No-Target Switch; serial search: Target Only No-Switch/Target 1st No-Switch/Target Switch/No-Target Switch), with a total of 160 trials. To provide the opportunity for breaks, trials were divided into five blocks. Trials were randomized within blocks. Participants completed fourteen practice trials prior to the experimental trials.

2.2.3 Data analysis

Data were analysed using Statistical Package for Social Sciences (SPSS 21). Participants’ median VS RTs (ms) on trials where responses were correct on both the VS and RSVP tasks were extracted using E-Prime data viewing application E-DataAid. Participants’ proportions of correct VS target identifications, RSVP identifications and proportions of RSVP target false positives in the No-Target Switch condition were also extracted.

Differences in median VS RTs across VS conditions and RSVP conditions were analysed in a 2 × 4 (VS condition: serial/pop-out × RSVP condition: Target Only No-Switch/Target 1st No-Switch/Target Switch/No-Target Switch) repeated measures ANOVA. Multiple comparisons were corrected for with Bonferroni correction. Where Mauchly’s Test of Sphericity was significant, indicating that the assumption of sphericity had been violated, Greenhouse-Geisser corrected statistics were reported.

2.2.4 Results

Overall participants correctly identified over 96% of VS targets in each of the eight conditions and 90% of RSVP targets in each of the three target conditions (Target Only No-Switch/Target 1st No-Switch/Target Switch). No further analysis was carried out on VS accuracy nor RSVP target identification as it was unrelated to the current hypotheses.

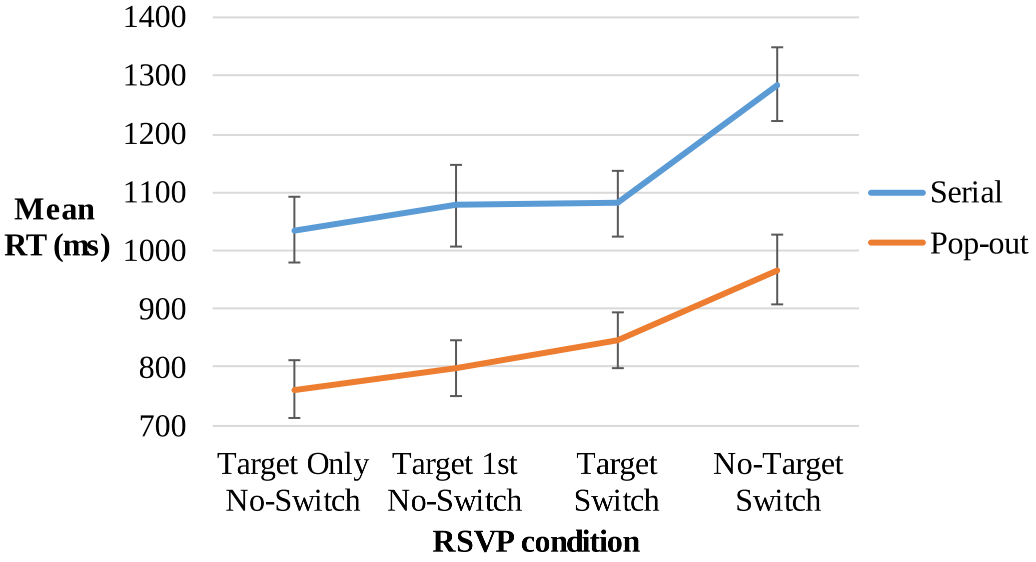

Figure 2.2. Means of participants' median VS RTs. Vertical bars represent the standard error of the mean (SE).

A 2 x 4 (VS condition × RSVP condition) within subjects ANOVA on participants' median VS RTs was conducted to explore the effects of VS and RSVP conditions on RTs. Serial search RTs were significantly slower than pop-out search RTs ($F(1,19)=294.96$, $p<.001$, $\eta^2_p=.94$). There was a significant main effect of RSVP condition on RT ($F(3,37.071)=24.95$, $p<.001$, $\eta^2_p=.568$).

Post hoc comparisons revealed that RTs were significantly slower in the No-Target Switch condition compared to all other conditions ($p<.001$), and in the Target Switch condition in comparison the Target Only No-Switch condition ($p=.038$). There were no other significant differences in RT between RSVP conditions ($p>.10$). There was no significant interaction between VS condition and RSVP condition ($p>.10$).

2.2.5 Discussion

Consistent with hypotheses, RTs were significantly slower in the No-Target Switch condition compared to all other conditions, a result of participants attending to the RSVP stream until the end of the stream, inducing a cost of switching. Although RTs were slower in the Target Switch condition in comparison to the Target Only No-Switch condition, there was no difference in RTs between Target Switch and Target No-Switch conditions. The Target Switch condition therefore induced only a marginal cost of switching. In the Target Switch condition the target digit was either the fourth, fifth, sixth or seventh item in the stream, providing a 300-600ms delay between the RSVP target presentation and VS onset. This delay likely provided enough time to anticipate the VS onset and distribute attention spatially. It was expected that presenting the target digit later in the RSVP stream in the Target Switch condition would elicit greater costs of switching.

2.3 Experiment 2: Pilot with Simple Response Time

2.3.1 Aims

In Experiment 1, RTs were significantly slower in the No-Target Switch condition compared to both No-Switch conditions (Target Only No-Switch/Target 1st No-Switch). In contrast, there was no significant difference in RTs between the Target Switch condition and the Target 1st No-Switch condition. This could be due to participants having 300-600ms to process the RSVP target and prepare for the VS. In version 2 of the task, described below (Section 2.3.2), the target digit was later in the stream as either the seventh, eighth or ninth item in the RSVP stream, which reduced the time between the RSVP target and VS onset to between 100-300ms.

It was expected that in version 2 of the task, where Target Switch RSVP targets appeared later in the stream, VS RTs would be significantly slower in both the Target Switch and No-Target Switch conditions compared to the Target 1st No-Switch condition, as participants were required to attend to the RSVP stream until near the end of the stream. It was hypothesised that serial search RTs would again be significantly slower than pop-out search RTs.

In addition to changing the position of RSVP target, the Target Only No-Switch condition was removed from the paradigm. There was no significant difference between Target Only and Target 1st No-Switch RTs, and so the Target Only No-Switch condition failed to be informative. Henceforth the Target 1st No-Switch condition will be referred to as the No-Switch condition.

The VS response was changed to a single spacebar response, which differed from the previous two-choice response (K or Z key). There is typically greater variability in CRT compared to SRTs (e.g. Hope, Bates, Dykiert, Der, & Deary, 2015). Older participants have been shown to display increased intra-individual variability in RTs (Hultsch, MacDonald, & Dixon, 2002). Higher variability in CRTs could potentially be inflated in older more than younger participants. Thus, it is important to minimise any variability in RTs resulting from response modality.

2.3.2 Methods

Participants

Twenty participants (8 males, 12 females) age 21-30 years (mean=24.5 years, SD=2.52) were recruited from Aston University staff and students and the community. Participants with photosensitive epilepsy or visual impairments were excluded.

Materials and procedures

Attention switching task version 2

Apart from the changes described below, version 2 of the attention switching task was the same as version 1, which is described in Section 2.2.2.

In Experiment 1 there was no significant difference in RTs between the Target 1st No-Switch and Target Switch conditions. In version 2 of the task, the Target Switch target digit appeared later in the RSVP steam, as either the seventh, eighth or ninth item. In Experiment 1, there was no difference between Target Only No-Switch and Target 1st No-Switch RTs. In version 2 we removed the Target Only No-Switch condition so that there were only three RSVP conditions (Target 1st No-Switch/Target Switch/No-Target Switch). The Target 1st No-Switch condition will now be referred to as the "No-Switch" condition. There were 30 trials of each of the six conditions (pop-out search: No-Switch/Target Switch/No-Target Switch; serial search: No-Switch/Target Switch/No-Target Switch), with a total of 180 trials. To provide the opportunity for breaks, trials were divided into ten blocks. Trials were randomised within blocks.

Two changes were made to participants' responses. In the new version of the task, instead of making a two-choice response to the VS by typing in the VS target (K or Z), participants first pressed the spacebar to indicate that they had seen the target. Participants then typed on the keyboard whether it was a 'K' or a 'Z' in the display. RTs to participants' spacebar responses were recorded. To prevent participants from attempting to guess the RSVP target when they had failed to detect one, participants were first asked to indicate whether they had seen a target digit in the RSVP stream by typing 'Y' if they had and 'N' if they had not. If a digit was correctly detected, participants then typed on the keyboard which number they saw. Accuracy throughout the task was recorded.

To make the task more engaging, participants wore headphones through which a 'ding' sound was played after a correct response and a chord sound was played after an incorrect response. Participants completed ten practice trials before starting the experimental trials.

2.3.3 Data analysis

The analysis procedure for the current experiment was the same as was implemented in Experiment 1 (described in Section 2.2.3) with the exception that one RSVP condition was removed, changing the model to a 2 × 3 (VS condition: serial/pop-out × RSVP condition: No-Switch/Target Switch/No-Target Switch) repeated measures ANOVA.

2.3.4 Results

Overall participants correctly identified over 94% of VS targets in each of the six conditions and 93% of RSVP targets in both target conditions (No-Switch/Target Switch). No further analysis was carried out on VS accuracy nor RSVP target identification as it was unrelated to the current hypotheses.

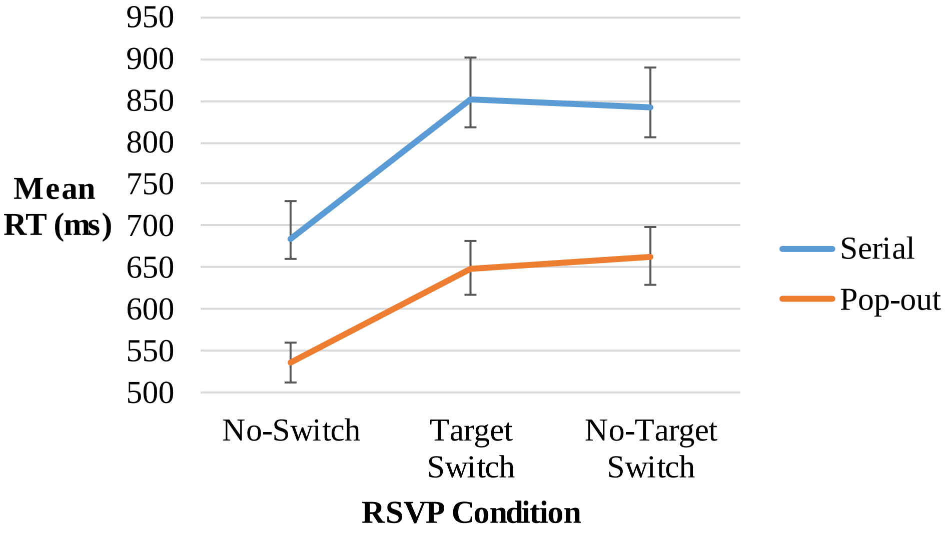

Figure 2.3. Means of participants' median VS RTs. Vertical bars represent the SE.

A 2 x 3 (VS condition × RSVP condition) within subjects ANOVA on participants' median VS RTs was conducted to explore the effects of VS and RSVP conditions on RTs. The main effect of VS condition showed that serial search RTs were significantly slower than pop-out search RTs ($F(1,19)=69.33$, $p<.001$, $\eta^2_p=.79$). There was a significant main effect of RSVP condition on RT ($F(2, 38)=50.35$, $p<.001$, $\eta^2_p=.73$). Post hoc comparisons demonstrated that the main effect of RSVP condition resulted from significantly slower RTs in both the Target Switch and No-Target Switch conditions compared to the No-Switch condition ($p<.001$). The interaction between VS condition and RSVP condition did not reach significance ($F(2,38)=3.11$, $p=.056$, $\eta^2_p=.14$).

2.3.5 Discussion

The hypothesis that the two Switch conditions would be significantly slower than the No-Switch condition was supported. Placing the RSVP target digit later in the stream succeeded in inducing a cost of switching. In the two Switch conditions participants were required to attend to the stream of letters until the end of the stream and were therefore required to rapidly switch from orienting their attention in time to distributing attention spatially to the VS. In contrast, in the No-Switch condition where the RSVP target is the first item in the stream, participants could disengage from the stream after identifying the target digit and had time to prepare to refocus attention spatially.

2.4 Comparison of Experiment 1 and 2

2.4.1 Aims

The aim of changing the VS response from a two-choice response to a single spacebar response in Experiment 2 was to minimise intra-individual variability. It has been argued that intra-individual variability increases with increased age (Hultsch et al., 2002). It is important to minimise variability in RTs that results from response modality. For this reason we compared the variability in RTs in Experiment 1 and Experiment 2.

It was hypothesised that there would be greater variability, reflected in larger SDs in RTs, in Experiment 1 compared to Experiment 2. Variability was expected to be higher in serial compared to pop-out search RTs and in the Target Switch condition compared to other RSVP conditions. In the Target Switch condition the RSVP target appears in three possible positions in the stream. It was expected that the exact position of the RSVP target would affect VS RTs, introducing variability, as the preparation time participants had to refocus attention varied with target position.

2.4.2 Methods

Participants

Twelve participants age 21-30 (mean=24.68 years, SD=2.53) took part in both Experiment 1 and Experiment 2 (12 males, 16 females) and so could be included in the comparison of the two experiments. Descriptions of Experiment 1 and 2 can be found in Sections 2.2.2 and 2.3.2.

2.4.3 Data analysis

Data were analysed using SPSS 21. Participants' SDs of mean VS RTs on trials where responses were correct on both the VS and RSVP tasks were extracted for both Experiment 1 and 2 using E-Prime data viewing application E-DataAid. As the Target Only No-Switch condition was removed from version 2 of the task in Experiment 2, Target Only No-Switch RTs were excluded from analyses.

Differences in SDs across experiments, VS conditions and RSVP conditions were analysed in a 2 × 2 × 3 (Experiment: version 1/version 2 × VS condition: serial/pop-out × RSVP condition: No-

Switch/Target Switch/No-Target Switch) repeated measures ANOVA. Multiple comparisons were corrected for with Bonferroni correction.

2.4.4 <u>Results</u>

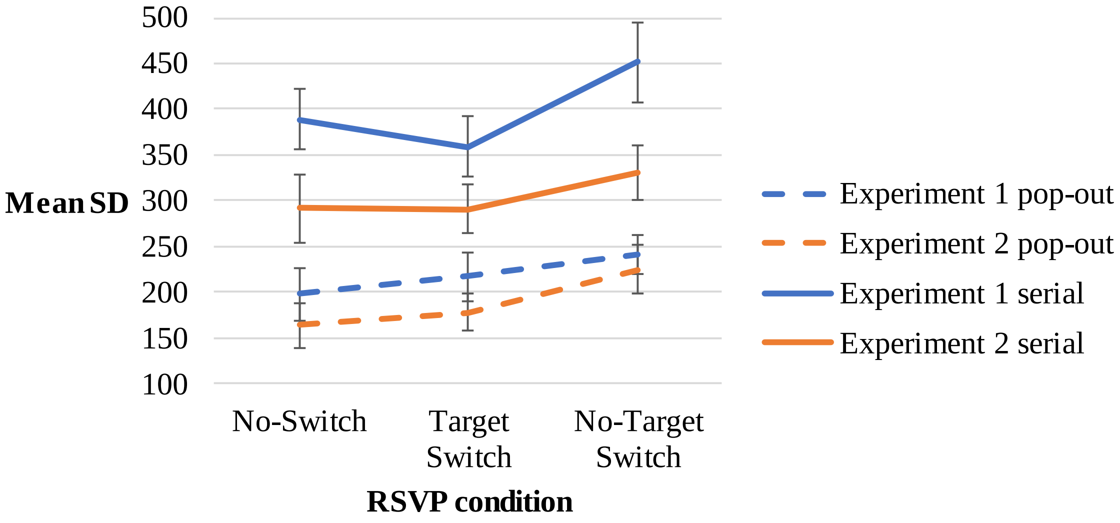

Figure 2.4. Mean SDs for each condition for Experiment 1 and Experiment 2. Vertical bars represent the SE.

To test the hypothesis that Experiment 2 would display lower variability in RTs compared to Experiment 1, a 2 × 2 × 3 within subjects ANOVA was carried out on participants' SDs of RTs. A significant main effect of experiment version resulted from higher SDs in Experiment 1 compared to Experiment 2 ($F(1, 11)=6.05$, $p=.032$, $\eta^2_p=.36$), as can be seen in Figure 2.4. A significant main effect of VS resulted from higher SDs in serial than pop-out search RTs ($F(1, 11)=189.79$, $p<.001$, $\eta^2_p=.95$). The effect of RSVP condition on SD did not reach significance ($F(1, 22)=3.03$, $p=.069$, $\eta^2_p=.22$) and post hoc comparisons detected no significant differences in SD between RSVP conditions ($p>.10$). There was a significant experiment version × VS condition interaction ($F(1, 11)=5.88$, $p=.034$, $\eta^2_p=.35$).

To further explore the interaction between experiment version and VS condition, the percentage increase in SD from Experiment 2 to Experiment 1 was calculated and compared for serial and pop-out search conditions and entered into paired t-tests. Paired t-tests revealed that, compared to pop-out VS RTs, serial VS RTs displayed disproportionally greater variability in version 1 compared to version 2.

There were no other significant interactions between experiment version, VS condition and RSVP condition ($p>.10$).

2.4.5 Discussion

Older participants are thought to show increased intra-individual variability in RTs (Hultsch et al., 2002). Greater variability in RTs from a two-choice response could therefore be further inflated by increased age. It is important to minimize this variability by favouring a single spacebar VS response.

Supporting our hypothesis, on comparison of Experiment 1 and 2 we found that, while the overall pattern of means was the same, there was higher variability in Experiment 1 than 2 that likely resulted from participants making a two-choice response in Experiment 1 in contrast to a single spacebar response in Experiment 2.

Higher variability in RTs in serial compared to pop-out searches was consistent with our hypotheses and with previous literature (Hope et al., 2015). In pop-out searches, the target is visually distinct from distractors and attention is automatically and rapidly drawn to the target through bottom-up processes. In contrast, a serial VS requires a slower, top-down strategy introducing more variability. It is widely acknowledged in the literature that serial but not pop-out search ability deteriorates with increased age (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt, 1989). The inflated increase in variability in serial search RTs when participants are required to make a choice response rather than a single response could be further exaggerated with increased age.

Contrary to our hypothesis, Figure 4 illustrates that variability was highest in the No-Target Switch condition despite the variability in the latency of Target Switch target presentation. Increased variability in the No-Target Switch condition may result from variability in the time participants take to redistribute their attention spatially or to process the absence of a target. However, this effect did not reach significance and therefore should be interpreted carefully.

It should be noted that although the No-Switch and No-Target Switch conditions were not changed across tasks, in the Target Switch condition the position of the target in the RSVP stream appeared later in Experiment 2 compared to Experiment 1 which could affect RT variability in this condition. However, this change was intended to make switching more difficult and should therefore increase RTs and SDs in Experiment 2 compared to Experiment 1. Instead we found higher overall variability in Experiment 1 compared to Experiment 2. In Experiment 1 the position of the target digit was in four possible locations, whereas in Experiment 2 it was in three possible locations. This could have introduced higher variability in RTs in the Target Switch condition in Experiment 1. However, no interaction was seen between experiment version and RSVP condition, suggesting that changes made to the Target Switch condition did not have a significant effect on variability.

It should be noted that only 12 participants took part in both experiments. The comparison was intended only to help inform our choice in experiment design. To make sound conclusions regarding intra-individual variability within each design requires a larger sample size.

One limitation of implementing a single spacebar response is that participants may modify their decision after their response with the aid of visual memory. It is not known whether the ability to adopt this strategy is greater in young adults than older adults. However, the opportunity to implement this strategy would be present in both switch and No-Switch trials and therefore should not affect the pattern of results.

2.5 Experiment 3: Comparison of five age groups

2.5.1 Aims

Experiment 3, which has been published in Callaghan et al. (2017), aimed to compare five age groups (21-30, 40-49, 50-59, 60-69, and 70+ years) on their ability to refocus from temporal to spatial attention by assessing their performance on the attention switching task developed in Experiments 1 and 2. If difficulties in refocusing attention are found in older age, then it could be that older age groups have similar impairments in more realistic settings such as while driving. If so, then it will be important to develop an intervention to improve switching between modalities of attention to help to improve driver performance and safety and prolong the length of time that people are able to continue to drive.

The literature investigating the ability to refocus from orienting attention in time to distributing attention spatially is limited across all ages. There is some evidence to suggest that the ability to refocus attention between time and space may become more difficult with increased age (Jefferies et al., 2015; Lee & Hsieh, 2009; Russell et al., 2013). For example, Lee and Hsieh (2009) found age-related difficulties in switching from attending to an RSVP stream to identify a target, to allocating attention in space to identify and point to a peripheral target.

Participants completed version 2 of the attention switching task, described in Section 2.3.2. It was hypothesised that an age-related decline in refocusing attention from time to space would be found, where older age groups would be impaired on switching from the RSVP task to the VS task. Deficits were expected to be reflected in greater increases in RTs from the No-Switch condition to each of the Switch conditions (i.e. Switch-Costs) in older groups compared to younger groups.

It is unclear whether the findings of Russell et al. (2013) and Lee and Hsieh (2009) were due to the an increased magnitude of the attentional blink with increased age (Lahar et al., 2001; Maciokas & Crognale, 2003; Shih, 2009; van Leeuwen et al., 2009) or due to deficits in the ability to switch from orienting attention in time to distributing attention spatially. In contrast to Lee and Hsieh's (2009) study, the inclusion of the No-Target Switch condition, where there was no target in the RSVP stream, enabled the investigation of whether any observed age group differences were due to difficulties in refocusing attention or an increased attentional blink. If there is a deficit in refocusing attention, then age-related inflated Switch-Costs would be present in both the No-Target Switch and Target Switch conditions. Conversely, if age-related increases in Switch-Costs result from an extended attentional blink after processing the RSVP target, then age differences in Switch-Costs would only be observable in the Target Switch and not the No-Target Switch condition.

Based on previous evidence that suggests that visual selective attention to temporal events is more difficult in those over the age of 70 years (Conlon & Herkes, 2008; Shih, 2009) but not in those aged 60-70 years (Lee & Hsieh, 2009; Quigley et al., 2012), it was expected that participants in the 70+ years group would detect and identify fewer RSVP targets digits compared to younger adults, but that RSVP target identification in the 60-69 years group would be unimpaired.

It is well established that there is a decline in working memory capacity with increased age (Richardson and Vercchi, 2002; Toepper et al., 2014). It could be argued that the increased working memory load from retaining the target digit in the current task could impair older participants' performance in switching. However, it is unlikely that retaining a single target would place enough demand on working memory to affect task performance. Furthermore, (Akyürek & Hommel, 2005) demonstrated that working memory load does not interact with the duration of the attentional blink, implying that working memory load should not affect temporal attention or the switch to spatial attention and VS target processing. Although working memory capacity is unlikely to affect task performance in the current task, performance may be affected by age-related declines to the central executive (Baddeley, 1992). Baddeley's (1992) working memory model proposed that the central executive controls the allocation of attentional resources. It may therefore be expected that a decline in executive function could affect the ability to switch from allocating attention to events changing in time (i.e. the RSVP stream) to distribute attention spatially (i.e. to VS stimuli). We therefore implemented the RNG task to measure executive functions of updating and inhibition (Miyake et al., 2000) in order to examine the effect of executive function on task performance. Performance on random generation tasks has previously been found to decline with age (Van der Linden et al., 1998).

Consistent with age-related declines in serial but not pop-out search performance (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt,

1989) and general slowing of RTs (Salthouse, 2000; Verhaeghen & Cerella, 2002), it was predicted that there would be an age-related increase in VS RTs that would be greater for serial than pop-out searches.

To establish an understanding of the mechanisms that underpin switching between modalities of attention, additional cognitive measures were recorded. The useful field of view (UFOV) task was implemented to measure visual processing speed, divided attention and selective attention. Performance on the UFOV tasks have been found to decline with age (Ball et al., 2006; Edwards et al., 2006; Rubin et al., 2007).

2.5.2 Methods

Participants

One hundred and five participants in five age groups (21-30, 40-49, 50-59, 60-69, and 70+ years) participated. The 19-30 years group were used as a comparison group for age-related cognitive changes for all other groups and the 40-49 and 50-59 years groups were used as middle-aged comparison groups for the 60-69 and 70+ years groups. Due to the study being advertised as research related to driving, many of the participants were regular drivers. The percentage of participants in each group who could drive are displayed next to participant demographics in Table 2.1. Participants with photosensitive epilepsy and visual impairments were excluded from participation, in addition to participants from the 50-59, 60-69, and 70+ years groups who scored equal to or less than the 87 cut-off for possible cognitive impairment on the Addenbrookes Cognitive Examination 3 (ACE-3; Noone, 2015). The ACE-3 consists of a series of short tasks which provide measures of language, memory, attention, fluency and visuospatial abilities.

Participants were recruited from Aston University staff and students and the community. Participants aged over 50 years were additionally recruited from the Aston Research Centre for Healthy Ageing (ARCHA) participation panel and University of the Third Age groups around the West Midlands. Participants received £7.50 towards their travel expenses. All participants provided written informed consent before participating. The research was approved by Aston University Research Ethics Committee.

One participant from the 60-69 years group and two from the 70+ years group scored equal to or lower than the 87 cut-off on the ACE-3 (Noone, 2015) and were therefore excluded from further analyses. One participant in the 40-49 years group scored lower than 87 on the ACE-3, however, this was due to English being their second language and so they were not excluded from the study. Their ACE-3 score was excluded from the analysis. All other participants scored over 87. After excluding participants with low ACE-3 scores, the mean age of the 60-69 years group was 66.00 years (SD=2.32), and the mean age for the 70+ years groups was 74.86 years (SD=5.72).

Table 2.1. Participant demographics

		Age Group (years)				
		21-30 (n=20)	40-49 (n=20)	50-59 (n=20)	60-69 (n=22)	70+ (n=23)
Age (years)	Mean	25.00	44.15	55.80	65.95	75.78
	SD	2.62	3.31	2.28	2.28	6.35
Gender	Male	10.00	9.00	8.00	11.00	9.00
	Female	10.00	11.00	12.00	11.00	14.00
Handedness	Right	19.00	18.00	17.00	22.00	20.00
	Left	1.00	2.00	2.00	0.00	3.00
	Ambidextrous	0.00	0.00	1.00	0.00	0.00
Level of Education	A-Level	1.00	4.00	8.00	5.00	4.00
	Degree	4.00	7.00	8.00	10.00	9.00
	Post degree qualification	15.00	9.00	4.00	7.00	9.00
ACE-3	Mean	na	na	95.9	94.27	94.57
	SD	na	na	2.49	4.04	3.22
Drivers	Regular drivers	17.00	19.00	20.00	21.00	23.00

The mean age of each age group, the number of participants who are male and female, the number of participants who are left and right handed, the number of people in each level of education and the number of drivers are presented for each age group. Mean ACE-3 scores are presented for the 50-59, 60-69, and 70+ years groups. One participant from the 40-49 years group was excluded from the ACE-3 analysis as their performance was impaired on vocabulary dependent sections of the task due to English being their second language.

Fisher's Exact test comparing group differences in level of education (A-level equivalent or lower/degree equivalent/post degree qualification) revealed a significant difference in the level of education between groups (*p*=.049). The number of participants in the 21-30 years group with post degree qualifications was greater than expected (z=2.1). A one-way ANOVA comparing group differences in general cognitive function measured with the ACE-3 revealed no significant group differences in ACE-3 scores (*p*>.05).

Materials and procedures

Attention switching task

The attention switching task in the current experiment was identical to the one described in Experiment 2 in Section 2.3.2. A full description of the equipment used and of the visual display can be found described in Section 2.2.2.

Participants completed ten practice trials before starting the experimental trials. One participant from the 40-49 years group, one from the 50-59 years group, five from the 60-69 years group and 11 from the 70+ years group required an additional ten practice trials.

Useful Field of View task

The UFOV (Ball et al., 1988) was administered to measure processing speed, selective attention, and divided attention. The UFOV consists of three sub-tasks on the computer, where the stimulus presentation duration begins at 500ms and reduces to 16.7ms until the participant achieves less than 75% accuracy. The shortest presentation duration at which the participant achieves 75% accuracy is recorded as the participant's processing speed threshold in each of the tasks.

On the processing speed task, either a picture of a car or a picture of a truck was presented in the centre of the screen. Participants then indicated whether the image presented to them was a car or a truck. The divided attention task was the same as the processing speed task with the addition of the simultaneous presentation of a peripheral stimulus, which was also either a car or a truck. Participants both identified the item presented in the centre of the screen and the location of the peripheral stimulus. The selective attention task was the same as the divided attention task with the addition of distractor stimuli simultaneously presented surrounding the two target stimuli. A full description of the UFOV has been described previously by Ball, Owsley, Sloane, Roenker and Bruni (1993).

Random Number Generation task

The RNG task (Towse & Neil, 1998) was administered to measure executive functions. For two minutes, participants were played a metronome beat at 60 beats per minute and called aloud random numbers from 1-9 in time with the beat. Random was defined using Horne, Evans and Orne's (1982) hat analogy.

Towes and Neil's (1998) software, Rgcalc, was used to calculate measures of randomness. In accordance with Miyake et al.'s (2000) Principal Components Analysis, Evans' (1978) *RNG score,* a measure of how frequently number pairs/triplets occurred, was selected to measure inhibition, and *Redundancy* (R), a measure of how frequently each number occurred, was selected to measure updating. Lower scores on each measure indicates poorer randomisation.

2.5.3 Data analysis

Data were analysed using SPSS 21.

Attention switching task

Participants' median VS RTs (ms) on trials where responses were correct on both the VS and RSVP tasks were extracted using E-Prime data viewing application E-DataAid. Participants' proportions of correct VS target identifications, RSVP target detections, RSVP target identifications and proportions of false positive RSVP targets detections on the No-Target Switch condition were also extracted.

Older adults display higher proportions of false positive responses than younger individuals (Bolton & Staines, 2012; Kenemans, Smulders, & Kok, 1995). D prime (d') was used as an unbiased measure of RSVP target detection sensitivity, as has been done in previous work on visual attention in the ageing population (Berardi, Parasuraman, & Haxby, 2001; Mouloua & Parasuraman, 1995; Parasuraman, Nestor, & Greenwood, 1989). Differences between age groups and RSVP conditions in both RSVP target detection and target identification were analysed in two 2 × 5 mixed ANOVA, with RSVP condition (Target Switch/No-Switch) as a within subjects factor, and age group (21-30, 40-49, 50-59, 60-69, 70+ years) as a between subjects factor.

Differences in median VS RTs between age groups, VS conditions and RSVP conditions were analysed in a 2 × 3 × 5 mixed ANOVA, where within subject factors were VS condition (serial/pop-out) and RSVP condition (No-Target Switch/Target Switch/No-Switch), and age group (21-30, 40-49, 50-59, 60-69, 70+ years) was a between subjects factor. Multiple comparisons were corrected for with Bonferroni correction. Where Mauchly's Test of Sphericity was significant, indicating that the assumption of sphericity had been violated, Greenhouse-Geisser corrected statistics were reported.

The data were expected to violate assumptions of equality of variance due to increases in inter-individual variability with age (Hale, Myerson, Smith, & Poon, 1988; Morse, 1993). There is evidence to support that the ANOVA is robust to violations to homogeneity of variance (Budescu, 1982; Budescu & Appelbaum, 1981). Levene's test for equality of variance is therefore not reported.

To further explore the interactions between independent variables that were identified from the ANOVA on RSVP accuracy, independent t-tests were implemented to compare age groups on target identification separately for Target Switch and No-Switch RSVP conditions.

To further explore the interactions that were identified between independent variables in the RT ANOVAs, percentage differences between conditions were calculated for each individual and independent t-tests were implemented to compare age groups' percentage differences in RTs. To further explore the age group × RSVP condition interaction, "Switch-Costs" were calculated as the percentage difference in RTs between Target Switch and No-Switch conditions (Target Switch-Costs) and between No-Target Switch and No-Switch conditions (No-Target Switch-Costs) for each individual. Independent t-tests were implemented to compare age groups' Switch-Costs. It is important to note that t-tests were exploratory rather than hypothesis driven, and hence Restricted Fisher's Least Significant Difference test was applied and corrections for multiple comparisons were not conducted (Snedecor & Cochran, 1967). Where Levene's test for equality in variance was significant ($p<.05$) when computing t-tests, 'Equality of variance not assumed' statistics were reported.

Cognitive measures

The relationship between Switch-Costs and each cognitive measure, including UFOV subtasks processing speed, divided attention and selective attention, and RNG task indices for updating (R) and inhibition (RNG), and the relationship between each UFOV subtask and pop-out search RTs on the No-Switch condition, were explored with Spearman's correlation analyses. It should be noted that correlations were exploratory and corrections for multiple comparisons were not conducted.

2.5.4 Results

Attention switching task

One participant in the 60-69 years group was excluded from the attention switching task analyses due to achieving chance level VS accuracy in several conditions, including the No-Target Switch pop-out search condition (mean=.40), the Target Switch pop-out search condition (mean=.53), and the Target Switch serial search condition (mean=.57). The participant's low proportion of correct VS responses indicates that they may not have understood the task. One participant from the 70+ years group was excluded from RT analyses due to poor VS and RSVP target identification, resulting in less than one third of serial search trials remaining in the No-Switch condition. Nineteen participants remained in the 70+ years group in the RT analysis and there were 20 participants in 60-69 years group in the remaining analysis.

RSVP accuracy

Both the ability to detect targets in the RSVP stream and the proportion of correctly identified targets, where the participant correctly reported the target digit, were examined. Poor target detection would suggest that participants have a deficit in temporal selective attention. Group differences in target identification and not target detection may indicate a deficit in consolidation or recall of the target. Thus, distinguishing between correctly detected and identified targets could reveal specific age-related deficits in different cognitive processes.

Target detection

A 2 × 5 (RSVP condition × age group) ANOVA was conducted on measures of d', an index of target detection sensitivity. D' provides a measure of detection sensitivity while controlling for false positive response rates, which has been shown to be inflated in older participants (Bolton & Staines, 2012; Kenemans et al., 1995). D' has previously been used as a measure of target sensitivity in work on visual attention in the ageing population (Berardi et al., 2001; Mouloua & Parasuraman, 1995; Parasuraman et al., 1989). D' for each RSVP condition are presented for each age group in Figure 2.5 (left).

There were significant main effects of age ($F(4, 95)=9.04$, $p<.001$, $\eta^2_p=.28$) and RSVP condition ($F(4, 95)=43.55$, $p<.001$, $\eta^2_p=.31$) on d'. There was no significant interaction between age and RSVP condition ($p>.10$).

Main effect of age

Post hoc comparisons illustrated that the main effect of age on detection sensitivity resulted from greater detection sensitivity in the 21-30 years group compared to the 50-59 ($p=.036$), 60-69 ($p<.001$) and 70+ years ($p<.001$) groups. The 40-49 years group displayed a significantly higher detection sensitivity than the 60-69 ($p=.005$) and 70+ years groups ($p=.001$). There were no other significant group differences in detection sensitivity ($p>.10$).

No further analysis was carried out on d'. Age differences in target detection suggest that difficulties derive from declines in selective attention that will similarly affect RSVP target identification, as is evident in Figure 2.5. Instead, target identifications were examined in more depth.

Target identification

Figure 2.5 (right) illustrates a decrease in target identification with increased age. A 2 × 5 (RSVP condition × age group) mixed ANOVA was conducted on the proportion of correctly identified RSVP targets. There was a significant main effect of age ($F(4, 95)=9.06$, $p<.001$, $\eta^2_p=.28$) and RSVP condition ($F(1, 95)=43.40$, $p<.001$, $\eta^2_p=.31$) on RSVP target identification, as well as a significant age × RSVP condition interaction ($F(4, 95)=3.15$, $p=.018$, $\eta^2_p=.12$).

Main effects of age and RSVP condition

It was hypothesised that the 70+ years group would identify fewer targets compared to younger groups but that there would be no difference in the proportion of targets identified in the 60-69 years group. Post hoc comparisons showed that the main effect of age resulted from the 21-30 years group identifying significantly more RSVP targets than the 50-59 ($p=.017$), 60-69 ($p=.001$) and 70+ years ($p<.001$) groups. The 40-49 years group identified significantly more targets than the 70+ years group (*p*=.002). The higher target identification in the 40-49 years group compared to the 60-69 years group did not reach significance (*p*=.078). There were no other significant group differences in target identification (*p*>.10). The main effect of RSVP condition resulted from participants identifying more targets in the No-Switch than the Target Switch condition.

Interaction between age and RSVP conditions

To further explore the interaction between age group and RSVP condition on target identification independent t-tests were implemented to compare age groups on RSVP target identification on each RSVP condition separately.

In the No-Switch condition, the 21-30 years group identified significantly more targets than the 40-49 (*t*(26.24)=2.46, *p*=.021), 50-59 (*t*(22.14)=2.65, *p*=.015), 60-69 (*t*(26.77)=4.49, *p*<.001) and 70+ (*t*(22.54)=4.79, *p*<.001) years groups, and the 40-49 years group identified more targets than the 70+ years group (*t*(38)=2.60, *p*=.013).

In the Target Switch condition, the 21-30 years group identified significantly more targets than the 50-59 (*t*(38)=3.93, *p*<.001), 60-69 (*t*(28.76)=5.00, *p*<.001) and 70+ (*t*(27.31)=5.39, *p*<.001) years groups, the 40-49 years group identified significantly more targets than the 50-59 (*t*(38)=2.38, *p*=.022), 60-69 (*t*(38)=3.45, *p*=.001) and 70+ (*t*(38)=3.92, *p*<.001) years groups, and there was a non-significant trend for the 50-59 years group to identify more targets than the 70+ years group (*t*(38)=1.77, *p*=.086).

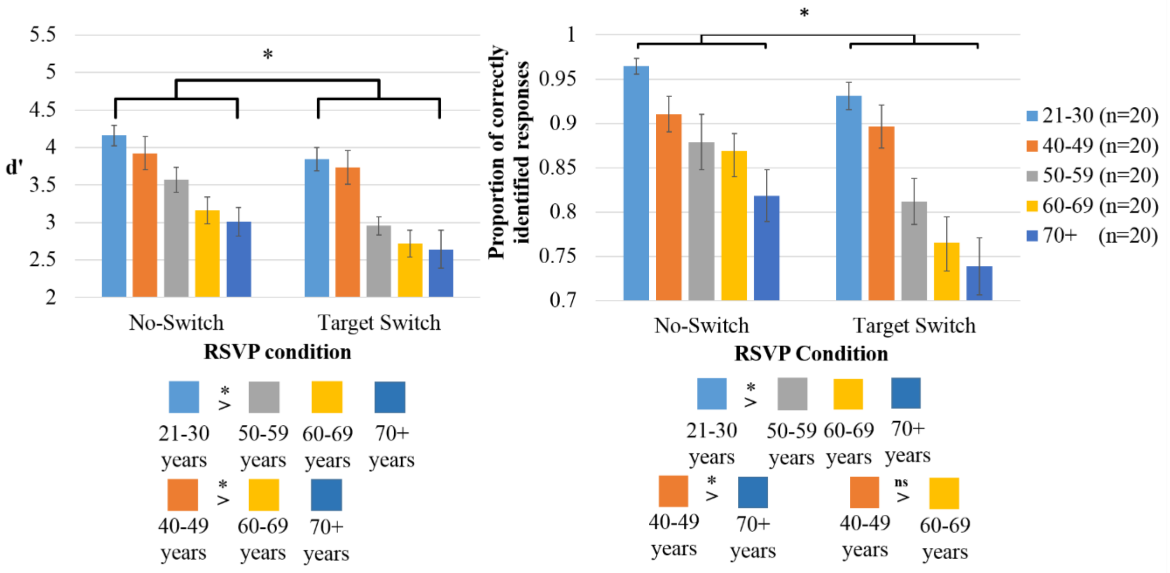

Figure 2.5. RSVP Accuracy. An index of RSVP target detection sensitivity, d’ (left) and the proportion of correctly identified RSVP targets (right) in each RSVP condition for each age group. The asterisk above each graph represents significant differences between RSVP conditions, collapsed across age groups. The colour coded boxes below each graph illustrate significant age group differences collapsed across RSVP conditions. Vertical bars represent the SE.

VS task

All groups correctly identified over 94% of VS targets in all six conditions. Thus, no further analysis was carried out on VS accuracy.

A 2 × 3 × 5 (VS condition × RSVP condition × age group) mixed ANOVA was conducted with participants' median RTs. Mauchly's Test of Sphericity was significant for RSVP condition ($\chi^2(2)=8.56$, $p=.014$) indicating that the assumption of sphericity has been violated. Greenhouse-Geisser corrected statistics were therefore reported. Mean VS RTs for each age group for serial and pop-out searches are presented in Figure 2.6.

Significant main effects of age ($F(4, 94)=13.39$, $p<.001$, $\eta^2_p=.36$), VS condition ($F(1, 94)=335.17$, $p<.001$, $\eta^2_p=.78$), and RSVP condition ($F(1.84, 172.80)=133.57$, $p<.001$, $\eta^2_p=.59$) on VS RTs were revealed, in addition to a significant age × VS condition interaction ($F(4, 94)=4.98$, $p=.001$, $\eta^2_p=.18$), a significant age × RSVP condition interaction ($F(7.35, 172.80)=2.72$, $p=.009$, $\eta^2_p=.10$), and a significant VS condition × RSVP condition interaction ($F(1.99, 187.19)=5.37$, $p=.005$, $\eta^2_p=.05$). There was no significant age × VS condition × RSVP condition interaction ($p>.10$).

Main effects of age, VS condition and RSVP condition

Based on widely acknowledged age-related slowing of RTs, RTs were expected to increase with increased age (Foster et al., 1995; Salthouse, 2000). Post hoc comparisons illustrated that the 21-30 years group was significantly faster than the 50-59 ($p=.024$), 60-69 ($p<.001$) and 70+ ($p<.001$) years groups, but not the 40-49 years group ($p>.10$). The 70+ years group was slower than both the 40-49 ($p=.001$) and 50-59 years groups ($p=.004$). There were no other significant group differences in RT ($p>.10$).

Participants were significantly faster on the pop-out compared to serial VS. We hypothesized that RTs would be faster on the No-Switch condition, when participants no longer need to attend to the RSVP stream after identifying the target digit, compared to when they are required to attend to the RSVP stream to the end of the stream in the two Switch conditions (Target Switch/No-Target Switch). The main effect of RSVP condition on VS RTs resulted from significantly faster RTs on the No-Switch condition compared to both the No-Target Switch ($p<.001$) and Target Switch ($p<.001$) conditions. There was no significant difference between the No-Target Switch and Target Switch conditions ($p>.10$).

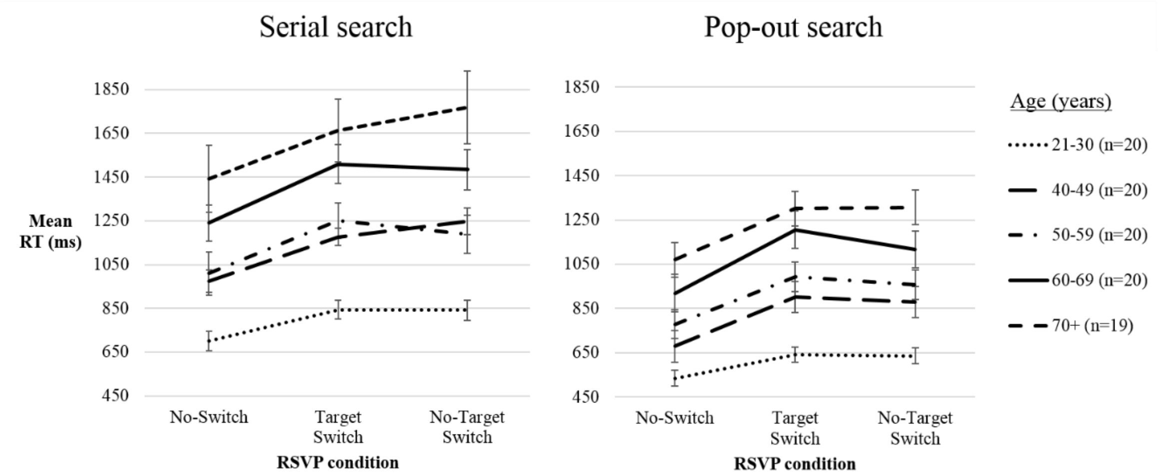

Figure 2.6. VS RTs. Means of participants' median VS RTs for each RSVP condition for each age group on serial (left) and pop-out VS (right). Vertical bars represent the SE.

Interaction between age and VS conditions

It is well established that older participants display deficits in serial but not in pop-out VS (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt, 1989). It was hypothesised that the increase in RTs on serial compared to pop-out search would be greater in older than younger groups. In support of this hypothesis, there was a significant age × VS condition interaction. To investigate this hypothesis further, the percentage increase in RTs from the pop-out to serial search, collapsed across RSVP conditions, was calculated and entered into independent t-tests to compare groups. To collapse VS RTs across RSVP conditions separately for serial and pop-out search RTs, each participant's median RTs were averaged across RSVP conditions separately for pop-out and serial search RTs. The mean percentage increase in RTs from pop-out to serial search is presented in Table 2.2.

Independent t-tests revealed that there was a significantly larger difference between serial and pop-out search RTs in the 40-49 years than the 50-59 (*t*(38)=2.89, *p*=.007). The larger difference between pop-out and serial search RTs in the 40-49 years group compared to the 21-30 (*t*(38)=-1.85, *p*=.072), 60-69 (*t*(38)=1.80, *p*=.080) and 70+ (*p*>.10) years groups did not reach significance. There were no further significant group differences in the percentage increase in RT from pop-out to serial search (*p*>.10).

Table 2.2. Means and SDs of the percentage difference from pop-out to serial search RTs for each group

		Age Group (years)				
		21-30 (n=20)	40-49 (n=20)	50-59 (n=19)	60-69 (n=20)	70+ (n=20)
Percentage	Mean	21.68	27.21	19.21	22.65	23.17
Difference	SD	11.01	7.61	9.95	8.41	8.58

Percentage difference indicates the percentage increase in serial search RTs compared to pop-out search RTs.

Interaction between age and RSVP conditions

It was hypothesized that there would be greater difficulties in switching between the temporal and spatial attention tasks with increased age. To investigate the hypothesis that Switch-Costs would be greater with increased age, the interaction between age and RSVP condition was further explored. Switch-Costs were calculated as the percentage difference in RTs between Target Switch and No-Switch conditions (Target Switch-Costs) and between No-Target Switch and No-Switch conditions (No-Target Switch-Costs) for each individual. Collapsing VS conditions to calculate Switch-Costs lead to finding no significant age group differences in Switch-Costs (*p*>.10). Thus, although there was no three-way interaction between age, VS condition and RSVP condition (*p*>.10), Switch-Costs were calculated separately for serial and pop-out search RTs to gain a detailed understanding of the interaction between age and RSVP conditions. Target Switch-Costs and No-Target Switch-Costs were entered into independent t-tests to compare groups. It is important to note that t-tests were exploratory, however, remain in the scope of current hypotheses. The means and SDs of each group's Switch-Costs on serial search and pop-out search RTs are presented in Table 2.3.

Pop-out search Target Switch-Costs were significantly greater for both the 40-49 (*t*(38)=-2.39, *p*=.022) and 60-69 years groups compared to the 21-30 years group (*t*(38)=-2.28, *p*=.028). The greater pop-out Target Switch-Costs in the 50-59 years group compared to the 21-30 years groups did not reach significance (*t*(38)=-1.73, *p*=.091). There were no significant differences in Target Switch-Costs or No-Target Switch-Costs between any other age groups for either VS condition (*p*>.10).

Table 2.3. Means and SDs of Switch-Costs for each age group

			Age Group (years)				
			21-30 (n=20)	40-49 (n=20)	50-59 (n=19)	60-69 (n=20)	70+ (n=19)
Serial	Target Switch-Costs	Mean	16.46	16.21	17.41	18.48	13.22
		SD	11.36	12.68	12.48	12.39	14.63
	No-Target Switch-Costs	Mean	15.94	20.65	12.78	16.30	18.15
		SD	13.26	10.85	21.23	14.33	12.68
Pop-out	Target Switch-Costs	Mean	15.39	23.89	21.51	23.33	18.44
		SD	11.57	10.87	10.75	10.41	9.71
	No-Target Switch-Costs	Mean	16.78	21.44	16.78	16.75	17.61
		SD	8.48	10.01	15.03	13.28	11.84

Switch-Costs were calculated as the percentage increase in RT from the No-Switch condition to each of the switch conditions (Target Switch/No-Target Switch) separately, and separately for each VS condition.

Interaction between VS conditions and RSVP conditions

No further analysis was carried out on the interaction between RSVP condition and VS condition, as it is unrelated to the current hypotheses.

Cognitive Function

The cognitive mechanisms that influence switching between modalities of attention were explored. Mean scores on UFOV processing speed, divided attention and selective attention, and the RNG index (inhibition) and R (updating) scores (Miyake et al., 2000) can be found in Table 2.4. Group comparisons of listed cognitive measures can be found in Appendix 2.1.

Table 2.4. Means and SDs for cognitive measures

		Age Group (years)				
		21-30 (n=20)	40-49 (n=20)	50-59 (n=20)	60-69 (n=21)	70+ (n=21)
Updating (R)	Mean	1.41	1.45	1.06	1.22	1.08
	SD	1.78	1.07	0.81	0.52	0.71
Inhibition (RNG)	Mean	0.33	0.34	0.32	0.34	0.36
	SD	0.03	0.50	0.05	0.03	0.04
Processing Speed	Mean	16.72	16.70	21.54	25.44	22.54
	SD	0.07	0.00	9.53	23.38	13.37
Divided Attention	Mean	24.22	39.05	58.20	49.26	79.04
	SD	31.30	53.87	63.24	51.25	76.34
Selective Attention	Mean	54.39	101.36	127.08	151.50	186.06
	SD	28.97	59.55	58.57	87.36	87.37

One participant in the 70+ years group did not complete the UFOV, resulting in 20 participants in this group for the processing speed, divided attention and selective attention measures.

The relationship between Switch-Costs and cognition

To identify cognitive functions that may affect switching ability, the relationships between Switch-Costs and cognitive measures were examined separately for each age group. Relationships were examined only for Target Switch-Costs in the pop-out search condition, as it was in this condition only that age group differences in Switch-Costs were found. Shapiro Wilks test of normality demonstrated that the distribution of scores from all cognitive measures except the RNG index violated the assumption of normality for one or more age groups ($p<.05$). Spearman's rho correlation coefficients are therefore reported, which can be found in Table 2.5. It should be noted that correlations were exploratory and corrections for multiple comparisons were not conducted.

Table 2.5. Spearman's rho correlation coefficients, correlating cognitive measures with Switch-Costs

	Age group (years)				
	20-29 (n=20)	40-49 (n=20)	50-59 (n=20)	60-69 (n=20)	70+ (n=19)
R	-0.03	-0.23	-0.03	0.13	-0.01
RNG	-0.16	-0.32	0.29	0.21	-0.14
Processing Speed	-0.06	.	-0.40	-0.49*	0.14
Divided Attention	0.22	0.04	-0.50*	0.07	-0.12
Selective Attention	-0.17	0.12	-0.73***	-0.43	0.02

*p<.05, **p<.01, ***p<.001; Updating (R), inhibition (RNG)

UFOV Processing Speed

There was a significant negative correlation between Target Switch-Costs and UFOV processing speed in the 60-69 years group (*p*=.033). Those with greater Switch-Costs displayed faster processing speeds. The correlation between Target Switch-Costs and processing speed did not reach significance in the 50-59 years group (*p*=.083). There were no other significant correlations between Switch-Costs and processing speed (*p*>.10). Correlation coefficients are reported in Table 2.5.

UFOV Divided Attention

In the 50-59 years group there was a significant negative correlation between Switch-Costs and UFOV divided attention (*p*=.027). Those with greater Switch-Costs performed better on the UFOV divided attention task (i.e. had faster processing thresholds). There were no other significant correlations between UFOV divided attention and Switch-Costs in any other age group (*p*>.10).

UFOV Selective Attention

There was a significant negative correlation between Target Switch-Costs and UFOV selective attention in the 50-59 years group (*p*<.001) and a non-significant negative correlation between Target Switch-Costs and selective attention in the 60-69 years groups (*p*=.061). Participants with greater Target Switch-Costs had faster processing thresholds in the selective attention task. There were no other significant correlations between UFOV selective attention and Target Switch-Costs in any other age group (*p*>.10).

The direction of the relationship between Target Switch-Costs and performance on processing speed, divided attention and selective attention UFOV tasks was unexpected. Poor performance on the

UFOV tasks was related to smaller Target Switch-Costs. These findings may be explained by a significant positive correlation between VS RTs in the No-Switch condition and UFOV processing speed (r=.445, p<.001, n=99), divided attention (r=.592, p<.001, n=99) and selective attention (r=.577, p<.001, n=99) measures. Those who performed poorly on the UFOV tasks had slower VS RTs on the No-Switch condition. Slow RTs on the No-Switch condition resulted in smaller Switch-Costs, as the difference between Switch and No-Switch conditions became smaller.

RNG task

There were no significant correlations between Switch-Costs and RNG measures R or RNG in any age group (p>.10).

2.5.5 **Discussion**

The aim of the current study was to investigate whether there was an age-related decline in the ability to switch between temporal and spatial attention and to explore the cognitive mechanisms that might underlie these changes. Identifying age-related cognitive changes that affect driving behaviour is an important first step in working towards developing a cognitive intervention to improve driving performance and prolong the time that people are able to continue to drive.

There were decreases in both RSVP target detection sensitivity and target identification with increased age. Deficits in target identification but not target detection would suggest that group differences are related to memory and not temporal attention. Results therefore indicate that older participants' impaired performance derives from temporal attention mechanisms and results are not due to memory difficulties. It was hypothesised that there would be age-related difficulties in target identification in the 70+ years group but not the 60-69 years group. On the contrary, the 21-30 years group identified more targets than all other age groups in both the No-Switch condition and the Target Switch condition. Age group differences were more extensive in the Target Switch condition compared to the No-Switch condition, and significantly fewer targets were identified in the Target Switch condition compared to the No-Switch condition overall. Poorer target identification in the Target Switch condition likely results from the presence of distractor stimuli both forward and backward masking Target Switch targets, whereas No-Switch targets were only backward masked. It is likely that the effect of distractors masking the target was further exacerbated by older adults' inhibitory deficits (Adamo et al., 2003; Aydin et al., 2013; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig et al., 2007; Maciokas & Crognale, 2003).

Consistent with previous research and with expectations, RTs were slower on serial than pop-out searches (Wolfe, 1998). These findings are due to attention being immediately drawn to the distinct target in pop-out searches, in contrast to when needing to complete a serial search (Treisman, 1985).

Consistent with age-related slowing of RTs (Salthouse, 2000; Verhaeghen & Cerella, 2002), and supporting current hypotheses, there was an age-related increase in VS RTs.

A greater increase in RTs from pop-out to serial search in the 40-49 years group compared to both younger and older groups was unexpected and contrasts with previous findings. Age-related deficits in serial but not pop-out search are well established (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Li et al., 2013; Plude & Doussardroosevelt, 1989). The absence of greater differences between VS conditions in the older groups may be due to ceiling effects, with slow RTs in both VS conditions in the older groups. Previous VS paradigms have not preceded VS tasks with an RSVP task, which could have further exacerbated participants' performance across all VS conditions. In contrast, RTs on the pop-out search in the 40-49 years group remain fast and result in a larger percentage increase in RT from the pop-out to serial search.

Consistent with predictions, RTs were faster when switching from the RSVP task when the target was the first item in the stream compared to when the target was absent or in the middle of the stream. This can be attributed to larger Switch-Costs when attending to the RSVP stream to near the end of the stream than when able to disengage from the stream. These finding show that costs in switching from the temporal attentional task cause a delay to initiating a VS.

Larger Switch-Costs in the 40-49 and 60-69 years groups compared to the youngest group for the Target Switch condition only partially supports the hypothesis that there would be increased Switch-Costs with age. Greater age-related Switch-Costs in only the 40-49 and 60-69 years groups raises the question of why the 70+ years groups did not also display greater Switch-Costs compared to the youngest group and why the larger Switch-Costs in the 50-59 years group compared to the youngest group did not reach significance. RTs in the 40-49 years group were not significantly slower than RTs in the youngest group. It may be that fast RTs in the No-Switch condition are inflating the Switch-Costs in the 40-49 years group, as the percentage increase in RTs when they have to switch is greater. In contrast, Switch-Costs in the 50-59 years group are partially masked by their slower RTs in the No-Switch condition.

The question remains as to why greater Target Switch-Costs are seen in the 60-69 years and not in the 70+ years group. The absence of significantly greater Switch-Costs cannot merely be explained by increased variability, as both means and variability of Target Switch-Costs were marginally lower in the 70+ (mean=18.44, SD=9.71) compared to the 60-69 (mean=23.33, SD=10.41) years group in the pop-out search condition (Table 2.3), although these differences were not significant. One explanation may be that the oldest group have developed efficient compensation strategies that are not yet present in the 60-69 years group. It may become necessary to adapt new strategies and recruit wider neural networks with older age due to increasingly impaired attentional mechanisms combined with slowed RTs, whereas faster RTs in younger participants are sufficient to compensate for switching demands. The recruitment of broader neural circuits with increased age is widely supported (Toepper et al., 2014), including in frontoparietal regions during attentional tasks (Madden, Spaniol, Whiting, et al., 2007), although it is unclear whether wider activation is due to compensation (Madden, 2007; Madden, Spaniol, Whiting, et al., 2007) or increased noise due to deficits in inhibitory mechanisms (Fabiani et al., 2006; Gazzaley et al., 2008; Shih, 2009). The presence of increased neural noise with increased age raises the possibility that greater Switch-Costs were not seen in the 70+ years group due to increased variability in RTs masking Switch-Costs. Increased variability masking greater Switch-Costs in the 70+ years group is supported by the increased variability observed with age in the current data (Figure 2.6).

A common limitation in aging research is self-selection bias. Older volunteers tend to be healthy, highly educated people who seek to stay active in later life. Both a physically, socially and cognitively active lifestyle, and higher levels of education and occupation have been shown to be protective factors against cognitive decline (Anstey & Christensen, 2000; Fratiglioni, Paillard-Borg, & Winblad, 2004; Lopez et al., 2014) and aspects of lifestyle such as level of education, video gaming habits and employment status have been shown to predict performance in visual attention tasks (Wilms & Nielsen, 2014). Thus, sample attributes may result in Switch-Costs in the 60-69 but not 70+ years group, in which there is less of a bias towards healthy, highly motivated people. However, the 70+ years group did not display a significantly higher level of education and did not perform better on the ACE-3, which is a basic measure of cognitive function.

As a third alternative, the difference between Switch and No-Switch conditions may have been reduced in the 70+ years group due to participants taking longer to process the No-Switch target and/or taking longer to disengage attention from the RSVP stream in the No-Switch condition due to difficulties in inhibiting distractor stimuli. In both scenarios, VS RTs in the No-Switch condition would be inflated, reducing the difference between Switch and No-Switch conditions. These explanations would be consistent with increased visual processing speeds with increased age (Ball et al., 2006; Rubin et al., 2007) and with evidence that suggests that temporal attention is impaired only in those over the age of 70 years and not in those aged 60-69 years (Lee & Hsieh, 2009; Shih, 2009), explaining why increases in Switch-Costs are seen in the 60-69 years group and not the 70+ years group. This explanation would also account for the surprising findings of increased Switch-Costs with faster processing speed thresholds in the UFOV processing speed and selective attention tasks that were seen in both the 50-59 and 60-69 years groups. This relationship was in the opposite direction to expectations. To perform well on the UFOV selective attention task, one is required to inhibit irrelevant distractors across the screen to selectively attend to the target. Thus, inhibitory deficits seem to be resulting in both a smaller difference between No-Switch and Switch conditions, due to difficulties in disengaging from the RSVP stream, and longer processing speeds in the UFOV selective attention task. However, it is important to note that correlation analyses were exploratory and corrections for multiple comparisons were not conducted. Further research with larger sample sizes is needed to corroborate these findings.

However, Switch-Costs did not correlate with the RNG index, which is a measure of inhibition. This may be because inhibitory mechanisms implemented in the RNG task to inhibit repetition and number sequences are separate from those involved in inhibiting visual distractors. Excitatory-inhibitory competition in the visual cortex is involved in selectively attending visual information (Luck et al., 1997; Reynolds et al., 1999), whereas inhibition during the RNG task is likely to involve the inhibition of response in working memory localized to the prefrontal cortex (Daniels, Witt, Wolff, Jansen, & Deuschl, 2003). This conclusion is supported by (Madden, Spaniol, Whiting, et al., 2007) who, in a serial VS task, found that whereas young adults' performance was associated with occipital lobe activation, older adults' performance was more strongly related to frontal and parietal activity. These findings are consistent with a specific decline in serial search performance with age caused by deficits in excitatory-inhibitory mechanisms during visual processing.

Age differences in Switch-Costs in the Target Switch condition and not in the No-Target Switch condition are likely due to the requirement to consolidate the RSVP target. It could be that increased Switch-Costs in this condition are due to slow processing speeds resulting in participants taking longer to process the target, which delays the switch to refocus attention spatially. On the contrary, fast processing speeds were related to increased Switch-Costs. Current findings therefore suggest that deficits in switching between temporal and spatial attention were not due to general slowing.

The current results support Lee and Hsieh's (2009) findings of an age-related increase in difficulties in switching from attending to an RSVP stream to identify a target, to allocating attention in space to identify and point to a masked peripheral target. However, Lee and Hsieh's (2009) aim was to investigate the attentional blink in older adults, and thus does not distinguish between impaired task performance resulting from an increased attentional blink, or due to deficits in switching between temporal and spatial attention. The inclusion of the No-Target Switch condition in the current task enabled the investigation of whether age-related deficits in switching were due to increases in the time taken to refocus attention spatially or an increased attentional blink. If there was a deficit in refocusing attention, then older adults should be impaired in switching in both the No-Target Switch and Target Switch conditions when compared with younger adults. Conversely, the current findings of increased Switch-Costs in the Target Switch condition only indicate that higher Switch-Costs may result from an increased attentional blink after processing the RSVP target. However, Figure 2.6 could also signify that increased variability in the No-Target Switch condition may have prevented group differences from emerging in the No-Target Switch condition (e.g. 70+ group). Despite attempts to minimise variability in RTs by using an initial spacebar response, high variability masking differences in statistical power is corroborated by generally increased variability in RTs with increased age in the current dataset (Figure 2.6). The absence of a significant difference in RTs between the No-Target Switch condition and the Target Switch condition further supports that group differences in Switch-Costs in the No-Target Switch condition were not seen due to variability in RTs masking differences in statistical power. The results of Experiment 4 described below in Section 2.6 further support that inflated Switch-Costs with increased age were indeed due to a decline in attention refocusing rather than an increased magnitude of the attentional blink.

Limitations

In contrast to previous VS paradigms (Humphrey & Kramer, 1997; Li et al., 2013), participants were required to make an initial spacebar response to indicate that they had identified the target and then report which letter they had seen. A limitation of this approach is that participants may modify their decision after they have made a response with the aid of visual memory. It is not known whether the ability to adopt this strategy is greater in young adults than older adults. However, the opportunity to implement this strategy was present in both Switch and No-Switch trials and therefore should not have affected our main findings.

It could be argued that, rather than an age-related impairment in refocusing attention between temporal and spatial modalities, higher Switch-Costs with increased age reflect either a difficulty in switching between different levels of task difficulty or between different target types. Firstly, it could be that switching from a task with high task demands to a task with lower task demands induces Switch-Costs that are greater with increased age. Accuracy data suggests that RSVP target identification placed more demand on cognitive processing than VS target identification. The percentage of correct VS target identifications was over 94% in all age groups. Although the percentage of correct RSVP target identifications was over 93% for the 21-30 years group, and over 90% for the 40-49 years group, all other age groups identified significantly fewer targets than this. Furthermore, target identification was significantly higher in the No-Switch condition compared to the Target Switch condition. Greater cognitive effort applied in the Target Switch condition compared to the No-Switch condition could have slowed RTs on the subsequent VS task. Additionally, there was a significant age group × RSVP condition interaction that stemmed from the two youngest groups identifying significantly more RSVP targets than the three oldest groups, a difference that was greater in the Target Switch condition than the No-Switch condition. Therefore, it could be that age-related increases in Switch-Costs actually result from age-related increases in cognitive effort required to identify targets in the Target Switch condition compared to the No-Switch condition. Experiment 4, described in Section 2.6, was carried out to establish whether inflated

Switch-Costs were a result of age-related difficulties in switching between temporal and spatial attention or are a result of age differences in RSVP task ability.

Secondly, we do not believe that switching between target types of numbers and letters impaired switching performance. Numbers and letters are in the same “alphanumeric” semantic category and should therefore require little cognitive effort to switch between the two. On the contrary, we expect that switching from identifying a target digit in the RSVP stream to identify a second target digit in the VS would employ a greater cognitive effort, as one must retain additional information about which number belonged to which task. Experiment 5, described in Section 2.7, was carried out to assess whether increased Switch-Costs were a result of refocusing attention between time and space or switching between different target types.

The 40-49 and 50-59 years groups were intended as middle-age comparison groups for the two oldest age groups and the 21-30 years group was intended as a comparison group for all other age groups. The finding of higher Switch-Costs in the 40-49 years group was unexpected, particularly as no differences in RTs were found between the 21-30 and 40-49 years groups. The 40-49 years group seem to present an intermediate stage of ageing, where they do not differ from the 19-30 years group in overall VS RTs, but display age-related declines when there are increased attentional demands when refocusing attention from time to space.

It is well established that working memory capacity declines with healthy ageing, including both verbal (Hultsch, Hertzog, Small, McDonald-Miszczak, & Dixon, 1992; Zacks, Hasher, & Li, 2000) and visual (Brockmole & Logie, 2013; Faubert, 2002) short term memory. A limitation of the current study is that no measure of verbal or visual working memory capacity was taken to look at the influence of memory on switching. However, the strain on working memory is very low, as the participant is only required to hold a single item in memory (i.e. the RSVP target digit). It is therefore unlikely that difficulties in working memory would affect switching performance. Furthermore, Akyürek and Hommel (2005) found that working memory load did not interact with the duration of the attentional blink. Additionally, working memory load remains constant across both the No-Switch and Target Switch conditions and so memory deficits should not have influenced our main findings.

Although age-related declines in working memory capacity are unlikely to have affected switching performance in the current task, it is possible that declines in executive function affected switching performance. In relation to Baddeley’s (1986) working memory model, the current task would require the top-down control of attention from the central executive. It was therefore expected that measures of executive function would predict switching performance. However, measures of executive function obtained from the RNG did not correlate with task performance. No age group differences were found in RNG measures that are presented in Appendix 2.1, despite age-related declines in executive function being widely acknowledged in the literature (Cepeda et al., 2001; Gamboz et al., 2009; Gold et al., 2010). It could be that switching deficits would be further exacerbated in a sample of older adults who have executive function impairments reflected in the RNG. Further research is needed to explore the relationship between executive function and switching between temporal and spatial attention to come to more sound conclusions.

Conclusions

The hypothesis that there would be greater Switch-Costs in older than younger groups was partially supported, as people aged 40-49 and 60-69 years displayed greater Switch-Costs than those aged 20-29 years. There was also a non-significant trend for greater Switch-Costs in the 50-59 years group. Increased Switch-Costs in the 40-49 and 60-69 years groups but not the 70+ years groups was surprising. However, switching difficulties in the oldest group may have been masked by slow RTs on the No-Switch condition due to a failure to inhibit and disengage from the RSVP stream. This conclusion would explain the surprising findings of decreased Switch-Costs with slower selective attention processing speeds. Poor selective attention could mask Switch-Costs due to difficulties with inhibiting the remainder of the RSVP stream in the No-Switch condition resulting in slow RTs.

Increased Switch-Costs in the Target Switch condition but not the No-Target Switch condition indicates that increased Switch-Costs could result from either an increased attentional blink following RSVP target identification, which delays the allocation of attentional resources to the VS, or increased variability in RTs in the No-Target Switch condition, although the results of Experiment 4 described below (Section 2.6) suggest the latter.

2.6 Experiment 4: Controlling for task difficulty

2.6.1 Aims

It could be argued that age-related increases in Switch-Costs observed in Experiment 3 resulted from age-related increases in the amount of cognitive effort required to identify targets in the RSVP task compared to the VS task, and in the Target Switch condition compared to the No-Switch condition. In Experiment 3, successful RSVP target identification was lower (groups means ranged between 73.9-93.9%; Figure 2.5) than VS target identification (groups means all >94%). Furthermore, RSVP target identification was lower in the Target Switch condition than the No-Switch condition, a difference that was inflated in the three oldest groups in comparison to the two younger groups (Section 2.5.4, Figure 2.5).

It is important to establish whether older groups' higher Switch-Costs reflect difficulties in refocusing from temporal to spatial attention or age differences in perceived RSVP task difficulty. In Experiment 4 we aimed to improve RSVP target identification so as to improve the similarity of target identification difficulty between VS and RSVP tasks, and No-Switch and Target Switch conditions. This was achieved by making the RSVP target red (among the black distractor letters) to enhance bottom-up processing of the target (Lien et al., 2011; Theeuwes, 1994, 2004).

Two age groups (18-25, 60+ years) were compared. If Switch-Costs were a result of switching between temporal and spatial attention, then the overall pattern of RTs should not change. VS RTs would be expected to be faster in the No-Switch condition compared to the Target Switch condition. Higher Switch-Costs would be expected in the 60+ compared to the 18-25 years group. In contrast, if Switch-Costs in Experiment 3 were a result of age differences in perceived RSVP task difficulty then one would expect Switch-Costs to be greatly reduced or eliminated in the current task and to be proportionate across age groups.

2.6.2 Methods

Participants

Twenty Aston University undergraduate psychology students (2 male, 18 female) aged 18-25 years (mean = 19.15 years, SD = 1.53) and 20 participants (11 male, 9 female) aged 60+ years (mean = 67.4, SD = 4.27) were recruited. Participants aged 60+ years were participants who had previously taken part in Experiment 3, 5 or experiments described in Chapter 3 or 4. All participants over the age of 60 years had scored over the 87% threshold for possible cognitive impairment on the ACE-3 (Noone, 2015) within the last two years. Participants with photosensitive epilepsy and visual impairments were excluded. Participants aged 18-25 years received course credits for participation. Participants aged 60+ years received £7.50 towards travel expenses.

Attention switching pilot Red

The attention switching task in Experiment 4 was identical to version 2 of the task used in Experiment 2 and Experiment 3 except for the target digit in the RSVP stream being red (RGB 178-34-34) instead of black. A full description of the experimental methods can be found in Section 2.3.2. Participants completed 18 practice trials prior to the experimental trials.

2.6.3 Data analysis

The analyses implemented for the current experiment were the same as those in Experiment 3, described in Section 2.5.3, however there were fewer age groups and so the model was a 2 × 3 × 2 (VS condition: serial/pop-out × RSVP condition: No-Switch/Target Switch/No-Target Switch × age group: 18-25 years/60+ years) mixed ANOVA.

2.6.4 Results

RSVP target identification

The proportion of correct RSVP target identifications for each age group are presented in Figure 2.7. A 2 × 2 (RSVP condition × age group) mixed ANOVA on the proportion of correctly identified RSVP targets revealed a significant main effect of age ($F(1, 38)=4.99$, $p=.031$, $\eta^2_p=.12$). RSVP target identification was significantly lower in the 60+ years compared to 18-25 years group.

There was no significant main effect of RSVP condition and no significant age × RSVP condition interaction ($p>.10$). The absence of a significant difference between RSVP conditions and the lack of a significant interaction between age and RSVP condition demonstrates that displaying the target digit in red succeeded in eliminating differences in target identification difficulty between RSVP conditions. Any age differences in Switch-Costs that are now observed in RTs cannot be attributed to differences in perceived task difficulty.

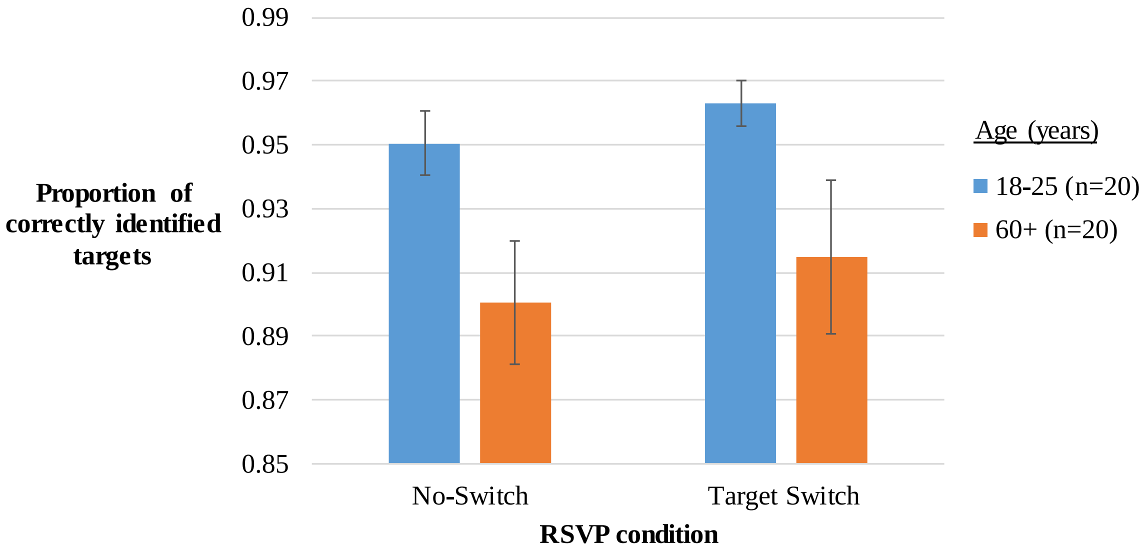

Figure 2.7. Proportion of correctly identified RSVP targets. Vertical bars represent the SE.

VS RTs

A 2 × 3 × 2 (VS condition × RSVP condition × age group) mixed ANOVA was conducted with participants' median RTs. Mauchly's Test of Sphericity was significant for RSVP condition ($\chi^2(2)=8.16$, $p=.017$) indicating that the assumption of sphericity has been violated. Greenhouse-Geisser corrected statistics were therefore reported. Mean VS RTs for each age group for serial and pop-out searches are presented in Figure 2.8.

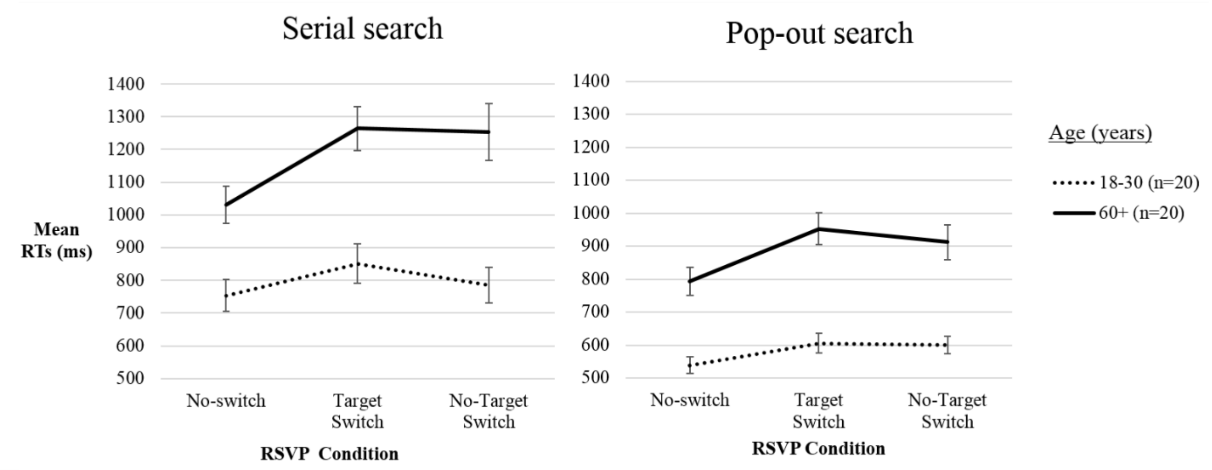

Figure 2.8. Means of median VS RTs. Vertical bars represent the SE.

There were significant main effects of age (*F*(1, 38)=26.16, *p*<.001, η^2_p=.41) VS condition (*F*(1, 38)=148.70, *p*<.001, η^2_p=.80) and RSVP condition (*F*(1.67, 63.44)=36.31, *p*<.001, η^2_p=.49) on RTs. There was a significant age × RSVP condition interaction (*F*(1.67, 63.44)=8.06, *p*<.001, η^2_p=.18) and a significant age × VS condition × RSVP condition interaction (*F*(1.87, 70.98)=4.05, *p*<.024, η^2_p=.10). The age × VS condition (*F*(1, 38)=3.79, *p*=.059, η^2_p=.09) and the VS condition × RSVP condition (*F*(1.87, 70.98)=2.52, *p*=.087, η^2_p=.06) interactions did not reach significance.

RTs were significantly slower in the 60+ years group compared to the 18-25 years group. Participants were significantly faster on the pop-out compared to serial VS. RTs were significantly faster in the No-Switch condition compared to both the No-Target Switch (*p*<.001) and Target Switch (*p*<.001) conditions. There was no significant difference between the No-Target Switch and Target Switch conditions (*p*>.10).

No further analysis was carried out on either the age × VS condition or the VS condition × RSVP condition interactions as they were unrelated to current hypotheses.

To investigate the hypothesis that Switch-Costs would be greater with increased age and that findings would replicate Experiment 3, the age × RSVP condition interaction was further explored. Switch-Costs were calculated for each individual, separately for serial VS RTs and pop-out VS RTs. Details of how Switch-Costs were calculated can be found with Experiment 3 in Section 2.5.4. Switch-Costs were entered into independent t-tests to compare groups. T-tests were exploratory, however, remain in the scope of current hypotheses. The means and SDs of each group's Switch-Costs on serial and pop-out search RTs are presented in Table 2.6.

Independent t-tests conducted on participants' Switch-Costs confirmed that the 60+ years group displayed significantly greater serial search Target Switch-Costs (*t*(38)=-2.52, *p*=.016) and serial search No-Target Switch-Costs (*t*(38)=-3.75, *p*<.001), as well as pop-out Target Switch-Costs (*t*(38)=-2.29, *p*=.028) compared to the 18-25 years group.

Table 2.6. Means and SDs of Switch-Costs for each age group

			Age group (years)	
			18-25 (n=20)	60+ (n=20)
Serial	Target Switch-Costs	Mean	12.28	24.16
		SD	10.65	18.17
	No-Target Switch-Costs	Mean	4.78	21.08
		SD	11.81	15.40
Pop-out	Target Switch-Costs	Mean	12.48	21.06
		SD	9.83	13.57
	No-Target Switch-Costs	Mean	12.24	15.48
		SD	10.64	14.62

2.6.5 Discussion

The aim of the current experiment was to establish whether age-related increases in Switch-Costs observed in Experiment 3 were a result of declines in the ability to switch between temporal and spatial attention or a result of age group differences in perceived task difficulty when switching between tasks of different levels of cognitive demands. In Experiment 3 we found that target identification was lower in the RSVP task compared to the VS task, and was lower in the Target Switch condition compared to the No-Switch condition, differences that were inflated with increased age (Figure 2.5). It was therefore important to identify whether Switch-Costs were still present when the RSVP target identification was less cognitively demanding.

The hypothesis that there would no longer be a significant difference in the proportion of correctly identified targets between RSVP conditions in either age group was supported. Displaying the target digit in red (among black letters) succeeded in eliminating differences between RSVP conditions and the interaction between RSVP condition and age group in the proportion of correct target identifications. It is likely that improved target identification was due to enhanced bottom-up processing achieved through presenting the target digit in colour (Lien et al., 2011; Theeuwes, 1994, 2004). Any age differences in Switch-Costs that are observed in the current task cannot be attributed to differences in RSVP task difficulty.

The hypothesis that there would be age-related increases in Switch-Costs was supported, despite the now seemingly equal RSVP task demands across RSVP conditions. These findings support the conclusions of Experiment 3 and suggest that the Switch-Costs observed in Experiment 3 were not due to switching between tasks with different task demands.

Differing from Experiment 3, in addition to higher Target Switch-Costs in the 60+ years group compared to the 18-25 years group, there were also higher No-Target Switch-Costs. Increased Target Switch-Costs but not No-Target Switch-Costs with increased age could have suggested that age differences were a result of an age-related increase in the magnitude of the attentional blink rather than a deficit in refocusing attention (Lahar et al., 2001; Maciokas & Crognale, 2003). Findings of age-related increases in No-Target Switch-Costs in the current study support that age group differences in No-Target Switch-Costs in Experiment 3 were masked by higher RT variability in the No-Target Switch condition. Additional age group differences were also found in serial VS Switch-Costs that were not seen in Experiment 3. Reducing task demands of the RSVP task therefore seems to have reduced variability in VS RTs and revealed No-Target Switch-Costs and Switch-Costs in the serial VS condition. Implementing a bottom-up strategy during RSVP target identification may have reduced variability in the time participants took to process that they had not seen a target in the RSVP stream in the No-Target Switch condition, therefore potentially reducing variability in VS RTs.

2.7 Experiment 5: Controlling for target type

2.7.1 Aims

The attention switching task implemented in Experiments 1-4 involved switching from identifying a number in the RSVP stream to identifying a letter in the VS display. It could be argued that difficulties in switching arise from switching between these different target types. The current experiment aimed to test this argument by comparing age groups (18-30 and 60+ years) on the ability to identify a target digit in the RSVP stream and identify a second target digit in the VS display. As letters and numbers come from within the same ‘alphanumeric’ semantic category, it is expected that switching between identifying numbers and letters added no additional costs of switching. On the contrary, it is expected that switching between identifying two targets in the same ‘numeric’ category will hinder performance, as participants have to additionally retain in which part of the task they identified each number. Furthermore, naming multiple objects from within the same semantic category in close succession hinders picture naming speed, likely due to the spread of activation to representations of semantically related objects creating more competition in word production networks (Maess, Friederici, Damian, Meyer, & Levelt, 2002). It was hypothesised that there would be significantly higher Switch-Costs in the 60+ years group compared to the 18-30 years group when switching from identifying a RSVP target digit to identifying a VS target digit.

2.7.2 Methods

Participants

Twenty Aston University undergraduate psychology students (4 male, 16 female) aged 18-30 years (mean = 22.65 years, SD = 3.69) and 20 participants (11 male, 9 female) aged 60+ years (mean = 66.60 years, SD = 3.76) took part. Participants aged 60+ years were participants who had previously taken part in Experiment 3, 4 or experiments described in Chapter 3 or 4. All participants aged 60+ years had scored over the 87% threshold for possible cognitive impairment on the ACE-3 (Noone, 2015) within the last two years. Participants with photosensitive epilepsy and visual impairments were excluded. Participants aged 18-30 years received course credits for participation. Participants aged 60+ years received £7.50 towards their travel expenses.

Attention switching Digit

The attention switching task in Experiment 5 was the same as version 2 of the task used in Experiment 2 and Experiment 3 apart from changes listed below.

To explore whether age-related increases in Switch-Costs remain when switching between temporal and spatial attention tasks when targets are from within the same 'numeric' category, participants switched from identifying a target digit in the RSVP stream to identifying a target digit in the VS display. Participants responded to the VS display by pressing the left arrow key if the target digit was on the left visual hemifield and the right arrow if the target digit was on the right visual hemifield. VS RTs were recorded. A left-right response was implemented instead of the spacebar response, as detecting a target digit in the RSVP stream could prime participants' responses to the VS display, causing a bias towards faster RTs in the Target Switch condition, where the delay between RSVP target presentation and VS onset is shorter than in the No-Switch condition. Implementing a left-right response minimises response priming as RSVP targets are presented centrally. Participants completed 24 practice trials before beginning the experimental trials.

2.7.3 Data analysis

Analyses implemented for the current experiment were the same as those in Experiment 3 and 4. Similarly to Experiment 4, there were only two age groups and so a 2 × 3 × 2 mixed ANOVA was conducted.

2.7.4 Results

Both groups correctly identified over 98% of VS targets in all six conditions and 82% of RSVP targets in both target conditions (No-Switch/Target Switch). No further analysis was carried out on VS accuracy nor RSVP target identification as it was unrelated to the current hypotheses.

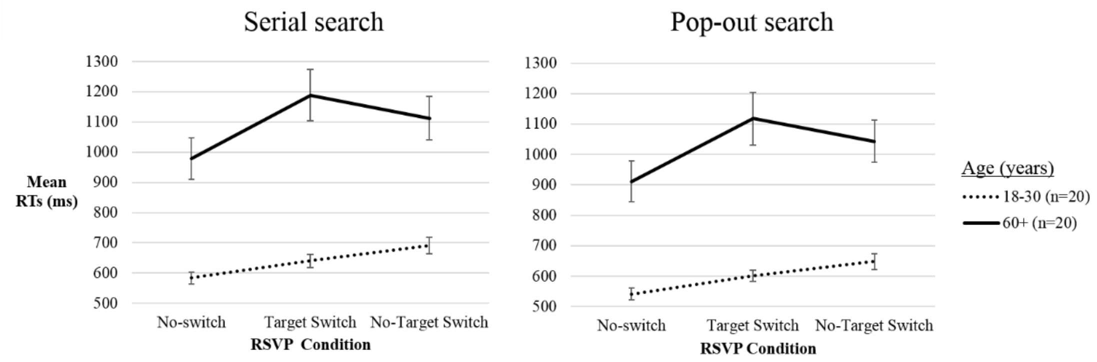

Figure 2.9. Means of median VS RTs. Vertical bars represent the SE.

A 2 × 3 × 2 (VS condition × RSVP condition × age group) mixed ANOVA was conducted with participants' median VS RTs. Mauchly's Test of Sphericity was significant for RSVP condition ($\chi^2(2)=6.46$, $p=.040$) indicating that the assumption of sphericity has been violated. Greenhouse-Geisser corrected statistics were therefore reported. Mean VS RTs for each age group for serial and pop-out searches are presented in Figure 2.9.

There were significant main effects of age ($F(1, 38)=34.65$, $p<.001$, $\eta^2_p=.48$) VS condition ($F(1, 38)=63.58$, $p<.001$, $\eta^2_p=.63$) and RSVP condition ($F(1.72, 65.51)=36.58$, $p<.001$, $\eta^2_p=.49$) on RTs. There was a significant age × VS condition interaction ($F(1, 38)=4.09$, $p=.050$, $\eta^2_p=.10$) and a significant age × RSVP condition interaction ($F(1.72, 65.51)=10.83$, $p<.001$, $\eta^2_p=.22$). There were no significant VS condition × RSVP condition or age × VS condition × RSVP condition interactions ($p>.10$).

RTs were significantly slower in the 60+ years group compared to the 18-30 years group. Participants were significantly faster on the pop-out compared to serial VS. RTs were significantly faster in the No-Switch condition compared to both the No-Target Switch ($p<.001$) and Target Switch ($p<.001$) conditions. There was no significant difference between the No-Target Switch and Target Switch conditions ($p>.10$).

No further analysis was carried out on either the age × VS condition or the VS condition × RSVP condition interactions, as they were unrelated to the current hypotheses.

It was hypothesized that age-related increases in Switch-Costs that were observed in Experiment 3 and 4 would be replicated in the current study. To investigate the hypothesis that Switch-Costs would be greater with increased age, the age × RSVP condition interaction was further explored. Measures of Switch-Costs were calculated separately for serial and pop-out VS RTs for each participant, consistent with the analysis implemented for Experiments 3 and 4 (Section 2.5.3 and 2.6.3). Details of how Switch-Costs were calculated can be found in Section 2.5.3. Switch-Costs were entered into independent t-tests to compare groups. T-tests were exploratory, however, remain in the scope of current hypotheses. The means and SDs of each group's Switch-Costs on serial search and pop-out search RTs are presented in Table 2.7.

Independent t-tests conducted on participants' Switch-Costs confirmed that there were significantly higher Target Switch-Costs in the 60+ years group compared to the 18-30 years group for both serial ($t(30.17)=-2.98$, $p=.006$) and pop-out ($t(38)=-2.54$, $p=.015$) VS RTs. Note that Levene's test for equality of variances was significant for serial search RTs in the Target Switch condition and so equal variances not assumed statistics were reported. There were no significant group differences in No-Target Switch-Costs ($p>.10$).

Table 2.7. Means and SDs of Switch-Costs for each age group

			Age group (years)	
			18-30 (n=20)	60+ (n=20)
Serial	Target Switch-Costs	Mean	9.99	21.99
		SD	8.93	15.68
	No-Target Switch-Costs	Mean	18.51	14.99
		SD	10.90	15.69
Pop-out	Target Switch-Costs	Mean	11.79	22.57
		SD	9.77	16.25
	No-Target Switch-Costs	Mean	20.18	16.16
		SD	14.90	16.28

2.7.5 Discussion

The aim of the current experiment was to investigate whether age-related increases in Switch-Costs were due to switching between temporal and spatial attention or a result of switching between identifying different target types (numbers and letters).

The hypothesis that Switch-Costs would be significantly higher in the 60+ years group compared to the 18-30 years group was supported. Findings demonstrate that age differences in Switch-Costs remain when switching from the RSVP task to the VS task to identify targets from matching semantic categories. These findings corroborate the conclusions of Experiments 3 and 4 and support that there is a decline in the ability to refocus attention from temporal to spatial attention with increased age.

In contrast to Experiment 3 but consistent with Experiment 4, age group differences were not only seen in pop-out search Switch-Costs but also in serial search Switch-Costs. From Figure 2.9 it is evident that the pattern of RTs and variability in RTs is very similar across VS conditions. In Experiment 3 the variability in serial VS RTs was greater than in pop-out VS RTs (Figure 2.6), possibly preventing age group differences in Switch-Costs from reaching significance.

2.8 Experiment 6: Speeded response to RSVP target

2.8.1 Aims

So far we have observed that there is an age-related decline in the ability to refocus from temporal to spatial attention that cannot be explained by differences in task difficulty nor switching between different target types. Further work is required to explore how age-related declines in switching translate to more ecologically valid behaviour such as driving behaviour. It may be that difficulties in refocusing from temporal to spatial attention are reflected in difficulties in switching from attending to traffic on the road ahead (i.e. engaging temporal attention) to attending to road signs and other surrounding objects (i.e. engaging spatial attention). The current study therefore aimed to mirror aspects of attention implemented while driving, i.e. by attending to events changing in time and responding to them (temporal attention), followed by distributing attention spatially and making decisions about information in the environment (spatial attention). Consistent with Experiments 1-5, participants switched from identifying a target digit in an RSVP stream to identifying a target letter in the VS display. In the current task, however, participants were required to respond to the detection of the RSVP target digit with a speeded spacebar response, similar to a driver braking in response to identifying an event on the road ahead. Participants were required to make a two choice left-right response to the VS display to signify whether the target was on the left or right of the visual hemifield, similar to a driver signalling left or right with their indicators after reading a road sign. Throughout Experiments 1-5 older participants responded significantly slower than younger adults. The 70+ years group's mean serial VS RT in the No-Target Switch condition in Experiment 3 was 1767.3ms (Figure 2.6). To allow time for older participants to respond to the RSVP target in the current task a blank grey screen was presented between the RSVP stream and the VS display and remained on the screen for 1800ms or until the participant responded with a spacebar press. In the current task the No-Target condition therefore behaved as a No-Switch condition, as there was a 1800ms delay between the RSVP offset and the VS onset.

It was hypothesised that RTs would be slower in the Switch condition in comparison to the two No-Switch conditions. It was hypothesised that there would be increased Switch-Costs with increased age, as reflected in disproportionately higher RTs in the Switch condition in comparison to each of the No-Switch conditions.

2.8.2 Methods

Participants

One hundred and twenty eight participants in five age groups (18-30, 40-49, 50-59, 60-69, and 70+ years) participated as part of the driving simulator study reported in Chapter 4. All participants had a full driving license, had experience driving in the United Kingdom (UK) and had driven in the last year. The 18-30 years group were used as a comparison group for age-related cognitive changes for all other groups and the 40-49 and 50-59 years groups were used as middle-aged comparison groups for the 60-69 and 70+ years groups. Participants with photosensitive epilepsy or visual impairments were excluded from participation, in addition to those who scored equal to or less than the 87 cut-off for possible cognitive impairment on the ACE-3 (Noone, 2015).

Participants from Experiment 3 and the MEG study described in Chapter 3 were invited to take part. Additional participants in the 21-30 and 40-49 years groups were recruited from Aston University staff and students and the community. The remaining participants aged over 60 years were recruited from the ARCHA panel. Participants received £7.50 towards their travel expenses or course credits. All participants provided written informed consent before participating. The research was approved by Aston University Research Ethics Committee.

Two participants from the 70+ years group scored equal to or lower than the 87 cut-off on the ACE-3 (Noone, 2015) and were therefore excluded from further analyses. The remaining participants' demographics are presented in Table 2.8.

Table 2.8. Participant demographics

		Age Group (years)				
		18-30 (n=34)	40-49 (n=22)	50-59 (n=24)	60-69 (n=25)	70+ (n=21)
Age (years)	Mean	21.21	44.05	54.96	64.96	75.10
	SD	3.36	3.08	2.56	2.82	4.44
Gender	Male	10	9	7	16	9
	Female	24	13	17	9	12
Handedness	Right	30	19	22	23	21
	Left	4	2	2	2	0
ACE-3	Mean	n/a	n/a	96.38	96.04	95.10
	SD	n/a	n/a	2.39	2.47	2.47

The mean age of each age group, the number of participants who are male and female, the number of participants who are left and right handed are presented for each age group. Mean ACE-3 scores are presented for the 50-59, 60-69, and 70+ years groups. Note that the handedness data is missing for one participant in the 40-49 years group.

Attention Switching Task

The current attention switching task was the same as version 2 of the task used in Experiment 2 and Experiment 3 apart from changes listed below.

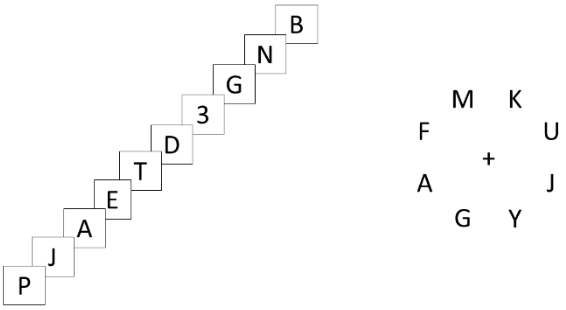

Figure 2.10. Illustration of examples of the stimuli set up. The RSVP stream illustration (left) displays a Target Switch RSVP stream. Each trial consisted of a fixation cross (2000ms) followed by an RSVP stream immediately followed by a blank grey screen (until the participant responds to the RSVP target), followed by a pop-out VS display (right).

To better represent cognitive processes that are implemented while driving, participants switched from identifying and responding to a target digit in the RSVP stream to identifying the location of a target in the VS display. Participants responded to the RSVP target with a spacebar response, and made a left-right response to the VS display to indicate whether the target was on the left or right of the visual hemifield. An example of the stimuli is illustrated in Figure 2.10. Both spacebar RTs and

VS RTs were recorded. If participants correctly detected and responded to an RSVP target they were instructed to type the number that they saw on the keyboard after the VS.

VS displays consisted only of pop-out VS, as this is the condition we have reliably found increased age-related Switch-Costs in previous experiments, in Experiments 3 - 5 (Sections 2.5-2.7). In contrast we failed to find significant age group differences in serial VS Switch-Costs in Experiment 3. A blank grey (RGB 192-192-192) screen was presented between the RSVP stream and the VS display and remained on the screen for 1800ms or until the participant responded with a spacebar press. This was to allow time for participants to respond to the RSVP target. The RSVP condition that contained no target behaved as a No-Switch condition in the current task, as the blank screen remained for 1800ms prior to the onset of the VS display.

There were 30 trials of each of the three conditions (Target No-Switch/Target Switch/No-No-Target Switch), with a total of 90 trials. To provide the opportunity for breaks, trials were divided into five blocks. All participants completed 18 practice trials prior to beginning the experiment. One participant each from the 50-59, 60-69 and 70+ years groups completed the practice trials twice.

2.8.3 <u>Data analysis</u>

The analyses implemented for the current experiment were the same as those in Experiments 3-5 described in Section 2.5-2.7. However this time there was only one VS condition (i.e. pop-out search) and there were five age groups, and so a 3 × 5 (RSVP condition × age group) mixed ANOVA was conducted.

A 2 × 5 (RSVP condition × age group) mixed ANOVA was conducted with participants' median spacebar simple RTs (SRTs) in response to detecting the RSVP target.

2.8.4 <u>Results</u>

All age groups correctly identified over 99% of VS targets in all three conditions. No further analysis was carried out on VS accuracy.

Attention switching task

RSVP accuracy

A 2 × 5 (RSVP condition × age group) mixed ANOVA was conducted with the proportion of correct RSVP target identifications. There was a significant main effect of age ($F(4, 117)=20.24$, $p<.001$, $\eta^2_p=.41$) and RSVP condition ($F(1, 117)=6.55$, $p=.012$, $\eta^2_p=.05$) on RSVP target identification, with significantly lower target identification in the Target Switch condition compared to the Target No-

Switch condition. There was no significant age × RSVP condition interaction (*p*>.10). The proportion of correctly identified RSVP targets are presented in Figure 2.11.

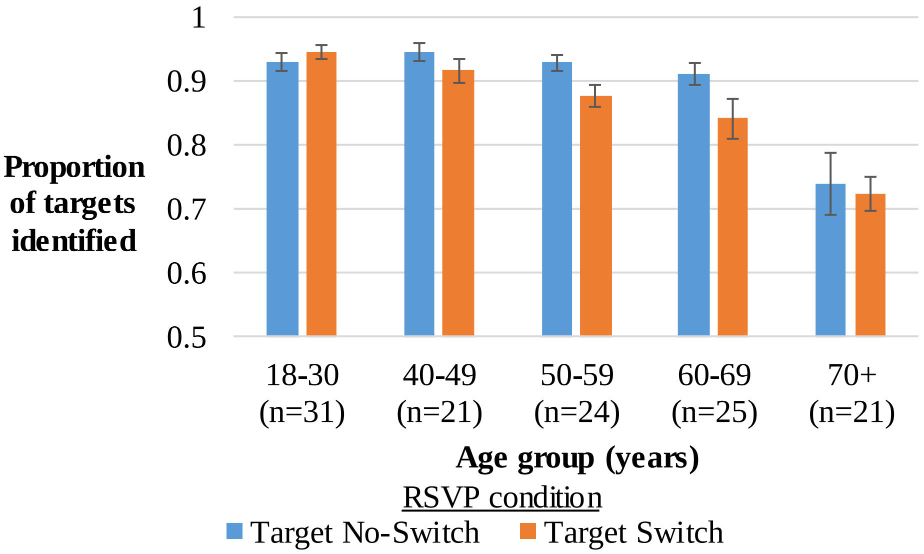

Figure 2.11. Proportion of correct RSVP target identifications. Vertical bars represent the SE.

Post hoc comparisons revealed that the main effect of age on RSVP target identification resulted from significantly smaller proportions of correctly identified targets in 70+ years group compared to all other age groups (*p*<.001).

RSVP SRTs

One participant in the 70+ years group correctly identified fewer than ten out of 30 RSVP targets in the Target No-Switch condition and so was excluded from RSVP spacebar RT analysis. A 2 × 5 (RSVP condition × age group) mixed ANOVA was conducted with participants' median SRTs in response to detecting the RSVP target. Mean RSVP RTs for each group are presented in Figure 2.12.

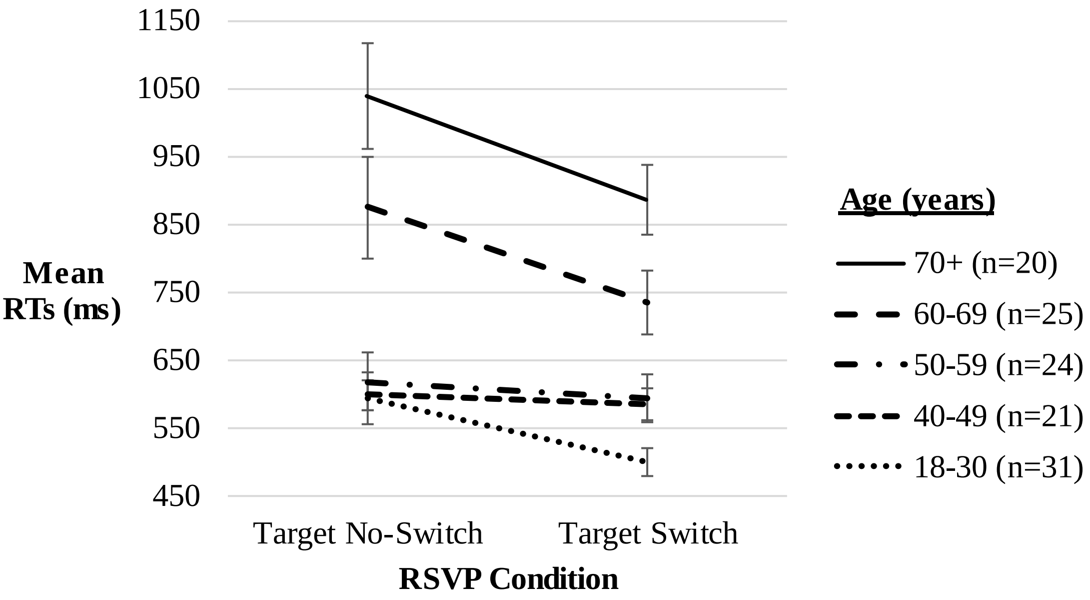

Figure 2.12. Means of median RSVP SRTs. Vertical bars represent SE.

There was a significant main effect of age ($F(4, 116)=15.31 p<.001$, $\eta^2_p=.35$) and RSVP condition ($F(1, 116)=39.22$, $p<.001$, $\eta^2_p=.25$) on RSVP RTs and a significant age × RSVP condition interaction ($F(4, 116)=4.30$, $p=.003$, $\eta^2_p=.13$). From Figure 2.12 it is evident that RSVP RTs were faster when the target was towards the end of the stream in the Target Switch condition in comparison to when the target was the first item in the stream in the Target No-Switch condition.

Post hoc comparisons demonstrated that RTs were significantly slower in the 70+ years group in comparison to the 18-30 ($p<.001$), 40-49 ($p<.001$) and 50-59 ($p<.001$) years groups. RTs were significantly slower in the 60-69 years group in comparison to the 18-30 ($p<.001$), 40-49 ($p=.011$) and 50-59 ($p=.016$) years groups. There were no other significant age group differences in RSVP RT ($p>.10$).

To investigate the age × RSVP condition interaction on RSVP RTs, paired t-tests were carried out to compare RTs between the two RSVP conditions separately for each age group. Paired t-tests revealed that RTs were significantly faster when the target was towards the end of the stream (Target Switch condition) in comparison to when it was the first item in the stream (Target No-Switch condition) only for the 18-30 ($t(30)=4.27$, $p<.001$), 60-69 ($t(24)=3.39$, $p=.002$) and 70+ ($t(19)=4.38$, $p<.001$) years groups, but not for the 40-49 or 50-59 years groups ($p>.10$).

VS RTs

One participant from the 60-69 years group and one from the 70+ years group identified only a small proportion of the RSVP targets resulting in fewer than ten out of 30 trials remaining in one or more conditions for the RT analysis. These participants were excluded from the remaining analysis.

A 3 × 5 (RSVP condition × age group) mixed ANOVA was conducted with participants' median RTs. Mauchly's Test of Sphericity was significant for RSVP condition ($\chi^2(2)=47.03$, $p<.001$) signifying that the assumption of sphericity has been violated. Greenhouse-Geisser corrected statistics were therefore reported. Mean VS RTs for each age group are presented in Figure 2.13.

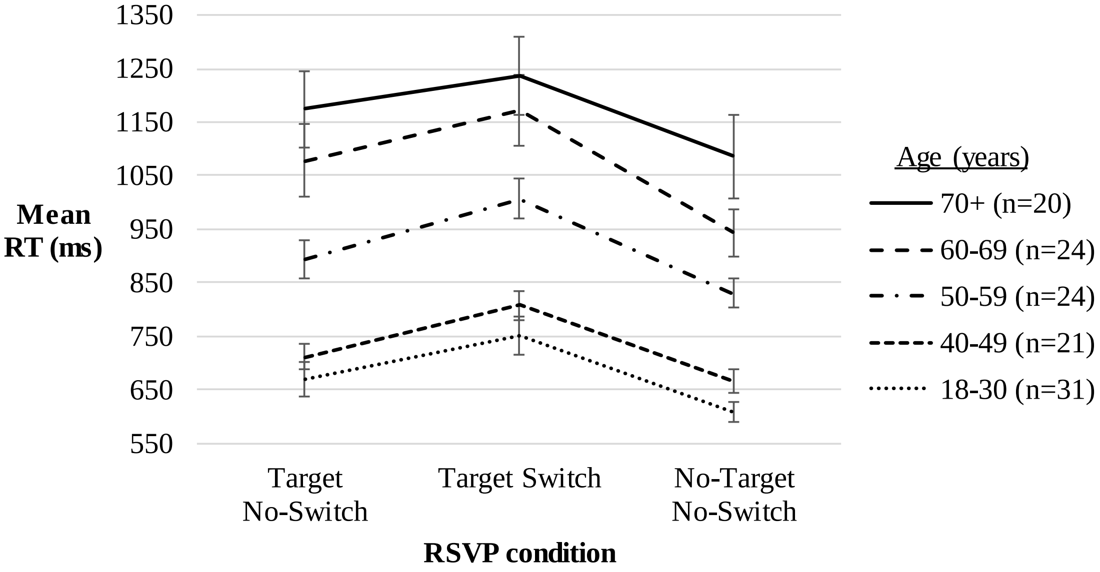

Figure 2.13. Means of median VS RTs. Vertical bars represent SE.

There was a significant main effect of age ($F(4, 115)=24.08$, $p<.001$, $\eta^2_p=.46$) and RSVP condition ($F(2, 171.89)=81.76$, $p<.001$, $\eta^2_p=.42$) on VS RTs. There was no significant age × RSVP condition interaction ($p>.10$).

Post hoc comparisons illustrated that the main effect of age on VS RTs resulted from significantly faster RTs in the 18-30 years group compared to all other age groups ($p<.001$), faster RTs in the 40-49 years group compared to the 50-59 ($p=.044$), 60-69 ($p<.001$) and 70+ years groups ($p<.001$) and faster RTs in the 50-59 years group compared to the 70+ years group ($p<.001$). There were no other significant age group differences in VS RTs ($p>.10$).

VS RTs were significantly slower in the Target Switch condition compared to both the Target No-Switch and No-Target No-Switch conditions ($p<.001$), and were significantly faster in the No-Target No-Switch condition compared to the Target No-Switch condition ($p<.001$).

2.8.5 Discussion

The current study aimed to mirror aspects of attention that are implemented while driving, i.e. by attending to events changing in time and responding to them (temporal attention), followed by the distribution of attention spatially and making decisions about information in the environment. Participants were required to respond to the identification of the RSVP target digit with a speeded spacebar response, similar to a driver braking in response to identifying an event on the road ahead. Participants were required to make a two choice left-right response to the VS display to signify whether the target was on the left or right of the visual hemifield, similar to a driver signalling left or right with their indicators after reading a road sign.

Replicating findings from Experiments 1-5, the hypothesis that RTs would be slower in the Switch condition in comparison to the two No-Switch conditions was supported. RTs were additionally faster in the No-Target No-Switch condition compared to the Target No-Switch condition, which is likely a result of having more time to prepare to switch when there was a 1800ms delay between the RSVP stream and the VS display.

Contrary to Experiments 1-5 and contradicting our hypotheses, there were no significant age group differences in Switch-Costs. It is likely that age groups did not differ due to the delay between the offset of the RSVP stream and the onset of the VS display providing time for participants to prepare to switch. Older participant were slower at responding and processing information than younger adults as shown in Figure 2.6 and as is widely acknowledged in the literature (Foster et al., 1995; Salthouse, 1991, 2000). It was important to allow time for older participants to make a speeded response to the RSVP target, hence, a delay between the RSVP stream and VS display was introduced. The length of delay varied systematically with participants' RTs on the RSVP task and therefore likely varied systematically with age. Those with greater overall age-related decline are likely to have responded slowly to the RSVP target, which would have systematically increased the delay between the RSVP stream and the VS display, in turn providing participants longer to prepare to switch to the VS.

SRTs to the RSVP target were found to be faster in the Target Switch condition compared to the Target No-Switch condition, for the 18-30, 60-69 and 70+ years groups only. There are two explanations for faster RTs in the Target Switch compared to the Target No-Switch condition. Firstly it could be that when the target appears towards the end of the stream, attention is already oriented to events changing in time and so participants process the target faster due to enhanced attentional focus. An alternative explanation could be that when the target is the first item in the stream there is ongoing interference from the RSVP distractor stimuli for a further 900ms as the nine distractor items are displayed successively, whereas in the Target Switch condition there is only a further 100-300ms of interference from distractor stimuli, as either one, two or three distractor stimuli are displayed, depending on whether the target was the 7th, 8th or 9th item in the stream.

From Figure 2.12 it appears that when making a speeded response to the detection of an RSVP target, the youngest group are faster than the two middle-aged groups when there is less interference from distractor items and more time to orient attention in time (i.e. when the target is towards the end of the stream). In contrast, the 18-30 years group have similar RTs to the 40-49 and 50-59 years groups when there is increased visual interference and less time to orient attention in time. Similar to the youngest age group the two oldest groups appear to be hindered by increased visual interference and having less time to focus attention, whereas the two middle-aged groups seem unaffected. It could be that the four older groups did not benefit from anticipatory attention in the same way the youngest age group did, possibly due to declining attention mechanisms, and the two older groups additionally experience increased interference from RSVP distractor stimuli due to deficits in the ability to inhibit irrelevant visual information (Adamo et al., 2003; Aydin et al., 2013; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig et al., 2007; Maciokas & Crognale, 2003).

Interestingly, the 50-59 years group’s VS RTs were significantly slower than the 18-30 years group (Figure 2.13), but their RSVP SRTs were not (Figure 2.12). This finding cannot be explained by slowing of SRTs occurring later in life than CRTs, as the 50-59 years group also displayed significantly slower VS RTs in Experiment 3 (Figure 2.6) when the VS response was a single spacebar response. Instead these findings could suggest that spatial attention deteriorates earlier in life than temporal attention, in both processing speed, as is reflected in the current task, and processing accuracy, as is reflected in previous findings of impaired target detection during temporal attention over the age of 70 years (Conlon & Herkes, 2008; Shih, 2009) but not in those aged 55-72 years (Lee & Hsieh, 2009; Quigley et al., 2012). In comparison, age-related deficits in VS performance have previously been observed at a mean age of 63 years (Bennett et al., 2012; Li et al., 2013).

2.9 General discussion and conclusions

The aim of the current chapter was to explore whether there are age-related changes in the ability to refocus from temporal to spatial attention and to understand the cognitive mechanisms that might underpin these changes.

Experiment 3 demonstrated that participants aged 40-49 and 60-69 years displayed greater Switch-Costs than those aged 21-30 years, but only when there was a target in the RSVP stream and when they were switching to a pop-out VS. There was also a non-significant trend for greater Switch-Costs in the 50-59 years group. Increased Switch-Costs in the 40-49, 50-59 and 60-69 years groups but not the 70+ years groups was surprising. However, as discussed in Section 2.5.5, switching difficulties in the oldest group may have been masked by slow RTs on the No-Switch condition due to a failure to inhibit and disengage from the RSVP stream, or due to RTs across RSVP conditions reaching ceiling levels.

There were two main limitations of Experiment 3. Firstly, on investigation of the proportion of correctly identified RSVP targets it was evident that RSVP target identification was more challenging than VS target identification and that Target Switch target identification was more challenging than No-Switch target identification, differences that were further exacerbated by increased age. It could therefore be argued that, rather than age-related increases in Switch-Costs resulting from difficulties in refocusing attention, age group differences could be a result of differences in perceived RSVP task difficulty. Experiment 4 was therefore designed to make RSVP target identification less challenging by presenting the target digit in red, which contrasts with the black letters. Contrasting the colour of the target digit allows participants to implement a bottom-up processing strategy which is faster and places less demand on cognitive resources than when implementing a top-down strategy (Lien et al., 2011; Theeuwes, 1994, 2004). In Experiment 4 there was no longer a significant difference between RSVP conditions in the proportion of correctly identified RSVP targets and no longer an interaction between age group and RSVP condition. The pattern of Switch-Costs in Experiment 4 remained similar to Experiment 3, with significantly higher Switch-Costs in the 60+ years group in comparison the 18-25 years group. These findings demonstrate that observed age related increases in Switch-Costs were not a result of differences in task difficulty.

The second key limitation of Experiment 3 was that, rather than a deficit in refocusing from temporal to spatial attention, it could be argued that age group differences were a result of switching between identifying different target types. In Experiment 3 participants were required to switch from identifying a target digit in the RSVP stream and identifying a target letter in the VS display. It is unlikely that switching between these two target types would add to cognitive load, as both targets types were in the shared “alphanumeric” semantic category. In Experiment 5 we tested this hypothesis. Participants were required to switch from identifying a target digit in the RSVP stream to identify a second target digit in the VS display. The results of Experiment 5 confirmed our expectations. Higher Switch-Costs in the 60+ years group compared to the 18-30 years group remained after controlling for target type.

In Experiment 3, increased Target Switch-Costs but not No-Target Switch-Costs could indicate that increased Switch-Costs resulted from an increased magnitude of the attentional blink following RSVP target identification (Lahar et al., 2001; Lee & Hsieh, 2009; Maciokas & Crognale, 2003; Shih, 2009; van Leeuwen et al., 2009). Although no significant age group differences in Switch-Costs were found for the No-Target Switch condition in Experiment 3, Experiment 4 revealed higher

No-Target Switch-Costs in the 60+ years group compared to the younger group. These findings support that observed increases in Switch-Costs with increased age are not due to an increased magnitude of the attentional blink with increased age, but are indeed a reduced ability to refocus from temporal to spatial attention.

Similarly, Experiment 3 found no significant group differences in serial VS Switch-Costs. However, age group differences in serial VS Switch-Costs were found in Experiments 4 and 5. It is likely that the higher variability in serial VS RTs and serial VS Switch-Costs in Experiment 3 (Figure 2.6 left and Table 2.3) prevented age group differences in Switch-Costs from reaching significance.

The 40-49 and 50-59 years groups seem to present an intermediate stage of ageing. Firstly, in Experiment 3, the 40-49 years group did not differ from the 19-30 years group in overall VS RTs but displayed age-related declines when there were increased attentional demands when refocusing attention from time to space. Secondly, in Experiment 6, the 50-59 years group displayed significant differences from the youngest age group in VS RTs, but not in RSVP RTs in response to detection of an RSVP target, possibly reflecting deterioration in spatial attention earlier in life than temporal attention (Bennett et al., 2012; Conlon & Herkes, 2008; Li et al., 2013; Shih, 2009). This finding further corroborates evidence that orienting attention in time and distributing attention spatially involve at least partly different underlying neural mechanisms (Coull & Nobre, 1998). The two middle-aged groups also differed from older and younger groups in Experiment 6 in that they showed no difference in RSVP RT across different RSVP conditions. The 18-30, 60-69 and 70+ years groups all showed slower RTs when responding to a target that was the first item in the RSVP stream compared to when it was towards the end of the stream, but the 40-49 and 50-59 years groups did not. One explanation for this could be that they differ from the youngest and the two older groups in different ways. Firstly, they may differ from the youngest group in that they gain no benefits from having longer to focus attention in time when the target is towards the end of the stream , either due to weaker or delayed attentional enhancement (>700ms). Secondly, they may differ from the 60-69 and 70+ years groups in that the older groups are impaired at inhibiting irrelevant visual information (Adamo et al., 2003; Aydin et al., 2013; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig et al., 2007; Maciokas & Crognale, 2003). The older two groups may therefore experience greater interference from the RSVP distractor stimuli that are presented after RSVP target onset. Interference would have been greater when the target was the first item of the stream when the target was followed by nine distractors, compared to when the target was towards the end of the stream and followed by only one, two or three distractor letters before a blank screen was presented. The 40-49 and 50-59 years groups therefore do not seem to be impaired at inhibiting irrelevant visual information. These findings warrant further research to corroborate these speculations.

Experiment 6 aimed to mirror aspects of attention implemented while driving, i.e. by attending to events changing in time and responding to them (temporal attention), followed by distributing attention spatially and making decisions about information in the environment. Participants responded to the detection of the RSVP target digit with a speeded spacebar response, similar to a driver braking in response to identifying an event on the road ahead. They then made a left-right response to the VS display to signify whether the target was on the left or right of the visual hemifield, similar to a driver signalling left or right with their indicators after reading a road sign. It was important to allow time for older participants to make a speeded response to the RSVP target, hence, a delay was introduced between the RSVP stream and VS display. Contrary to Experiments 1-5, there were no significant age group differences in Switch-Costs. As discussed in Section 2.8.5, it is likely that age groups did not differ due to the delay between the offset of the RSVP stream and the onset of the VS display providing time for participants to prepare to switch.

Together, Experiments 3-5 support our hypothesis of increased difficulties in refocusing attention from time to space with increased age. Older age groups were slower at switching from allocating their attention to events changing in time to refocusing their attention spatially. The question remains as to what changes to neural mechanisms underlie this difficulty in attentional refocusing. Exploring the neural mechanisms associated with difficulties in switching could provide insights that inform the development of interventions. In Chapter 3 we aimed to address this question by recording MEG while participants completed the attention switching paradigm.

Additionally, further work is required to explore how age-related declines in switching translate to more ecologically valid behaviour such as driving behaviour. It may be that difficulties in switching between temporal and spatial attention cause difficulties in switching from attending to traffic on the road ahead to attending to road signs and other surrounding objects. If difficulties in switching are found to affect driving performance, it will be important to develop an intervention to improve switching between modalities of attention to help to improve driver performance and safety. This would have the long-term benefit of prolonging the time that older drivers can continue to drive and help to preserve their independence. In Chapter 4 we aimed to assess whether difficulties in attentional refocusing with increased age are also seen when switching between temporal and spatial attention during simulated driving.

Chapter 3

Neural mechanisms underlying refocusing attention between time and space

3.1 MEG Experiment

3.1.1 Chapter aims

In Chapter 2 we demonstrated that switching between temporal and spatial attention becomes more difficult with increased age (Callaghan et al., 2017). Exploring the neural mechanisms that underpin age related impairments in switching performance could provide insights into the source of this difficulty. The aim of the current chapter was therefore to investigate the neural mechanisms that reflect age-related changes in the ability to refocus attention between time and space.

Consistent with the experiments conducted in Chapter 2, age groups were compared on their ability to switch from allocating attention in time, in order to identify a single target in a rapid serial visual presentation (RSVP) stream, to allocating attention spatially, to identify a target in a VS display. To manipulate the cost of switching (of attentional focus) from the RSVP stream to the VS display, the position of the target in the RSVP stream was either the first item in the stream, towards the end of the stream, or absent from the stream. When the target was the first item in the stream participants were no longer required to attend to the stream, and thus no cost of switching was expected (No-Switch condition). On the contrary, when the target was near the end of the stream or the stream consisted of only distractor items, participants needed to attend to the stream until towards the end of the stream, inducing a cost of switching (Target Switch condition/No-Target Switch condition). Longer VS RTs were therefore expected when switching from the RSVP task to the VS in both the Target Switch and No-Target Switch conditions in comparison to the No-Switch condition. It was hypothesized that there would be an age-related increase in the cost of switching from the RSVP task to initiate the VS, which would be reflected in greater increases in RTs from the No-Switch condition to the two Switch conditions in the older groups in comparison to the younger groups.

MEG was recorded while participants completed the attention switching task to enable the investigation of age-related changes in neural mechanisms that may explain deficits in switching. Based on previous literature, a network involving occipital, frontal, parietal and motor regions was expected to be involved in refocusing attention in time and space (Coull & Nobre, 1998; Fu et al., 2005; Gross et al., 2004; Li et al., 2013; Madden, Spaniol, Whiting, et al., 2007; Shapiro et al., 2002). According to the Neural Theory of Visual Attention (NTVA; Bundesen et al., 2005) as temporal expectation increases, temporal attention works to increase the firing rate of neuronal populations that represent certain features. In contrast, spatial attention alters the number of cell assemblies allocated to processing objects in the visual field (Bundesen et al., 2005; Vangkilde et al., 2012; Vangkilde et al., 2013). Switching between temporal and spatial attention in the current study may therefore require attention to efficiently re-allocate cell assemblies to receptive fields, as well as change the firing rates of feature-coding neuronal populations. Based on Dehaene et al.'s (2006) framework, fronto-parietal networks would be crucially involved in such top-down changes in selective enhancement, reflecting dynamic adjustments of expectations in space and time, by modulating the temporal and spatial dynamics of firing rates in posterior neuronal populations. In particular, the PFC and ACC may be involved in implementing top-down control of attention and attentional guidance (Badre & Wagner, 2004; Baluch & Itti, 2011; Bouvier, 2009; Kastner & Ungerleider, 2000; Kerns et al., 2004). The ACC has been shown to be especially important in guiding attention when there is conflict or ambiguity to be resolved (Badre & Wagner, 2004; Kerns et al., 2004).

The literature has frequently demonstrated more widely distributed cortical responses in older compared to younger adults, particularly in frontal regions (Adamo et al., 2003; Lague-Beauvais et al., 2013; Li et al., 2013; Madden, Spaniol, Whiting, et al., 2007). It has been debated as to whether this increase in activity reflects increased neural noise (Welford, 1981) or compensatory recruitment (Fabiani et al., 2006; Madden, Spaniol, Whiting, et al., 2007). Similar to a neural noise hypothesis of neural ageing, Cabeza, (2002) proposed a dedifferentiation hypothesis of neural ageing, where ageing results in a decreased specialisation of cortical processing. Although increased neural noise or dedifferentiation observed with increased age (Cabeza, 2002; Huettel et al., 2001; Polich et al., 1985; Shih, 2009; Welford, 1981) could provide an explanation of impaired selective attention (Shih, 2009), there is also evidence to suggest that older adults compensate for excitatory-inhibitory deficits with top-down control of attention, such as utilising cues more than younger people in selective attention (McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002). The "posterior to anterior shift in ageing hypothesis" (PASA; Davis et al., 2008) proposes that there is a compensatory shift in activity towards frontal regions in conjunction with declines in occipital sensory processing. Studies across several cognitive paradigms have seen decreases in posterior activity (Buckner et al., 2000; Cabeza et al., 2004; Davis et al., 2008; Huettel et al., 2001; Madden et al., 2002; Ross et al., 1997) and increases in anterior regions, including the pre-frontal cortex (PFC) and parietal regions (Cabeza et al., 2004; Grady, 2000; Madden, 2007).

It is often argued that the power of alpha (8-12Hz) oscillations plays an important role in attention mechanisms, where inhibition is partly achieved through increased alpha amplitudes (or frequency power), whereas an alpha decrease reflects enhanced attention (Capotosto et al., 2009; Hanslmayr et al., 2007; Hanslmayr et al., 2005; Klimesch et al., 2007; Sauseng et al., 2005; Thut et al., 2006; Yamagishi et al., 2003). Sustained attention has also typically been shown to involve alpha synchronisation (Dockree et al., 2007; Rihs et al., 2007, 2009), likely inhibiting unattended locations and irrelevant sensory information (Rihs et al., 2007). Evidence suggests that older adults fail to modulate alpha (Deiber et al., 2013; Hong et al., 2015; Pagano et al., 2015; Vaden et al., 2012; Zanto et al., 2010) and display slowed alpha frequency when measuring individual alpha peak frequencies

(Pons et al., 2010). In particular, older participants have been shown to fail to modulate alpha in anticipation of a visual target (Deiber et al., 2013; Zanto et al., 2010) and to inhibit irrelevant visual distractors (Vaden et al., 2012). It could be that impaired alpha modulation reflects impaired attentional mechanisms, as typical enhancement and inhibition of external stimuli is diminished. However, failure to modulate alpha oscillations does not seem to consistently impair performance (Hong et al., 2015; Vaden et al., 2012), possibly indicating the implementation of alternative compensatory neural mechanisms. Vaden et al. (2012) proposed that age-related changes in alpha band power and frequency could render alpha modulations redundant. This raises the question of what mechanisms could be available to the ageing brain that could compensate for decreased flexibility in the alpha range. One visual attention study by Deiber et al. (2013) found that rather than a posterior alpha modulation, the older group displayed a low beta frequency response to cues and targets (conforming to Gross et al., 2006). It could be that older adults were engaging alternative mechanisms that implement different frequencies to compensate for impaired alpha modulation, a notion that requires further investigation. It was expected that older adults would display abnormal alpha modulation, either through a weaker alpha power increase (Vaden et al., 2012) or through a weaker alpha power decrease (Deiber et al., 2013; Zanto et al., 2011). Age-related changes in alpha modulations were expected to either be unrelated to performance or be associated with poor performance in refocusing attention from time to space, reflected in a relationship between alpha power modulation and Switch-Costs (i.e. in increased RT costs to switch from attending to the RSVP stream to attending to the VS).

In addition to age-related changes in alpha oscillations, theta modulations (3-7Hz) deteriorate with increased age in both resting state and task related conditions, and particularly along the frontal midline (Cummins & Finnigan, 2007; Finnigan et al., 2011; Reichert et al., 2016; van de Vijver et al., 2014). Theta is associated with a broad array of task processes including pre-stimulus top-down control (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Min & Park, 2010), target processing (Demiralp & Başar, 1992), working memory (Sauseng et al., 2010) and selective attention (Green & McDonald, 2008). Frontal midline theta is thought to reflect medial PFC and ACC activity (e.g. Asada et al., 1999) which play an important role in attentional control (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Konishi et al., 1999; Pollmann, 2004). Functional connectivity of theta has been shown to be involved in attention and cognitive control (Cavanagh et al., 2009; Schack et al., 2005; Voloh et al., 2015; Wang et al., 2016). Voloh et al. (2015) found increases in phase amplitude coupling between ACC and PFC in theta-gamma frequencies before successful attentional shifts but not unsuccessful ones in non-human primates. Reduced frontal-midline theta with increased age are inconsistent with the simple framework of the PASA hypothesis of ageing (Davis et al., 2008). Age-related reductions in frontal midline theta have most commonly been observed in memory recall tasks and during resting state and mostly recorded with EEG (Cummins & Finnigan, 2007; Finnigan et al., 2011; Reichert et al., 2016; van de Vijver et al., 2014). Although there is an overall reduction in frontal midline theta power with increased age, there could be an increase in compensatory lateral PFC activation, which may not have not been picked up by previous EEG studies due to poor spatial resolution. It was hypothesised that there would either be a reduction in theta power, particularly across the frontal midline as has been demonstrated in previous EEG studies (Cummins & Finnigan, 2007; van de Vijver et al., 2014) or an increase in frontal theta activity reflecting additional top-down compensatory processing (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007).

In the light of the aforementioned inconsistencies we set out to clarify the notion of age-related deficiencies and compensatory mechanisms in relation to changes in alpha and theta frequencies. We used MEG to increase spatial resolution over previous EEG studies, while achieving the necessary temporal resolution for frequency-based analysis, thus, allowing for oscillatory analysis in source space. In addition to the hypotheses outlined above, functional oscillatory connectivity at theta and alpha frequencies was expected to either become weaker with increased age, as would be proposed by increased neural noise theories of ageing (Shih, 2009; Welford, 1981), or increase with increased age, as would be expected from compensatory recruitment (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007).

3.1.2 Methods

Participants

Participants who took part in Experiment 3 in Chapter 2 were invited to take part. Additional participants were recruited from Aston University staff and students and the community. Additional participants aged over 60 years were also recruited from the Aston Research Centre for Healthy Ageing participation panel. Participants received £7.50 towards their travel expenses. All participants provided written informed consent before participating and were screened for contraindications to having an MRI or MEG scan. The research was approved by Aston University Research Ethics Committee.

Seventy three participants in three age groups (19-30, 40-49, 60+ years) participated. Participants with visual impairments, photosensitive epilepsy, and a history of brain injury or stroke were excluded from participation. All participants in the 60+ years group scored over the 87 cut-off for possible cognitive impairment on the Addenbrookes Cognitive Examination 3 (ACE-3; Noone, 2015). The ACE-3 consists of a series of short tasks which provide measures of language, memory, attention, fluency and visuospatial abilities. Six participants were excluded from analysis due to low accuracy and/or noisy MEG data resulting in fewer than 30 out of 80 trials remaining for one or more conditions after data pre-processing. These five participants included two individuals aged 40-49 years and three participants aged 60+ years. Two participants withdrew from the study and in three data sets there was a recording error, one in which there was an error in the recording of triggers in the raw MEG data and two in which there was an error in the continuous recording of the head position indicator (HPI) coils. Demographics for the remaining 63 participants are presented in Table 3.1.

Table 3.1. Participant demographics

		Age Group (years)		
		19-30 (n=20)	40-49 (n=20)	60+ (n=23)
Age (years)	Mean	24.6	44.95	68.61
	SD	2.96	3.28	5.43
Gender	Male	08	07	10
	Female	12	13	13
Handedness	Right	16	19	22
	Left	04	01	01
ACE-3	Mean	n/a	n/a	95.5
	SD	n/a	n/a	2.69

Presented for each age group are participants’ mean age, the number of participants who are male and female, the number of participants who are left and right handed in addition to the mean ACE-3 scores for the 60+ years group.

Materials and procedures

Attention switching task and MEG recordings

The attention switching task that was implemented in Experiments 2 and 3 of Chapter 2, and published in Callaghan et al. (2017), was adapted for use with MEG. The methodology for the task is reiterated here. Participants alternated between attending to an RSVP stream and attending to a VS display. Each trial consisted of a fixation cross, presented for 2000ms, followed by the RSVP stream, which was immediately followed by the VS display. Stimuli were presented on stimulus presentation software E-Prime 2.0 Professional (Psychology Software Tool. Inc.) on a windows computer, projected onto a screen approximately 86cm in front of the participant at a resolution of 1400×1050. All stimuli were presented in black (RGB 0-0-0) on a grey background (RGB 192-192-192).

The RSVP stream consisted of a rapidly changing stream of letters in the centre of the display. There were ten items in each RSVP stream, each presented for 100ms with no inter-stimulus interval. Stimuli were presented in font size 30pt (0.75×0.75cm, 0.78°). On two thirds of the trials, one of the items in the stream was a target digit (1/2/3/4/6/7/8/9). Due to its visual similarity to the letter S, ‘5’ was excluded. The participant's task was to remember the digit. The remaining one third of the trials contained no target. Based on their visual similarity to certain numbers, letters I, O, and S were excluded from the stream, as well as VS targets K and Z. It should be noted that the current RSVP task differs from the attentional blink paradigm as the RSVP stream contains only a single target.

The VS display consisted of eight letters presented in a circle around a fixation cross in the centre of the screen, including seven distractors and one target. The target letter was always either a ‘K’ or a ‘Z’ and distractors were always a ‘P’, rendering a “pop-out” VS. Stimuli were presented in font size 20pt (0.50×0.50cm, 0.52°) and the centre of each stimulus was 2.3cm (2.40°) from the centre of the fixation cross.

Participants were seated comfortably with each of their fingers resting on one of eight buttons on a response pad that was placed in front of them. Participants pressed a button with their right index finger once they had identified the VS target. Participants’ RTs to press the button were recorded. Participants then pressed a button to indicate whether it was a ‘K’ (right index finger response) or a ‘Z’ (left index finger response) in the display. Participants were then prompted to indicate whether they had seen a target digit in the RSVP stream (yes: right index finger response; no: left index finger response). If a digit was correctly detected in the RSVP stream, participants then pressed the button that corresponded with the number that they saw. Participants wore earphones through which a ‘ding’ sound was played after a correct response and a chord sound was played after an incorrect response. Accuracy throughout the task was recorded. Participants were instructed to keep their eyes fixed on the cross at the centre of the screen while they completed the VS and to respond as quickly as possible.

To manipulate the cost of switching, the position of the target in the RSVP stream that preceded the VS was either the first item in the stream (No-Switch condition) or the target was either the seventh or ninth item in the stream (Target Switch condition) or absent from the stream (No-Target Switch condition). Illustrations of the RSVP stream and of the VS display are presented in Figure 3.1.

There were 80 trials of each of the three conditions (No-Switch/Target Switch/No-Target Switch), with a total of 240 trials. To provide the opportunity for breaks, trials were divided into ten blocks. Trials were randomized within blocks. Participants completed 24 practice trials before starting the experimental trials.

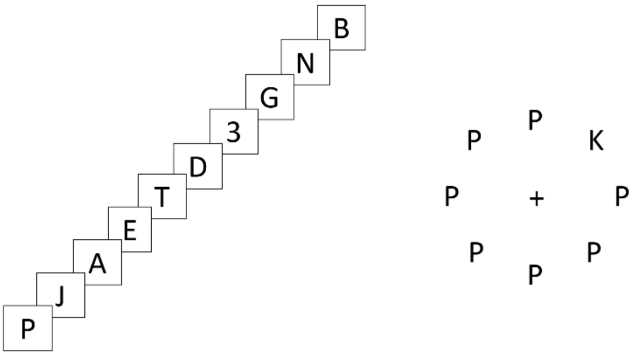

Figure 3.1. Illustration of examples of the stimuli set up. The RSVP stream illustration (left) displays a Target Switch RSVP stream. Each trial consisted of a fixation cross (2000ms) followed by an RSVP stream immediately followed by a pop-out VS display (right).

MEG data were recorded with a 306-channel Elekta Neuromag system (Vectorview, Elekta, Finland) in a magnetically shielded room at a sampling rate of 1000Hz. The 306 sensors were made up of 102 triplets incorporating one magnetometer and two orthogonal planar gradiometers. Data were recorded in two halves within the same session.

Head position was recorded continuously throughout data acquisition via the location of five HPI coils. Three HPI coils were positioned across the participant's forehead and one on each mastoid. The position of each HPI coil, three fiducial points, and 300-500 points evenly distributed across the head surface were recorded prior to the MEG recording with Polhemus Fastrak head digitisation. A T1 structural MRI was obtained for each participant, acquired using a 3T Siemens MAGNETOM Trio MRI scanner with a 32-channel head coil.

3.1.3 <u>Data analysis</u>

Response times

Participants' median VS RTs (ms) on trials where both VS and RSVP responses were correct were extracted using E-Prime data viewing application E-DataAid. Participants' proportions of correct VS target identifications and RSVP target identifications were also extracted.

Differences in median VS RTs between age groups and RSVP conditions were analysed in a 3 × 3 mixed ANOVA, where RSVP condition (No-Switch/Target Switch/No-Target Switch) was a within subjects factor and age group (19-30, 40-49, 60+ years) was a between subjects factor. Multiple comparisons were corrected for with Bonferroni correction.

The data were expected to violate assumptions of equality of variance due to increases in inter-individual variability with age (Hale et al., 1988; Morse, 1993). There is evidence to support that the ANOVA is robust to violations to homogeneity of variance (Budescu, 1982). Levene's test for equality of variance is therefore not reported. Where Mauchly's Test of Sphericity was significant, indicating that the assumption of sphericity had been violated, Greenhouse-Geisser corrected statistics were reported.

To further explore the age group × RSVP condition interactions, “Switch-Costs” were calculated as the percentage difference in RTs between Target Switch and No-Switch conditions (Target Switch-Costs) and between No-Target Switch and No-Switch conditions (No-Target Switch-Costs) for each individual. Independent t-tests were implemented to compare age groups’ Switch-Costs. It is important to note that t-tests were exploratory rather than hypothesis driven, and hence Restricted Fisher’s Least Significant Difference test was applied and corrections for multiple comparisons were not conducted (Snedecor & Cochran, 1967). Where Levene’s test for equality in variance was significant ($p<.05$) when computing t-tests, ‘Equality of variance not assumed’ statistics were reported.

MEG

MEG data were preprocessed in Elekta software using MaxFilter (temporal signal space separation, .98 correlation) to remove noise from sources inside and outside the sensor array. Seventeen participants displayed magnetic interference from dental work and so a tsss correlation of .90 was applied. This included five participants from the 19-30 years group, six from the 40-49 years group and six from the 60+ years group. Movement correction was applied to one participant in the 40-49 years group due to head movement (>7mm).

Data were read into the Matlab® toolbox Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011), band-pass filtered between 0.5 - 85Hz and epoched from 3.5s preceding VS onset (i.e. 2.5s preceding RSVP stream onset) to 2s after the onset of the VS display. Trials were visually inspected for artefacts and any noisy trials were removed.

Sensor level analysis

Prior to analysis independent components analyses (ICA) were implemented and components with eye blink or heartbeat signatures were omitted. Noisy MEG channels were interpolated with averaged signal from neighbouring sensors. Time-frequency analysis was carried out on signal from the planar gradient representation of 102 gradiometer pairs using a Hanning taper from 2-30Hz (for every 1Hz), with four cycles per time-window in stages of 50ms. For each participant trials were averaged within each condition (No-Switch/Target Switch/No-Target Switch).

Source level analysis

For the source level analysis noisy sensors were excluded. Due to size restrictions of the MEG data file, each data set was recorded in two halves within the same session and were therefore MaxFiltered separately prior to concatenating the data, which could lead to different components being removed in each half of data. To reduce potential artefacts due to applying Maxfiltering to the two halves of data separately, a PCA was implemented to reduce data dimensionality to components that accounted for 99% of the variance.

Using an in house Matlab script and Elekta software MRI Lab, individual MRIs were aligned with the sensor array, by aligning the individual's MRI with the fiducial positions and head shape that were recorded with Polhemus Fastrak head digitisation. Individual single-shell head-models were created from these coregistered MRIs. Head-models were normalised to MNI space (Montreal Neurological Institute template). Voxels were 5mm.

Time-frequency tiles were selected based on the results from the sensor level analysis. To localise sources of theta (3-5Hz; 550-1550ms) and upper alpha (10-14Hz; 450-950ms) oscillations, two separate Dynamic Imaging of Coherent Sources (DICS; Gross et al., 2001) beamformers were implemented. Spatial filters were calculated based on cross-spectral densities obtained from the fast-fourier-transform (FFT) of signals from 204 gradiometers using a Hanning taper, spectral smoothing of +/-2Hz and 2s of data padding.

Connectivity

Functional connectivity between each pair of 116 parcellated cortical and subcortical atlas regions (Automated Anatomical Labelling: AAL; Tzourio-Mazoyer et al., 2002) was estimated with weighted Phase Lag Index (wPLI; Vinck, Oostenveld, van Wingerden, Battaglia, & Pennartz, 2011). WPLI measures the extent that phase leads or lags between two signals. Findings show that wPLI is both less sensitive to noise and less vulnerable to the estimation of spurious connectivity due to volume conduction compared to measures of PLV, PLI and imaginary coherence, due to the suppression of zero-phase lag synchrony and weighting estimates of phase lag consistence with the magnitude of the imaginary part of coherence (Vinck et al., 2011). A detailed description of wPLI can be found in Vinck et al. (2011). Spatial filters for each of the 116 regions were computed with a linearly constrained minimum variance (LCMV) beamformer (Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997). Separately for each trial, spatial filters were applied to the raw data to compute virtual electrodes for each condition for each of the 116 regions. Fourier analysis was computed (with a Hanning taper) from the virtual electrodes between 0-2s from 2-16Hz. Consistent with source analyses, data at 3-5Hz (0.55-1.55s) and 10-14Hz (0.45-0.95s) were selected for further analysis. WPLI values were averaged across time and frequencies.

Minimum Spanning Trees (MST)

To explore age group differences in the topology of Switch and No-Switch networks Kruskal's algorithm (Kruskal, 1956) was applied to the 116×116 wPLI matrices to construct an MST for each RSVP condition for each age group. MST is a graph theoretical approach that enables the comparison of network topologies while controlling for the number of nodes (i.e. atlas regions) and edges in a network and avoiding the requirement to select an arbitrary threshold (Tewarie et al., 2014). Networks that contain different numbers of nodes and/or edges bias graph theoretical metrics such as degree and path length. A more detailed discussion of MST analysis can be found in Tewarie et al. (2014).

From the MST three local metrics (degree/betweenness centrality/eccentricity) and two global metrics (mean eccentricity/leaf fraction) were extracted. Degree can be defined as the number of edges (i.e. connections) to a node. Betweenness centrality quantifies the extent to which a node is a hub in the network based on both the degree and the degree of adjoining nodes. Eccentricity quantifies the extent to which the node is central in the network in terms of the path lengths to all other nodes. Low eccentricity reflects short path lengths to all other nodes in the network and indicates greater centrality.

From the MST, two global metrics, mean eccentricity and leaf fraction, were extracted. Mean eccentricity was computed to provide an indication of the topology of all paths in the network. Lower mean eccentricity values signify that the network is characterised by efficient local connectivity, whereas higher values signify that on average nodes have longer path lengths to other nodes. Leaf fraction is the proportion of nodes in the network that are connected to only one other node. Higher leaf fraction implies that networks are characterised by efficient local connectivity directly between nodes, rather than a network characterised by chain-like, long range connectivity (Tewarie et al., 2014; Tewarie et al., 2015).

Statistics

Power

During sensor and source level analysis, two-tailed dependent t-tests were carried out to compare each of the switch conditions (Target Switch/No-Target Switch) with the No-Switch condition separately for each age group. Multiple comparisons were corrected for with non-parametric cluster permutations (Maris & Oostenveld, 2007).

Second level analysis was carried out with differences in differences comparisons (Bögels, Barr, Garrod, & Kessler, 2014; Wang, Callaghan, Gooding-Williams, McAlliste, & Kessler, 2016). For each participant the No-Switch condition was subtracted from each of the Switch conditions separately. These differences were entered into two two-tailed independent cluster permutation t-tests (2000 permutations) to compare age groups (19-30 years vs 40-49 years/19-30 years vs 60+ years).

To explore the relationship between behavioural performance and power changes in theta and alpha frequencies, differences between each of the Switch conditions and the No-Switch condition in theta and alpha power at source analysis cluster peaks were entered into Spearman's correlation analysis with Target and No-Target RTs Switch-Costs. An explanation of how Switch-Costs were calculated is described in the current chapter below (Section 3.1.1). Correlation analyses were exploratory and so multiple comparisons were not corrected for, however analyses were related to current hypotheses and will inform future research trajectories.

Network connectivity

To investigate whether there were any changes in the extent of network connectivity between Switch and No-Switch conditions, 116×116 wPLI matrices were entered into non-parametric Network Based Statistics analysis (NBS; Zalesky, Fornito, & Bullmore, 2010). NBS analysis controls for the multiple comparisons problem through cluster permutation analysis. Instead of clustering based on spatial information, clustering is performed on network based information. Clusters were formed from connected edges that exceed a selected *t*-threshold when compared across groups. A null distribution was derived from 5000 permutations to determine the probability that group differences in the extent of the network was greater than by chance (p<.05). Two-tailed hypotheses were evaluated.

The output of NBS is highly sensitive to the *t*-threshold selected, with lower *t*-thresholds passing a greater number of edges into the network. The selection of *t*-threshold is arbitrary (Nelson, Bassett, Camchong, Bullmore, & Lim, 2017; Verstraete, Veldink, Mandl, van den Berg, & van den Heuvel, 2011; Ye, Leung, Schäfer, Taylor, & Doesburg, 2014; Zalesky, Cocchi, Fornito, Murray, & Bullmore, 2012; Zalesky et al., 2010). Although all *t*-values selected in the current analysis met the criteria of p<.05, consistent with Nelson et al. (2017) a range of *t*-thresholds were sampled (*t*-thresholds 2.1-5) to understand the implications of thresholding on resulting networks. The range of thresholds at which clusters were significant are reported in Figures 3.7 and 3.8.

Consistent with the statistical comparisons of power, to explore the interaction between RSVP condition and age, age groups were compared on the differences between Switch and No-Switch conditions. To enable us to compare age groups on the networks that were strongest for each condition, when calculating differences between conditions for each participant the No-Switch wPLI matrix was subtracted from the Target Switch wPLI matrix and in a separate analysis the Target Switch wPLI matrix was subtracted from the No-Switch wPLI matrix. In each output negative values were set to zero. This allowed us to first compare age groups on the networks that were stronger in the Target Switch than the No-Switch condition, followed by comparing age groups on networks that were stronger in the No-Switch than the Target Switch condition. The same procedure was applied to compare No-Target Switch and No-Switch conditions.

To further characterise networks that significantly differed between age groups, nodes were categorised into eight anatomical regions (frontal, occipital, parietal, temporal and hippocampal, cerebellum, insula, striatum, thalamus), consistent with Verdejo-Román, Fornito, Soriano-Mas, Vilar-López, & Verdejo-García, (2017) and Ye et al. (2014). Categories of each atlas region are presented in Table A3.1.1 in Appendix 3.1. It should be noted that the total number of connections incorporated in each network is determined by the arbitrary *t*-threshold selected in the NBS analysis and each network has a different total number of nodes and edges (Nelson et al., 2017; Verstraete et al., 2011; Zalesky et al., 2012; Zalesky et al., 2010). The aim of the matrix plots is to better characterise which cortical regions are most strongly connected in each network.

MST

Two-tailed dependent t-tests were carried out to compare each of the switch conditions (Target Switch/No-Target Switch) with the No-Switch condition on local MST metrics in each node separately for each age group. Multiple comparisons were controlled for with permutation analysis with 10000 permutations.

To compare age groups in the difference between Switch and No-Switch conditions in local MST metrics, each local metric in the No-Switch condition was subtracted from each of the Switch conditions at each node for each participant. This is consistent with the analysis procedure implemented to compare age groups in sensor power, source power and NBS. Differences in local metrics between conditions were then entered into independent samples t-tests where multiple comparisons were controlled for with 10000 permutations.

Global metrics, mean eccentricity and leaf fraction, were analysed in SPSS 21. For both theta and alpha frequency, MSTs Two 3×3 (age group × RSVP condition) ANOVAs were performed on leaf fraction and mean eccentricity, to investigate the effects of age and RSVP condition on overall network topology, where RSVP condition (No-Switch/Target Switch/No-Target Switch) was a within subjects factor and age group (19-30, 40-49, 60+ years) was a between subjects factor. Multiple comparisons were corrected for with Bonferroni correction. To further explore the interactions between independent variables that were identified from the ANOVA on mean eccentricity independent t-tests were implemented to compare age groups on mean eccentricity separately for each RSVP condition. There is evidence to support that the ANOVA is robust to violations to homogeneity of variance (Budescu, 1982; Budescu & Appelbaum, 1981). Levene's test for equality of variance is therefore not reported. Where Mauchly's Test of Sphericity was significant, indicating that the assumption of sphericity has been violated, Greenhouse-Geisser corrected statistics were reported.

Global MST metrics and local metrics at nodes in which significant group differences were found were entered into Spearman's correlation analysis with Target and No-Target Switch-Costs. Correlation analyses were exploratory and so multiple comparisons were not corrected for, however were directly related to hypotheses.

3.1.4 Results

Attention switching task RTs

All groups correctly identified over 96% of VS targets in all three conditions. Thus, no further analysis was carried out on VS accuracy. All groups correctly identified over 73% of VS targets in both RSVP conditions. RSVP accuracy was unrelated to the aims and hypotheses of the current chapter and no further analysis was carried out on RSVP accuracy, however the proportion of correct RSVP target identifications in the two Target conditions are presented in Figure A3.2.1 in Appendix 3.2. Group means of participants' median VS are presented in Figure 3.2.

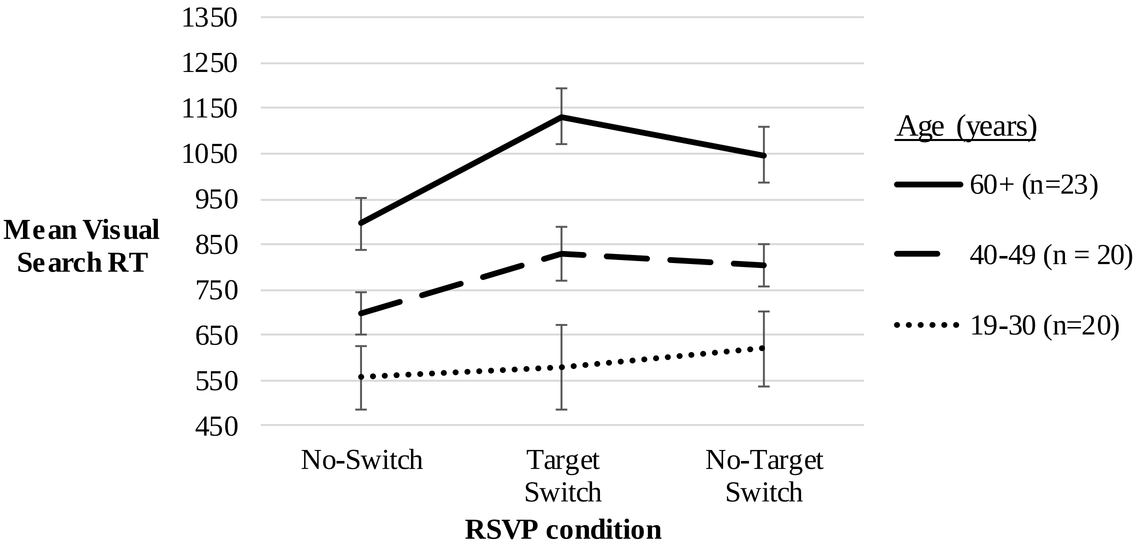

Figure 3.2. Group means of participants' median VS RTs. Vertical bars represent the SE.

The 3 × 3 (RSVP condition × age group) mixed ANOVA on participants' median VS RTs revealed a significant main effect of age ($F(2, 60)=11.36$, $p<.001$, $\eta^2_p=.28$), a significant main effect of RSVP condition ($F(2,120)=35.21$, $p<.001$, $\eta^2_p=.37$) and a significant interaction between age and RSVP condition ($F(4,120)=7.05$, $p<.001$, $\eta^2_p=.19$).

Post hoc comparisons revealed that the main effect of age resulted from significantly slower RTs in the 60+ group in comparison to both the 19-30 (*p*<.001) and 40-49 years (*p*=.029) groups. There was no significant difference between the 19-30 and 40-49 years groups (*p*>.10).

The main effect of RSVP condition resulted from significantly slower RTs in both the Target Switch (*p*<.001) and No-Target Switch (*p*<.001) conditions in comparison to the No-Switch condition. There was no significant difference in RTs between the Target Switch and No-Target Switch conditions (*p*>.10).

To investigate the hypothesis that there would be significantly greater Switch-Costs in both the 40-49 and 60+ years groups in comparison to the 19-30 years group, and to further explore the interaction between age and RSVP condition, independent t-tests were carried out comparing Switch-Costs across age groups. Refer to the methods section for a description of how Switch-Costs were calculated for each participant. Means and SDs of participants Switch-Costs are presented in Table 3.2.

Target Switch-Costs were significantly greater in both the 40-49 (*df*=38, *t*=-3.45, *p*<.001) and 60+ (*df*=41, *t*=-5.15, *p*<.001) years groups in comparison to the 19-30 years group. There were no significant age group differences in No-Target Switch-Costs (*p*>.10).

Table 3.2. Means and SDs of Switch-Costs for each age group

		Age group (years)		
		19-30 (n=20)	40-49 (n=20)	60+ (n=23)
Target Switch-Costs	Mean	4.02	19.67	26.65
	SD	12.72	15.78	15.67
No-Target Switch-Costs	Mean	12.59	17.29	17.98
	SD	15.24	15.66	18.43

MEG results

The RT results replicated findings from Callaghan et al. (2017) demonstrating deficits in switching in both the 40-49 years and 60+ years groups in comparison to the 19-30 years group. To explore the interaction between age and RSVP condition that was observed in the behavioural results, a two level analysis approach was implemented on MEG data (Bögels et al., 2014; Wang et al., 2016). Firstly, possible effects of switching were explored by contrasting each of the Switch conditions with the No-Switch condition (i.e. Target Switch - No-Switch/No-Target Switch - No-Switch) for each age group. The contrasts from the first stage of analysis in the 40-49 and 60+ years groups were compared with the contrasts in the 19-30 years group. The two Switch conditions were not compared with each other and the 40-49 years and 60+ years groups were not compared with each other, as these comparisons were unrelated to the current hypotheses. Frequencies from 2-30Hz were explored. From the TFRs presented in Figures 3.3 - 3.6, frequency bands of 3-5Hz (lower theta) and 10-14Hz (upper alpha) were selected to enter into cluster based permutation analysis of time-frequency sensor data and source power. Time windows entered into source analysis were selected based on the latencies of effects observed in cluster based permutation analysis of time-frequency sensor data.

Theta power

Target Switch vs No-Switch

Statistical results comparing theta power in Target Switch and Target No-Switch conditions, and exploring the interaction between RSVP condition and age group, are presented in Figure 3.3.

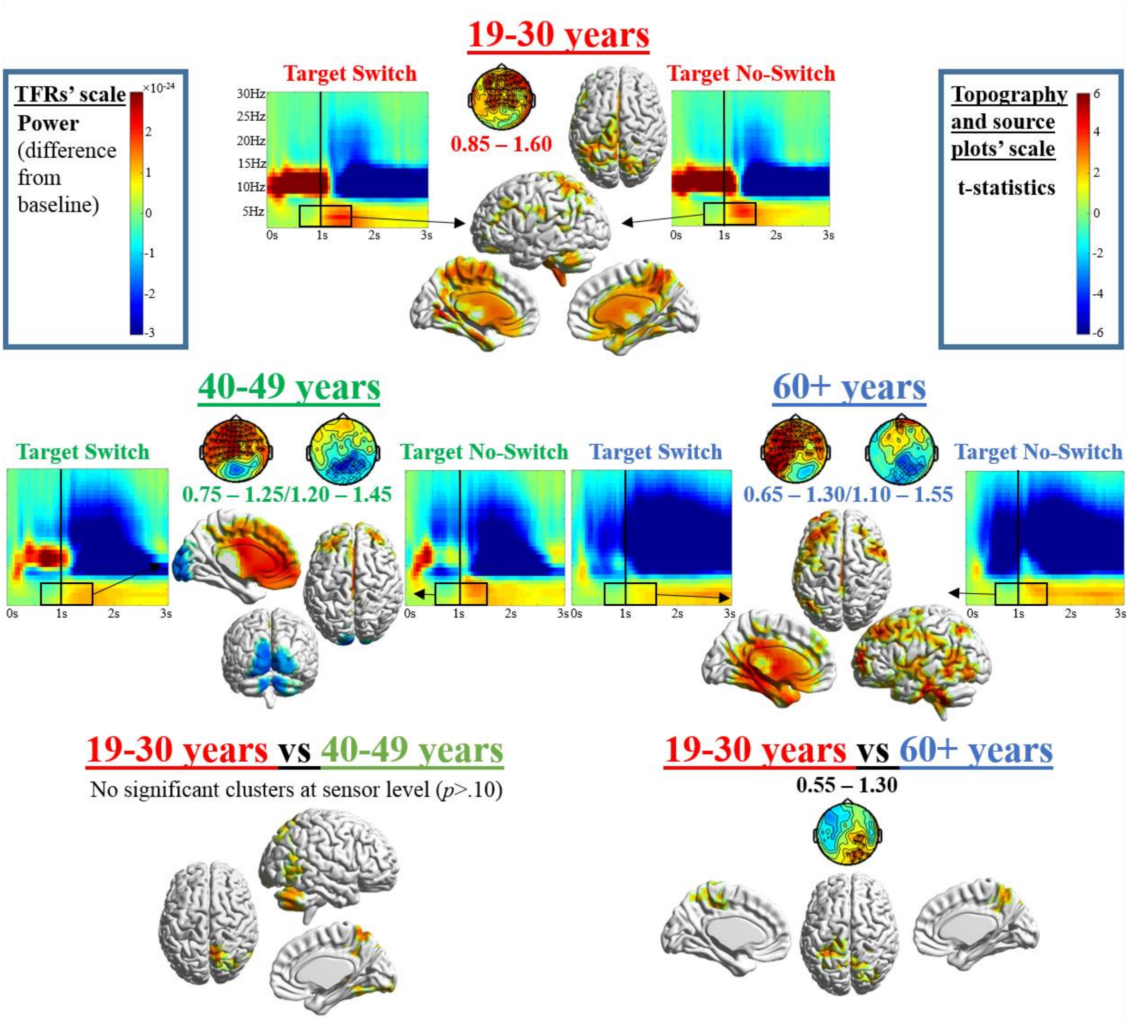

Figure 3.3. Effects in lower theta (3-5Hz) when contrasting Target Switch and No-Switch conditions in each age group (top two rows) and when exploring the Target Switch condition × age interaction (bottom row). Time-frequency representations (TFRs) present power in relation to a baseline period of -0.6s - -0.01s in a group of four posterior gradiometer pairs. The onset of the RSVP stream occurred at 0.0s. Black lines placed over TFRs indicate the onset of the VS display, and RSVP target onset occurred at either 0.7 or 0.9s. Topographical and source plots present *t*-statistics of significant clusters (*p*<.025 in source plots and *p*<.05 in sensor plots). Rectangles placed over TFRs highlight the time-frequency tile entered into source localisation.

The TFRs in Figures 3.3 and 3.4 illustrate that there was a theta increase in response to the VS display onset in all conditions. All age groups displayed a significantly higher theta increase in the Target Switch condition in comparison to the No-Switch condition, which localised to superior and inferior parietal gyri, occipital gyri, and the MFG in the 19-30 years group, bilateral frontal cortex and the ACC in the 40-49 years group and the SFG, temporal gyri and the cerebellum in the 60+ years group. Whereas the 19-30 years group displayed higher theta in parietal regions, the two older groups demonstrated more extensive frontal recruitment. The 60+ years group displayed higher temporal lobe theta that was not present in the two younger groups. The two older groups additionally presented with posterior negative clusters, which reflect lower theta in the Target Switch condition in comparison to the No-Switch condition, and localised to occipital regions in the 40-49 years group.

No significant negative cluster was seen in the 60+ years group in source space, however, this could be due to difficulties with cluster permutation analyses localising both positive and negative clusters.

Age group comparisons of differences between Target Switch and No-Switch conditions, which are presented in Figure 3.3 (bottom row), confirmed that the higher theta increase in the Target Switch condition was significantly greater in the 19-30 years group in parietal regions in comparison to both the 40-49 and 60+ years groups.

No-Target Switch vs No-Switch

Results of statistical comparisons of No-Target Switch and No-Switch theta power and investigations of the interaction between RSVP condition and age group, are presented in Figure 3.4.

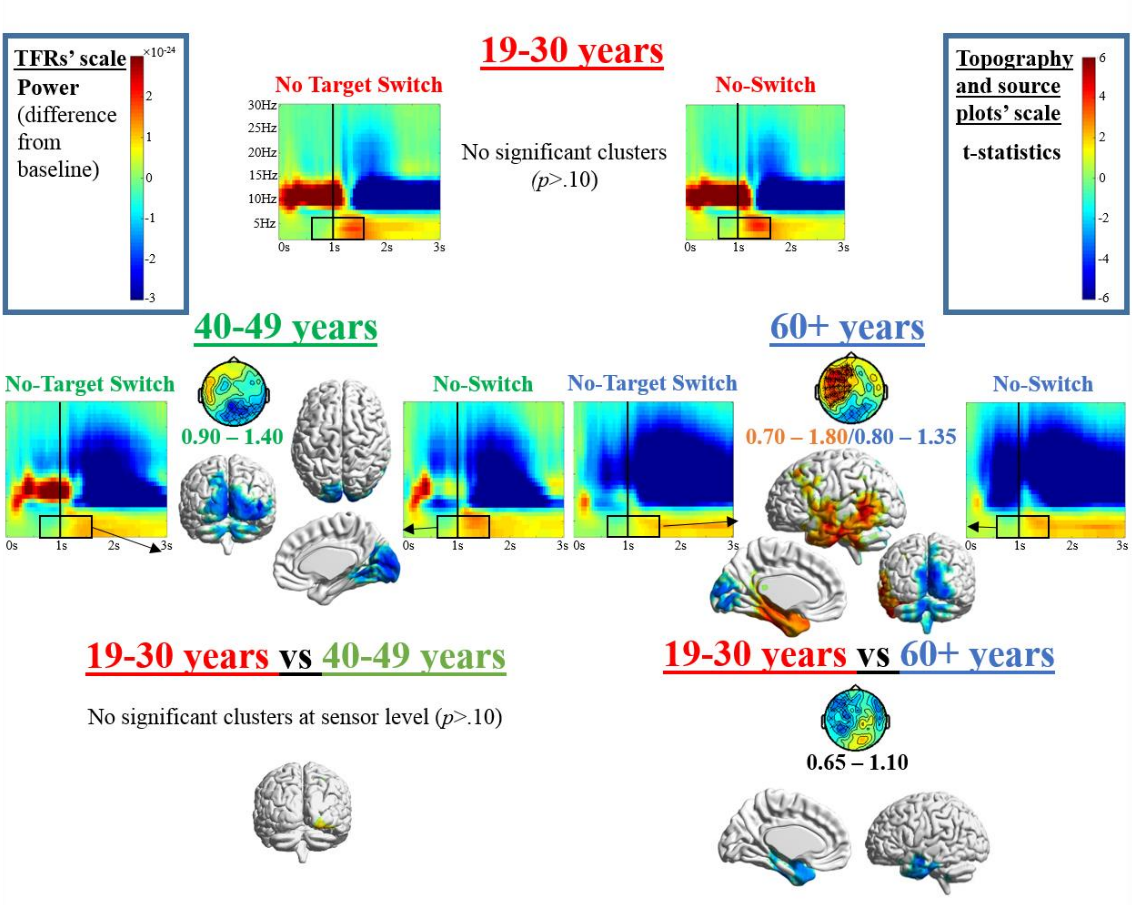

Figure 3.4. Effects in lower theta (3-5Hz) when contrasting No-Target Switch and No-Switch conditions in each age group (top two rows) and when exploring the No-Target Switch condition × age interaction (bottom row). TFRs present power in relation to a baseline period of -0.6s - -0.01s in a group of four posterior gradiometer pairs. The onset of the RSVP stream occurred at 0.0s. Black lines placed over TFRs indicate the onset of the VS display, and RSVP target onset occurred at either 0.7 or 0.9s. Rectangles placed over TFRs highlight the time-frequency tile entered into source localisation. Topographical and source plots present *t*-statistics of significant clusters (p<.025 in source plots and p<.05 in sensor plots). Note that No-Switch TFRs are identical to those presented in Figure 3.3.

There was no significant difference between No-Target Switch and No-Switch conditions in theta frequency in the 19-30 years group, suggesting that the differences observed in theta between Target Switch and No-Switch conditions in this age group were a result of processing the RSVP target in the Target Switch condition.

In contrast, both the 40-49 and 60+ years groups again display negative clusters that localise to the occipital lobes, indicating deficient theta increases in the No-Target Switch condition, a finding that cannot be due to RSVP target processing. The 60+ years group again showed higher theta in the No-Target Switch condition in comparison to the No-Switch condition that localised to frontal regions and the left temporal lobe.

In summary, the 19-30 years group showed higher Target Switch related theta in parietal regions in comparison to the two older groups, however this increase seems to be related to RSVP target processing, as no significant difference in theta was seen between No-Target Switch and No-Switch conditions in the 19-30 years group. The left intraparietal sulcus has been shown to participate in both top-down and bottom-up mechanisms of attentional control (Imaruoka et al., 2003) suggesting that younger adults may implement more efficient attentional mechanisms during RSVP target detection compared to older adults.

Both the 40-49 and 60+ years groups showed significantly lower occipital theta in both Switch conditions (in comparison the No-Switch condition) that was not present in the 19-30 years group. It could be that occipital theta deficits in the two Switch conditions are related to increased VS RTs in the two older groups when switching, possibly through deficient attentional guidance modulating the temporal and spatial dynamics of activity in feature-coding neuronal populations (Bundesen et al., 2005). Based on the Dehaene et al. (2006) framework, this deficient attentional guidance in visual processing regions could be related to parietal theta deficits (Figure 3.3 bottom row).

The 60+ years group additionally showed significantly higher frontal and temporal theta in the two Switch conditions in comparison to the No-Switch condition, and the 40-49 years group showed higher frontal theta in the Target Switch condition. It could be that this additional recruitment of the frontal cortex reflects the two older groups relying more on top-down attentional control (McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002). The additional recruitment of temporal gyri in the 60+ years group may indicate the implementation of further strategies to cope with task demands, such as enhanced episodic memory encoding (Schacter & Wagner, 1999) or silent vocalisation (Graves, Grabowski, Mehta, & Gordon, 2007; Hickok & Poeppel, 2007; Hocking & Price, 2009; Smith, Jonides, Marshuetz, & Koeppe, 1998).

Alpha power

Target Switch vs No-Switch

Statistical results comparing alpha power in Target Switch and No-Switch conditions, and exploring the interaction between RSVP condition and age group, are presented in Figure 3.5.

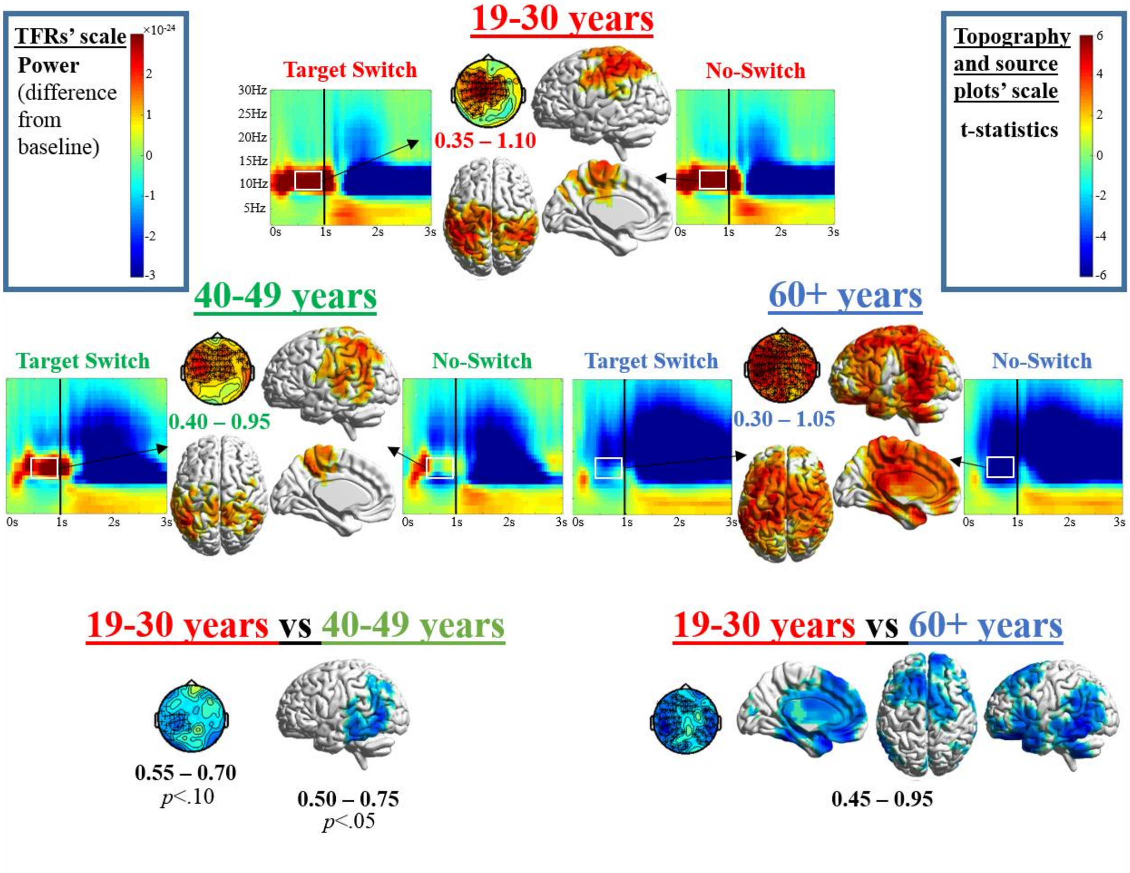

Figure 3.5. Effects in alpha (10-14Hz) when contrasting Target Switch and No-Switch conditions in each age group (top two rows) and when exploring the Target Switch condition × age interaction (bottom row). TFRs present power in relation to a baseline period of -0.6s - -0.01s in a group of four posterior gradiometer pairs. The onset of the RSVP stream occurred at 0.0s. Black lines placed over TFRs indicate the onset of the VS display, and RSVP target onset occurred at either 0.7 or 0.9s. Rectangles placed over TFRs highlight the time-frequency time entered into source localisation. Topographical and source plots present *t*-statistics of significant clusters. Note that TFRs are identical to those presented in Figure 3.3.

All age groups show significantly higher alpha in the Target Switch condition in comparison to the No-Switch condition which localised to parietal regions in all age groups and was widely distributed across the cortex in the 60+ years group. The TFRs in Figure 3.5 suggest that in the 19-30 and 40-49 years groups, this difference in alpha resulted from an alpha increase throughout the RSVP stream that was higher in the Target Switch condition than the No-Switch condition, whereas in the 60+ years group higher alpha in the Target Switch condition resulted from a greater alpha decrease in the No-Switch condition than the Target Switch condition throughout RSVP presentation. In contrast to the 19-30 years group both the 40-49 and 60+ years groups displayed higher temporal lobe alpha in the Target Switch condition in comparison to the No-Switch condition.

Group comparisons of differences highlighted that the higher alpha in the Target Switch condition in comparison to the No-Switch condition was significantly greater in both the 40-49 and 60+ years groups in comparison to the 19-30 years group, as is reflected by the negative clusters on the bottom row in Figure 3.5.

No-Target Switch vs No-Switch

Statistical results comparing alpha power in No-Target Switch and No-Switch conditions, and exploring the interaction between RSVP condition and age group, are presented in Figure 3.6.

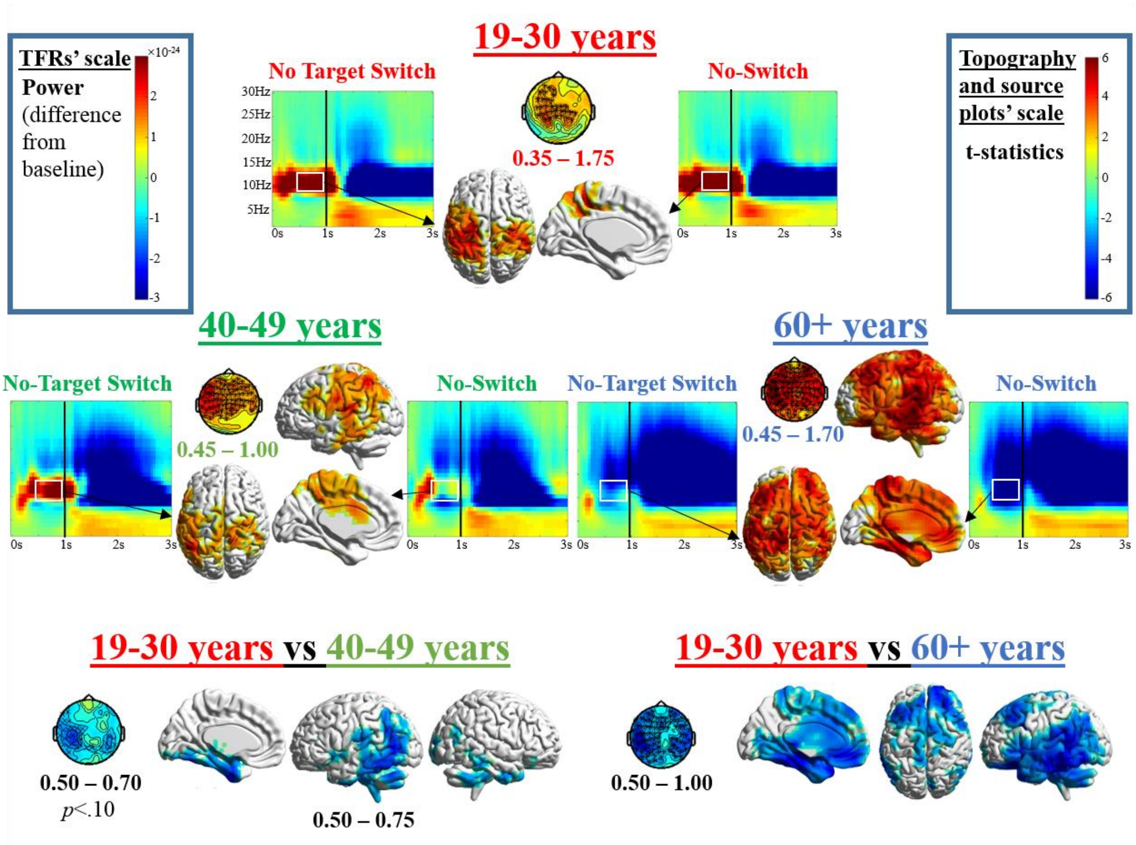

Figure 3.6. Effects in alpha (10-14Hz) when contrasting No-Target Switch and No-Switch conditions in each age group (top two rows) and when exploring the No-Target Switch condition × age interaction (bottom row). TFRs present power in relation to a baseline period of -0.6s - -0.01s in a group of four posterior gradiometer pairs. The onset of the RSVP stream occurred at 0.0s. Black lines placed over TFRs indicate the onset of the VS display, and RSVP target onset occurred at either 0.7 or 0.9s. Rectangles placed over TFRs highlight the time-frequency tile entered into source localisation. Topographical and source plots present *t*-statistics of significant clusters. Note that TFRs are identical to those presented in Figure 3.4.

All age groups show significantly higher alpha in the No-Target Switch condition in comparison to the No-Switch condition which localised to parietal regions in all age groups and was widely distributed across the cortex in the 60+ years group. Similar to the pattern seen when comparing Target Switch and No-Switch conditions in Figure 3.5, lower alpha in the No-Switch condition in comparison to the No-Target Switch condition appears to have resulted from a greater alpha increase in the Target Switch condition in the 19-30 and 40-49 years groups and a greater alpha decrease in No-Switch condition in the 60+ years group.

Group comparisons revealed that the higher alpha in the No-Target Switch condition in comparison to the No-Switch condition was significantly higher in both the 40-49 and 60+ years groups in comparison to the 19-30 years group, as is reflected by the negative clusters on the bottom row in Figure 3.6. While alpha effects were contained to parietal regions in the 19-30 years group, in the 40-49 and especially in the 60+ years groups the higher alpha effects were both stronger and more widely distributed across the cortex. In the 40-49 years group the distribution extended primarily into the ventral processing stream in occipito-temporal cortex, whereas in the 60+ years group the wider distribution also comprised prefrontal areas.

Correlations between power and Switch-Costs

To explore the relationship between theta and alpha power modulation and Switch-Costs, for each participant differences in theta power between each of the Switch conditions and the No-Switch condition were extracted at several MNI coordinates and entered into Spearman’s correlation analyses with Target and No-Target Switch-Costs. MNI coordinates were selected based on the peak *t*-values of significant clusters from cluster permutation analyses that compared Switch and No-Switch conditions in each age group. Target Switch-Costs were correlated with power differences between Target Switch and No-Switch conditions and No-Target Switch-Costs were correlated with power differences between No-Target Switch and No-Switch conditions. MNI coordinates and corresponding atlas labels that were selected for correlation analyses in theta power can be found in Table A3.3.1 and Table A3.3.2 in Appendix 3.3 and those selected for correlation analyses in alpha power can be found in Table A3.3.4 and Table A3.3.5 in Appendix 3.3. Correlations were exploratory and multiple comparisons were not corrected for.

Correlations between Target Switch-Costs and theta power change

There were greater theta power increases in frontal regions in the two older groups but weaker theta increases in parietal regions in comparison to the younger adults (Figure 3.3). In the 60+ years group, decreased Target Switch-Costs were associated with greater theta power increases in the left superior parietal gyrus (r=-.53, p=.010) and left MFG (r=-.40, p=.057), which both supports that additional frontal recruitment in the oldest group reflects compensation and suggests that deficits in parietal theta modulation were related to impaired switching. The two older groups displayed posterior negative clusters that localised to occipital regions and the cerebellum. The negative correlation between Target Switch-Costs and theta power modulation in the right cerebellum (crus II; r=-.44, p=.035) in the 60+ years group may therefore reflect increased Switch-Costs with increased theta deficiencies when switching.

In the 19-30 years group, there was a positive correlation between Target Switch-Costs and power change in the left insula (*r*=.44, *p*=.056) and a negative correlation between Target Switch-Costs and power change in the left superior occipital gyrus (*r*=-.41, *p*=.071) that did not reach significance. In the insula, as power differences between conditions decreased, Switch-Costs decreased, whereas as power differences in the occipital lobe increased, Switch-Costs decreased.

There were no other significant correlations between Target Switch-Costs and theta power change in any coordinates in any age group (*p*>.10).

Correlations between No-Target Switch-Costs and theta power change

There were no significant differences in theta power between No-Target Switch and No-Switch conditions in the 19-30 years group and so correlations between power differences between these conditions and No-Target Switch-Costs were not explored.

In the 60+ years group, a significant negative correlation was found between No-Target Switch-Costs and theta modulation in the left cerebellum (crus II; *r*=-.60, *p*=.002). This relationship again reflects increased Switch-Costs with greater negativity of posterior clusters. There were no other significant correlations between No-Target Switch-Costs and theta power change in any coordinates in the 60+ years group (*p*>.10).

Correlations between Target Switch-Costs and alpha power change

In contrast to theta power correlations, none of the correlations between Target Switch-Costs and alpha power changes reached significance (*p*>.05). In the 40-49 years group there was a positive correlation between power modulation in the left paracentral lobule and Target Switch-Costs that did not reach significance (*r*=.41, *p*=.077), and non-significant negative correlations between Target Switch-Costs and alpha power modulation in the left middle occipital2 (*r*=-.40, *p*=.083) and the orbital part of the right MFG (*r*=-.43, *p*=.060). As alpha power difference in the left paracentral lobule increased, Switch-Costs increased, consistent with the increase in power change observed with increased age. In contrast Switch-Costs decreased as power change in the left middle occipital gyrus and right MFG increased.

There were no other significant correlations between Target Switch-Costs and alpha power in any age group (*p*>.10).

Correlations between No-Target Switch-Costs and alpha power change

In the 19-30 years group there was a significant positive correlation between No-Target Switch-Costs and alpha modulation in the left postcentral gyrus2 (r=.45, p=.048). As power change increased, Switch-Costs increased. There were no other significant correlations between No-Target Switch-Costs and power change in any age group (p>.10).

Although the older age groups display stronger alpha modulations in comparison to the younger adults, this modulation does not appear to have a clear relationship with Switch-Costs. Only non-significant correlations were observed between alpha power modulation and Target Switch-Costs in the 40-49 years group, which was in the direction of increased Switch-Costs with increased alpha modulation in the left paracentral lobule but decreased Switch-Costs with increased alpha modulation in the right MFG and left middle occipital gyrus. The absence of a correlation between Switch-Costs and alpha power modulation in the oldest group is consistent with Vaden et al.'s (2012) proposition that alpha becomes redundant with increased age. However, the stronger task related alpha modulation in the two older groups implies that alpha oscillations are still utilised in older age, despite the seemingly weak benefits on performance. Rather than compensation it could therefore be that his strong modulation of alpha power reflects increased neural noise (Shih, 2009) and the dedifferentiation hypothesis (Cabeza, 2002).

Network connectivity (NBS) analysis

Having observed age-related changes in both theta and upper alpha power, age-related changes in functional connectivity were explored. If more extensive neural activation is due to increased neural noise, functional connectivity may be weaker with increased age. On the other hand, if more extensive neural activation is due to compensatory recruitment then it may be that functional connectivity is greater with increased age, as communication across the cortex increases.

Functional connectivity between 116 AAL atlas regions was estimated with wPLI. To investigate whether there were any changes in functional connectivity between Switch and No-Switch conditions, non-parametric NBS was applied (Zalesky et al., 2010). NBS comparisons of Target Switch and No-Switch network connectivity, and of No-Target Switch and No-Switch network connectivity in each age group, can be found in Figure A3.4.1 and Figure A3.4.3 in Appendix 3.4. Investigations of the main effect of age on wPLI, achieved through age group comparisons of network connectivity (with NBS) in each of the Switch conditions, can be found Figure A3.4.2 and Figure A3.4.4 in Appendix 3.4.

To explore the interaction between RSVP condition and age, age groups were compared on the differences between Switch and No-Switch conditions, consistent with the analysis implemented for sensor and source power in the current Chapter (Section 3.1.4). A description of how this was implemented can be found in the Data Analysis section (Section 3.1.3).

Significant networks are presented in Figures 3.7 - 3.10. To further characterise networks that were found to be significantly different between age groups, nodes were categorised into eight anatomical regions (frontal, occipital, parietal, temporal and hippocampal, cerebellum, insula, striatum, thalamus), consistent with Verdejo-Román et al. (2017) and Ye et al. (2014). The matrix plots in Figures 3.7 - 3.10 illustrate the number of connections within each network between each of the eight regions. The total number of connections incorporated in each network is determined by the arbitrary *t*-threshold selected in the NBS analysis and each network has a different total number of nodes and edges (Tewarie et al., 2014; Tewarie et al., 2015). The scales of each matrix plot are therefore different across networks and should be interpreted with caution. A more detailed discussion of NBS can be found in the Methods Section 3.1.3.

Theta network connectivity

NBS results (theta network connectivity) investigating the RSVP condition (Target Switch/No-Switch) × age interaction are presented in Figure 3.7, and investigating the RSVP condition (No-Target Switch/No-Switch) × age interaction are presented in Figure 3.8.

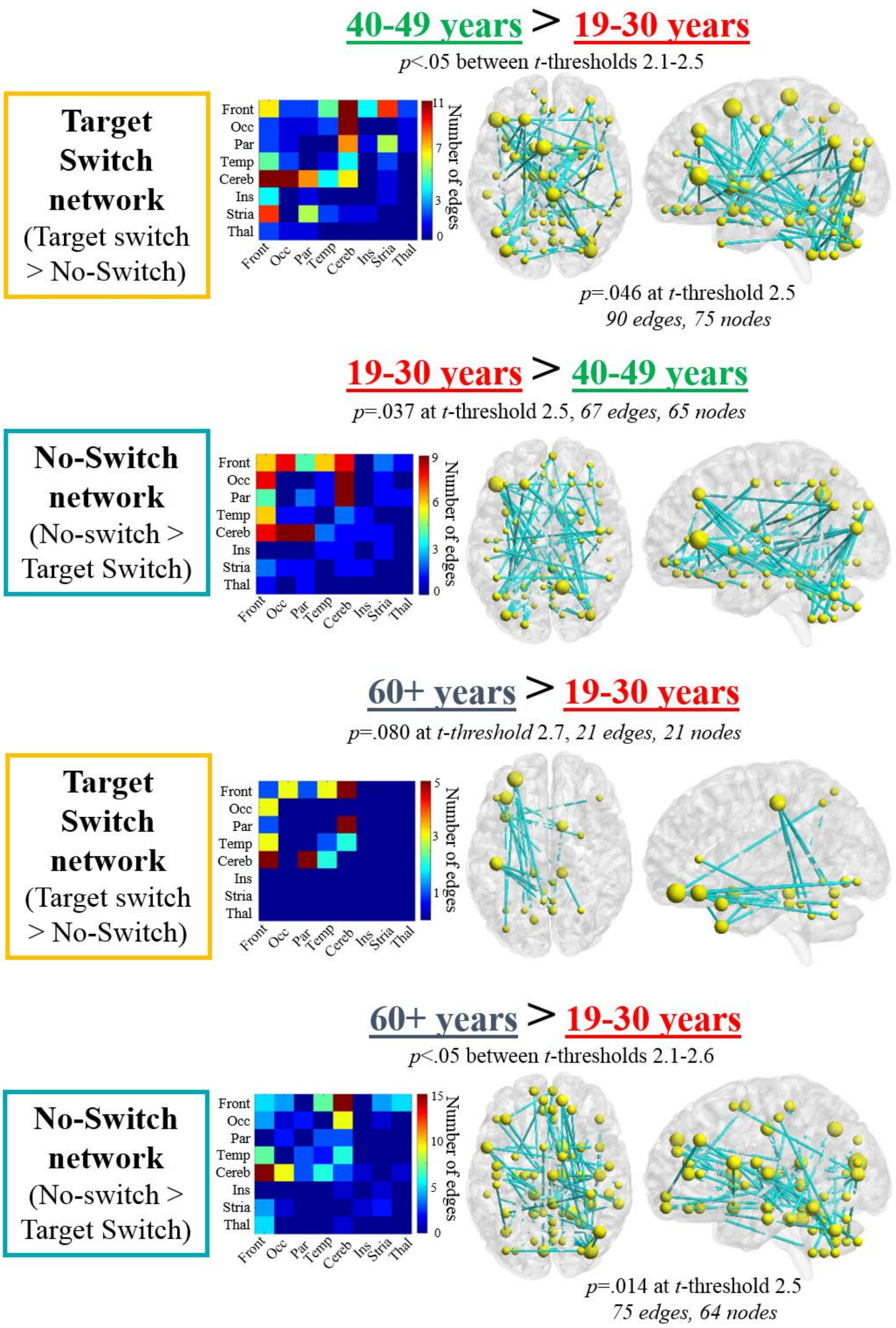

Figure 3.7. NBS results exploring the interaction between Target Switch condition and age group in theta (3-5Hz) connectivity (wPLI) between 0.55-1.55s. Group comparisons of Target Switch (Target Switch > No-Switch) networks (top and third rows) and No-Switch (No-Switch > Target Switch) networks (second and bottom row). Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria) and thalamus (Thal). Note that the number of connections in each network vary and so the scales of matrix plots differ.

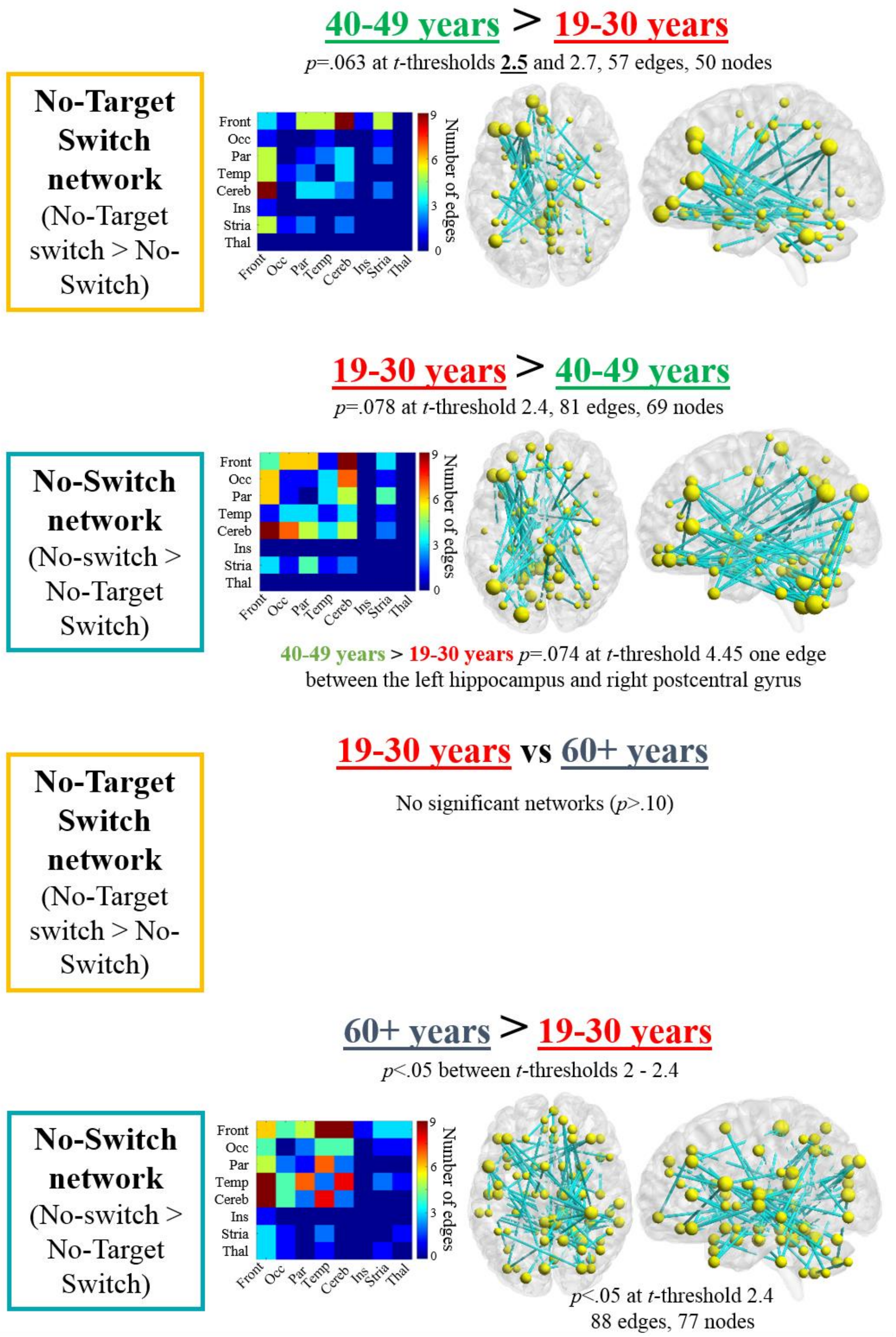

Figure 3.8. NBS results exploring the interaction between No-Target Switch condition and age group in theta (3-5Hz) connectivity (wPLI) between 0.55-1.55s. Group comparisons of Target Switch (No-Target Switch > No-Switch) networks (top and third row) and No-Switch (No-Switch > No-Target Switch) networks (second and bottom row). Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria) and thalamus (Thal). Note that the number of connections in each network vary.

The 60+ years group displayed more widely distributed theta networks (including Target Switch > No-Switch, No-Switch > Target Switch and No-Switch > No-Target Switch networks) than the 19-30 years group, particularly in frontal and temporal regions and the cerebellum. These findings are consistent with the additional recruitment of temporal and frontal regions that was seen in theta source statistics, and could reflect older participants relying more on top-down attentional control from the frontal lobe to cope with task demands (Badre & Wagner, 2004; Baluch & Itti, 2011; Bouvier, 2009; Kastner & Ungerleider, 2000; Kerns et al., 2004). These findings support compensatory models of ageing (Davis et al., 2008; Madden, 2007), rather than more widely distributed activity being a result of increased neural noise (Shih, 2009; Welford, 1981). If activity seen in additional regions was merely due to increased noise in the network, one would expect weaker connectivity between nodes in the 60+ years group in comparison to the 19-30 years group, which is contrary to our findings.

The 40-49 years group also showed more widely distributed theta networks than the 19-30 years group when there was increased attentional demands in the two Switch conditions, as can be seen in Figures 3.7 and 3.8 (top row), particularly between frontal nodes and temporal and parietal regions and between the cerebellum and frontal parietal and temporal regions. Again it could be that this is reflecting compensatory recruitment. In the No-Switch networks, however, the 40-49 years group showed weaker connectivity in comparison to the 19-30 years group (second row Figures 3.7 and 3.8). It should be noted that there was no significant difference in RT overall between the 19-30 and 40-49 years groups. It could be that this weaker connectivity is reflecting an initial decline in attentional networks that is not yet seen in behaviour, and therefore not yet compensated for with an increase in top-down attentional control.

Alpha network connectivity

NBS results (alpha network connectivity) investigating the RSVP condition (Target Switch/No-Switch) × age interaction are presented in Figure 3.9, and investigating the RSVP condition (No-Target Switch/No-Switch) × age interaction are presented in Figure 3.10.

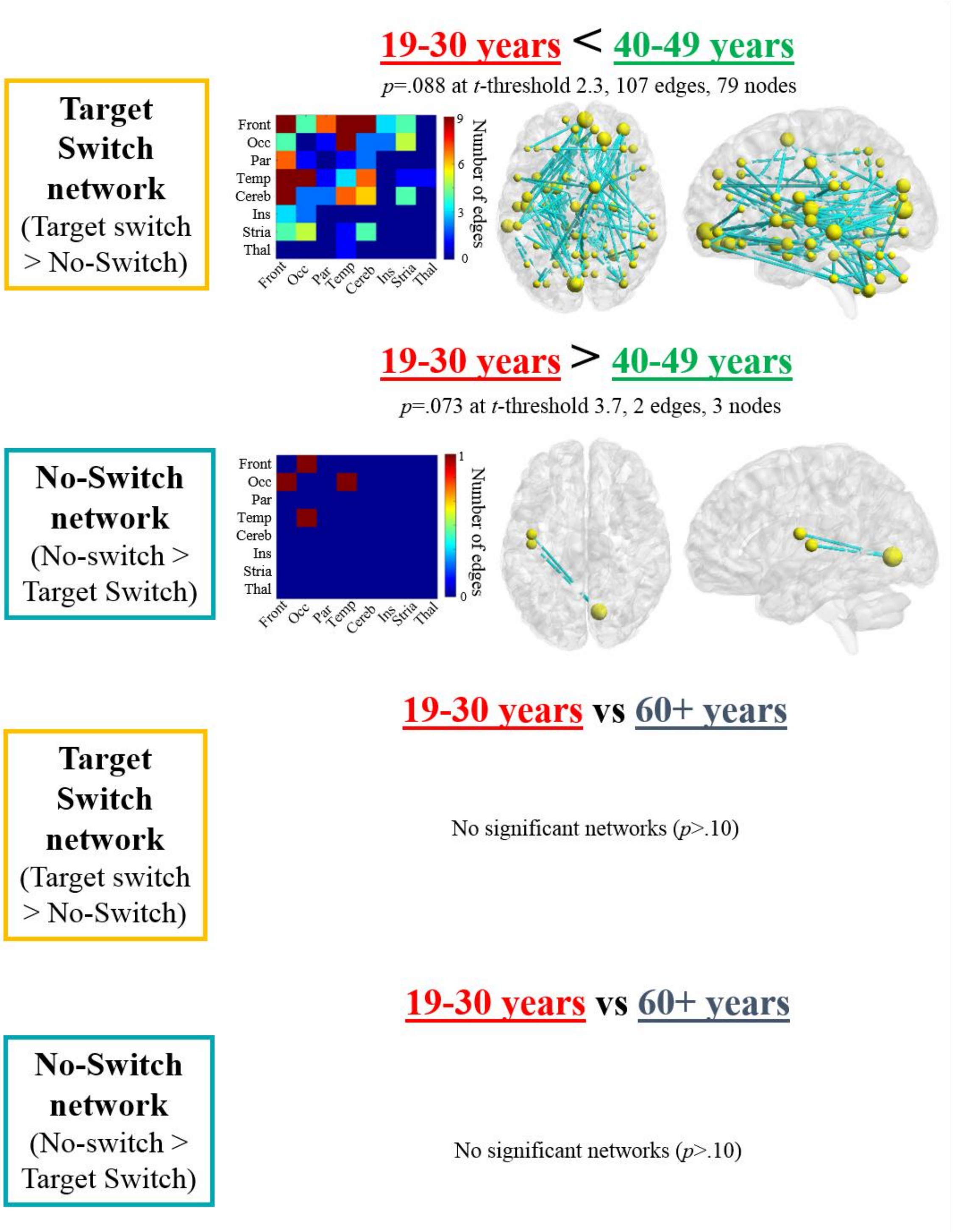

Figure 3.9. NBS results exploring the interaction between Target Switch condition and age group in alpha (10-14Hz) connectivity (wPLI) between 0.45-0.95s. Group comparisons of Target Switch (Target Switch > No-Switch) networks (top and third row) and No-Switch (No-Switch > Target Switch) networks (second and bottom row). Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria) andthalamus (Thal). Note that the number of connections in each network vary and so the scales of matrix plots differ.

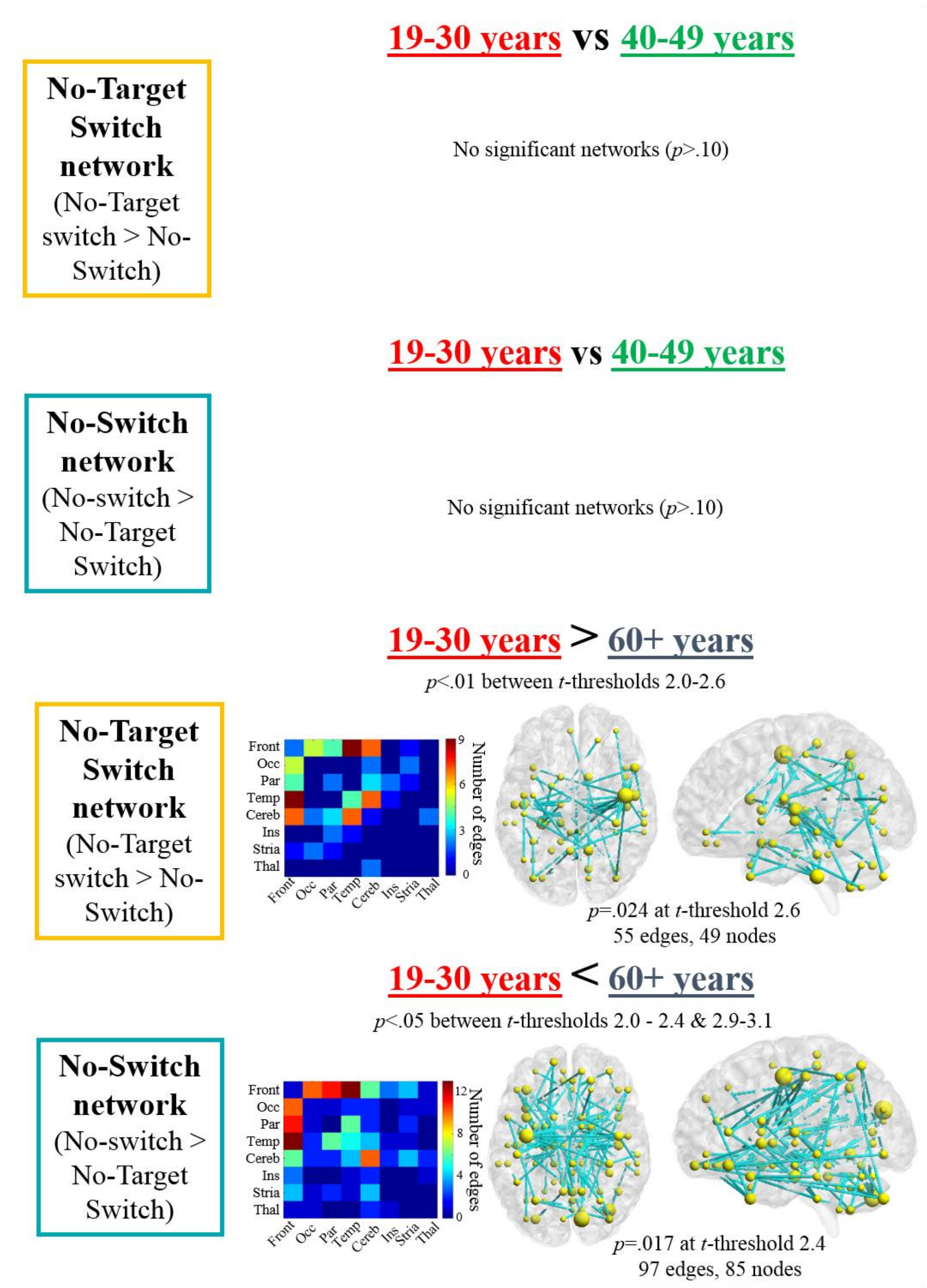

Figure 3.10. NBS results exploring the interaction between Target Switch condition and age group in alpha (10-14Hz) connectivity (wPLI) between 0.45-0.95s. Group comparisons of No-Target Switch (No-Target Switch > No-Switch) networks (top and third row) and No-Switch (No-Switch > No-Target Switch) networks (second and bottom row). Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria) and thalamus (Thal). Note that the number of connections in each network vary and so the scales of matrix plots differ.

Similar to the pattern of connectivity in theta band, the 40-49 years group showed weaker connectivity in comparison to the 19-30 years group in the No-Switch network (No-Switch > Target Switch; Figure 3.9 second row), but more widely distributed networks than the 19-30 years group when there was increased attentional demands in the Target Switch network (Figure 3.9 top row). Increased connectivity was particularly seen between frontal nodes and temporal regions and the cerebellum and between temporal and occipital nodes. Again it could be that this is reflecting compensatory recruitment.

There were no significant differences between the 19-30 and 60+ years groups when contrasting Target Switch and No-Switch networks (*p*>.10). The 19-30 years group displayed significantly greater No-Target Switch connectivity in comparison to the 60+ years group, particularly to frontal nodes and temporal nodes and to the cerebellum. Together these findings suggest that the observed increases in alpha power modulation may reflect increased neural noise (Shih, 2009; Welford, 1981) and dedifferentiation (Cabeza, 2002) rather than compensatory recruitment (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007). However the 60+ years group displayed greater No-Switch connectivity (No-Switch > No-Target Switch) in comparison to the 19-30 years group, between frontal nodes and occipital, parietal and temporal nodes.

There were no significant differences between the 19-30 and 40-49 years groups when contrasting Target Switch and No-Switch networks (*p*>.10).

Minimum Spanning Tree (MST) analysis

To explore age group differences in the topology of Switch and No-Switch networks MSTs were formed from alpha and theta wPLI matrices for each RSVP condition for each age group. MSTs were made of 116 nodes corresponding to the 116 AAL atlas regions. A list of the 116 nodes can be found in Table A3.1.1 in Appendix 3.1.

Local MST metrics, degree, betweenness centrality and eccentricity were computed for each node in each MST. To investigate the main effect of RSVP condition on network centrality (i.e. degree, betweenness centrality and eccentricity) of all nodes, *t*-tests were implemented to compare each of the Switch conditions with the No-Switch condition separately for each age group. Results can be found in Figure A3.6.1 in Appendix 3.6. To explore the interaction between RSVP condition and age, the difference in each local metric (degree, betweenness centrality and eccentricity) between each of the Switch conditions and the No-Switch condition, was compared across age groups. This protocol corresponds to the analysis procedure implemented to compare age groups in sensor power, source power and NBS. Differences between conditions in local MST metrics were then entered into permutation t-tests. The local MST metric analyses results are presented in Appendix 3.6.

Global MST metrics leaf fraction and mean eccentricity were computed for each MST both for theta and alpha MSTs. Separately for theta and alpha MSTs, two 3×3 (age group × RSVP condition) ANOVAs were performed on leaf fraction and mean eccentricity, to investigate the effects of age and RSVP condition on network topology.

There were no significant effects of age or RSVP condition, and no interactions between age and RSVP condition on either mean eccentricity or leaf fraction ($p>.10$) in theta MSTs, which indicates that the topology of a theta driven network is similar across age groups and RSVP conditions. Group means of mean eccentricity and leaf fraction in theta MSTs are presented in Figure A3.5.1 Appendix 3.5. Group means of mean eccentricity and leaf fraction in alpha MSTs are presented in Figure 3.11.

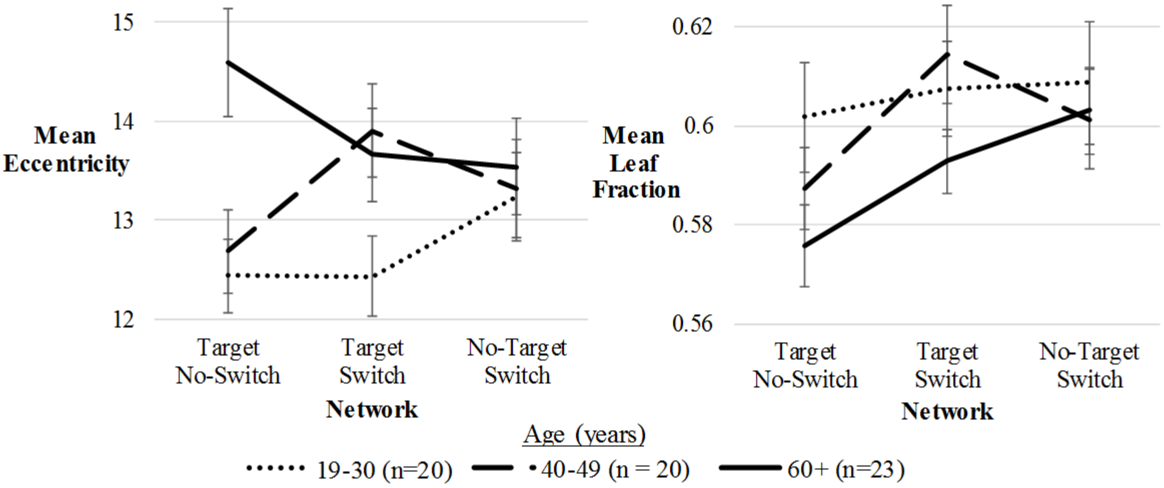

Figure 3.11. Group means of global alpha MSTs' metrics mean eccentricity (left) and leaf fraction (right) for networks in each RSVP condition. Vertical bars represent the SE.

Mean eccentricity

The RSVP condition × age group ANOVA on mean eccentricity in alpha MSTs revealed no significant main effect of RSVP condition ($p>.10$), however revealed a significant main effect of age ($F(2,60)=3.77$, $p=.029$, $\eta^2_p=.11$) and a significant interaction between age and RSVP condition ($F(4,120)=2.73$, $p=.032$, $\eta^2_p=.08$).

Post-hoc comparisons revealed that the 19-30 years group had significantly lower eccentricity in comparison to the 60+ years group ($p=.024$). There were no other significant age group differences in mean eccentricity. Shorter overall path lengths in the 19-30 years group in comparison to the 60+ years group indicates stronger connectivity on a local level rather than a longer range network (Tewarie et al., 2015).

To further explore the interaction between age and RSVP condition, independent t-tests were carried out to compare groups on mean eccentricity in each of the RSVP conditions separately. Independent t-tests revealed that the overall pattern of eccentricity mirrors age group differences in RTs and Switch-Costs. The 19-30 and 40-49 years groups did not significantly differ in the No-Switch condition in mean eccentricity (*p*>.10) and overall did not differ in RT, whereas the older group showed both significantly slower RTs (*p*<.001) and higher eccentricity than both the 19-30 (*t*(41)=-3.18, *p*=.003) and 40-49 (t(41)=-2.75, *p*=.009) years groups. In the Target Switch condition both the 40-49 (*t*(38)=-2.39, *p*=.022) and 60+ years (*t*(41)=-1.94, *p*=.059) groups show higher eccentricity in comparison to the 19-30 years group, as well as higher Switch-Costs in RT (the statistics for which are reported in Section 3.1.4: 'Attention switching task RTs'). In the No-Target Switch condition the 40-49 years and 60+ years groups show no significant differences in Switch-Costs in comparison to the 19-30 years group, and show no significant difference in mean eccentricity (*p*>.10).

There were no significant correlations between participants' mean eccentricity and Switch-Costs for any age group (*p*>.10).

Leaf fraction

As shown in Figure 3.11 (right), the RSVP condition × age group ANOVA on leaf fraction revealed a significant main effect of RSVP condition (*F*(2,120)=3.97, *p*=.021, η^2_p=.06). There was no significant main effect of age, and no significant interaction between age and RSVP condition on leaf fraction (*p*>.10). Post hoc comparisons revealed that leaf fraction was lower in the No-Switch condition in comparison to both the Target Switch (*p*=.023) and No-Target Switch (*p*=.075) conditions, although the latter failed to reach significance. Higher leaf fraction in the two Switch conditions implies that networks are characterised by efficient connectivity directly between nodes, indicating local connectivity, rather than a network characterised by chain-like, long range connectivity (Tewarie et al., 2014; Tewarie et al., 2015).

3.1.5 Discussion

In Chapter 2 we demonstrated that older adults find refocusing attention from time to space more difficult than younger adults (Callaghan et al., 2017). In the current chapter we replicated these results and found that the 40-49 and 60+ years groups had increased Switch-Costs in comparison to the 19-30 years group as reflected by disproportionally increased RTs when required to refocus attention from a temporal RSVP task to a spatial VS task. The primary aim of the current chapter was to investigate the age-related changes in neural mechanisms that may underlie this age-related difficulty in refocusing attention from events changing in time to stimuli distributed spatially.

Also consistent with Chapter 2, the 60+ years group's RTs were overall slower in comparison to the 19-30 years group. On the other hand, the 40-49 and 19-30 years groups' RTs did not significantly differ, implying that the 40-49 years group found the baseline No-Switch condition no more demanding than younger adults. However, they presented significantly higher Switch-Costs than the 19-30 years group, suggesting that they found the Target Switch condition disproportionality more demanding than the No-Switch condition, contrasting with the 19-30 years group. The 40-49 years group therefore seem to present an intermediate stage of ageing, where some aspects of attentional control are affected very little by age and participants function at a similar level to younger adults, whereas other aspects of attentional control are already affected by age and RTs and neural mechanisms coincide more with patterns observed in older adults. This general pattern was mirrored in both NBS and MST functional connectivity data in both theta and alpha frequencies and is discussed in further detail below, as well as in the Appendix 3.6 in regards to local MST metric eccentricity.

Conforming to our hypotheses based on previous reports (Cummins & Finnigan, 2007; Deiber et al., 2013; Vaden et al., 2012; van de Vijver et al., 2014), we indeed observed modulations of theta and alpha oscillatory power at sensor level as well as in source space. The hypothesis that there would be reduced theta power was supported. The enhanced spatial resolution of MEG compared to EEG warranted further analysis in source space, which revealed that reduced theta power localised to occipital and parietal regions. Instead of a reduction in frontal midline theta power, as proposed by previous literature, increased frontal midline theta was observed with increased age, particularly in the 40-49 years group. Findings were consistent with hypotheses of increased frontal theta activity reflecting additional compensatory processing (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007), particularly supporting the PASA compensation hypothesis of ageing (Davis et al., 2008). As anticipated, there were age-related changes in task related alpha modulation, where the oldest age group failed to show an alpha increase to inhibit irrelevant visual information (Vaden et al., 2012) and instead showed a stronger and widely distributed alpha desynchronization. The middle-aged group presented a similar pattern to the older group, with a weaker alpha increase in comparison to younger adults and a stronger and more widely distributed alpha modulation across the cortex. Thus, both theta and alpha signatures revealed widely distributed processing networks in older participants, with a stronger propensity towards frontal involvement compared to the youngest group. Overall, our study therefore both observed deficiencies in processing in the older groups that are in part related to behavioural Switch-Costs and supports compensatory notions of oscillatory aberrations that have been observed in the context of age-related functional decline (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007). In the following sections we will discuss various aspects of our results in more detail, before reaching final conclusions.

Theta power and network connectivity

As shown in Figure 3.3 and 3.4, the 40-49 and 60+ years groups appear to have a theta deficit in comparison to the 19-30 years group. The 19-30 years group showed higher Target Switch related theta in parietal regions in comparison to the two older age groups. Reduced parietal activity in older compared to younger groups contrasts with Cabeza et al.'s (2004) findings of increased posterior parietal activity. Posterior parietal activity is usually observed during enhanced attention (Coull and Nobre, 1998; Li et al., 2013; Madden et al., 2007; Shapiro et al., 2002). However this increase seems to be related to RSVP target processing rather than refocusing attention, as no significant difference in theta was seen between No-Target Switch and No-Switch conditions in the 19-30 years group. It could be that this parietal theta increase in younger adults reflects enhanced attention directed towards the RSVP target and RSVP target processing (Imaruoka et al., 2003).

In addition to a deficit in target processing related theta, both the 40-49 and 60+ years groups showed significantly lower occipital and cerebellar theta in both Switch conditions (compared to the No-Switch condition), a difference that was not present in the 19-30 years group. It could be that posterior theta deficits in the two Switch conditions are linked to age-related increases in VS RTs in these conditions, a notion that is supported by the correlation between increased Switch-Costs and reduced cerebellar theta power in the 60+ years group. Furthermore, there was a trend towards decreased network node centrality (measured as local MST measure betweenness centrality), in the right occipital gyrus in the 60+ years group in comparison to the 19-30 years group (see Appendix 3.6 for details). Reduced activity in the occipital lobe is consistent with previous findings of age-related reductions in visual cortex activity during visual processing (Davis et al., 2008; Huettel et al., 2001; Madden et al., 2002; Ross et al., 1997).

Current findings were consistent with the recruitment of additional cortical regions with increased age (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007). Despite the theta deficit in the occipital lobe, the 60+ years group showed significantly higher frontal and temporal theta power in the two Switch conditions in comparison to the No-Switch condition, and the 40-49 years group showed higher frontal theta power in the Target Switch condition compared to the No-Switch condition (Figures 3.3 and 3.4). These findings were corroborated by more extensive theta connectivity in the 60+ years group in comparison to the 19-30 years group, across almost all conditions, reflected in NBS results, particularly in frontal and temporal regions and the cerebellum. The 40-49 years group also showed more extensive connectivity than the younger group in the two Switch conditions, again predominantly between frontal, temporal and parietal regions, as well as the cerebellum. Additional recruitment of frontal regions could reflect compensatory recruitment of top-down mechanisms to bias attention (Hopfinger, Buonocore, & Mangun, 2000). The additional temporal lobe activity in the 60+ years group on the other hand could reflect further compensatory strategies to complete the task, such as episodic memory encoding (Schacter & Wagner, 1999) or silent vocalisation (Graves et al., 2007; Hickok & Poeppel, 2007; Hocking & Price, 2009; Smith et al., 1998). Increased frontal theta with increased age contrasts with Cummins and Finnigan's (2007) findings of reduced theta in frontal electrodes, and instead support compensatory models of ageing such as PASA (Davis et al., 2008). Increased theta functional connectivity with increased age also opposes the notion that more widely distributed activity in the current study was a result of increased neural noise (Shih, 2009; Welford, 1981). If activity seen in additional regions was merely due to increased neural noise, one would expect weaker connectivity in the 60+ years group in comparison to the 19-30 years group rather than increased phase synchronisation, which is not the case (Figures 3.7 and 3.8). Additional evidence for compensatory recruitment of temporal cortex in the 60+ years group comes from a correlation between Switch-Costs and increased network centrality of the left middle temporal pole (as reported in the Appendix 3.7), suggesting that those participants with stronger connectivity to the temporal pole have lower Switch-Costs. Furthermore, as theta power in the frontal lobe increased, Switch-Costs decreased in the 60+ years group.

The "middle-aged" group (40-49 years) represents an interesting case that presented characteristics set between the youngest and the oldest groups, with some patterns being closer to the younger and some patterns being closer to the older group. This was discussed in the context of RTs, where 40-49 years group did not differ significantly overall from the youngest group, yet showed increased Target Switch-Costs. For instance, theta connectivity was weaker in the 40-49 years group in comparison to the 19-30 years group for networks that were stronger when No-Switch was required (Figure 3.7 and 3.8 second row). However, connectivity was increased in the 40-49 years group in comparison to the 19-30 years group in a frontal, temporal, parietal and cerebellar network, when a Switch was required (Figure 3.7 and 3.8 top row). Weaker connectivity could reflect the start of a decline in attentional networks that is not yet seen in behaviour, and therefore not yet compensated for with recruitment of additional top-down mechanisms that are only recruited when attentional demands increase. Furthermore, several nodes were more central in the No-Target Switch network in the 40-49 years group in comparison to the 19-30 years group (see Appendix 3.6). Importantly, as the network centrality of these nodes increased across individuals, Switch-Costs in the 40-49 years group decreased (see correlations reported in Appendix 3.7), further supporting the compensatory role of this additional recruitment.

Both 40-49 and 60+ years groups displayed increased connectivity to the cerebellum reflected in both theta NBS results (Figures 3.7 and 3.8) and node centrality measures reported in Appendix 3.6. The role of the cerebellum in cognitive processing is still poorly understood, but recent reviews suggest that the cerebellum monitors and regulates cortical processing (Rao, Mayer, & Harrington, 2001), especially when timing is required (Keren-Happuch, Chen, Ho, & Desmond, 2014). This could be crucial in the current context for sustaining temporal attention and for a timely switch to spatial attention. Increased connectivity between the cortex and the cerebellum in older groups could therefore be due to a greater need to regulate and time cortical activity as excitatory mechanisms across the cortex are less efficient (Shih, 2009). However, cerebellar activity should be interpreted with caution due to it being close to the edge of the MEG sensor array; hence, such activity could be due to spatial leakage from occipital generators.

Alpha

In addition to age group differences in theta networks, prior to switching to attend to the VS, modulations of alpha power were both stronger and more widely distributed across the cortex in the 40-49 and 60+ years groups in comparison to the 19-30 years group (Figures 3.5 and 3.6). In contrast to these power changes, there was no significant difference between the 19-30 and 60+ years groups in alpha connectivity for the Target Switch network (Figure 3.9). Furthermore, the 19-30 years group recruited a more widely distributed No-Target Switch network than the 60+ years group (Figure 3.10). These two results seem inconsistent with source power and could suggest that the widely distributed alpha power in the 60+ years group reflects increased neural noise rather than compensation. This conclusion would support Vaden et al.'s (2012) proposal that alpha modulation becomes redundant with increased age, and is further supported by the absence of a correlation between alpha power (difference) and Switch-Costs in the 60+ years group. It can be seen from the TFRs in Figure 3.5 that the older groups exhibited greater alpha power decreases in comparison to the younger group. Rather than increased neural noise it could therefore be that group differences in mere signal amplitude (much lower in the 60+ years group than in the 19-30 years group) or signal-to-noise ratio (SNR) resulted in a less sensitive estimation of connectivity in the 60+ years group in comparison to the 19-30 years group.

Contrary to the non-significant relationship between Switch-Costs and alpha modulation in the 60+ years group, in the 40-49 years group Switch-Costs increased with increased alpha power differences in the left paracentral lobule, suggesting that high alpha power preceding the VS results in inefficient switching. This pattern is consistent with literature that demonstrates that pre-stimulus alpha desynchronisation predicts successful target stimulus processing (Sauseng et al., 2005). In contrast, Switch-Costs decreased as occipital and right MFG power change increased. It could be that power changes in the occipital lobe and MFG reflect efficient inhibition of distractor stimuli leaving more processing resources available to switch to distributing attention spatially, whereas alpha desynchronization in the paracentral lobule reflects preparation of task set information and attention. Previous literature has shown that prestimulus alpha desynchronization no longer predicts successful stimulus processing in older age (Deiber et al., 2013) as it does in younger adults (Sauseng et al., 2005). The current findings call into question whether pre-stimulus alpha desynchronisation predicts successful target stimulus processing in middle-age. Questions also arise as to how alpha is functionally relevant in older age, and what alternative mechanisms are implemented to gate sensory processing (Jensen & Mazaheri, 2010) and enhance attention to visual stimuli (Capotosto et al., 2009; Hanslmayr et al., 2007; Hanslmayr et al., 2005; Klimesch et al., 2007; Sauseng et al., 2005; Thut et al., 2006; Yamagishi et al., 2003) if not alpha oscillations.

Alpha network connectivity in the 40-49 years group provides further evidence that this age group reflects an intermediate stage of ageing, where in some aspects they are similar to younger adults and in some aspects they are closer to older adults. For example, similarly to patterns observed in theta network connectivity, the 40-49 years group showed a wider distributed alpha network than the 19-30 years group in the Target Switch network (Figure 3.9 top row), but a weaker alpha network than the 19-30 years group in the No-Switch network. In contrast, comparisons of the No-Target Switch and No-Switch conditions revealed no significant network differences between 40-49 and 19-30 years groups, consistent with no significant behavioural differences in No-Target Switch-Costs. From these findings it therefore seems that there is no effect of age on alpha power modulation at the age of 40-49 years during monitoring of the RSVP stream when there is no target present, but there is more extensive alpha connectivity compared to the younger group when target processing and switching after target processing is required.

The pattern of similarity between the 40-49 and 19-30 years groups in the No-Switch condition, but significant differences between these groups in the Target Switch condition was again mirrored in the global MST metric of mean eccentricity (Figure 3.11). In contrast to the 60+ years group the 40-49 and 19-30 years groups did not significantly differ in mean eccentricity in the No-Switch condition. However, in the Target Switch condition, both of the older groups showed significantly higher mean eccentricity in comparison to the youngest group, indicating on average longer path lengths between nodes, which could be tied to recruitment of larger, less focal networks. Thus, alpha network measures corroborate the recruitment of compensatory networks despite alpha connectivity age group differences reflected in NBS (60+ vs 19-30 years; Figure 3.10) potentially suggesting increased neural noise.

3.1.6 Conclusions

We have replicated the findings of Chapter 2 and Callaghan et al. (2017), observing age-related declines in the ability to switch between temporal and spatial attention. Difficulties in refocusing attention between time and space seem to be accompanied by a deficit in lower theta frequency in occipital and cerebellar regions. Older and middle-aged adults seem to partially compensate for this posterior theta deficit by recruiting a more extensive frontal network, possibly reflecting increased reliance on top-down attentional control. In addition to more extensive frontal recruitment, the 60+

years group showed recruitment (in both power and connectivity) of the temporal lobes, possibly reflecting further compensation strategies such as episodic memory encoding or silent vocalisation. Contrary to the notion of functional connectivity becoming weaker with age due to increased neural noise, increased connectivity was predominantly observed in older age groups, particularly at theta frequency and with increased attentional demands in the Switch conditions. This increase in connectivity further corroborates that more widely distributed activity reflects compensatory mechanisms. Stronger and more extensive alpha band power was found across the cortex with increased age. In contrast to theta oscillations, alpha power modulations were not correlated with Switch-Costs and functional connectivity was not stronger with increased age, signifying that increases in the extent of power modulation could merely be neural noise. Further research is required to explore this further as group differences in SNR could have affected alpha connectivity estimates.

Chapter 4

Age-related changes in refocusing attention from temporal to spatial attention when driving

4.1 Driving Simulator Experiment

4.1.1 Chapter aims

The series of experiments presented in Chapter 2 demonstrated an age-related decline in the ability to refocus attention from attending to events changing in time to distributing attention spatially. In Chapter 3, MEG was recorded while participants completed the attention switching paradigm, enabling the investigation of age-related changes in neural mechanisms that may underlie difficulties in switching between temporal and spatial attention that are seen with increased age. Further work is required to explore how age-related declines in switching translate to driving behaviour. It may be that difficulties in switching between temporal and spatial attention cause difficulties in switching from attending to traffic on the road ahead to attending to road signs and other surrounding objects. If difficulties in switching are found to affect driving performance, it will be important to develop an intervention to improve switching between modalities of attention to help to improve driver performance and safety. This will have the long-term benefit of prolonging the time that older drivers can continue to drive and help to preserve their independence.

The aim of the current chapter was to investigate whether age-related changes in the ability to switch between temporal and spatial attention that were observed in Chapter 2 are also observed during simulated driving. Age groups were compared on their ability to switch from allocating attention in time, where participants must attend to the fast changing traffic in front of them, to allocating attention spatially, in order to complete a VS of a road sign (the target city name “Birmingham” was embedded within 11 other city names). In Dual-Task Switch trials, the road sign VS task was preceded by a “braking event” task, where participants were required to brake in response to a car suddenly pulling in front of them from the over-taking lane and braking. Shortly after the braking event, participants were required to refocus their attention spatially in order to complete the road sign VS that appeared either a further 3.04m (~142ms; Immediate Switch) or a further 30.48m (~1420ms; Delayed Switch) in front of the driver. This sequence of events is evident in Figure 4.2 A, which pictures the participant shortly after the braking event, from which the vehicle is still visible, and shortly after the road sign onset. In “Single-Task” trials the road sign VS task was carried out without a preceding braking event task. It is important to note that due to the interval between the braking event and the road sign being specified in distance in Dual-Task trials, the time delay between the braking event and the road sign varied with participants’ driving speeds. RTs to indicate either left or right in response to the road sign were recorded. Note that the Single-Task condition still involved an attention switching element, where participants attended to the road ahead before switching to attend to the road sign. However, Dual-Task trials were expected to require a heightened effort to refocus attention due to a greater enhancement of attention towards temporal events (i.e. towards braking). It was therefore hypothesised that RTs to indicate in response to the road sign would be slower when the sign was preceded by a braking event (1st task) in the two Dual-Task conditions, in comparison to when the sign appeared without a preceding braking event task in the Single-Task condition. We refer to this slowing of RTs in the Dual-Task conditions compared to the Single-Task condition as Dual-Task Costs. It was hypothesised that there would be an age-related decline in refocusing attention from a temporal event to spatially distributed stimuli while driving, reflected in greater increases in RTs from the Single-Task condition to both the Immediate Switch and Delayed Switch Dual-Task conditions. Although it was expected that participants would learn that a road sign would follow a braking event, the Delayed Switch condition was included to prevent participants predicting exactly when the road sign would appear. It was expected that participants' RTs would be faster on the Delayed Switch condition in comparison to the Immediate Switch condition as participants had longer to refocus attention after the braking event.

EEG was recorded in a subset of participants aged 18-30 and 60+ years as a pilot study that aimed to fulfil two main agendas. Firstly, we sought to assess the feasibility of recording EEG in the driving simulator, where data is susceptible to interference from environmental noise and movement artefacts. Previous literature has successfully recorded EEG in driving simulator environments outside of Aston University (Campagne et al., 2004; Lowden et al., 2009). Secondly, we aimed to investigate whether the oscillatory signatures observed with MEG in Chapter 3 when switching between temporal and spatial attention in a computer based task are also seen when switching between temporal and spatial attention during simulated driving. Corroborating the increased MEG theta power upon VS presentation in Chapter 3, we expected an increase in EEG theta power when the appearance of the road sign initiated VS, which could reflect top-down guided attentional control and target processing (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Demiralp & Başar, 1992; Green, Conder, & McDonald, 2008; Min & Park, 2010). Mirroring the decreased MEG alpha that was observed in Chapter 3 and signifying enhanced attention to the VS (Capotosto et al., 2009; Hanslmayr et al., 2007; Hanslmayr et al., 2005; Klimesch et al., 2007; Sauseng et al., 2005; Thut et al., 2006; Yamagishi et al., 2003), we expected alpha or beta desynchronization after the onsets of the braking event and the road sign, respectively, as attention and motor preparation (Donoghue et al., 1998; Farmer, 1998; Kühn et al., 2004; Park et al., 2013) toward stimuli is enhanced.

In Chapter 3 we found age group dependent changes in task-related MEG theta power modulation that correlated with Switch-Costs. According to the PASA hypothesis (Davis et al., 2008) and our MEG findings, an age-related decrease in posterior theta was expected to be accompanied by an increase in frontal and temporal lobe recruitment with increased age. Chapter 3's MEG findings also presented a stronger and more widely distributed alpha response which is consistent with previous findings of age-related impairments in alpha modulation (Deiber et al., 2013; Hong et al., 2015;

Pagano et al., 2015; Vaden et al., 2012). Age-related changes in alpha modulation appear to be general rather than specific to switching, as alpha modulations did not correlate with Switch-Costs.

In contrast to the PASA hypothesis (Davis et al., 2008) it has been proposed that ageing is associated with a change in strategy away from a “proactive control” strategy, which applies top-down information such as cues, towards a more “reactive control” strategy (Braver et al., 2009; Dew et al., 2012). Although this theory of ageing is supported by evidence that older adults display impaired anticipatory attention (Deiber et al., 2013; Gamboz et al., 2010; Zanto et al., 2011), it is inconsistent with the extensive literature that suggests that older participants implement top-down attentional control more than younger adults in order to compensate for a decline in lower level attention mechanisms (McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002). It could be that the strategy implemented by older participants is task dependent. For example, it may be that older participants move towards a reactive control strategy when there is more demand on cognitive resources, such as in more realistic scenarios. Further investigation is required to develop our understanding of the situations that such a change in strategy is apparent in.

Beta frequency has been implicated in visual attention and perception (Gola et al., 2012; Gola et al., 2013; Gross et al., 2004; Kamiński et al., 2012; Park et al., 2016), motor preparation, and motor response (Donoghue et al., 1998; Farmer, 1998; Kühn et al., 2004; Park et al., 2013). Whereas lower pre-stimulus alpha power improves target detection (Hanslmayr et al., 2007; Hanslmayr et al., 2005; Sauseng et al., 2005), the role of beta modulations has been less clear. Where some studies have observed a beta decrease prior to and during enhanced attention or during motor preparation (Kühn et al., 2004; Park et al., 2013; Park et al., 2016; ; Zaepffel et al., 2013) other studies have observed increased beta power in anticipation of a target stimulus (Basile et al., 2007; Gross et al., 2006) and high beta power during alertness (Kamiński et al., 2012). There is evidence to suggest that this discrepancy may depend on task difficulty, where higher beta synchronisation is observed during high task demands when stimuli require further evaluation, and greater beta desynchronization occurs when there is less demand (Park et al., 2013; Tzagarakis et al., 2010). Increased alpha power is observed during periods of sustained attention (Dockree et al., 2007; Rihs et al., 2007, 2009), likely as one inhibits irrelevant sensory information and spatial locations (Rihs et al., 2007). Similarly, increased beta synchronisation during anticipation of a target or during evaluation of stimuli could reflect inhibition of prepared motor responses and attention to sustain the current attention and motor state (Engel & Fries, 2010).

Changes in the modulation of beta frequency has been found with increased age (Christov & Dushanova, 2016; Gola et al., 2012; Gola et al., 2013; Karrasch, Laine, Rapinoja, & Krause, 2004). Christov and Dushanova (2016), for instance, found a greater beta desynchronization in comparison to younger adults in an auditory discrimination task. Similarly, in a visual attention task where participants signified whether a target was present in a visual array or not, Gola et al. (2013) found that, in contrast to younger adults and high performing older adults, low performing older adults displayed occipital beta desynchronization instead of beta synchronisation during the presentation of a cue that preceded target onset. Regarding motor preparation, Deiber et al. (2014) found reduced beta lateralisation with increased age when preparing for voluntary actions, an effect that correlated with slow RTs. It was therefore expected that age-related deficits in task related beta modulation might be present when switching from temporal to spatial attention while driving, possibly related to impaired preparatory mechanisms (Deiber et al., 2014; Gola et al., 2013).

In addition to the driving simulator task participants completed a version of the computer based attention switching task. The methods and results for this experiment are described in detail in Chapter 2, Experiment 6 (Section 2.8.2). The task was designed to better mirror aspects of attention implemented while driving, i.e. by attending to events changing in time and responding to them (temporal attention), followed by distributing attention spatially and making decisions about information in the environment (spatial attention). Participants switched from identifying a target digit in an RSVP stream to identifying a target letter (K) in the VS display. Participants were required to respond to the detection of the RSVP target digit with a speeded spacebar response, similar to a driver braking in response to identifying an event on the road ahead. Participants were required to make a two choice left-right response to the VS display to signify whether the target was on the left or right of the visual hemifield, similar to a driver signalling left or right with their indicators after reading a road sign. To manipulate the cost of switching, the position of the target in the RSVP stream that preceded the VS was either the first item in the stream (No-Switch condition) or the target was either the seventh, eighth or ninth item in the stream (Target Switch condition) or absent from the stream. To allow time for older participants to respond to the RSVP target, a blank grey screen was presented between the RSVP stream and the VS display and remained on the screen for 1800ms or until the participant responded with a spacebar press. The condition in which the target was absent from the stream therefore behaved as a No-Switch (No-Target No-Switch) condition, as the participant had 1800ms to prepare to refocus their attention to the VS. Implementing a computer based attention switching paradigm in the same participants as the driving simulator task allowed us to evaluate how well the computer based attention switching task relates to attention switching performance while driving.

To provide a better understanding of the cognitive processes underlying switching from temporal to spatial attention in an ecologically valid setting, the relationships between certain cognitive abilities and Dual-Task Costs while driving were explored. As mentioned in Chapter 1, the ability to inhibit irrelevant information deteriorates with increased age (Hasher & Zacks, 1988). In Chapter 2

Experiment 3 we failed to observe well documented executive functioning inhibitory deficits in older adults with the RNG task (Van der Linden et al., 1998). In the current chapter, the Stroop task was instead implemented to assess inhibition (Coubard et al., 2011; Stroop, 1935). Healthy older adults have previously demonstrated exaggerated Stroop interference (Coubard et al., 2011; Verhaeghen & Cerella, 2002). Several measures of the Cambridge Neuropsychological Test Automated Battery (CANTAB) were implemented, including Simple Response Time (SRT) and Choice Response Time (CRT) tasks to obtain standardized measures of RTs, the Attention Switch Task (AST), to obtain a standardized measure of attention switching, and the Rapid Visual Presentation (RVP) task, to obtain a standardized measure of sustained attention and updating. The CANTAB is a set of standardized neuropsychological measures that have been developed for assessing cognition in the elderly (Robbins et al., 1994).

To explore how age-related declines in refocusing attention between time and space might affect self-perceived driving behaviour, participants completed the Driving Behaviour Questionnaire (DBQ), from which we analysed subscales that measure frequency of errors and attentional lapses while driving.

4.1.2 Methods

Participants

Participants completed Experiment 6 of Chapter 2 and the current driving simulator study as part of the same study and so participants have previously been described in Chapter 2 Section 2.8.2. To reiterate, 128 participants in five age groups (18-30, 40-49, 50-59, 60-69, and 70+ years) participated. All participants had a full driving license, had experience driving in the UK and had driven in the last year. The 18-30 years group were used as a comparison group for age-related cognitive changes for all other groups and the 40-49 and 50-59 years groups behaved as middle-aged comparison groups for the 60-69 and 70+ years groups. Participants with photosensitive epilepsy or visual impairments were excluded from participation, in addition to those who scored equal to or less than the 87 cut-off for possible cognitive impairment on the ACE-3 (Noone, 2015).

Participants from Experiment 3 and the MEG study described in Chapter 3 were invited to take part. Additional participants in the 21-30 and 40-49 years groups were recruited from Aston University staff and students and the community. The remaining participants aged over 60 years were recruited from the ARCHA panel. Participants received £7.50 towards their travel expenses. All participants provided written informed consent before participating. The research was approved by Aston University Research Ethics Committee.

Two participants from the 70+ years group scored equal to or lower than the 87 cut-off on the ACE-3 (Noone, 2015) and were therefore excluded from further analyses. The remaining participants' demographics are presented in Table 4.1. Note that the same table was previously displayed in Chapter 2 Table 2.8.

Table 4.1. Participant demographics

		Age Group (years)				
		18-30 (n=34)	40-49 (n=22)	50-59 (n=24)	60-69 (n=25)	70+ (n=21)
Age (years)	Mean	21.21	44.05	54.96	64.96	75.10
	SD	3.36	3.08	2.56	2.82	4.44
Gender	Male	10	9	7	16	9
	Female	24	13	17	9	12
Handedness	Right	30	19	22	23	21
	Left	4	2	2	2	0
ACE-3	Mean	n/a	n/a	96.38	96.04	95.10
	SD	n/a	n/a	2.39	2.47	2.47

The mean age of each age group, the number of participants who are male and female, and the number of participants who are left and right handed for each age group. Mean ACE-3 scores are presented for the 50-59, 60-69, and 70+ years groups. Note that the handedness data is missing for one participant in the 40-49 years group.

Materials and procedures

Attention switching task

A full description of the attention switching paradigm can be found in Chapter 2 Sections 2.2.2 and 2.8.2. A brief overview of the task is reiterated here. Similarly to previous versions of the attention switching task, described in Chapters 2 and 3, participants switched from identifying a target digit in an RSVP stream to identifying a target letter (K) in a VS display. Participants were required to respond to the detection of the RSVP target digit with a speeded spacebar response. VS displays were always pop-out VS displays, where all the distractor stimuli were the letter 'P'. The VS target letter was always the letter 'K' and it was presented either on the left or right of the visual hemifield. Participants were required to make a two choice left-right response with the arrow keys on the keyboard to signify whether the VS target was on the left or right of the visual hemifield. Both VS RTs and RSVP RTs were recorded.

To manipulate the cost of switching, the position of the target in the RSVP stream that preceded the VS was either the first item in the stream (No-Switch condition) or the target was either the seventh, eighth or ninth item in the stream (Target Switch condition) or absent from the stream (No-Target

No-Switch condition). To allow time for older participants to respond to the RSVP target in the current task a blank grey screen was presented between the RSVP stream and the VS display and remained on the screen for 1800ms or until the participant responded with a spacebar press. In the current task the No-Target condition therefore behaved as a No-Switch condition, as there was a 1800ms delay between the RSVP offset and the VS onset. Illustrations of the RSVP stream and of the VS display are presented in Figure 4.1.

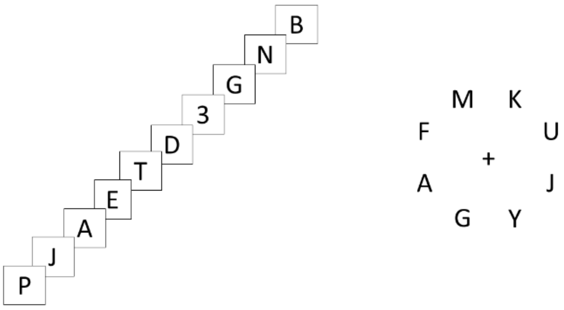

Figure 4.1. Illustration of examples of the stimuli set up. The RSVP stream illustration (left) displays a Target Switch RSVP stream. Each trial consisted of a fixation cross (2000ms) followed by an RSVP stream immediately followed by a blank grey screen (until the participant responds to the RSVP target), followed by a pop-out VS display (right). Note that the current figure was presented previously in Chapter 2 (Figure 2.10).

Driving Simulator

Participants completed a driving simulator task where they switched from allocating their attention to events changing in time (i.e. temporal attention), as they attended to the fast changing traffic on the road ahead, to distributing attention spatially, in order to complete a VS of a road sign as part of a route finding exercise.

An example of experiment setup is displayed in Figure 4.2. Participants were seated comfortably in an adjustable GT Omega Art Racing Simulator Cockpit (RS6 seat), complete with a Logitech G27 Force feedback wheel and pedal set, which incorporated a steering wheel, gear stick, clutch, brake and accelerator pedals. The indicators were paddles to the left and right of the steering wheel that participants could pull towards them to turn on and off. A manual gearstick was to the left of the participant and was programmed to go up to 5th gear. Driving simulator software STISIM Drive™ by Systems Technology Inc. was used to record driving simulator data and to render the driving simulations, which were projected at a resolution of 1280 × 1024 pixels onto three 1.30 × 2.27m projection screens at a refresh rate of 75Hz. Data were sampled at a frequency of 60Hz. The central projection screen was positioned facing the driving seat 2.2m away from the participant. To fabricate the perception of movement through 3D space, the two peripheral projection screens were positioned adjacent to the central screen, rotated 40 degrees away from the central screen towards the driving seat. The projection included a dashboard which contained a speedometer displaying miles per hour (mph) and a rev counter displaying revolutions per minute (RMP). The driving seat was surrounded by a speaker system through which engine and braking sound-effects were produced.

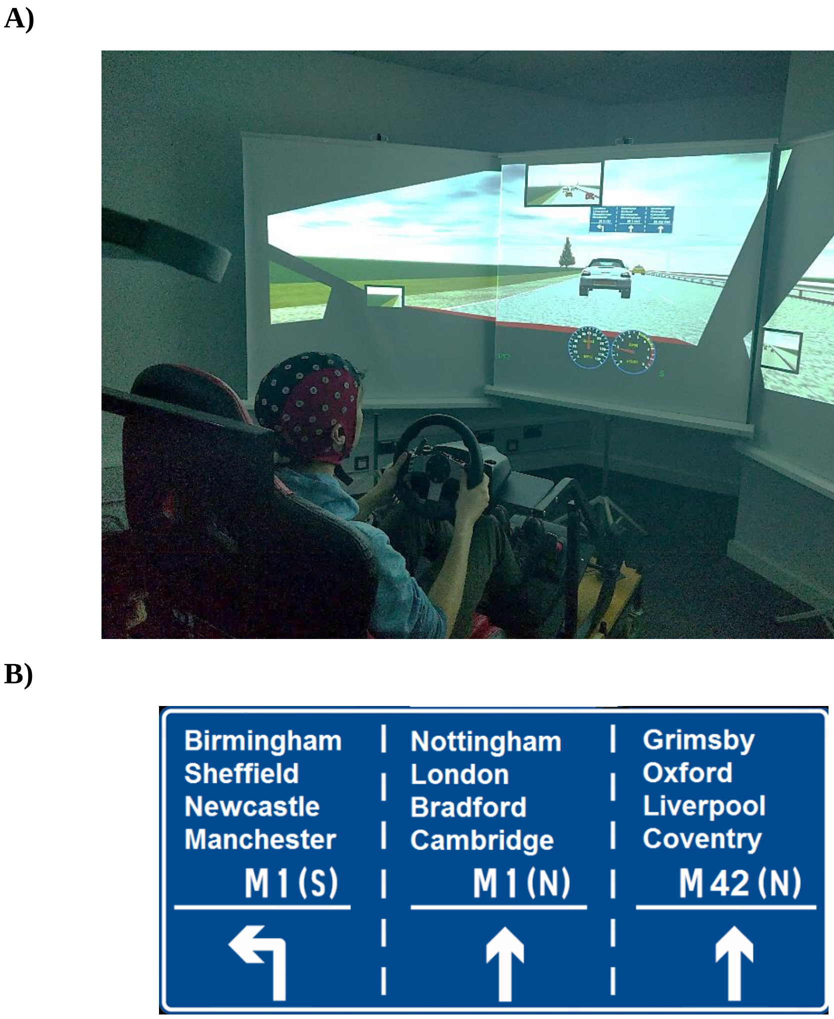

Figure 4.2. Example of A) the experiment setup, where the participant is seated in the driving simulator wearing an EEG cap, and the vehicle involved in the “braking event” is displayed on the projector screen along with the road sign; and B) the road sign stimuli: The target word “Birmingham” is in the left column, requiring a speeded left indicator response.

Participants drove on a simulated dual-carriageway. In “Dual-Task” trials, participants were required to brake in response to a car suddenly pulling in front of them from the over-taking lane. Participants were instructed to brake as quickly as possible and RTs to brake initiation were recorded. Shortly after this “braking event”, participants were required to refocus their attention spatially to complete a VS of a road sign, which appeared in front of the driver after they had travelled either another 3.04m (~142ms; Immediate Switch condition) or another 30.48m (~1420ms; Delayed Switch condition) after the braking event. In “Single-Task” trials the sign appeared without a preceding braking event. In Dual-Task trials, the delay between the braking event and the road sign was specified in distance, resulting in the time delay between the braking event and the road sign varying with participants’ driving speeds.

An example of the road sign is displayed in Figure 4.2. When the road sign appeared, participants were required to identify the location of the target word "Birmingham" and indicate left if it was in the left column, to signal that they would exit the dual-carriageway, and right if it was in either the middle column or the right hand column to signal that they would stay on the dual-carriageway. Participants were instructed to indicate as quickly and accurately as possible and indicator RTs and accuracy were recorded. The speed at which participants were travelling when the sign appeared was also recorded.

The city name "Birmingham" was chosen as a VS target word, as this was the city where the study took place and was therefore familiar to all participants. The target was embedded among 11 distractor names. The stimuli remained the same on all trials and only the order of the stimuli on the sign differed across trials. Distractor stimuli were UK city names. To avoid advantaging participants who were more familiar with certain roads than others, the order of the names on the sign was random.

On 50% of trials the target was in the left column and on 50% of the trials the target was in one of the two right hand columns. There were 36 trials in total and trials were divided into three blocks of 12 trials to provide opportunities for breaks.

Prior to beginning the task participants took part in two practice driving scenarios. In the first scenario, participants were given the opportunity to familiarise themselves with the controls of the driving simulator while driving around a virtual town. Participants continued driving in the town scenario until they felt confident with the controls, particularly with changing gear, steering and braking. The aim of the second practice scenario was to familiarise participants with the task instructions. Participants completed six practice trials of the switching task, however, trials differed from experimental trials as they contained no traffic on the road and so there were no braking events and therefore no Dual-Task switching element to the task.

To help to prevent feelings of nausea produced by the driving simulator, participants wore acupressure bands around their wrists, which have previously been shown to help to prevent simulator sickness, although through a placebo effect (Wesley & Tengler, 2005).

UFOV

Participants completed the UFOV (Ball et al., 1988) task. A description of the UFOV task can be found in Chapter 2 Section 2.5.2.

CANTAB

To obtain standardized measures cognitive processes that may influence switching performance, several CANTAB® (Cambridge cognition, 2017) measures were administered, including Simple Reaction Time (SRT), Choice Reaction Time task (CRT), Attention Switching Task (AST) and the Rapid Visual Processing (RVP) tasks. CANTAB tasks are completed on a touch screen tablet which was placed on the desk 50cm in front of the participant. Participants responded on a button response pad. Throughout each task participants were instructed to sit with their index finger(s) resting on the button ready to press and to respond as quickly and accurately as possible. On each task stimuli were presented in white on a black background. CANTAB tasks are described in brief below. Detailed descriptions and interactive examples of the tasks can be found on the manufacturer's website (Cambridge cognition, 2017).

SRT

On each trial a white square appeared in the centre of the screen. As soon as the square appeared participants pushed the button as quickly as possible. RTs were recorded. The inter-stimulus interval varied so the onset of the square was unpredictable. There were 24 practice trials followed by two blocks of 50 trials each.

CRT

On each trial a white arrow appeared either on the left visual hemifield pointing left or on the right visual hemifield pointing right. Participants were required to make a speeded response to the arrow by pressing the left button if the arrow was on the left side of the screen and the right button if the arrow was on the right side of the screen. RTs were recorded. There were 24 practice trials followed by two blocks of 50 trials each.

AST

The AST was divided into three assessment stages. On each trial an arrow appeared on the screen pointing either to the left or to the right. The arrow was positioned in the centre of the screen throughout the first practice block and on either the left or right visual hemifield throughout all remaining blocks. The direction that the arrow was pointing was either congruent or incongruent with the visual hemifield that it was presented on. Participants were required to make a speeded button press response to the arrow.

On the first assessment stage, the arrow was presented either on the left or right visual hemifield and the instruction "Which direction?" was displayed at the top of the screen before each arrow. Participants pressed the button on the press-pad corresponding to the direction that the arrow was pointing (left or right). The first assessment stage was preceded by two practice stages that were similar to the assessment stage. In the first practice stage arrows were presented in the centre of the screen and in the second practice stage arrows were presented either on the left or right visual hemifield. In the second assessment stage the instruction “Which side?” was displayed at the top of the screen before each arrow, and participants pressed the press-pad button corresponding to the visual hemifield of the arrow (left or right). On the third section of the task, either the instruction “Which direction?” or “Which side?” was displayed at the top of the screen before each arrow, and participants were required to respond according to the instruction. The instruction could be either the same (on no-switch trials) or different (on switch trials) from the preceding trial. RTs were recorded. Assessment stages 2 and 3 were also preceded by practice stages. There were 8 trials in each practice stage in assessment stages 1 and 2 and 16 practice trials in stage 3. There were 40 trials in assessment stages 1 and 2 and 80 trials in assessment stage 3. In each practice stage participants were provided with audio-feedback, where they heard a high tone after a correct response and a low tone after an incorrect response.

RVP

Participants were presented with a number (2-9) one at a time in the centre of the screen at a rate of 100 digits per minute. Participants were required to detect target sequences of three consecutive numbers and responded with a button press each time they detected a target sequence. Sequences were 2-4-6, 4-6-8 and 3-5-7. The task lasted for four minutes, which included 400 presentations, the first 100 of which were not scored. Prior to completing the assessment, participants completed two minutes of practice in which they were required to detect only sequences of 3-5-7.

Stroop

The Stroop task was implemented to obtain a measure of inhibition. Consistent with Coubard et al. (2011) stimuli consisted of three sheets of A4 paper, corresponding to three conditions, containing either 100 colour words or coloured crosses. Consistent with Coubard et al. (2011), in Condition 1 the sheet of paper contained coloured crosses. Crosses were printed in red (RGB: 255, 0, 0), blue (RGB: 0, 112, 192), green (RGB: 0, 176, 80), yellow (RGB: 255, 255, 0), orange (RGB: 255, 192, 0), brown (RGB: 192, 145, 0) and purple (RGB: 204, 0, 153) ink, and participants were asked to name the colour of the ink. In Condition 2 the sheet of paper contained colour words (red, blue, green, yellow, orange, brown and purple) printed in black ink and participants were asked to read the colour words. In Condition 3 the sheet of paper contained the same colour words printed in incongruent coloured ink and participants were asked to name the colour of the ink each word was written in and inhibit the automatic reading of the word. The order that participants completed conditions was randomised. The number of each written word and each colour of ink was counterbalanced across conditions. The order of the words was randomised within conditions. Participants were instructed to read the words/name the colour of the ink of all the words on the page as quickly as they can. The time taken to complete the page, errors and corrected errors were recorded.

Driving questionnaire

Prior to coming to take part, participants completed the DBQ. The DBQ is a 28 item scale that can be divided into three subscales, including violations, errors and lapses. Participants rate how often the statement has applied to them over the past year on a six-point scale ranging from 0-5, where 0 = Never; 1 = Hardly ever; 2 = Occasionally; 3 = Quite often; 4 = Frequently; 5 = Nearly all the time. The total scores on each subscale are recorded. The violations subscale was excluded from the analysis, as violations are unrelated to the research question.

EEG acquisition

In 17 participants aged 18-30 years (mean=22.88 years, SD=4.05) and 13 participants aged 60+ years (mean=71.23 years, SD=5.49) EEG pilot data was recorded while participants completed the driving simulator task. EEG was recorded on a 64 channel eego™ sports mobile EEG system (ANT Neuro, Enschede, The Netherlands), digitised at a sampling rate of 500Hz). Sensors were Ag/AgCl electrodes arranged in accordance with the International 10-10 system. Electrode CPz was taken as an online reference electrode and the ground electrode was positioned at AFz. Participants were instructed to keep their face as relaxed as possible throughout the recording and to keep their head movements to the minimum necessary while driving to minimise muscle artefacts.

4.1.3 Data analysis

Attention switching task and Driving Simulator task RTs and accuracy

On the computer based attention switching task, participants' median VS RTs (ms) on trials where responses were correct on both the VS and RSVP tasks were extracted. Participants median RSVP RTs (ms) were extracted on trials on where target identification was correct. Participants' proportions of correct VS target identifications, RSVP target detections, RSVP target identifications were also recorded.

A 3 × 5 (RSVP condition × age group) mixed ANOVA was conducted on VS RTs, and a 2 × 5 (RSVP condition × age group) mixed ANOVA was conducted with participants' median spacebar simple RTs (SRTs) in response to detecting the RSVP target. To investigate the age × RSVP condition interaction on RSVP RTs, paired t-tests were carried out to compare RTs between the two RSVP conditions separately for each age group.

In the driving simulator task, participants' median indicator RTs on trials where they had both braked successfully in the braking event and indicated correctly in response to the road sign were extracted from raw driving simulator outputs, as well as their braking RTs. The proportion of correct indicator responses, braking responses and participants' median driving speeds (mph) when passing the road sign were also recorded. RT and accuracy data were analysed using SPSS 21.

Differences in median indicator RTs between event conditions and age groups were analysed in a 3 × 5 mixed ANOVA, where event condition (Immediate Switch/Delayed Switch/Single-Task) was a within subjects factor and age group (18-30/40-49/50-59/60-69/70+ years) was a between subjects factor. Multiple comparisons were corrected for with Bonferroni correction. Differences in median braking RTs between age groups were analysed in a one-way ANOVA. Multiple comparisons were corrected for with Bonferroni correction.

The data were expected to violate assumptions of equality of variance due to increases in inter-individual variability with age (Hale et al., 1988; Morse, 1993). There is evidence to support that the ANOVA is robust to violations to homogeneity of variance (Budescu, 1982; Budescu & Appelbaum, 1981). Levene's test for equality of variance is therefore not reported. Where Mauchly's Test of Sphericity was significant, indicating that the assumption of sphericity has been violated, Greenhouse-Geisser corrected statistics were reported.

To further explore the age group × event condition interaction that was identified in the indicator RT ANOVAs, percentage differences from the Single-Task condition to each of the Dual-Task conditions were calculated as measures of "Dual-Task Costs" for each individual and independent t-tests were implemented to compare age groups' Dual-Task Costs. It is important to note that t-tests were exploratory rather than hypothesis driven, and hence Restricted Fisher's Least Significant Difference test was applied and corrections for multiple comparisons were not conducted (Snedecor & Cochran, 1967). Where Levene's test for equality in variance was significant ($p<.05$) when computing t-tests, 'Equality of variance not assumed' statistics were reported.

Cognitive and self-report measures

CANTAB outputs of median RTs and SDs for SRT, CRT and AST tasks were recorded, as well as CANTAB outputs of AST costs and RVP accuracy (proportion correct).

Consistent with Coubard et al. (2011) Stroop interference ratio was calculated as the number of correct responses in Condition 3 (incongruent colour naming) divided by the correct number of responses in Condition 1 (coloured crosses colour naming). In addition to interference ratio, interference cost was calculated as the percentage increase from Condition 1 completion time to Condition 3 completion time.

The relationship between Dual-Task Costs while driving and each cognitive measure, including UFOV subtasks processing speed, divided attention and selective attention, and CANTAB measures SRT, CRT, AST costs, and RVP accuracy, and Stroop measures interference ratio and interference cost, were explored with Spearman's correlation analyses. It should be noted that correlations were exploratory and multiple comparisons were not corrected for. Relationships between Dual-Task Costs and self-reported DBQ measures attention lapses and driving errors were explored with Spearman's correlation analyses. Correlation analyses between Dual-Task costs and CANTAB, DBQ and Stroop measures are reported in Appendix 4.1. Missing values on questionnaire items were imputed by taking the average score of the subscale's completed items.

Age group differences in the cognitive and self-report measures listed in the previous paragraph were investigated with 11 one-way ANOVAs which are reported in Appendix 4.1. Bonferroni correction for multiple comparisons was applied during post hoc comparisons.

EEG preprocessing and analysis

EEG data were read into the Matlab® toolbox Fieldtrip (Oostenveld et al., 2011), band pass filtered between 0.5 - 36.0Hz and epoched from -7.0-3.0s, where 0.0s corresponded to the onset of the road sign. Trials were visually inspected for artefacts and trials with large artefacts were removed.

Prior to analysis, ICA was implemented and components with eye blink or heartbeat signatures were omitted. Noisy electrodes were interpolated with averaged signal from neighbouring sensors. Time-frequency analysis was carried out applying a Hanning taper from 2-30Hz (for every 1Hz), with three cycles per time-window in stages of 50ms. For each participant trials were averaged within each condition (Single-Task/Immediate Switch/Delayed Switch).

For source localisation, noisy electrodes were excluded instead of interpolated. Data were referenced to the average of all remaining electrodes. A generic Boundary Element Method head-model was created from a template T1 weighted MRI. Head-models were normalised to MNI space (Montreal Neurological Institute template). Voxels were 5mm. Time-frequency tiles were selected based on the results from the sensor level analysis. Sources of theta (3-7Hz; 0.0-1.0s), beta (15-25Hz; 0.0-0.5s and 1.0-2.0s) and alpha (8-12Hz; 1.0-2.0s) oscillations were localised with exact Low Resolution Electromagnetic Tomography (eLORETA; Pascual-Marqui, 2007). LORETA (Pascual-Marqui, Michel, & Lehmann, 1994) was developed to map the sources of electrical potentials recorded from the scalp. LORETA results have been shown to correlate with sources detected with fMRI and PET (Dierks et al., 2000; Gamma et al., 2004). In comparison to LORETA, eLORETA is less susceptible to noise (Pascual-Marqui, 2007). Analysis in alpha frequency revealed a similar pattern as was observed in beta frequency and it is therefore reported in Appendix 4.2.

4.1.4 Results

Attention Switching Task

Analyses of RTs and accuracy on the computer based attention switching task can be found in Chapter 2 Section 2.8.4, including the statistical outcomes. A brief summary of the results are reiterated below and are presented in Figures 4.3.

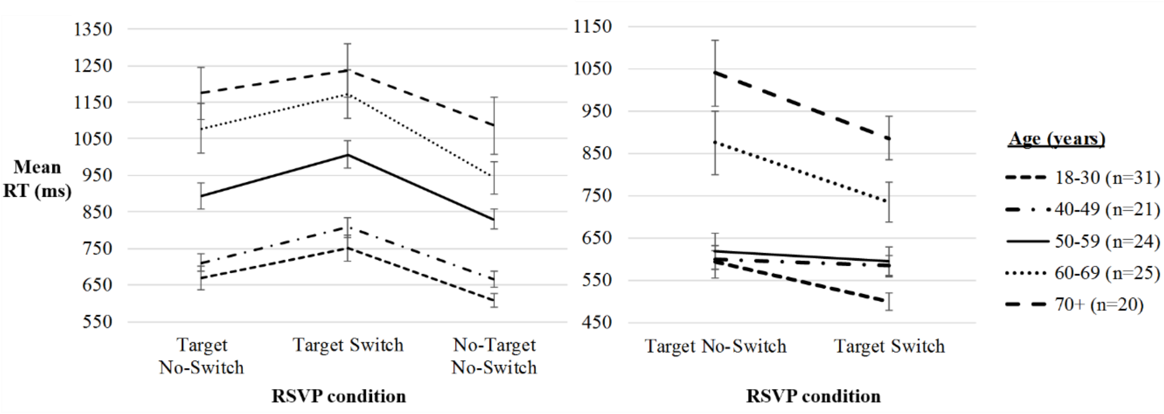

Figure 4.3. Means of median RSVP SRTs (left) and means of median VS RTs (right). Vertical bars represent SE.

RSVP RTs were significantly faster when the target was towards the end of the stream (Target Switch condition) in comparison to when it was the first item in the stream (Target No-Switch condition) for all groups except the 40-49 and 50-59 years groups, resulting in a significant RSVP condition × age group interaction. RSVP RTs were significantly slower in the 70+ years group in comparison to the 18-30, 40-49 and 50-59 years groups and in the 60-69 years group in comparison to the 18-30, 40-49 and 50-59 years groups.

VS RTs were significantly faster in the 18-30 years group compared to all other age groups and in the 40-49 years group compared to the 50-59, 60-69 and 70+ years groups, and in the 50-59 years group compared to the 70+ years group. VS RTs were significantly slower in the Target Switch condition compared to both the Target No-Switch and No-Target No-Switch conditions and were significantly faster in the No-Target No-Switch condition compared to the Target No-Switch condition. There was no RSVP condition × age group interaction (*p*>.10).

Driving simulator task

All age groups achieved greater than 97% accuracy to respond to the braking event and greater than 95% accuracy overall in response to the road sign and so no further analysis was conducted on accuracy data.

Indicator RTs

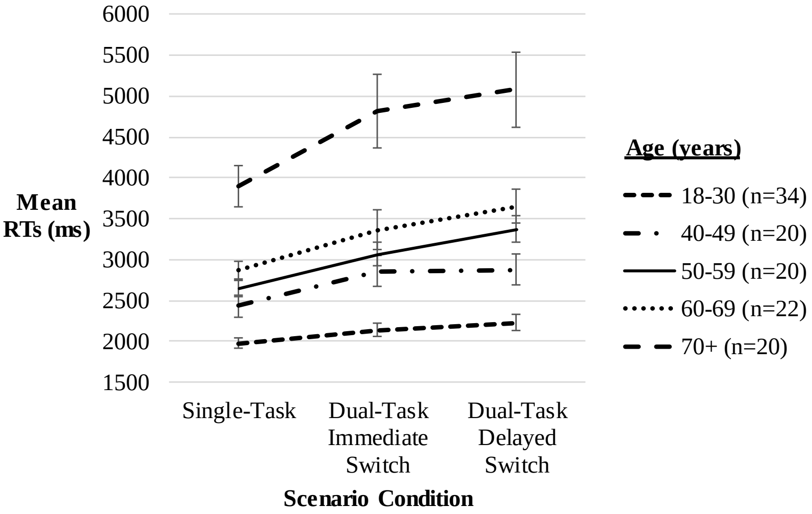

Figure 4.4. Group means of participants' median indicator RTs. Vertical bars represent the standard error of the mean.

A 3 × 5 (event condition × age group) ANOVA was conducted on participants indicator RTs. Mauchly's Test of Sphericity was significant for event condition ($\chi^2(2)=24.51$, $p<.001$) signifying that the assumption of sphericity has been violated. Greenhouse-Geisser corrected statistics were therefore reported. Mean indicator RTs for each age group are presented in Figure 4.4.

There was a significant main effect of age ($F(4, 111)=25.96$, $p<.001$, $\eta^2_p=.48$) and event condition ($F(1.67, 185.04)=57.75$, $p<.001$, $\eta^2_p=.34$) on indicator RTs and a significant interaction between age and event condition ($F(6.67, 185.04)=3.79$, $p<.001$, $\eta^2_p=.12$).

Post hoc comparisons revealed that the significant main effect of age resulted from significantly faster indicator RTs in the 18-30 years group in comparison to the 50-59 ($p=.004$), 60-69 ($p<.001$) and 70+ ($p<.001$) years groups, and significantly slower indicator RTs in the 70+ years group in comparison to all other groups ($p<.001$). There were no other significant age group differences in indicator RTs ($p>.10$).

The significant main effect of event condition resulted from significantly faster indicator RTs in the Single-Task condition in comparison to both Dual-Task Switch conditions ($p<.001$) and faster RTs in the Immediate Switch condition in comparison to the Delayed Switch condition ($p<.001$).

To investigate the hypothesis that age-related increases in Dual-Task Costs would be seen while driving, the interaction between age and RSVP condition was further explored. Each participant's percentage increase in RTs from the Single-Task condition to the Immediate Switch condition

(Immediate Dual-Task Costs) and from the Single-Task condition to the Delayed Switch condition (Delayed Dual-Task Costs) were calculated as measures of Dual-Task Costs. Dual-Task Costs were entered into independent t-tests to compare groups. T-tests were exploratory and multiple comparisons were not corrected for. The means and SDs of each group's Immediate and Delayed Dual-Task Costs are presented in Table 4.2.

Table 4.2. Means and SDs of Dual-Task Costs for each age group

		Age Group (years)				
		21-30 (n=34)	40-49 (n=20)	50-59 (n=20)	60-69 (n=22)	70+ (n=20)
Immediate Dual-Task Costs	Mean	8.62	17.68	15.21	16.80	22.76
	SD	16.50	21.34	11.56	28.50	24.35
Delayed Dual-Task Costs	Mean	12.67	18.59	26.81	27.28	30.50
	SD	20.30	20.31	14.31	22.86	32.37

Dual-Task Costs were calculated as the percentage increase in RT from the Single-Task condition to each of the Dual-Task conditions (Immediate Switch/Delayed Switch) separately.

There were significantly higher Immediate Dual-Task Costs in the 70+ years group in comparison to the 18-30 years group (*t*(52)=-2.54, *p*=.014). Higher Immediate Dual-Task Costs in the 40-49 years group in comparison to the 18-30 years group did not reach significance (*t*(52)=-1.75, *p*=.087). There were no other significant age group differences in Immediate Dual-Task Costs between any age group (*p*>.10).

In comparison to the 18-30 years group, there were significantly higher Delayed Dual-Task Costs in the 50-59 (*t*(52)=-2.74, *p*=.008), 60-69 (*t*(54)=-2.50, *p*=.015) and 70+ (*t*(27.95)=-2.22, *p*=.035) years groups. Note that 'equal variances not assumed' statistics are reported for the comparison of Delayed Dual-Task Costs in the 18-30 and 70+ years group, as Levene's test for equality of variances was significant (*F*=4.69 *p*=.035) signifying that the assumption of equal variances was violated. No other significant age group differences in Delayed Dual-Task Costs were found between any age group (*p*>.10).

Braking RTs and driving speed

A one-way ANOVA was conducted to compare age groups on RTs to brake in response to the vehicle braking. Means of participants' median braking RTs are presented in Figure 4.5.

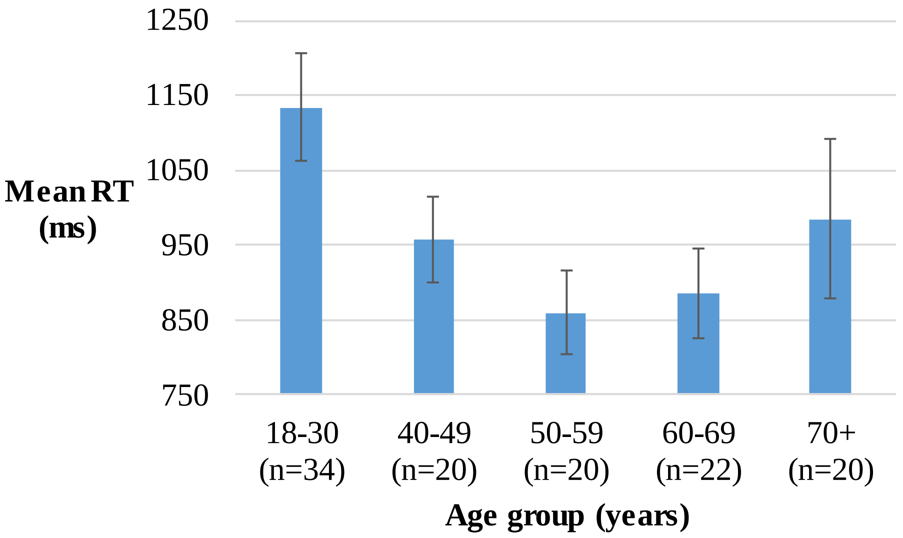

Figure 4.5. Group means of participants' median braking RTs. Vertical bars represent the SE.

A significant effect of age was found on braking RTs (*F*(4, 115)=2.53, *p*=.045). Post-hoc comparisons revealed that braking RTs were faster in the 50-59 years group compared to the 18-30 years group (*p*=.077), however this did not reach significance. There were no other significant age group differences in braking RTs (*p*>.10).

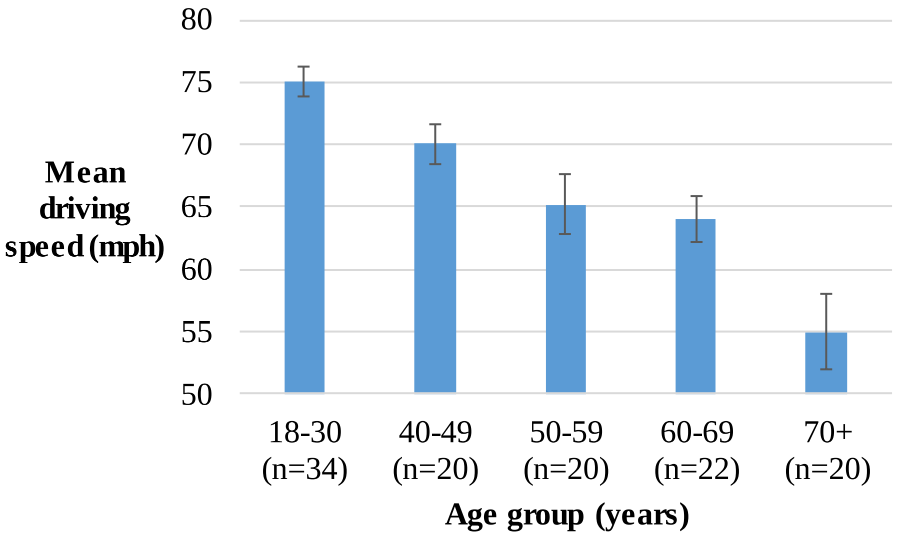

Figure 4.6. Group means of participants' median driving speeds when they passed the road sign. Vertical bars represent the SE.

A one-way ANOVA revealed age group differences in median driving speeds when participants passed the road sign (*F*(4, 115)=15.56, *p*<.001). Group means of median driving speeds are presented in Figure 4.6. The mean driving speed of the 18-30 years group was significantly higher than the 50-59 (*p*=.003), 60-69 (*p*<.001) and 70+ years groups (*p*<.001).

Correlations between performance across tasks

In addition to age-related difficulties in switching between temporal and spatial attention in a computer based task, which were evident from Experiments 3-5 in Chapter 2, we have demonstrated that age-related difficulties in switching are also present in the more realistic scenario of simulated driving. To explore whether performance on the computer based task was related to performance on the driving simulator task Spearman's correlation analyses were carried out between VS RTs in the two Switch conditions in the computer based switching task and indicator RTs in the two Dual-Task conditions the driving simulator task, as well as between RSVP SRTs in the computer based task and RTs to brake in the driving simulator task.

There were 111 participants who were included in the correlation analyses. There was no significant correlation between RSVP SRT and braking RT (p>.10). There were however significant positive correlations between Target Switch VS RTs and both Immediate Switch (r=.55, p<.001) and Delayed Switch (r=.57, p<.001) indicator RTs, and between No-Target Switch VS RTs and both Immediate Switch (r=.62, p<.001) and Delayed Switch (r=.67, p<.001) indicator RTs. These correlations demonstrate that performance on the VS administered in the computer based task is related to performance in reading the road sign in the driving simulator. In contrast, speeded SRTs in response to the detection of an RSVP target do not reflect participants' braking speed performance.

The relationship between driving Dual-Task Costs and cognition

The cognitive mechanisms that underpin switching between modalities of attention were explored via measures of UFOV processing speed, divided attention and selective attention, CANTAB measures SRT, CRT, AST costs and RVP accuracy, and Stroop measures interference ratio (Coubard et al., 2011) and interference cost. Refer to the methods section of the current chapter for descriptions of each measure. To identify cognitive functions that may affect switching ability while driving, the relationship between cognitive measures and both Immediate Dual-Task Costs and Delayed Dual-Task Costs were examined separately for each age group. Significant Spearman's rho correlation coefficients are reported. The same analysis was implemented to explore the relationship between Dual-Task Costs and DBQ self-report measures of attention lapses and driving errors to explore how difficulties in switching may affect on-road driving performance. Twenty two correlations were performed. It should be noted that correlations were exploratory and multiple comparisons were not corrected for.

Out of the cognitive measures and self-report measures listed above, only UFOV performance displayed significant correlations with Dual-Task Costs in the two oldest groups. Significant correlations between UFOV measures and Dual-Task Costs are therefore reported below. Means and SDs of UFOV measures are presented in Table 4.3. Means of the remaining cognitive and self-report measures can be found in Figures A4.1.1-A4.1.4 in Appendix 4.1, along with group comparisons, and correlations between these measures and Dual-Task Costs, as well as group comparisons of UFOV measures.

Table 4.3. Means and standard deviations for cognitive measures

		Age Group (years)				
		21-30 (n=30)	40-49 (n=20)	50-59 (n=23)	60-69 (n=25)	70+ (n=19)
Processing Speed	Mean	16.81	16.87	17.42	20.30	40.04
	SE	0.11	0.17	0.47	1.44	12.07
Divided Attention	Mean	23.69	29.03	32.68	36.84	86.82
	SE	2.89	5.97	5.69	5.82	19.45
Selective Attention	Mean	47.92	84.18	110.77	110.19	169.45
	SE	5.73	10.46	10.46	8.35	18.71

In the 70+ years group there was a significant negative correlation between Delayed Dual-Task Costs and UFOV selective attention (*r*=-.53, *p*=.023), and non-significant negative correlations between Delayed Dual-Task Costs and UFOV processing speed (*r*=-.40, *p*=.091) and between Immediate Dual-Task Costs and UFOV selective attention (*r*=-.47, *p*=.052).

In the 50-59 years group there was a negative correlation between UFOV divided attention and Delayed Dual-Task Costs that did not reach significance (*r*=-.41, *p*=.079).

In both the 50-59 and 70+ years groups, as participants' performance in processing speed, divided attention or selective attention UFOV measures becomes slower, Dual-Task Costs while driving increase. There were no other significant correlations between Dual-Task Costs while driving and UFOV performance in any age group (*p*>.10).

EEG

EEG was recorded in a subset of participants aged 18-30 and 60+ years as a pilot study to both investigate the feasibility of recording EEG in the driving simulator and to explore whether the oscillatory signatures observed with MEG when switching between temporal and spatial attention (described in Chapter 3) are also seen when switching between temporal and spatial attention during simulated driving. The demographics of the subgroups of participants who took part in EEG recordings are presented in Table 4.4. Oscillatory analysis in theta and beta frequency bands are reported below. Analysis in alpha frequency in a later time window (1.0-2.0s) revealed a similar pattern in alpha frequency as was observed in beta frequency and so is reported in Appendix 4.2.

Table 4.4 EEG participant demographics

		Age group (years)	
		18-30 (n=17)	60+ (n=13)
Age (years)	Mean	22.88	71.23
	SD	4.04	5.49
Gender	Male	4	7
	Female	13	6
Handedness	Right	15	13
	Left	2	0
ACE-3	Mean	n/a	95.23
	SD	n/a	2.52

The mean age of each age group, the number of participants who are male and female and the number of participants who are left and right handed are presented for each age group. Mean ACE-3 scores are presented for the 60+ years group.

Indicator RTs and driving speed

To explore the behavioural effects in the subgroup of participants from which we recorded EEG, a 3 × 2 (event condition × age group) ANOVA was conducted on participants indicator RTs. Mauchly's Test of Sphericity was significant for event condition ($\chi^2(2)=11.08$, $p<.004$) signifying that the assumption of sphericity has been violated. Greenhouse-Geisser corrected statistics were therefore reported. Mean indicator RTs for each age group are presented in Figure 4.7.

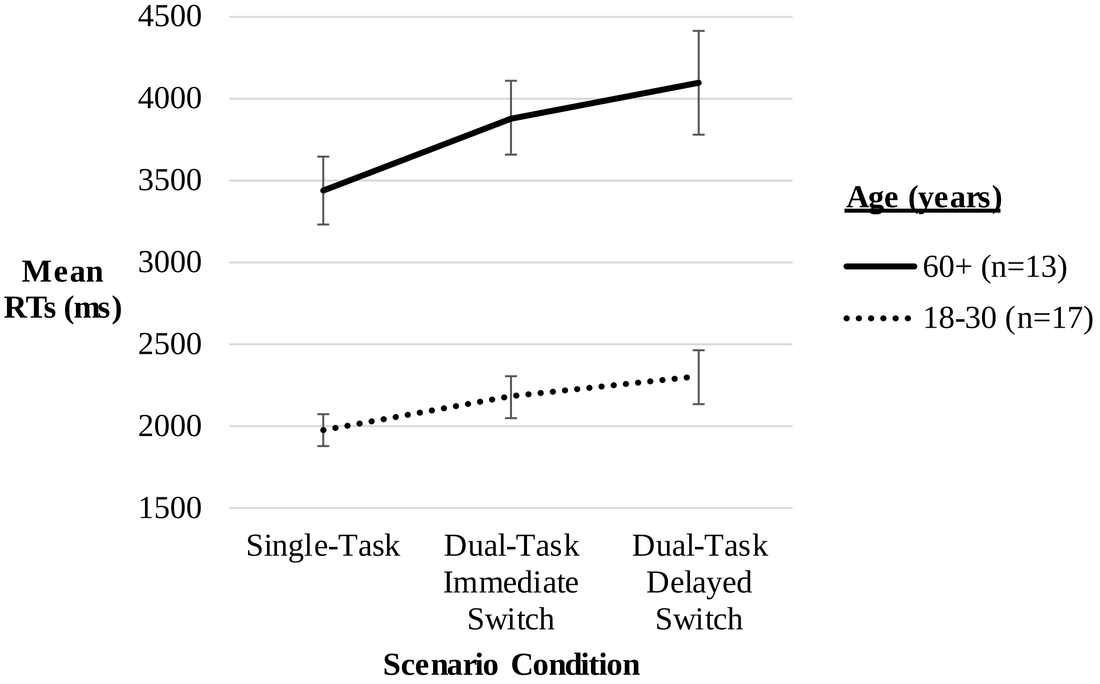

Figure 4.7. Group means of participants' median indicator RTs. Vertical bars represent the SE.

The 60+ years group was significantly slower than the 18-30 years group (*F*(1, 28)=45.11, *p*<.001, η^2_p=.62). There was a significant main effect of event condition (*F*(1.50, 41.90)=14.64, *p*<.001, η^2_p=.34) on indicator RTs, but no age × event condition interaction (*p*>.10). Post hoc comparisons demonstrated that indicator RTs in the Single-Task condition were significantly faster than RTs in the two Dual-Task conditions (*p*<.001). There was no significant difference between Immediate and Delayed Switch condition RTs (*p*>.10).

The means and SDs of each group's Immediate and Delayed Dual-Task Costs are presented in Table 4.5. From Table 4.5 it can be seen that, although Dual-Task Costs are higher in the 60+ years group compared to the 18-30 years group, variability in Dual-Task Costs is very high, reflected in large SDs. It is likely that a combination of a small number of participants in the 60+ years group and high variability in Dual-Task Costs across both age groups prevented group differences in Dual-Task Costs from reaching statistical significance.

Table 4.5. Means and SDs of Dual-Task Costs for each age group

		Age group (years)	
		21-30 (n=17)	60+ (n=13)
Immediate Dual-Task Costs	Mean	10.38	13.79
	SD	15.55	14.16
Delayed Dual-Task Costs	Mean	15.97	19.27
	SD	23.72	21.36

Dual-Task Costs were calculated as the percentage increase in RT from the Single-Task condition to each of the Dual-Task conditions (Immediate Switch/Delayed Switch) separately.

Braking RTs and driving speed

There was no significant difference in braking RTs between the subsets of EEG participants aged 18-30 years and 60+ years (*p*>.10). The mean braking RT was 1027.90ms (SD = 358.60) for the 18-30 years group and 1055.40ms (SD = 541.33) for the 60+ years group.

Median driving speeds when participants passed the road sign were significantly higher in the subset of EEG participants aged 18-30 years compared to the subset of EEG participants aged 60+ years (*t*(28)=6.00, *p*<.001). The mean driving speed of the 18-30 years group was 74.44mph (SD = 6.84) whereas the mean driving speed of the 60+ years group was 60.00mph (SD = 6.08).

Theta

Single-Task vs Dual-Task conditions

Figure 4.8 presents theta (3-7Hz) EEG power effects when A) contrasting Immediate Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Immediate Switch/Single-Task) × age interaction (bottom row), and B) contrasting Delayed Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Delayed Switch/Single-Task) × age interaction (bottom row).

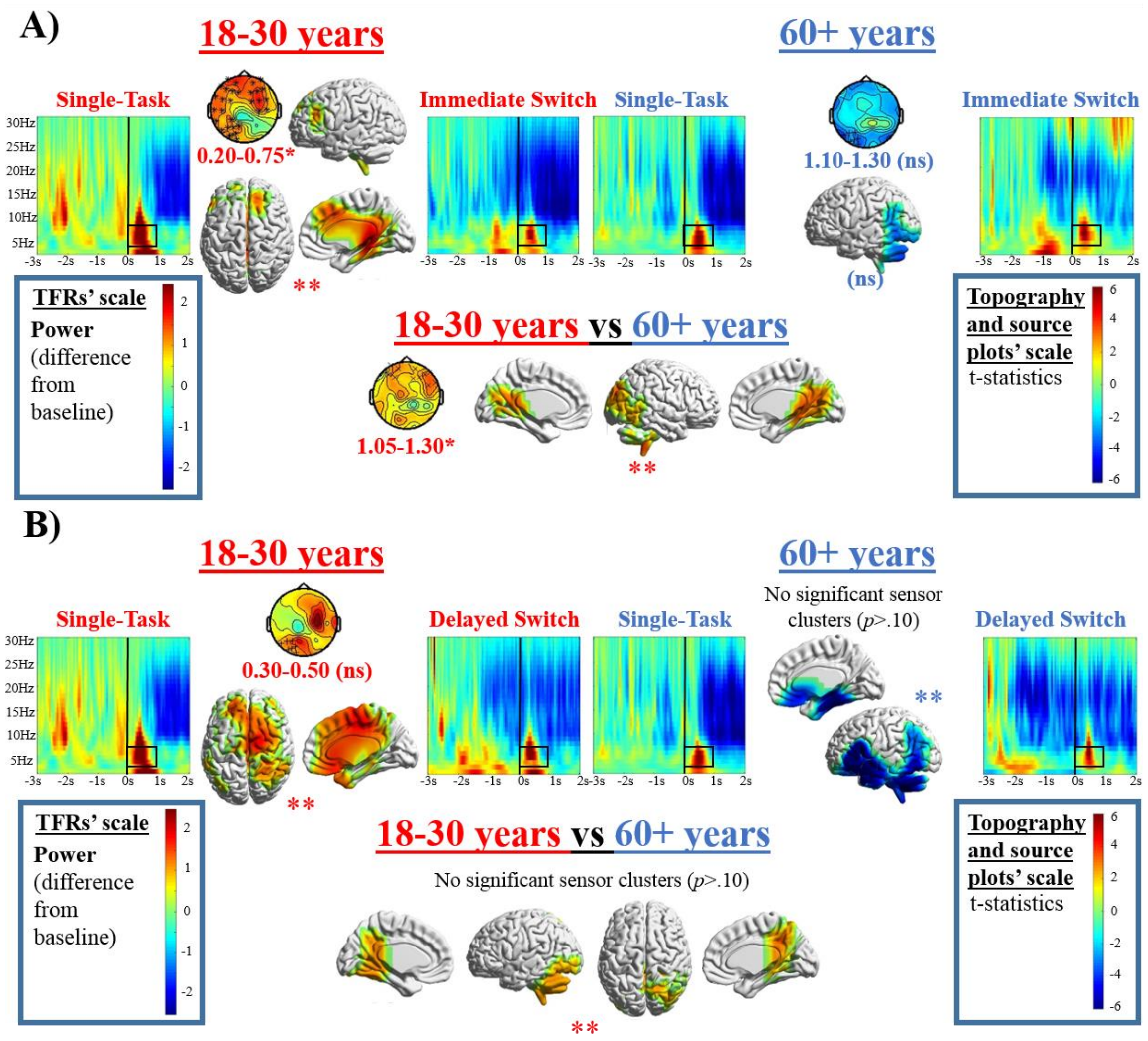

Figure 4.8. Effects in theta (3-7Hz) EEG power when A) contrasting Immediate Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Immediate Switch/Single-Task) × age interaction (bottom row), and B) contrasting Delayed Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Delayed Switch/Single-Task) × age interaction (bottom row). TFRs present power in relation to a baseline period of -5.5s - -3.5s in a group of 10 anterior electrodes (AF3, AF4, F1, F2, F3, F4, FC1, FC2, FC3, FC4). Black lines placed over TFRs signify the onset of the road sign VS display at 0.0s. In the Switch conditions the car pulled in front of the participant at either 3.04m (~0.14s; Immediate Switch) or 30.48m (~1.42s; Delayed Switch) prior to the onset of the road sign. Topographical and source plots present *t*-statistics of significant clusters. Rectangles placed over TFRs highlight the time-frequency tile entered into source localisation. Note that the Single-Task TFRs for each age group are presented in both A and B. Significance levels are indicated as (ns)p<.10, *p<.050, **p<.025.

The TFRs in Figure 4.8 display a theta response shortly after the road sign appears, which is consistent with top-down guided attentional control and target processing (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Demiralp & Başar, 1992; Green et al., 2008; Min & Park, 2010). In the Dual-Task conditions, there was an earlier theta increase that reflects processing of the braking event, which is initiated approximately 0.9s prior to the onset of the VS in the Immediate Switch condition and between -3.0 and -2.0s in the Delayed Switch condition. Although the vehicle did not brake in front of the participant until either ~0.14s prior to the onset of the sign in the Immediate Switch condition or ~1.42s prior to the onset of the sign in the Delayed Switch condition, the earlier onset of theta modulation likely reflects detection of and attention to the vehicle. Surprisingly, this early theta response did not differ significantly between conditions in either age group. This could be due to inter-individual variability in when and whether the vehicle is detected, in addition to variability in the time that the braking event occurred in relation to the road sign onset, caused by differences in participants' driving speeds.

The 18-30 years group displayed a significantly greater theta increase in response to the road sign in the Single-Task condition in comparison to both Dual-Task conditions, which localised to the SFG, lingual gyrus and the median cingulate cortex (MCC) and ACC in the Immediate Switch condition, consistent with regions implicated in visual processing and top-down attentional control (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Mechelli, Humphreys, Mayall, Olson, & Price, 2000). In the Delayed Switch condition, theta modulation localised to the cerebellum, right parietal gyri, bilateral SMA, right frontal gyri, and the ACC, consistent with an attentional control network (Coull & Nobre, 1998; Gross et al., 2004; Li et al., 2013; Madden, Spaniol, Whiting, et al., 2007; Shapiro et al., 2002).

A stronger theta response in the Single-Task condition in comparison to Dual-Task conditions for younger drivers was surprising, although could be explained by a number of reasons. Firstly, it could be that there are fewer resources available to process the sign in the Dual-Task conditions after attending to the braking event. Alternatively, the opposite may be the case, where only young participants have the attentional resources available to learn that the sign will follow the braking event and prepare by engaging relevant attention networks prior to the road sign onset, perhaps in conjunction with the beta modulations described below. Finally, it could be that participants slowing down in response to the braking event in the Switch conditions made the sign easier to read for younger adults in comparison to when participants were driving at high speeds as they approached the sign in the Single-Task condition. In contrast, the 60+ years group compensate for attentional deficits by driving slowly to read the road sign. Age group comparisons of participants' median driving speeds, which are presented in Figure 4.6, confirmed that the average driving speed of the 18-30 years group was indeed significantly higher than the 50-59, 60-69 and 70+ years groups, as well as significantly higher in the subset of EEG participants aged 18-30 years compared to the subset of EEG participants aged 60+ years.

Presenting an opposite pattern to the younger adults, the 60+ years group show a weaker theta increase in the Single-Task condition in comparison to the Dual-Task conditions, although differences between the Delayed Switch condition and the Single-Task condition were only significant in source space (Figure 4.8 B) and differences between the Immediate Switch and the

Single-Task condition did not reach significance in either source or sensor space (Figure 4.8 A). Theta modulation in the 60+ years group localised to the cerebellum, temporal gyri, the inferior occipital gyrus, the left IFG, right parahippocampal gyri, and left rolandic operculum. Stronger theta modulation in the Dual-Task condition in comparison to the Single-Task condition is in line with expectations and with our MEG findings outlined in Chapter 3. Greater Dual-Task related theta modulation could reflect the requirement of greater cognitive effort to attend to the road sign when switching from attending to and responding to temporal events. The 18-30 years group differed in that they required little additional effort to switch to implement spatial attention after responding to a temporal event, possibly due to better engaging attentional networks in preparation of the road sign, which is reflected in their reduced theta effects as well as the beta frequency modulations described below.

Group contrasts (Figure 4.8 A and B, bottom rows) show that in comparison to the 60+ years group, the 18-30 years group display a significantly greater theta increase in the Single-Task condition in comparison to Dual-Task conditions in the right middle occipital gyrus, cerebellum and PCC in the Immediate Switch condition and in the right occipital lobe in the Delayed Switch condition. In comparison to the 18-30 years group the 60+ years group appears to present with lower theta power in the cerebellum and temporal lobes in the Delayed Switch condition compared to the Single-Task condition. It should be noted that there were discrepancies between age group differences in sensor and source power in the Immediate Switch comparison. When comparing age groups on the Immediate Switch condition, there is an anterior positive theta cluster in sensor space, however theta oscillations localised to posterior regions. Differences between Single-Task and Immediate Switch conditions failed to reach significance in the older age group, likely due to low participant numbers. It could be that low participant numbers also prevented all age group differences from reaching significance. On inspection of Figure 4.8, it could be that the anterior positive cluster in sensor space reflects the theta increase in the frontal lobe in the younger adults (Single-Task > Immediate Switch; Figure 4.9 A top left), whereas the posterior positive cluster in source space reflects the negative posterior cluster in the older group (Immediate Switch > Single Task; Figure 4.8 A top right).

Overall, the 18-30 years group display higher theta in the Single-Task condition in comparison to the Dual-Task conditions, likely reflecting increased cognitive effort to read the road sign when travelling at high speeds as well as efficiently enhancing attention in the Dual-Task condition (thus not “requiring” enhanced theta in the latter). In contrast, the 60+ years group show higher theta in the Dual-Task Switch conditions in comparison to the Single-Task conditions, likely due to difficulty in switching from temporal to spatial attention.

Beta

Single-Task vs Dual-Task conditions

Figure 4.9 displays effects in beta (15-25Hz) EEG power when A) contrasting Immediate Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Immediate Switch/Single-Task) × age interaction (bottom row), and B) when contrasting Delayed Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Delayed Switch/Single-Task) × age interaction (bottom row).

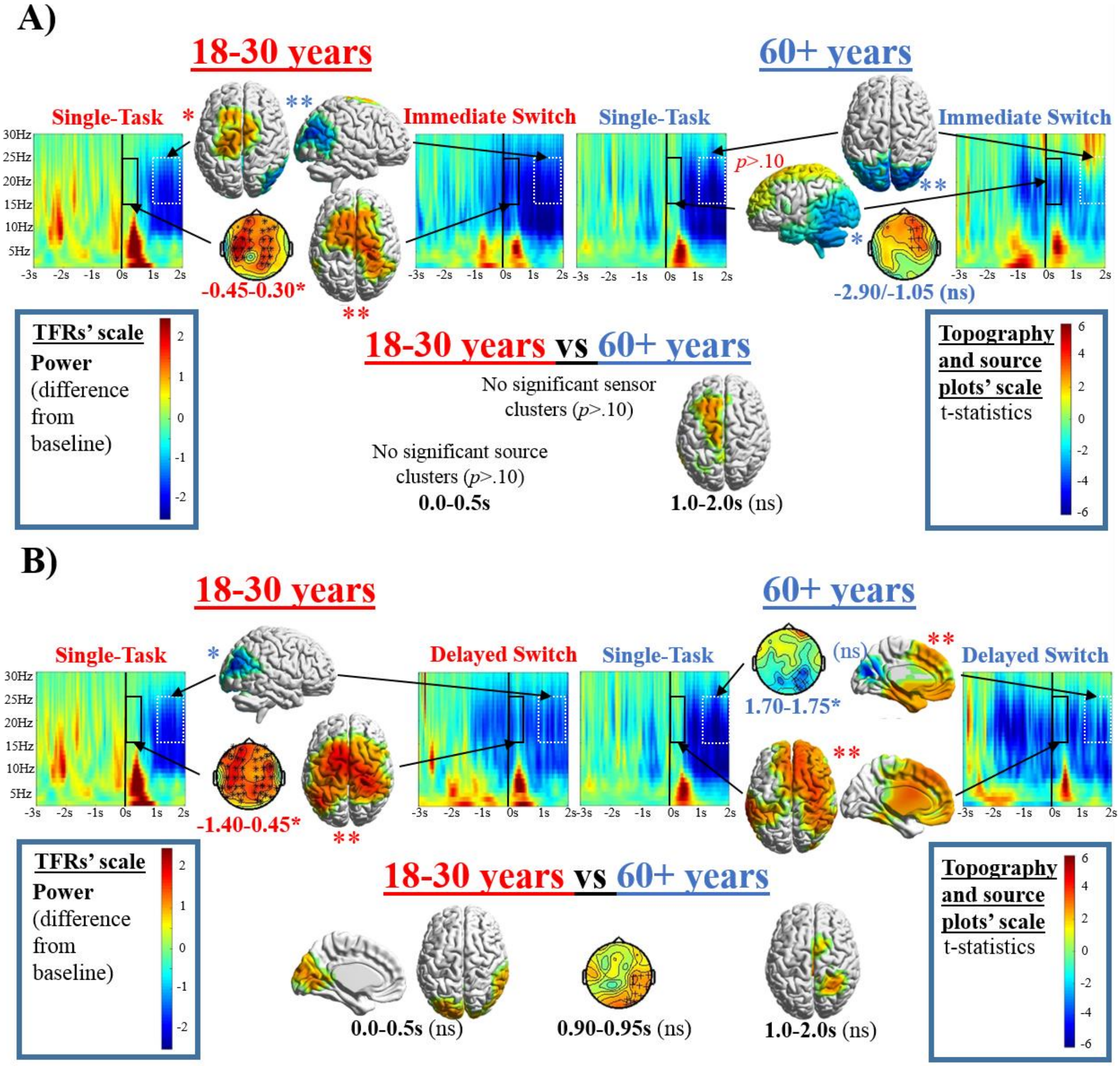

Figure 4.9. Effects in beta (15-25Hz) EEG power when A) contrasting Immediate Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Immediate Switch/Single-Task) × age interaction (bottom row), and B) when contrasting Delayed Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Delayed Switch/Single-Task) × age interaction (bottom row). TFRs present power in relation to a baseline period of -5.5s - -3.5s in a group of 10 anterior electrodes (AF3, AF4, F1, F2, F3, F4, FC1, FC2, FC3, FC4). Black lines placed over TFRs signify the onset of the road sign VS display at 0.0s. In the Switch conditions the car pulled in front of the participant at either 3.04m (~0.14s; Immediate Switch) or 30.48m (~1.42s; Delayed Switch) prior to the onset of the road sign. Topographical and source plots present *t*-statistics of significant clusters. Rectangles placed over TFRs highlight the time-frequency tile entered into source localisation. Note that the Single-Task TFRs for each age group are presented in both A and B. Significance levels are indicated as (ns)p<.10, *p<.050, **p<.025.

TFRs in Figure 4.9 highlight a beta power decrease in a late time window (from 0.5s) in response to the onset of the road sign in the Single-Task condition and in an earlier time window in response to the braking event in the Dual-Task conditions. A beta power decrease is consistent with enhanced attention (Gola et al., 2012; Gola et al., 2013; Gross, et al., 2004) and motor preparation and motor response (Donoghue et al., 1998; Farmer, 1998; Kühn et al., 2004; Park et al., 2013).

The 18-30 years group show a greater beta decrease in the Dual-Task conditions in comparison to the Single-Task condition in an early time window (in both Delayed and Immediate Switch conditions) and in an additional late time window in the Immediate Switch condition. The cluster analysis on sensor data (topographical plots in Figure 4.9 A and B top left) revealed that beta was higher in the Single-Task condition in comparison to the Dual-Task conditions, from -0.45-0.30s in the Immediate Switch condition and from -1.30-0.45s in the Delayed Switch condition. It appears that the stronger beta decrease in the Dual-Task conditions in comparison to the Single-Task condition reflects enhanced attention or motor preparation in response to the braking event which is then maintained in anticipation of the road sign appearing. In the 18-30 years group, beta modulations in both an early (0.0-0.5s) and a later (1.0s-2.0s) time window localised to parietal regions, mirroring the source localisation of MEG alpha modulation seen in Chapter 3 Figures 3.5 and 3.6. In the later time window a posterior negative cluster was also apparent in source space, which reflected a greater beta desynchronization in the Single-Task condition compared to the Dual-Task condition. It therefore seems that the Dual-Task condition involves the recruitment of a frontoparietal network as anticipatory attention and motor preparation is engaged early, whereas the Single-Task condition engages visual attention regions in a stronger more reactive response to the unpredictable onset of the road sign. In contrast to the Immediate Switch condition, in the Delayed Switch condition the positive parietal clusters are no longer apparent in the 18-30 years group (Figure 4.9 B left), possibly due to the degradation of the benefits of a cue (i.e. the braking event) on attention with increased time elapsed (Correa & Nobre, 2008; Coull & Nobre, 1998; Griffin, Miniussi, & Nobre, 2001; Woodrow, 1914).

In the Immediate Switch condition the beta decrease appears weaker in the 60+ years group in comparison to the younger group, with sensor data analysis revealing that conditions only differed at -2.90s and -1.05s relative to road sign onset, differences that did not reach significance. The positive frontoparietal cluster in source space was not significant (*p*>.10). Group comparisons confirmed that the stronger beta desynchronization in the Dual-Task condition compared to the Single-Task condition that was seen in the parietal cortex during the later time window was significantly greater in the 18-30 years group compared to the 60+ years group (Figure 4.9, B bottom row). This finding further supports that the 60+ years group is impaired at engaging in attention and motor preparation in anticipation of the road sign, as argued previously in the current chapter.

In the 60+ years group, source analysis revealed that the greater posterior beta decrease in the Single-Task condition compared to the Immediate Switch condition occurred earlier in the older group compared to the younger group - i.e. in the early time window of 0.0-0.5s as well as the later 1.0-2.0s window that is observed in both age groups. This greater beta decrease in the Single-Task condition localised to the cerebellum, left temporal gyri, left fusiform area, and the left occipital gyri. Note that this seems to contradict what is visible on the TFRs in Figure 4.9 A (top right), however the TFRs display data from a group of anterior electrodes, whereas lower beta localised to posterior regions. This localisation should be interpreted with caution as, although kept to a minimum, posterior sensors were effected by neck muscle and movement artefacts while in the driving simulator. Poor SNR could also explain the absence of any group differences in Immediate Switch beta modulation in sensor or source analysis (p>.10).

In contrast to the Immediate Switch condition, in both an early and a later time window the 60+ years group showed lower beta in the Delayed Switch condition compared to the Single-Task condition (Figure 4.9 B right), which is consistent with the 18-30 years group and reflects a greater beta decrease in the Dual-Task in comparison to the Single-Task condition. To reiterate, it is likely that this beta decrease reflects anticipatory preparation for the onset of the road sign after the braking event. Beta modulation appears more widely distributed in the 60+ years group in comparison the 18-30 years group, incorporating additional bilateral temporal and frontal gyri, although these differences were not significant in group contrasts (p>.10). Increased recruitment of frontal and temporal regions is consistent with our MEG findings in theta oscillations, and could reflect an increased reliance on top-down attentional guidance and compensatory strategies (McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002).

In the later time window the 60+ years group displayed a posterior negative cluster that reflects greater beta desynchronization in the Single-Task condition in comparison to the Delayed Switch condition (Figure 4.9, B, right), which is consistent with the 18-30 years group and the contrast between the Immediate Switch and Single-Task conditions. In addition to the posterior negative cluster, the older group displayed positive clusters in the ACC and frontal and temporal gyri, reflecting a greater beta desynchronization in the Delayed Switch condition compared to the Single-Task condition. This pattern differs from the younger adults and could signify the recruitment of compensatory top-down attentional control mechanisms (Davis et al., 2008; Madden, Spaniol, Bucur, & Whiting, 2007; McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002). There was a discrepancy between the source and sensor analysis in the 60+ years group. During the

0.0-1.0s period that was localised in source analysis, no significant clusters in sensor analysis were found. However, Figure A4.4.1 in Appendix 4.4 illustrates that there were positive clusters during this time period that did not reach significance (*p*<.10). It could be that the small number of participants and the small number of trials resulted in poor SNR that prevented these clusters from reaching significance.

Group comparisons of Delayed Switch related beta modulation revealed that beta modulation was greater in the 18-30 years group in comparison to the 60+ years group, including in the PCC (bilateral), right precuneus and the right occipital lobe in the early time window and in the MCC, right SMA, the right SFG and right superior parietal gyrus in the late time window.

In summary, the 18-30 years group displayed a greater beta decrease in response to the braking event in comparison to the 60+ years group, which may reflect enhanced attention and motor preparation that is maintained in anticipation of the road sign (Gross, et al., 2004; Gola et al., 2012; Gola et al., 2013; Donoghue et al., 1998; Farmer, 1998; Kuhn et al., 2004).

Correlations between power modulation and Dual-Task Costs

To explore the relationship between theta modulation and beta modulation and Dual-Task Costs, for each participant differences in theta and beta power between the Single-Task condition and each of the Dual-Task conditions were extracted at several MNI coordinates and entered into Spearman's correlation analyses with Immediate and Delayed Dual-Task Costs. MNI coordinates were selected based on the peak *t*-values of significant (*p*<.05) clusters from the cluster permutation analysis that compared Dual-Task and Single-Task conditions in each age group. Separately for the 18-30 years group (n=17) and the 60+ years group (n=13), differences in power between Immediate Switch and Single-Task conditions were correlated with Immediate Dual-Task Costs, and differences in power between Delayed Switch and Single-Task conditions were correlated with Delayed Dual-Task Costs. MNI coordinates and corresponding atlas labels that were selected for correlation analyses can be found in Tables A4.3.1 - A4.3.6 in Appendix 4.3. Correlations were exploratory and multiple comparisons were not corrected for.

Theta power correlations

There were no significant correlations between theta power modulation and Immediate Dual-Task Costs in either age group (*p*>.10)

In the 18-30 years group there was a positive correlation between Delayed Dual-Task Costs and theta power modulation in the orbital part of the right SFG (*r*=.43, *p*=.088), although this correlation did not reach significance. It is evident from Figure 4.8B (top left) that the younger group showed a higher theta increase in the Single-Task condition in comparison to the Delayed Switch condition. As this power difference increased, Dual-Task Costs increased. There were no other significant correlations between theta power modulation and Delayed Dual-Task Costs in any age group (*p*>.10).

Beta power correlations

In the 18-30 years group in the early time window (0.0s-0.5s), there was a significant negative correlation between Immediate Dual-Task Costs and beta power modulation in both the left MFG (*r*=-.52, *p*=.033) and the left cerebellum (*r*=-.42, *p*=.096), however the latter failed to reach significance. A significant negative correlation was also found between Immediate Dual-Task Costs and beta power modulation in the left MFG in the late time window of 1.0-2.0s (*r*=-.57, *p*=.017). As seen in Figure 4.9 A (top left) the 18-30 years group showed significantly higher frontal beta power in the Single-Task condition in comparison to the Immediate Switch condition, reflecting a greater beta decrease in the Dual-Task condition. As this difference became larger in the left MFG and cerebellum, Dual-Task Costs decreased, suggesting that a stronger beta decrease in the Immediate Switch condition is related to more efficient attention refocusing. There were no other significant differences between beta modulation and Immediate Dual-Task Costs in any age group (*p*>.10).

In the 18-30 years group in the late time window (1.0-2.0s), there was a significant negative correlation between Delayed Dual-Task costs and beta power modulation in both the right superior temporal gyrus and (*r*=-.65, *p*=.005) and the right middle occipital gyrus (*r*=-.44, *p*=.080), however the latter failed to reach significance. Figure 4.9 B (left) illustrates that there was a greater beta decrease in the Single-Task condition compared to the Delayed Switch condition. As this beta decrease became stronger (i.e. the clusters became more negative) Delayed Dual-Task Costs increased, implying that participants with a weaker beta decrease in temporal and occipital gyri in the Delayed Switch are less efficient at refocusing attention between time and space.

In the 60+ years group, in the early time window, there was a positive correlation between Delayed Dual-Task Costs and beta power modulation in both the left SFG (*r*=.59, *p*=.035) and the medial part of the right SFG (*r*=.52, *p*=.067). However, the latter failed to reach significance. It is evident from Figure 4.9 B (top right) that the 60+ years group showed higher beta in the Single-Task condition in comparison to the Delayed Switch condition, reflecting a greater beta desynchronization in the Dual-Task condition. As this difference increased (i.e. beta desynchronization in the Delayed Switch condition increased) Delayed Dual-Task Costs increased. The direction of this relationship is opposite to expected and opposite to the direction of the relationship between Immediate Dual-Task Costs and left MFG beta modulation in the 18-30 years group. One explanation could be that those with deficits in refocusing attention in the Dual-Task condition attempt to require increased beta modulation in the SFG due to increased cognitive effort in refocusing their attention. This could particularly be the case in the Delayed Switch condition, as participants may have a stronger focus of attention on the road ahead after the absence of an immediate road sign. However, there were only a small number of participants in the older group (*n*=13) and multiple comparisons were not corrected for. More research is needed before any conclusions can be made. There were no other significant differences between beta modulation and Delayed Dual-Task Costs in any age group (*p*>.10).

In summary, in the 18-30 years group, stronger beta desynchronization in the left MFG, cerebellum, temporal gyri and occipital gyri was related to more efficient attention refocusing. In the older group, a greater beta desynchronization in the SFG in the Dual-Task conditions was associated with higher Dual-Task Costs.

4.1.5 Discussion

The series of experiments presented in Chapter 2 demonstrated an age-related decline in the ability to refocus attention from attending to events changing in time to distributing attention spatially. The aim of the current chapter was to investigate whether these age-related difficulties in switching from temporal to spatial attention are also seen in a more ecologically valid setting, during simulated driving. In Chapter 3 MEG was recorded while participants completed the attention switching paradigm, facilitating the investigation of age-related changes in neural mechanisms that may underlie difficulties in switching. In the current study EEG was recorded in a subset of participants while they completed the driving simulator task, permitting the investigation of whether oscillatory signatures underlying switching from temporal to spatial attention while driving resemble those observed with MEG in the computer based switching task.

As hypothesised, RTs to complete the VS of the road sign were significantly slower in the two Dual-Task conditions in comparison to the Single-Task condition, reflecting costs of switching from a temporal attention task to a spatial attention task. Unexpectedly, RTs in the Delayed Switch condition were significantly slower than in the Immediate Switch condition. This was surprising, as faster RTs were expected when participants had more time to refocus their attention spatially after the braking event. It is likely that participants learned that the road sign followed the braking event and the braking event behaved as a cue. There is a vast literature that demonstrates that temporal orienting of attention is enhanced at shorter than longer time intervals between a cue and a target, and RTs to detect a target decrease if the time of stimulus onset is predictable (Correa & Nobre, 2008; Coull & Nobre, 1998; Griffin et al., 2001; Woodrow, 1914). When the distance between the braking event and the road sign onset is farther in the Delayed Switch condition, the variability in the time of the road sign onset increases due to variability in the speed that participants are driving. Variability in the onset time of the road sign (making it less predictable), combined with a longer time period between the braking event and the road sign onset, likely resulted in increased RTs in the Delayed

Switch condition in comparison to the Immediate Switch condition. In addition, it could be that at long delays participants focused their attention back on the road traffic and therefore had to re-switch to a spatial focus of attention when the sign appeared.

The hypothesis that there would be an age-related decline in switching from temporal to spatial attention while driving was supported, reflected in a greater increase in RTs from the Single-Task condition to both the Immediate and Delayed Switch conditions in the 40-49 and 70+ years groups in comparison to the 18-30 years group. Greater Delayed Dual-Task Costs were found in the 50-59, 60-69 and 70+ years groups in comparison to the 18-30 years group. These findings demonstrate that age-related declines in refocusing from temporal to spatial attention are not only observed in the computer based switching task but are also present in a more realistic setting such as when driving, particularly in those aged 70+ years. Findings of significantly increased Delayed Dual-Task Costs but not Immediate Dual-Task Costs in the 50-59 and 60-69 years groups signifies that these age groups present less of a difference in RTs between the Single-Task and Immediate Switch conditions, when the onset time of the stimulus is predictable, but are more impaired when the time of stimulus onset is ambiguous. These findings are in line with older age groups relying more on top-down guidance to control attention, such as implementing the use of temporal cues (McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002), as well as evidence towards impaired anticipatory attention mechanisms (Deiber et al., 2013; Gamboz et al., 2010; Zanto et al., 2011). It is likely that higher variability in Dual-Task Costs that are evident in Table 4.2 prevented Immediate Dual-Task Costs from reaching significance in older age groups. In contrast, participants aged 40-49 years displayed higher Immediate Dual-Task Costs compared to participants aged 18-30 years, but showed no difference in Delayed Dual-Task Costs. Note that Figure 4.4 illustrates that there is little difference between Immediate Switch and Delayed Switch RTs in the 40-49 years group. It is likely that Delayed Dual-Task Costs were not significantly greater than the 18-30 years group due to higher Delayed Dual-Task Costs in comparison to Immediate Dual-Task Costs in the 18-30 years group, as is evident in Table 4.2.

Delayed Dual-Task Costs but not Immediate Dual-Task Costs correlated with UFOV measures of processing speed, divided attention and selective attention in the 50-59 and 70+ years groups, where those with poor performance had higher Dual-Task Costs. A correlation between UFOV measures and Delayed but not Immediate Dual-Task Costs may imply that the relationship results from increased Delayed Dual-Task Costs in those who rely more on top-down attentional control due to impaired lower level attentional mechanism, such as those quantified with the UFOV. In the Immediate Switch condition, participants are better able to predict when the road sign will appear, enabling top-down attentional guidance to orient attention towards this time point, which may compensate for deficits in attention. In the Delayed Switch condition participants are less able to predict the time of the sign onset and must rely on lower level attentional mechanisms to cope with switching between temporal and spatial attention, possibly inflating Dual-Task Costs in this condition in those with less efficient lower level attentional mechanisms.

In addition to demonstrating the presence of age-related declines in switching between temporal and spatial attention in a computer based task in Experiments 3-5 in Chapter 2, the current chapter has demonstrated that age-related difficulties in refocusing attention between time and space are also present in the more realistic scenario of simulated driving. The question remained as to whether performance on the computer based task was related to performance in the driving simulator. Although VS RTs in the computer based task were indeed related to indicator RTs in response to the road sign VS in the driving simulator, speeded SRTs in response to the detection of an RSVP target did not reflect participants' braking speed performance. One explanation for this regards limitations in the methodology. To maintain ecological validity, participants were given control over the driving simulator vehicle and were therefore free to brake and accelerate at any time. Although the car did not brake in front of the participant until either ~0.14s prior to the onset of the sign in the Immediate Switch condition or ~1.42s prior to the onset of the sign in the Delayed Switch condition it is likely the participant detected the vehicle as a possible hazard prior to these time points. Older drivers have been shown to adjust their driving behaviour to compensate for slowed RTs (Andrews & Westerman, 2012) and may therefore have begun to brake at the earliest sign of a possible hazard, affecting measures of braking RT. This explanation is consistent with the unusual pattern of braking RTs observed across age groups (Figure 4.5), where the youngest age group display slower braking speeds than older groups.

EEG was recorded in a subset of participants to obtain pilot data investigating the feasibility of recording EEG in the driving simulator, where there is a large amount of environmental noise and movement artefacts. It is important to note that there were only 17 participants in the 18-30 years group and 13 participants in the 60+ years group in which we recorded EEG. Furthermore, there were only 12 trials in each condition. It is likely that the small number of trials and participants contributed to the failure of some of the observed differences in EEG power and RTs reaching significance, particularly in the 60+ years group. Although the interaction between event condition and age did not reach significance when comparing the EEG subsets of participants, the overall pattern of indicator RTs remained the same. Furthermore, despite the outlined limitations, age group differences in task-related modulation of theta, alpha (presented in Appendix 4.2) and beta frequency were found, which warrant further investigation. Additional research is needed with a greater number of participants and trials to be able to make firm conclusions about the age-related changes in neural mechanisms that contribute towards difficulties in switching between temporal and spatial attention while driving.

Supporting current hypotheses and consistent with the MEG findings in Chapter 3, pilot EEG recordings revealed a theta increase shortly after the road sign onset, consistent with the notion of theta involvement in top-down guided attentional control and VS processing (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Demiralp & Başar, 1992; Green et al., 2008; Min & Park, 2010). An early beta decrease was seen that was initiated in response to the braking event and was maintained throughout the VS of the road sign, which likely reflects enhanced attention or motor preparation as participants have learned that a road sign will follow the breaking event (Gross, et al., 2006 Gola et al., 2012; Gola et al., 2013; Donoghue et al., 1998; Farmer, 1998; Kühn et al., 2004). A later broad-band alpha-beta desynchronization after road sign onset was also observed.

There were age group differences in patterns of theta modulation. Whereas the 18-30 years group displayed higher frontal and parietal theta in the Single-Task condition in comparison to each of the Dual-Task conditions, the 60+ years group displayed the reverse pattern with higher theta in the Dual-Task conditions in comparison to the Single-Task condition, in frontal, temporal and occipital regions. The greater theta modulation in the Single-Task condition compared to Dual-Task conditions that was observed in the younger group was unexpected. In the 18-30 years group theta modulation localised to a fronto-parietal network including the ACC, regions that are frequently observed in the VS literature (Coull and Nobre, 1998; Gross et al., 2004; Li et al., 2013; Madden et al., 2007; Shapiro et al., 2002) and during top-down attentional control (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Mechelli et al., 2000). Higher theta power in the Single-Task condition could reflect enhanced cognitive effort to attend to the road sign when driving at high speeds, in contrast to when participants brake shortly before the road sign onset in response to the braking event in the Dual-Task conditions. The 60+ years group, on the other hand, compensate for attentional deficits with decreased driving speeds to allow themselves more time to read the road sign, as is evident from reduced driving speeds that were observed with increased age. Instead, the 60+ years group require greater cognitive effort in the Dual-Task conditions to compensate for their deficit in switching between temporal and spatial attention.

Dual-Task Costs positively correlated with theta power modulation only in the 18-30 years group in the orbital part of the right SFG. As theta modulation increased, Dual-Task Costs increased. If increased theta modulation in the Single-Task condition is due to increased cognitive effort when driving at high speeds, it could be that those same participants also find switching between temporal and spatial attention while driving more cognitively demanding. It is likely that the small number of participants contributed to the absence of significant correlations between Dual-Task Costs and theta power modulation in other cortical regions and in the 60+ years group.

The TFRs in Figures 4.8 and 4.9 display a theta increase in response to the braking event in the two Dual-Task conditions. It was therefore surprising not to have found significant differences between Dual-Task and Single-Task conditions in theta modulation preceding the road sign. The braking event occurred either 3.04m or 30.48m before the road sign onset, causing the time between the braking event and the road sign onset to vary with the participants' driving speed. The timing of the early theta response relative to the road sign onset therefore varied across trials and participants. It may be that this variability prevented differences in this early theta modulation between Dual-Task and Single-Task conditions from becoming significant. If epochs were aligned in relation to the onset of the braking event, then it is likely we would see significant theta modulation differences between Dual-Task and Single-Task conditions following the braking event, however such an analysis is outside the scope of the current hypotheses.

In an early time window, greater beta (15-25Hz) desynchronization was observed in the Dual-Task conditions in comparison to the Single-Task condition, a difference that was initiated by the detection of the vehicle involved in the braking event. Participants likely learn that a braking event will shortly be followed by the onset of a road sign. Beta desynchronization was localised to bilateral parietal lobes and likely reflects motor preparation (Kühn et al., 2004; Park et al., 2013; Zaepffel et al., 2013) or attentional enhancement (Park et al., 2016) as participants prepare to refocus attention spatially to attend and respond to the road sign. In a later time window, a greater broad-band alpha-beta desynchronization was again seen in the Dual-Task conditions compared to the Single-Task condition, localising to fronto-parietal regions, but also in the Single-Task condition compared to the Dual-Task conditions, localising to occipital lobes. Beta modulation in the occipital lobe signifies a role in enhancement of visual attention to the road sign (Gross et al., 2006; Gola et al., 2012; Gola et al., 2013) rather than motor preparation. Note that the same pattern of findings were observed in alpha (8-12Hz) frequency, which are presented in Appendix 4.2. It appears that a stronger alpha-beta response occurs in visual processing regions when the onset of the road sign is unpredictable in the Single-Task condition compared to when it is predicted in the Dual-Task conditions, possibly due to the absence of anticipatory beta desynchronization that is observed in the Dual-Task conditions.

In the early time window, immediately after the onset of the road sign, the 60+ years group displayed a weaker beta decrease in Dual-Task conditions compared to the younger group, particular in posterior regions (Figure 4.9 B bottom row). Greater beta desynchronization in the Immediate Switch compared to the Single-Task condition was not significant in the older group (p>.10), and although Delayed Dual-Task beta modulation was more widely distributed and involved additional frontal and temporal regions in the older group (Figure 4.9. B), power modulation was significantly weaker compared to the 18-30 years group. It could be that the smaller number of participants prevented differences from reaching significance (n=13 compared to 17 in the younger group), however, impairments in preparatory beta desynchronization is consistent with impaired anticipatory attention mechanisms seen in older age (Deiber et al., 2013; Gamboz et al., 2010; Zanto et al., 2011). It could be that this age group difference in beta modulation is related to differences in theta oscillations reported in the current chapter. The older group but not the younger group demonstrate a greater theta increase in the Dual-Task condition compared to the Single-Task condition, reflecting the allocation of more attentional resources in the Dual-Task conditions. It appears that the younger group engage in efficient preparatory mechanisms, reflected in beta desynchronization, in anticipation of the road sign in the Dual-Task conditions, reducing cognitive effort applied when the road sign appears. In contrast, the older group presents weaker beta desynchronization, which possibly reflects poor preparatory mechanisms that lead to increased cognitive effort, evident in a greater theta increase in the Dual-Task conditions compared to the Single-Task condition. This pattern of a weaker preparatory beta desynchronization and an enhanced theta response in the older age group is consistent with theories that posit that older adults move away from “proactive control” which utilises top-down information such as cues to prepare for a response, and move towards a “reactive control” in response to an event (Braver et al., 2009). Older participants failed to display “proactive” beta desynchronization and instead showed a more “reactive” theta response.

Age-related changes in beta oscillations are consistent with previous literature (Gola et al., 2012; Gola et al., 2013; Karrasch et al., 2004; Christov and Dushanova, 2016), particularly with a failure to modulate beta during motor preparation reflected in reduced lateralisation (Deiber et al., 2013). In an auditory discrimination task Christov and Dushanova (2016) found that, in comparison to younger adults, older adults demonstrated a weaker beta increase during sensory processing of an auditory target (50-250ms) and a greater beta decrease during cognitive processing of the same target (400-600ms). Similarly, in a visual attention task, Gola et al. (2013) observed that, in contrast to younger adults and high performing older adults, low performing older adults displayed occipital beta desynchronization instead of beta synchronisation during the presentation of a cue that preceded target onset. Increased beta oscillations preceding a target stimulus has previously been associated with improved target perception of visual targets (Hanslmayr et al., 2007; Kamiński et al., 2012). Although we did not observe a beta increase prior to road sign onset, current findings further corroborate age-related reductions in task related beta modulation, while additionally demonstrating that older participants display a weaker parietal beta desynchronization to prepare for target processing and response. Further research is required to distinguish whether this beta desynchronization reflects enhanced visual attention or motor response preparation.

Contrary to the MEG findings and our hypotheses, we did not find substantial evidence to support a PASA hypothesis of cognitive ageing in the EEG oscillatory signatures. In the MEG data we observed a posterior theta deficit accompanied by increased anterior theta power, both of which correlated with performance (i.e. Switch-Costs). Although we observed some additional frontal and temporal EEG beta desynchronization in the older group (Figure 4.9 B top right), as well as greater posterior beta desynchronization in the younger age group compared to the older age group (Figure 4.9 B bottom row), these were not seen consistently across conditions and did not correlate with Dual-Task Costs. Furthermore, a posterior to anterior shift was not observed in theta frequency. Therefore, the EEG data only partially support PASA hypotheses.

In addition to limitations that have been outlined above, there were a number of further limitations to the study. Firstly, due to the STISIM drive software providing only the option to programme events into the scenario in distance travelled rather than time elapsed, the sign appeared either 3.04m or 30.48m after the braking event. This resulted in the temporal dynamics of each trial being effected by the speed that the participant was driving. This has been taken into careful consideration when interpreting findings.

Despite the increased ecological validity of participants switching between temporal and spatial attention in the driving simulator in comparison to in the computer based switching paradigm, the scenario is still very different from on-road driving. For example, not all individuals would prioritise trying to read a road sign immediately after braking harshly in response to another vehicle. However, the task was designed to measure switching between temporal and spatial attention while driving, which would be difficult to do safely in an on-road driving study. The driving simulator enabled us to measure switching performance while driving, in a controlled and safe environment.

A further limitation of the study is that the VS road sign (displayed in Figure 4.2) contained three columns of names that the target could occur in, with the left-hand column corresponding to a left indicator response and the two right-hand columns corresponding to a right indicator response. On 50% of trials a right-hand indicator response was required and on 50% of trials a left-hand indicator response was required. This enabled participants to apply a strategy of only reading words in the left column. It is not expected that this affected our main findings for two reasons. Firstly, the number of occurrences of the target word in each column of the sign was matched across conditions, trials were pseudo-randomised within each of the three blocks and the order that the three blocks were completed in was counterbalanced across participants. Therefore this strategy could not have been systematically implemented in one condition more than the others. Secondly, there is no evidence to suggest that older participants would be less able to identify and implement this strategy in comparison to younger adults. Conversely, evidence consistently shows that older participants utilise top-down cues more than younger adults, including contextual cues in a realistic VS (Neider & Kramer, 2011). Older age groups displayed slower RTs and higher Dual-Task Costs in comparison to younger adults, suggesting that, if they were more likely to implement such a strategy, it did not affect our findings.

4.1.6 Conclusions

The aim of the current chapter was to investigate whether age-related difficulties in switching from temporal to spatial attention are also seen in a more ecologically valid setting, during simulated driving. Consistent with hypotheses, RTs were slower in the two Dual-Task conditions in comparison to the Single-Task condition. Unexpectedly, RTs were slower in the Delayed Switch condition in comparison to the Immediate Switch condition, likely due to the two well-known phenomena of increased RTs with increased time elapsed between the presentation of a cue (i.e. the braking event) and a target stimulus (i.e. the road sign) and increased RTs when the temporal onset of a target stimulus is unpredictable (Correa & Nobre, 2008; Coull & Nobre, 1998; Griffin et al., 2001; Woodrow, 1914). The hypothesis that there would be an age-related decline in switching from temporal to spatial attention while driving was supported, reflected in greater Dual-Task Costs in older age groups in comparison to the youngest age group. These findings support that age-related declines in refocusing from temporal to spatial attention are not only observed in the computer based switching task but are also present in a more realistic setting such as when driving. Age-related changes in task-related theta and beta modulations were found. Whereas the younger adults displayed greater theta increases in the Single-Task condition in comparison to the Dual-Task conditions, the older group showed higher theta in the Dual-Task conditions in comparison to the Single-Task condition. Furthermore, the older group displayed a weaker beta desynchronization in preparation for the road sign onset. It appears that the younger group engaged in efficient preparatory mechanisms, reflected in beta desynchronization, in anticipation of the road sign in the Dual-Task conditions, reducing cognitive effort applied when the road sign appears. In contrast, the older group presented weaker beta desynchronization, which possibly reflected poor preparatory mechanisms that lead to increased cognitive effort, evident in a greater theta increase in the Dual-Task conditions compared to the Single-Task condition. Despite the small number of trials and the small number of EEG participants age group differences in task-related modulation of theta, alpha (presented in Appendix 4.2) and beta frequency were found, which warrant further investigation. Further research is needed with increased numbers of both participants and trials to corroborate current findings of age group differences in oscillatory signatures underlying switching between temporal and spatial attention in simulated driving.

Chapter 5

General Discussion

5.1 General Discussion

5.1.1 Summary of aims and background

Despite the vast literature investigating spatial attention and temporal attention and how these change with age (Bennett et al., 2012; Foster et al., 1995; Humphrey & Kramer, 1997; Lahar et al., 2001; Lee & Hsieh, 2009; Li et al., 2013; Maciokas & Crognale, 2003; Plude & Doussardroosevelt, 1989), there has been very little research looking at our ability to switch or refocus between these two types of attention within any age group. The ability to efficiently refocus attention between temporal events and spatial locations is likely to be important for driving. For example, it is often necessary to refocus attention from attending to the fast changing traffic and events on the road ahead, to distributing attention to attend to road signs, pedestrians and other hazards in the surroundings. Older drivers have previously reported finding it difficult to read road signs in time (Musselwhite & Haddad, 2010). Consistent with self-reports, yet despite an overall reduced risk of collisions in older compared to younger drivers, older drivers have a disproportionately high risk of causing collisions at intersections as well as collisions by failing to give way, or to notice other objects, stop signs or signals (Arai & Arai, 2015; Guo et al., 2010; Hakamies-Blomqvist, 1993; McGwin & Brown, 1999). These at-fault collision statistics support Parasuraman and Nestor’s (1991) conclusions that older drivers’ accidents were often due to failures in attention, particularly selective attention and switching. Together these findings warranted further investigation into age-related changes in the ability to refocus attention from attending to events changing in time on the road ahead (i.e. temporal attention) to attending to spatial locations such as road signs or other vehicles at intersections (i.e. spatial attention).

The aim of the current project was therefore to investigate whether there is indeed an age-related decline in the ability to refocus attention between temporal and spatial attention, and if so, firstly to explore the neural mechanisms that might help to explain this difficulty in attentional refocusing, and secondly to explore whether such a decline is present during simulated driving. Considering the at-fault collision statistics outlined above, revealing difficulties in attentional refocusing while driving would stress the importance of developing an intervention to improve switching between modalities of attention while driving to help to improve driver performance and safety in older age, as well as the safety of other drivers on the road. This would have the long-term benefit of prolonging the time that older drivers can continue to drive and help to preserve their independence.

5.1.2 Principal findings

Refocusing attention between time and space

A series of experiments in Chapter 2 confirmed our hypotheses of an age-related decline in refocusing attention from attending to events changing in time to distributing attention across spatial locations. Such difficulties were apparent in a task where participants switched from focusing attention in time, in order to identify a target in an RSVP stream, to focusing attention spatially, to identify a target in a VS display. VS RTs were slower when participants had to rapidly switch to the VS task from attending to the RSVP stream (i.e. when the RSVP target was towards the end of the stream or absent from the stream), compared to when they were no longer required to attend to the RSVP stream (i.e. when the RSVP target was the first item in the stream). We have referred to this VS RT cost of refocusing as “Switch-Costs”. Age-related declines in refocusing attention between time and space were reflected in increased Switch-Costs in older age groups (40-49, 50-59, 60+ years) compared to younger adults. The 40-49 and 50-59 years groups were initially intended as middle-aged comparison groups for the older groups. Findings of higher Switch-Costs in participants aged 40-49 and 50-59 years compared to those aged 21-30 years in Experiment 3 of Chapter 2 were therefore surprising and meant that it was more appropriate to compare the 40-49 years group with the younger age group throughout the MEG data, particularly as there were no significant differences in Switch-Costs between the 40-49 years and older age groups. As we were not expecting to find age group differences in participants age 40-49 years we did not explore the ability to refocus attention in a 30-39 years group. Future research could include a 30-39 years group to observe how attentional refocusing changes throughout the adult lifespan.

Two previous studies have compared age groups on switching from temporal to spatial attention. Lee and Hsieh (2009) and Russel et al. (2013) found that, compared to younger adults, older adults’ responses were slower and less accurate when pointing to a peripheral target (i.e. a spatial attention task) up to 450ms after detecting a target in an RSVP stream (i.e. a temporal attention task). Both of these studies aimed to investigate age-related changes to the attentional blink. It was not clear from their findings whether age-related impairments were due to an increased magnitude of the attentional blink (i.e. an extended time of impaired target processing after processing a preceding target) or due to a decline in the ability to refocus attention from temporal to spatial attention. Throughout the current work, the addition of the No-Target Switch condition, where the target was absent from the RSVP stream, allowed us to distinguish between deficits in an increased magnitude of the attentional blink and deficits in refocusing attention between time and space. Age group differences in switching from the Target RSVP stream but no age group differences in switching from the No-Target RSVP stream could signify that deficits were due to an increased magnitude of the attentional blink. On the contrary, in Experiment 4 in Chapter 2, we found that the 60+ years group was impaired at switching to the VS task both from Target and No-Target RSVP streams compared to younger adults. Our findings therefore corroborate previous findings (Lee & Hsieh, 2009; Russel et al., 2013) and provide novel information that in addition to an increased magnitude of the attentional blink, there are further age-related difficulties in refocusing attention from time to space.

Driving

After finding age group differences in refocusing from temporal to spatial attention in a computer based task, it was important to identify whether such deficits were also present when switching between attentional modalities in a more ecologically valid scenario, during simulated driving. Confirming our hypotheses, in Chapter 4 we found that older participants were impaired at refocusing attention from attending to events changing in time to distributing attention across spatial locations during simulated driving. Such difficulties were apparent in a driving simulator task where participants refocused from attending to events changing in time, where participants attended to the fast changing traffic in front of them, to allocating attention spatially, in order to complete a VS of a road sign. Road sign VS RTs were slower in Dual-Task conditions, when participants switched from reacting to a temporal event (i.e. braking in response to a vehicle braking in front of them) in comparison to the Single-Task condition, when there was no preceding "braking event" and participants completed the road sign VS only. We have referred to this RT cost as "Dual-Task Costs". We found significantly higher Dual-Task Costs in older age groups (40-49, 50-59, 60-69 and 70+ years) compared to a younger age group (18-30 years). Our findings therefore support that age-related declines in refocusing attention from time to space are present during simulated driving.

Conflicting with our predictions, the three oldest age groups were impaired further when they had more time to prepare for the onset of the road sign after the braking event. It seems that the older participants' ability to maintain top-down attentional guidance after the onset of a cue (i.e. the braking event) diminishes after a more prolonged period of time. This conclusion is consistent with the notion that older adults move away from "proactive control" which utilises top-down information such as cues to prepare for a response, and move towards a "reactive control" in response to an event (Braver et al., 2009). It therefore seems that the frequently observed increased utilisation of cues and top-down attentional guidance in older age is task dependent. The current findings seem to suggest that older participants are impaired when top-down attentional guidance is required for a prolonged period of time, which was further reflected in age group differences in preparatory beta modulation (discussed in more detail below). Overall, our findings have important implications for future research, as it could be that deficits in refocusing attention contribute towards older drivers' disproportionately higher risk of collisions at intersections and impair their ability to process other objects in the environment, not just road signs (Arai & Arai, 2015; Guo et al., 2010; Hakamies-Blomqvist, 1993; McGwin & Brown, 1999; Musselwhite & Haddad, 2010; Parasuraman & Nestor, 1991), as participants cannot efficiently refocus from attending to and reacting to the traffic ahead to spatially distribute attention in order to process information in multiple surrounding spatial locations. This deficit could be further exacerbated by difficulties in anticipating events over longer periods of time.

Neural mechanisms

There is a fast growing literature demonstrating that older adults display more widely distributed activity across the cortex in comparison to younger adults (Adamo et al., 2003; Lague-Beauvais et al., 2013; Li et al., 2013; Madden, Spaniol, Whiting, et al., 2007). It has been debated as to whether this increased activity reflects neural noise and dedifferentiation (Cabeza, 2002; Huettel et al., 2001; Polich et al., 1985; Shih, 2009; Welford, 1981) or compensatory recruitment (Fabiani et al., 2006; Madden, Spaniol, Whiting, et al., 2007).

The PASA hypothesis of neural ageing (Davis et al., 2008) proposes that throughout healthy ageing there is a reduction in posterior activity accompanied by a compensatory increase in anterior activity. There is evidence for decreases in posterior activity across a range of tasks (Buckner et al., 2000; Cabeza et al., 2004; Davis et al., 2008; Huettel et al., 2001; Madden et al., 2002; Ross et al., 1997) including reduced magnitude and spatial extent of visual cortex response during visual processing (Buckner et al., 2000; Huettel et al., 2001; Ross et al., 1997). There is also ample evidence for increased activity in frontal regions (Cabeza et al., 2004; Grady, 2000; Madden, 2007). Cabeza et al. (2004) found an age-related increase in the right posterior parietal cortex which was positively correlated with task performance in working memory and visual attention tasks, as well as with PFC activity. Furthermore, Madden et al. (2007) found that, whereas an occipital hemodynamic response was associated with young participants’ performance, frontoparietal activity correlated with older adults’ performance. It is thought that as lower level sensory processing deteriorates, recruitment of the frontal lobe increases to compensate for functional decline (Cabeza et al., 2004; Davis et al., 2008; Madden et al., 2007).

In contrast to a compensatory account of more widely distributed activity, it has been argued that increased activity reflects neural noise and dedifferentiation (Cabeza, 2002; Huettel et al., 2001; Polich et al., 1985; Shih, 2009; Welford, 1981). Shih (2009) proposed that both increased neural noise and inhibitory deficits result in increased activation thresholds to select visual stimuli. Increased neural noise is supported by the reduced amplitudes that are observed in event related potentials as a result of increased age-related variability (Polich et al., 1985) and increased variability and higher noise levels found with fMRI in older age groups (Huettel et al., 2001). Similarly, Cabeza (2002) proposed a dedifferentiation hypothesis of neural ageing, where ageing results in a decreased specialisation of cortical processing.

In light of the contradictory theories of ageing, combined with evidence towards age-related deficits in alpha, theta and beta modulation (Cummins & Finnigan, 2007; Finnigan et al., 2011; Reichert et al., 2016; van de Vijver et al., 2014) we hypothesised that MEG and EEG would reveal age-related changes in alpha, beta and theta oscillations that would help to explain age group differences in refocusing attention in both the computer based task and during simulated driving, which are summarised above in the current chapter. It was expected that there would either be an age-related reduction in theta power, particularly across the frontal midline as has been demonstrated in previous EEG studies (Cummins & Finnigan, 2007; van de Vijver et al., 2014) or an increase in frontal theta activity reflecting additional top-down compensatory processing (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007). Based on previous literature it was expected that older adults would display abnormal alpha modulation, either through a weaker alpha power increase (Vaden et al., 2012) or through a weaker alpha power decrease (Deiber et al., 2013; Zanto et al., 2011). Age group differences in beta modulation were expected, possibly with a greater beta desynchronization with increased age (Christov & Dushanova, 2016). In MEG data, functional oscillatory connectivity at theta and alpha frequencies was expected to either become weaker with increased age, as would be proposed by increased neural noise theories of ageing (Shih, 2009; Welford, 1981), or increase with increased age, as would be expected from compensatory recruitment (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007).

The MEG findings outlined in Chapter 3 regarding theta oscillations further support the PASA compensatory hypothesis of ageing. We observed both task related occipital theta deficits and task related increased frontal theta in the two older groups compared to the younger groups. Furthermore, in the oldest group, increased switch-related frontal theta power was correlated with reduced Switch-Costs and reduced switch-related occipital power correlated with increased Switch-Costs. Consistent with increased MEG frontal theta power, older adults displayed more extensive functional network connectivity in comparison to younger adults. An increase in frontal activity is consistent with behavioural evidence of increased reliance on top-down attentional control in older age (Neider & Kramer, 2011; McLaughlin et al., 2010). In addition to compensatory frontal recruitment, the 60-69 years group displayed additional temporal recruitment, which could reflect the implementation of further compensatory strategies with increased cognitive decline, such as silent vocalisation (Graves et al., 2007; Hickok & Poeppel, 2007; Hocking & Price, 2009; Smith et al., 1998) or episodic memory encoding (Schacter & Wagner, 1999). In contrast to Cabeza et al.'s (2004) findings of increased parietal activity accompanying reduced occipital activity, in both the MEG and EEG recordings in Chapters 3 and 4 we found older age groups failed to display parietal activity that is usually observed during enhanced attention (Coull & Nobre, 1998; Li et al., 2013; Madden et al., 2007; Shapiro et al., 2002).

In contrast to the clear compensatory functionalities of MEG theta, the role of the widely distributed alpha power in the MEG findings was less clear. In contrast to theta connectivity, alpha connectivity was not stronger and more widely distributed in older than younger adults. This could either suggest that the widely distributed alpha power that was observed in the older group reflects neural noise, or it could reflect poor estimation of alpha connectivity due to lower alpha power and a lower SNR (stronger alpha decrease = smaller relative amplitudes). Furthermore, task-related alpha power differences did not correlate with Switch-Costs and therefore appeared unrelated to switching performance. Alpha power reflecting increased neural noise would be consistent with Vaden et al.'s (2012) proposition that alpha becomes redundant with increased age. Previous literature has shown that prestimulus alpha desynchronization no longer predicts successful stimulus processing in older age (Deiber et al., 2013) as it does in younger adults (Sauseng et al., 2005). If pre-stimulus alpha desynchronization no longer predicts successful target stimulus processing in older age (Deiber et al., 2013) the question remains as to whether alpha desynchronization predicts target processing in middle-age. Questions also arise as to how alpha is functionally relevant in older age, and what alternative mechanisms are implemented to gate sensory processing (Jensen & Mazaheri, 2010) and enhance attention to visual stimuli if not alpha oscillations (Capotosto et al., 2009; Hanslmayr et al., 2007; Hanslmayr et al., 2005; Klimesch et al., 2007; Sauseng et al., 2005; Thut et al., 2006; Yamagishi et al., 2003).

Deiber et al. (2013) found that older adults' reduced posterior alpha desynchronization in response to a cue was accompanied by increased beta modulation. The authors concluded that older adults compensate for poor posterior alpha anticipatory attention mechanisms with increased motor preparation in beta frequency. However, age-related deficits in beta modulation have also been found (Christov & Dushanova, 2016; Gola et al., 2012; Gola et al., 2013; Karrasch et al., 2004). Furthermore, in Chapter 4 during simulated driving, rather than an increase in motor preparation reflected in beta frequency (conforming to Deiber et al., 2013), older adults displayed reduced beta desynchronization in anticipation of the VS road sign onset. In addition, alpha and beta power displayed similar neural signatures (in terms of task modulation and cortical distribution), with modulation appearing to occur over a broad alpha-beta band, suggesting that age-related changes would be concomitant across an alpha and beta frequencies. Deiber et al.'s (2013) conclusions of older adults' compensatory motor preparation in beta frequency can therefore not be generalised across tasks and further research is required to investigate both age group differences in beta frequency and in mechanisms associated with sensory gating in older age.

Although evidence supporting a PASA hypothesis of ageing was less substantial in the EEG data that was recorded during simulated driving, the older group did show beta desynchronization in the Dual-Task conditions in additional frontal and temporal regions (Chapter 4 Figure 4.9 B), but weaker posterior beta desynchronization compared to the younger adults. Furthermore, participants seemed to compensate for a decline in preparatory beta desynchronization with an increased theta response to the road sign onset, supporting a "reactive" rather than a "proactive" control strategy (Braver et al., 2009; Dew et al., 2012). Driving is also more open to alternative behavioural compensation strategies compared to computer based tasks. For example, the younger age group allocated more resources to processing the sign in the Single-Task condition compared to the Dual-Task condition (reflected in a stronger theta signature), possibly due to increased attentional demands of reading the road sign when driving at high speeds compared to when participants have slowed down in response to the braking event. The 60+ years group on the other hand compensated for these attentional demands by driving more slowly. These findings highlight that, in more ecologically valid settings, older participants may adjust behaviour to compensate for functional decline to reduce the pressure on processing resources during a more demanding task, in turn reducing the amount of compensatory recruitment required throughout completion of the task. In contrast, in computer based tasks there is less opportunity to implement such compensatory behavioural strategies and so compensatory recruitment on a neural level is more prominent throughout task processing.

An intermediate stage of ageing

The 40-49 and 50-59 years groups seem to present an intermediate stage of ageing, where some cognitive processes are less efficient but not others. It could be beneficial to take advantage of these age groups to reveal which cognitive mechanisms decline earlier or faster than others. For example, in Experiment 3 in Chapter 2 the 40-49 years group did not differ from the 21-30 years group in overall VS RTs, but display age-related declines in the form of increased attentional Switch-Costs. Presenting a second example, in Experiment 6 in Chapter 2 the 50-59 years group differed significantly from the youngest age group in VS RTs, but not in RSVP RTs in response to RSVP target detection, possibly reflecting deterioration in spatial attention earlier in life compared to temporal attention (Bennett et al., 2012; Conlon & Herkes, 2008; Li et al., 2013; Shih, 2009). Additionally, this finding further corroborates evidence that orienting attention in time and distributing attention spatially involve in part different underlying neural mechanisms (Coull & Nobre, 1998). To advance our understanding of how temporal and spatial attentional mechanisms differ, future research trajectories could further investigate age group differences between temporal and spatial attention to find out how the mechanisms of different modalities of attention deteriorate with increased age. For example, it would be interesting to identify precisely which neural mechanisms decline to lead to a faster deterioration of spatial than temporal attention.

The two middle-age groups also differed from older and younger groups in that they showed no difference in RSVP RT across different RSVP conditions in Experiment 6. Whereas both the younger group and the two older groups all presented with slower RTs to respond to the RSVP target when it was the first item in the stream compared to when it was towards the end of the stream, the 40-49 and 50-59 years age groups showed no difference between RSVP conditions. One explanation for this could be that they differ from the youngest and the two older groups in different ways. Firstly, they may differ from the youngest group as they gain no benefits from having longer to focus attention in time, either due to weaker temporal attentional enhancement or delayed temporal attentional enhancement (>700-900ms, i.e. after RSVP target presentation). Secondly, they may differ from the 60-69 and 70+ years groups in that the older groups are additionally impaired in inhibiting irrelevant visual distractors from the stream of letters that are presented after RSVP target onset (Adamo et al., 2003; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig et al., 2007; Maciokas & Crognale, 2003). It therefore seems that participants in the two middle-age groups may show equivalent RSVP RTs across the two RSVP conditions due to gaining no benefit from having longer to orient attention in time but also due to preserved inhibitory mechanisms for inhibiting the RSVP distractor stimuli efficiently.

Furthermore, during simulated driving, whereas the 50-59 and 60-69 years groups displayed increased Delayed Dual-Task Costs but not Immediate Dual-Task Costs compared to the 18-30 years group, the 40-49 years group displayed higher Immediate Dual-Task Costs but showed no difference in Delayed Dual-Task Costs. Note that the 70+ years group showed significantly higher Delayed and Immediate Dual-Task Costs compared to the younger adults. The Delayed Switch condition differed from the Immediate Switch condition in that there was a larger distance to travel between the braking event, which behaved as a cue, and the road sign onset. A longer distance resulted in a longer time delay between the braking event and the road sign, in addition to increased variability in the time delay with variability in participants' driving speeds. It is well known that RTs increase with increased time elapsed between the presentation of a cue (i.e. the braking event) and a target stimulus (i.e. the road sign) and when the temporal onset of a target stimulus is unpredictable (Correa & Nobre, 2008; Coull & Nobre, 1998; Griffin et al., 2001; Woodrow, 1914). It could be that these phenomena influence attention refocusing in the three oldest age groups but not the 40-49 years group. Recall that indicator RTs in the Immediate and the Delayed Dual-Task conditions differed very little in the 40-49 years group (Figure 4.4 Chapter 4) contrary to the other age groups. Inflated effects of longer and unpredictable time delays between a cue and a target in older age groups coincides with evidence towards impaired anticipatory attention mechanisms with increased age (Deiber et al., 2013; Gamboz et al., 2010; Zanto et al., 2011) and a greater dependence on top-down guidance to control attention, such as implementing the use of temporal cues (McLaughlin & Murtha, 2010; Neider & Kramer, 2011; Watson & Maylor, 2002). EEG recorded during simulated driving demonstrated that, compared to the younger group, the older group displayed weaker beta desynchronization in anticipation of the road sign onset. It could be that the younger and middle-aged adults were able to maintain efficient anticipatory attention mechanisms during this extended time period, but the impaired anticipatory mechanisms in the older groups, reflected in weaker beta desynchronization in a subset of participants aged 60+ years, resulted in longer and more variable time delays between the braking event cue and the road sign target hindering older age groups' performance.

The presentation of the 40-49 years group as an intermediate stage of ageing was also evident in the MEG data, particularly in network connectivity. The 60+ years group displayed more extensive theta network connectivity compared to the youngest age group across almost all conditions as they compensated for functional decline. The 40-49 years group on the other hand displayed weaker connectivity in the No-Switch condition in comparison to the younger age group, when there were low task demands, but displayed more extensive theta network connectivity compared to the younger age group when there were increased cognitive demands in the two Switch conditions. A similar pattern was apparent in network topology. Only the 40-49 years group displayed significant differences between Switch and No-Switch conditions in network topology in both local measures of eccentricity presented in Appendix 3.6, and global measures of mean eccentricity in Chapter 3 Section 3.1.4. It may be that no differences were seen in the younger age group as they require few additional resources in the Switch condition compared to the No-Switch condition as they are efficient at refocusing their attention. In contrast, the oldest group display minimal differences in network topology between No-Switch and Switch conditions, due to impaired attentional mechanisms resulting in the requirement to implement similar attentional resources in the No-Switch condition that are applied in the Switch condition. The 40-49 years age group on the other hand display efficient attentional performance when there are low cognitive demands in the No-Switch condition, as is evident in both network connectivity and RT data, but are impaired on the Switch conditions when there are increased attentional demands and therefore recruit additional attentional resources.

The 40-49 and 50-59 years groups displaying age-related decline in some aspects of cognition and neural functioning but not others has implications for future research. Firstly, previous studies have included participants in their 50s in an “elderly” group to investigate the decline of certain cognitive functions in older age (Bennett et al., 2012; Li et al., 2013). Our findings highlight the need to provide better justification for the age-ranges selected as age groups, as including those aged 52 years in a group with participants aged 75 years does not seem appropriate, particularly in groups of fewer than 20 participants (Bennett et al., 2012; Li et al., 2013). Secondly, there is relatively little work that has explored cognitive ageing in middle-age groups compared to the literature that has investigated age-related changes in cognition in participants over the age of 60 years. In addition to taking more of an evidence based approach in selecting age groups, future research should aim to include middle-aged comparison groups to develop a better understanding of how distinct cognitive processes (e.g. temporal vs. spatial attention) may present with different trajectories of decline throughout the adult lifespan.

5.1.3 Limitations and future directions

Throughout the current work we have investigated age group differences only in switching from temporal to spatial attention. Jefferies et al. (2015) found that older participants took longer to narrow their focus of attention from two RSVP streams to one stream compared to younger adults, which could reflect difficulties in switching from distributing attention to multiple locations in space (i.e. spatial attention) to orienting attention in time. Although, an alternative possibility is that older adults' took longer to refocus attention due to their impaired inhibition of and slow disengagement from the no longer relevant RSVP stream (Adamo et al., 2003; Gazzaley et al., 2008; Greenwood & Parasuraman, 1994; Hasher & Zacks, 1988; Lustig et al., 2007; Maciokas & Crognale, 2003). While it is expected that impairments in refocusing attention would also be apparent when refocusing attention from spatial to temporal attention, further work is needed to investigate this hypothesis. This hypothesis remains relevant to driving behaviour, as drivers are often required to refocus from attending to a road sign (i.e. spatial attention) to attending to and reacting to a vehicle in front of them (i.e. temporal attention). Impairments in refocusing attention from spatial locations to temporal events would be particularly hazardous at intersections and roundabouts.

In the computer based switching task, we did not explore how switching affects the ongoing VS processes, as the number of distractor stimuli in the VS display was not manipulated. In the current project we were interested in the efficiency of switching to initiate a search. Further research is required to investigate how switching influences ongoing search processes. It may be that switching has a large effect on search speed at the beginning of a search but the effect on search speed plateaus with increasing numbers of distractors, as time since the switch increases. Alternatively, if there is only a cost in initiating the VS, it may be that Switch-Costs remain constant or get proportionally smaller with increasing numbers of distractors.

Furthermore, it may be that Switch-Costs are not specific to switching between types of attention, but would also affect performance in other cognitive functions. The decision to investigate refocusing attention from temporal to spatial attention specifically was based on evidence from on road driving performance and collision statistics that implicated impairments in the flexibility of attention in at-fault collisions (Arai & Arai, 2015; Guo et al., 2010; Hakamies-Blomqvist, 1993; McGwin & Brown, 1999; Musselwhite & Haddad, 2010; Parasuraman & Nestor, 1991). Although this difficulty may generalise to other tasks, it is switching between temporal and spatial attention that is important to driving, where declines in efficiency may have a negative impact on a person's life and jeopardise their safety.

As the current thesis focuses on age-related changes in flexible attentional control of visual processing, the current focus remains on the lower frequency oscillations of theta, alpha and beta frequencies and does not explore gamma oscillations. However, gamma oscillations have been shown to play a key role in visual processing (Cabral-Calderin et al., 2015; Gruber et al., 1999; Womelsdorf et al., 2006). It has been suggested that higher level cognitive control guides lower level visual processing though a mechanism in which gamma oscillations are modulated by long-range synchronisation with lower frequency oscillations such as theta and alpha oscillations (Canolty et al., 2006; Canolty & Knight, 2010; Doesburg et al., 2009b; Doesburg et al., 2015; Osipova et al., 2008; Voytek et al., 2010). It is therefore likely that the age related changes in theta, alpha and beta oscillations have a direct effect on gamma oscillations. Future work could benefit from additionally investigating how age-related changes in theta, alpha and beta frequencies interact with gamma oscillations.

We have demonstrated that there is an age-related decline in refocusing attention between time and space that is present both in a computer based task and during simulated driving. It could be that impairments in attention refocusing are partly responsible for the disproportionately high at-fault collisions at intersections and collisions caused by failing to give way, or to notice other objects, stop signs or signals (Arai & Arai, 2015; Guo et al., 2010; Hakamies-Blomqvist, 1993; McGwin & Brown, 1999; Musselwhite & Haddad, 2010; Parasuraman & Nestor, 1991). Our driving simulator results have demonstrated that impairments in refocusing attention slows older and middle-aged participants' ability to read road signs. Future research should aim to investigate how impairments in switching between temporal and spatial attention while driving effect their ability to navigate intersections. For example, it might be expected that older drivers are slower at processing vehicles in their surroundings following a real life braking event, or slower at braking in response to sudden hazards after reading a road sign. Such hypotheses can be tested safely with simulated driving.

Despite the compensatory recruitment observed in the MEG data, older participants still display poorer performance compared to younger adults, reflected in increased Switch-Costs in the computer based task and increased Dual-Task Costs in the driving simulator paradigm. Compensatory activity demonstrates that older brains remain capable of neural plasticity (Cabeza et al., 2004; Davis et al., 2008; Madden et al., 2007). It may therefore be beneficial to utilise this plasticity in training programmes to help to improve attentional refocusing in older age. Previous literature has demonstrated that training programmes can be beneficial to cognition in an ageing population, including interventions that train visual processing speed, task switching and visual attention (Dennis, Scialfa, & Ho, 2004; Dorbath, Hasselhorn, & Titz, 2011; Edwards, Delahunt, & Mahncke, 2009; Edwards et al., 2013; Elliott, O'Connor, & Edwards, 2014; Karbach & Kray, 2009; Karbach, Mang, & Kray, 2010; Neider et al., 2010; Roenker, Cissell, Ball, Wadley, & Edwards, 2003). Training in computer based visual attention and processing speed tasks have been shown to transfer to simulated driving (Cassavaugh & Kramer, 2009), reduce the risk of having at-fault collisions and delay driving cessation (Ball, Edwards, Ross, & McGwin, 2010; Edwards, Perkins, Ross, & Reynolds, 2009). Furthermore, training programmes that utilise driving simulators or driving video games have been shown to result in greater improvements in driving performance than computer based training programmes, including when training multi-tasking and attention switching while driving (Anguera et al., 2013; Casutt, Theill, Martin, Keller, & Jaencke, 2014). Together the evidence outlined above supports that the development of an intervention to train attention refocusing in a driving simulator could be beneficial. It may also be advantageous to attempt to enhance the benefits of training with brain stimulation techniques such as TMS and transcranial direct current stimulation (tDCS). For example, Tayeb and Lavidor (2016) found that increasing excitability of the dorsolateral PFC with tDCS enhanced the benefits of practice on a switching task. Further supporting the benefits of brain stimulation throughout training, Cappelletti et al. (2013) found that transcranial random noise stimulation to the parietal lobe improved both short- and long-term training benefits in a numerosity task.

Taken together, examples of successful training programmes in older populations and our current findings warrant the development of an intervention to help to improve older adults' ability to refocus attention between time and space while driving. Evidence from the current project, suggests that improving switching performance could help older drivers solely by helping them to read road signs more efficiently, in turn improving drivers' confidence. Improving confidence could have the long-term benefit of prolonging the time that older drivers can continue to drive and help to preserve their independence, in turn reducing their risk of developing depression (Marottoli et al., 1997; Ragland et al., 2005; Windsor et al., 2007). If further research corroborates our hypothesis of a link between impaired refocusing and at-fault collisions at intersections, then developing an intervention to improve switching performance while driving would additionally be paramount for improving the safety of older drivers and of other road users.

5.1.4 Conclusions

The aim of the current project was to investigate whether there is an age-related decline in the ability to refocus attention between temporal and spatial attention, and if so, firstly to explore the neural mechanisms that might help to explain this difficulty in attentional refocusing, and secondly to explore whether such a decline is present during simulated driving. Our hypothesis that there would be increased difficulties in refocusing attention from time to space with increased age was supported, both in computer based tasks and during simulated driving. Older age groups were slower at switching from allocating their attention to events changing in time to refocusing their attention spatially. Such findings warrant a trajectory of research that first investigates how deficits in switching between temporal and spatial attention affect older drivers' performance in navigating intersections, and secondly to develop a training programme to improve refocusing between modalities of attention while driving, to help to improve driver performance and safety in older age.

Observed MEG oscillatory signatures were consistent the PASA hypothesis of ageing, where older and middle-aged groups displayed both a switch-related theta deficit in the occipital lobe and compensatory increases in frontal recruitment, likely as they place more weight on top-down attentional guidance. The oldest age group displayed additional temporal recruitment, which likely reflect additional compensation strategies. The EEG data displayed similar oscillatory signatures as the MEG data, where a theta synchronisation and an alpha-beta desynchronization was observed upon VS road sign onset. Whereas a theta deficit seemed to explain attentional impairments in the computer based task (recorded with MEG), in the driving simulator task the older group displayed primarily a deficit in EEG beta desynchronization in anticipation of the road sign onset after the braking event, which provides a possible explanation for poorer attention refocusing. Reduced beta desynchronization in the older group in the two Dual-Task conditions was accompanied by a greater theta increase compared to the Single-Task condition, possibly utilising more attentional resources after a diminished anticipation of the road sign compared to younger drivers. In contrast, younger drivers, displayed a greater theta increase in the Single-Task condition compared to the Dual-Task conditions, partly due to efficient preparatory mechanisms before road-sign onset (reflected in beta desynchronization) and partly due to an increase in cognitive demands when processing the road sign while driving at higher speeds. The older age group on the other hand compensated for attentional demands in the Single-Task condition by driving more slowly.

The 40-49 and 50-59 years groups display intermediate stages of ageing, evident in both behavioural and network connectivity (observed with MEG), where some cognitive mechanisms are impaired by age, such as refocusing attention between time and space, but some cognitive mechanisms are unaffected by age, for example when there is less demand on attention. These findings have future implications for the design of research that aims to explore cognition and neural functioning in healthy ageing.

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Appendix 1

There was no supplementary material for Chapter 1.

Appendix 2

Supplementary material for Chapter 2.

Appendix 2.1

Group comparisons of scores on cognitive measures

Participants' scores on five cognitive measures, including UFOV processing speed, divided attention and selective attention, and RNG task R and RNG index, were entered into five one-way ANOVAs to compare age groups.

There was a significant effect of age ($F(3, 80)=4.67$, $p=.005$) on UFOV selective attention thresholds. Post hoc comparisons illustrated that the 40-49 years group displayed significantly faster selective attention processing thresholds in comparison to the 70+ years age group ($p<.01$). There was also a non-significant tendency for participants in the 50-59 years group to have faster selective attention processing thresholds than the 70+ years age group ($p=.088$). There were no other age group differences in selective attention processing thresholds ($p>.10$).

There were no main effects of age on any other cognitive measure ($p>.10$).

Appendix 3

Supplementary material from Chapter 3.

Appendix 3.1

Table A3.1.1. Atlas labels, short form abbreviations and anatomical categorisation

Region	Category
Left Precental gyrus	f
Right Precental gyrus	f
Left Superior frontal gyrus, dorsolateral	f
Right Superior frontal gyrus, dorsolateral	f
Left Superior frontal gyrus, orbital part	f
Right Superior frontal gyrus, orbital part	f
Left Middle frontal gyrus	f
Right Middle frontal gyrus	f
Left Middle frontal gyrus, orbital part	f
Right Middle frontal gyrus, orbital part	f
Left Inferior frontal gyrus, opercular part	f
Right Inferior frontal gyrus, opercular part	f
Left Inferior frontal gyrus, triangular part	f
Right Inferior frontal gyrus, triangular part	f
Left Inferior frontal gyrus, orbital part	f
Right Inferior frontal gyrus, orbital part	f
Left Rolandic operculum	f
Right Rolandic operculum	f
Left Supplementary motor area	f
Right Supplementary motor area	f
Left Olfactory cortex	f
Right Olfactory cortex	f
Left Superior frontal gyrus, medial	f
Right Superior frontal gyrus, medial	f
Left Superior frontal gyrus, medial orbital	f
Right Superior frontal gyrus, medial orbital	f
Left Rectal Gyrus	f
Right Rectal Gyrus	f
Left Insula	I
Right Insula	I
Left Anterior cingulate and paracingulate gyri	f
Right Anterior cingulate and paracingulate gyri	f
Left Median cingulate and paracingulate gyri	f
Right Median cingulate and paracingulate gyri	f

Left Posterior cingulate gyrus	f
Right Posterior cingulate gyrus	f
Left Hippocampus	t
Right Hippocampus	t
Left Parahippocampal gyrus	t
Right Parahippocampal gyrus	t
Left Amygdala	t
Right Amygdala	t
Left Calcarine fissure and surrounding cortex	o
Right Calcarine fissure and surrounding cortex	o
Left Cuneus	o
Right Cuneus	o
Left Lingual gyrus	o
Right Lingual gyrus	o
Left Superior occipital gyrus	o
Right Superior occipital gyrus	o
Left Middle occipital gyrus	o
Right Middle occipital gyrus	o
Left Inferior occipital gyrus	o
Right Inferior occipital gyrus	o
Left Fusiform gyrus	c
Right Fusiform gyrus	c
Left Postcentral gyrus	p
Right Postcentral gyrus	p
Left Superior parietal gyrus	p
Right Superior parietal gyrus	p
Left Inferior parietal, but supramarginal and angular gyri	p
Right Inferior parietal, but supramarginal and angular gyri	p
Left Supramarginal gyrus	p
Right Supramarginal gyrus	p
Left Angular gyrus	p
Right Angular gyrus	p
Left Precuneus	p
Right Precuneus	p
Left Paracentral lobule	p
Right Paracentral lobule	p
Left Caudate nucleus	s
Right Caudate nucleus	s
Left Lenticular nucleus, putamen	s
Right Lenticular nucleus, putamen	s
Left Lenticular nucleus, pallidum	s
Right Lenticular nucleus, pallidum	s
Left Thalamus	Th
Right Thalamus	Th
Left Heschl gyrus	t

Right Heschl gyrus	t
Left Superior temporal gyrus	t
Right Superior temporal gyrus	t
Left Temporal pole: superior temporal gyrus	t
Right Temporal pole: superior temporal gyrus	t
Left Middle temporal gyrus	t
Right Middle temporal gyrus	t
Left Temporal pole: middle temporal gyrus	t
Right Temporal pole: middle temporal gyrus	t
Left Inferior temporal gyrus	t
Right Inferior temporal gyrus	t
Left Cerebelum Crus I	c
Right Cerebelum Crus I	c
Left Cerebelum Crus II	c
Right Cerebelum Crus II	c
Left Hemispheric lobule III	c
Right Hemispheric lobule III	c
Left Hemispheric lobule IV/V	c
Right Hemispheric lobule IV/V	c
Left Hemispheric lobule VI	c
Right Hemispheric lobule VI	c
Left Hemispheric lobule VIIb	c
Right Hemispheric lobule VIIb	c
Left Hemispheric lobule VIII	c
Right Hemispheric lobule VIII	c
Left Hemispheric lobule IX	c
Right Hemispheric lobule IX	c
Left Hemispheric lobule X	c
Right Hemispheric lobule X	c
Vermic lobule I/II	c
Vermic lobule III	c
Vermic lobule IV/V	c
Vermic lobule VI	c
Vermic lobule VII	c
Vermic lobule VIII	c
Vermic lobule IX	c
Vermic lobule X	c

Standardised node labels and anatomical category for plotting in the matrix plots. Categories were frontal (f), occipital (o), parietal (p), temporal (t), cerebellum (c), insula (i), striatum (s) and thalamus (th).

Appendix 3.2

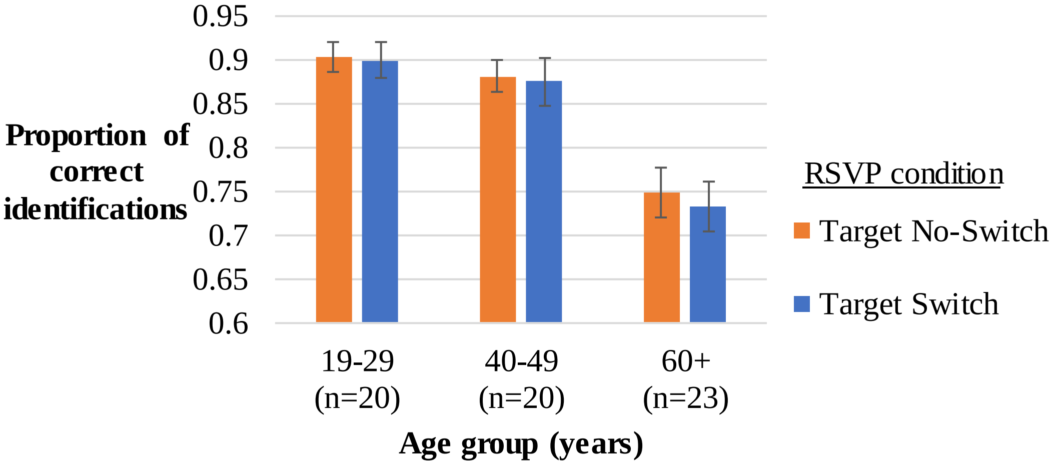

Figure A3.2.1. Proportion of correct RSVP target identifications. Vertical bars represent the standard error of the mean.

Appendix 3.3

Table A3.3.1. MNI coordinates and atlas labels from which theta power differences between Target Switch and No-Switch conditions were extracted for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
40-49	+	-0.6 3.8 0.4	Left anterior cingulate and paracingulate gyri
40-49	+	0.6 0.8 -0.6	Right caudate
40-49	+	-0.4 -1.2 1.8	Left thalamus
60+	+	-4.4 -4.2 -4.6	Left hemispheric lobule VIIb
60+	+	-1.0 -4.2 -0.6	Left lingual gyrus
60+	+	-5.0 -1.6 -1.2	Left middle temporal gyrus
60+	+	0.2 -1.2 0.4	Right thalamus
60+	+	5.6 0.8 3.4	Right precentral gyrus
60+	+	-3.0 5.8 0.8	Left middle frontal gyrus
60+	+	-4.6 -6.6 4.8	Left angular gyrus
60+	+	-2.2 0.8 -4.2	Left temporal pole: middle temporal gyrus
60+	+	-2.2 -6.2 2.4	Left superior occipital gyrus
19-30	+	-0.4 -5.6 0.4	Left calcarine fissure and surrounding cortex
19-30	+	-3.0 4.2 0.6	Left middle frontal gyrus2
19-30	+	-3.4 2.2 2.4	Left inferior frontal gyrus, triangular part
19-30	+	-3.0 -6.2 4.8	Left superior parietal gyrus
19-30	+	0.0 -5.2 5.4	Left precuneus
19-30	+	-3.4 -1.2 1.8	Left insula
19-30	+	3.0 -5.6 -3.2	Right hemispheric lobule VI
40-49	-	0.8 -8.8 -2.6	Right cerebelum crus II
40-49	-	-1.2 -8.4 1.6	Left cuneus

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A3.3.2 MNI coordinates and atlas labels from which theta power differences between No-Target Switch and No-Switch conditions were extracted for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
60+	+	-6.0 -5.2 0.4	Left middle temporal gyrus
60+	+	-4.6 -1.0 -1.6	Left superior temporal gyrus
60+	+	-4.4 -2.0 -3.4	Left inferior temporal gyrus
60+	+	-1.2 -4.2 1.4	Left posterior cingulate and paracingulate gyri
60+	+	-3.8 -3.6 -4.6	Left hemispheric lobule VIII
60+	+	-3.6 -3.8 1.8	Left rolandic operculum
60+	+	-4.0 0.6 1.0	Left inferior frontal gyrus, opercular part
60+	+	-4.0 1.8 -3.6	Left temporal pole: middle temporal gyrus
60+	+	-3.4 2.8 4.4	Left middle frontal gyrus
40-49	-	4.4 -7.4 0.6	Right middle occipital gyrus
40-49	-	-1.4 -7.8 2.6	Left cuneus
40-49	-	-1.2 -8.8 -3.4	Left cerebelum crus II
40-49	-	1.0 -5.4 -0.4	Right Hemispheric lobule IV/V
60+	-	0.8 -7.4 1.2	Right calcarine fissure and surrounding cortex
60+	-	-0.4 -6.0 -3.8	Left Hemispheric lobule VIII
60+	-	2.6 -8.8 -2.4	Right cerebelum crus I

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A3.3.3 MNI coordinates and atlas labels from which alpha power differences between Target Switch and No-Switch conditions were extracted for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
19-30	+	0.0 -2.6 7.8	Right paracentral lobule
19-30	+	-4.0 -3.6 4.8	Left postcentral gyrus
19-30	+	-2.4 -6.2 3.8	Left middle occipital gyrus
19-30	+	6.0 -4.6 4.8	Right inferior parietal gyrus
19-30	+	-1.2 -7.8 4.8	Left precuneus
19-30	+	3.2 -2.8 5.4	Right precentral gyrus
19-30	+	0.0 -3.2 4.8	Left median cingulate and paracingulate gyri
19-30	+	-2.4 0.4 5.4	Left middle frontal gyrus
40-49	+	-1.0 -5.2 4.8	Left precuneus2
40-49	+	-4.4 -5.6 5.4	Left inferior parietal gyrus
40-49	+	5.0 -6.2 4.4	Right angular gyrus
40-49	+	-6.0 -2.6 -0.2	Left middle temporal gyrus
40-49	+	1.6 -6.2 5.8	Right superior parietal gyrus
40-49	+	-5.8 -6.2 2.4	Left angular gyrus
40-49	+	-6.6 -3.4 2.4	Left supramarginal gyrus
40-49	+	-4.0 -7.6 3.8	Left middle occipital gyrus2
40-49	+	1.0 -3.2 3.4	Right median cingulate and paracingulate gyri
40-49	+	3.6 -0.2 5.4	Right middle frontal gyrus
60+	+	-5.4 -4.2 1.8	Left temporal pole: middle temporal gyrus
60+	+	-3.4 1.4 -3.2	Left inferior temporal gyrus
60+	+	-4.0 -3.2 -1.6	Right inferior frontal gyrus, triangular part
60+	+	6.0 3.8 1.4	Left paracentral lobule
60+	+	-1.6 -3.2 6.8	Left middle frontal gyrus2
60+	+	-2.8 2.8 5.8	Right middle frontal gyrus, orbital part
60+	+	3.0 3.4 -2.2	Left median cingulate and paracingulate gyri2
60+	+	-0.8 -2.2 3.2	Left posterior cingulate and paracingulate gyri
60+	+	-0.4 -4.2 1.4	Right middle frontal gyrus2

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A3.3.4 MNI coordinates and atlas labels from which alpha power differences between No-Target Switch and No-Switch conditions were extracted for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
19-30	+	-2.4 -5.6 4.4	Left superior parietal gyrus
19-30	+	5.0 -4.2 4.8	Right inferior parietal
19-30	+	0.6 -2.2 7.8	Right paracentral lobule
19-30	+	-2.8 -0.6 7.4	Left superior frontal
19-30	+	1.0 -5.4 7.8	Right precuneus
19-30	+	-4.6 0.4 2.8	Left inferior frontal gyrus, opercular part
40-49	+	1.0 -4.6 7.8	Right precuneus2
40-49	+	-4.4 -6.2 5.4	Left inferior parietal gyrus
40-49	+	-4.0 -2.6 1.4	Left rolandic operculum
40-49	+	-6.6 -1.6 2.8	Left postcentral gyrus
40-49	+	-1.4 -5.6 7.8	Left superior parietal gyrus2
40-49	+	-1.4 -5.6 5.4	Left precuneus
40-49	+	5.0 -3.6 5.8	Right superior parietal gyrus
40-49	+	-6.6 -5.2 -2.2	Left inferior temporal gyrus
40-49	+	4.0 -1.6 5.8	Right precentral gyrus
40-49	+	-0.2 0.6 2.6	Left anterior cingulate and paracingulate gyri
40-49	+	-5.4 1.8 2.4	Left inferior frontal gyrus, triangular part
40-49	+	7.0 -4.8 -1.2	Right inferior temporal gyrus
60+	+	-5.4 -3.6 -0.6	Left middle temporal gyrus
60+	+	-4.4 -4.2 2.2	Left supramarginal gyrus
60+	+	-2.4 -4.2 4.8	Left postcentral gyrus
60+	+	-4.4 1.4 3.4	Left inferior frontal gyrus, opercular part2
60+	+	-3.4 2.8 -3.2	Left temporal pole: superior temporal gyrus
60+	+	-1.0 -4.4 1.4	Left posterior cingulate and paracingulate gyri
60+	+	4.0 -3.2 3.8	Right supramarginal gyrus
60+	+	-4.8 -6.2 -1.2	Left inferior occipital gyrus
60+	+	3.0 4.4 4.4	Right middle frontal gyrus

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Appendix 3.4

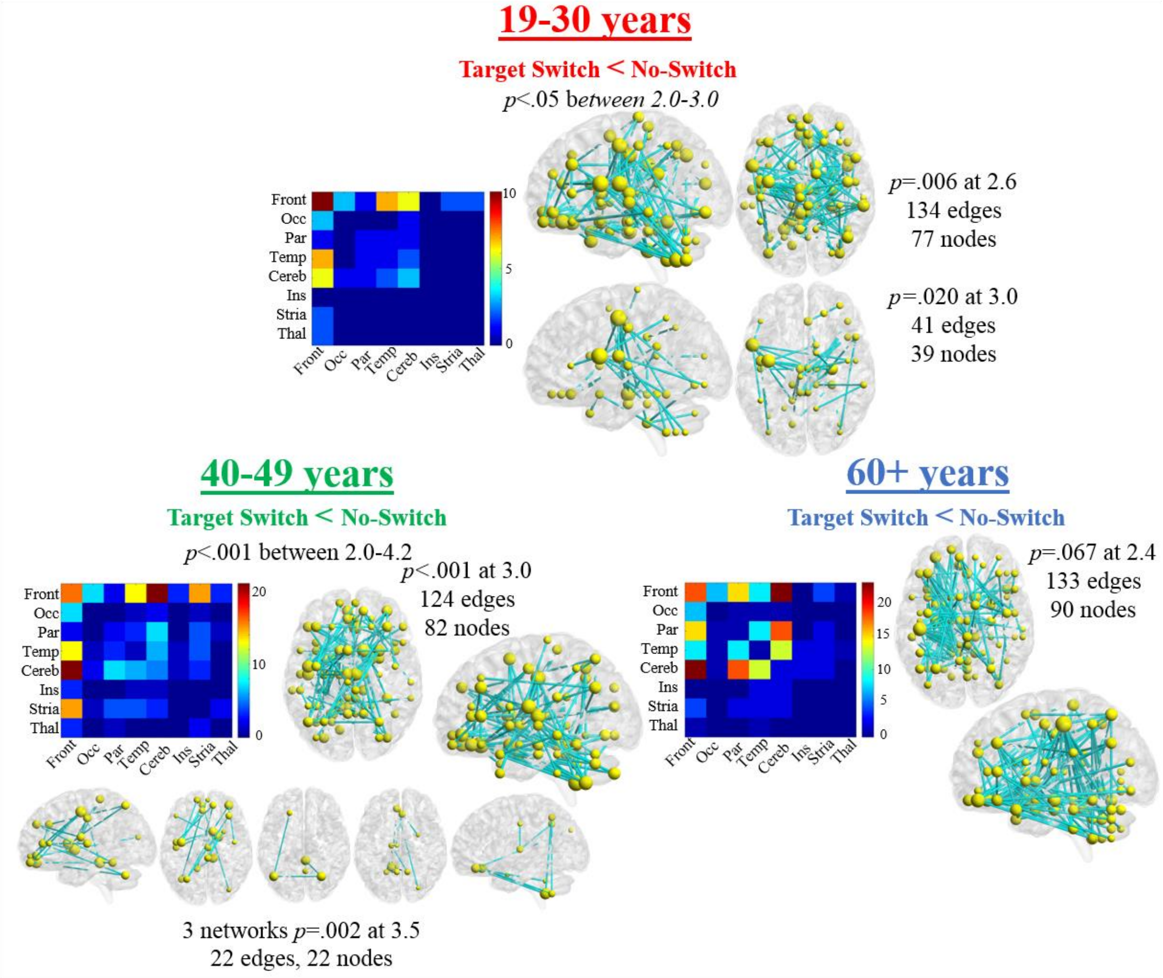

Figure A3.4.1 NBS results exploring differences in network connectivity between Target Switch and No-Switch conditions in each age group in theta (3-5Hz) connectivity (wPLI) between 0.55-1.55s. Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria), thalamus (Thal). Note that the number of connections in each network vary and so the scales of matrix plots differ.

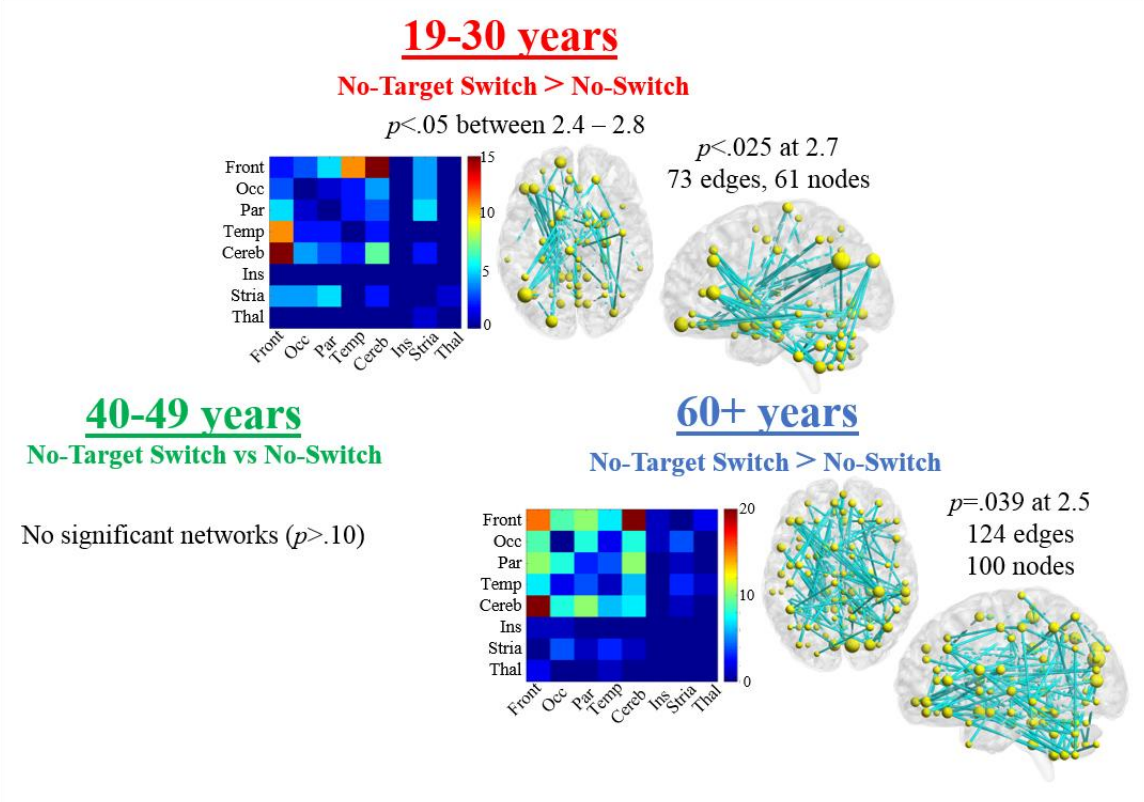

Figure A3.4.2. NBS results exploring differences in network connectivity between No-Target Switch and No-Switch conditions in each age group in theta (3-5Hz) connectivity (wPLI) between 0.55-1.55s. Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria), thalamus (Thal). Note that the number of connections in each network vary and so the scales of matrix plots differ.

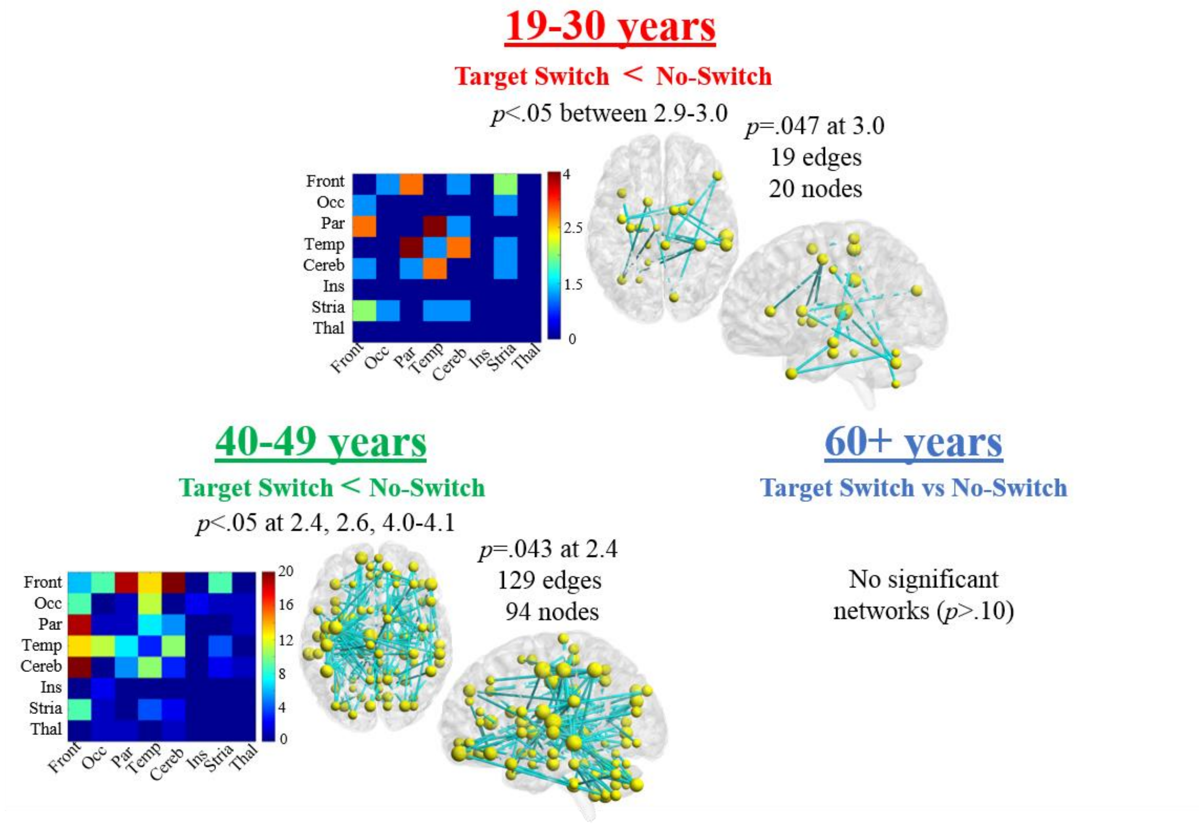

Figure A3.4.3 NBS results exploring differences in network connectivity between Target Switch and No-Switch conditions in each age group in alpha (10-14Hz) connectivity (wPLI) between 0.45-0.95s. Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria), thalamus (Thal). Note that the number of connections in each network vary and so the scales of matrix plots differ.

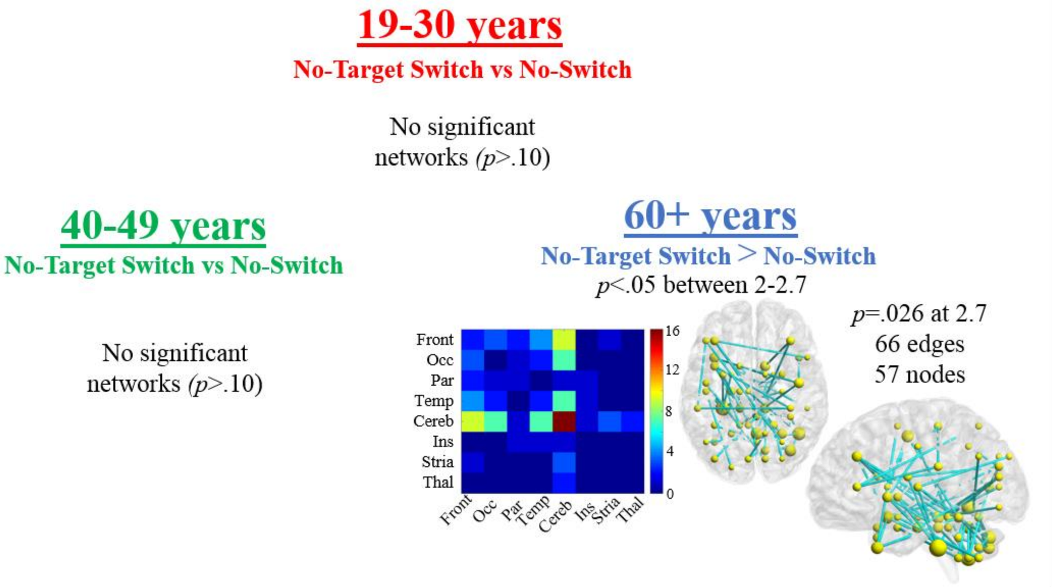

Figure A3.4.4 NBS results exploring differences in network connectivity between No-Target Switch and No-Switch conditions in each age group in alpha (10-14Hz) connectivity (wPLI) between 0.45-0.95s. Significant networks are plotted in BrainNet on surface plots. Node sizes represent node degree, where larger nodes have a higher degree. Matrix plots illustrate the number of connections between eight categories of neural regions, including frontal (Front), occipital (Occ), parietal (Par), temporal (Temp), cerebellar (Cereb), insula (Ins), striatum (Stria), thalamus (Thal). Note that the number of connections in each network vary and so the scales of matrix plots differ.

Appendix 3.5

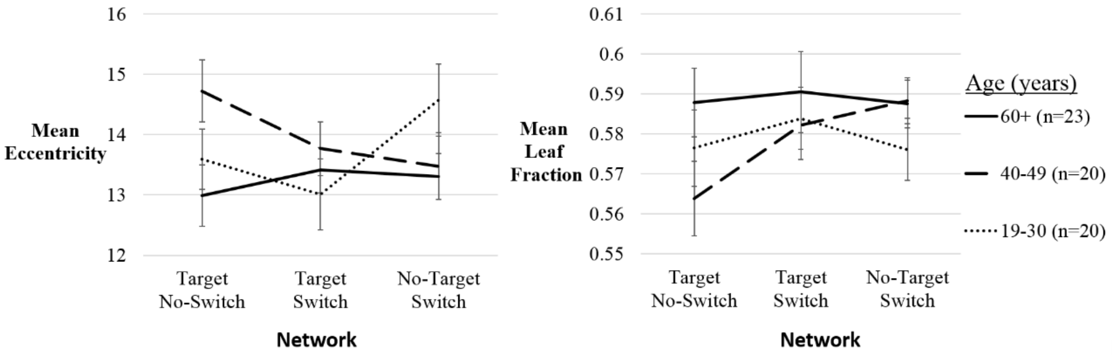

Figure A3.5.1 Group means of global theta MSTs' metrics mean eccentricity (left) and leaf fraction (right) for networks in each RSVP condition. Vertical bars represent the standard error of the mean.

Appendix 3.6

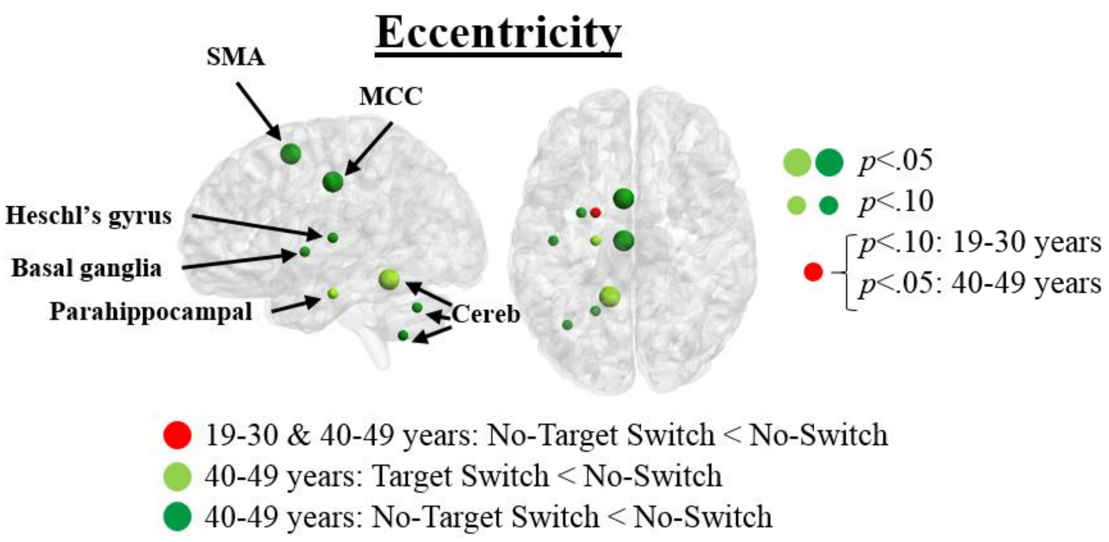

Figure A3.6.1. Theta (3-5Hz, 0.55-1.55s) MST comparisons (permutation t-tests) of eccentricity across RSVP conditions: Nodes with differences in eccentricity between No-Target Switch and No-Switch conditions in the 19-30 years group (red), and 40-49 years group (dark green) and between Target Switch and No-Switch conditions in the 40-49 years group. Nodes are plotted in BrainNet on surface plots. Node sizes represent significance level, where larger nodes p<.05 and smaller nodes p<.10. There were no significant differences between the No-Switch and either of the Switch conditions in degree or betweenness centrality in any age group.

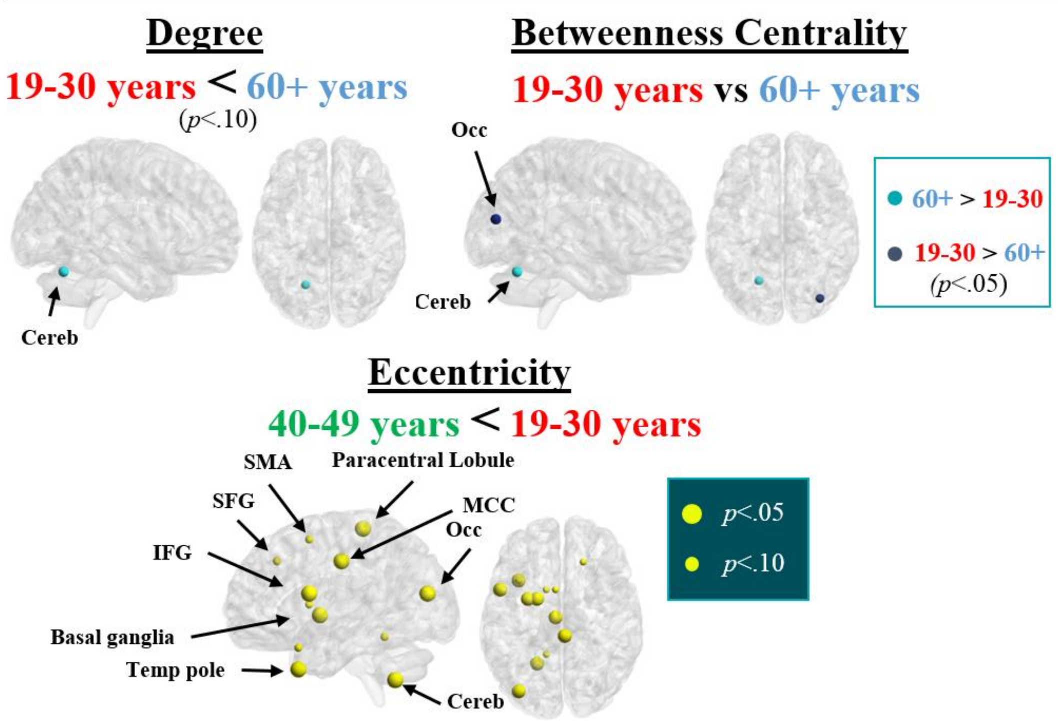

Figure A3.6.3. Theta (3-5Hz, 0.55-1.55s) MST group comparisons (permutation t-tests): Nodes with age group differences in the difference between No-Target Switch and No-Switch conditions in local MST metrics degree (top left), betweenness centrality (top right) and eccentricity (bottom). Nodes are plotted in BrainNet on surface plots. Node sizes represent significance level, where larger nodes *p*<.05 and smaller nodes *p*<.10.

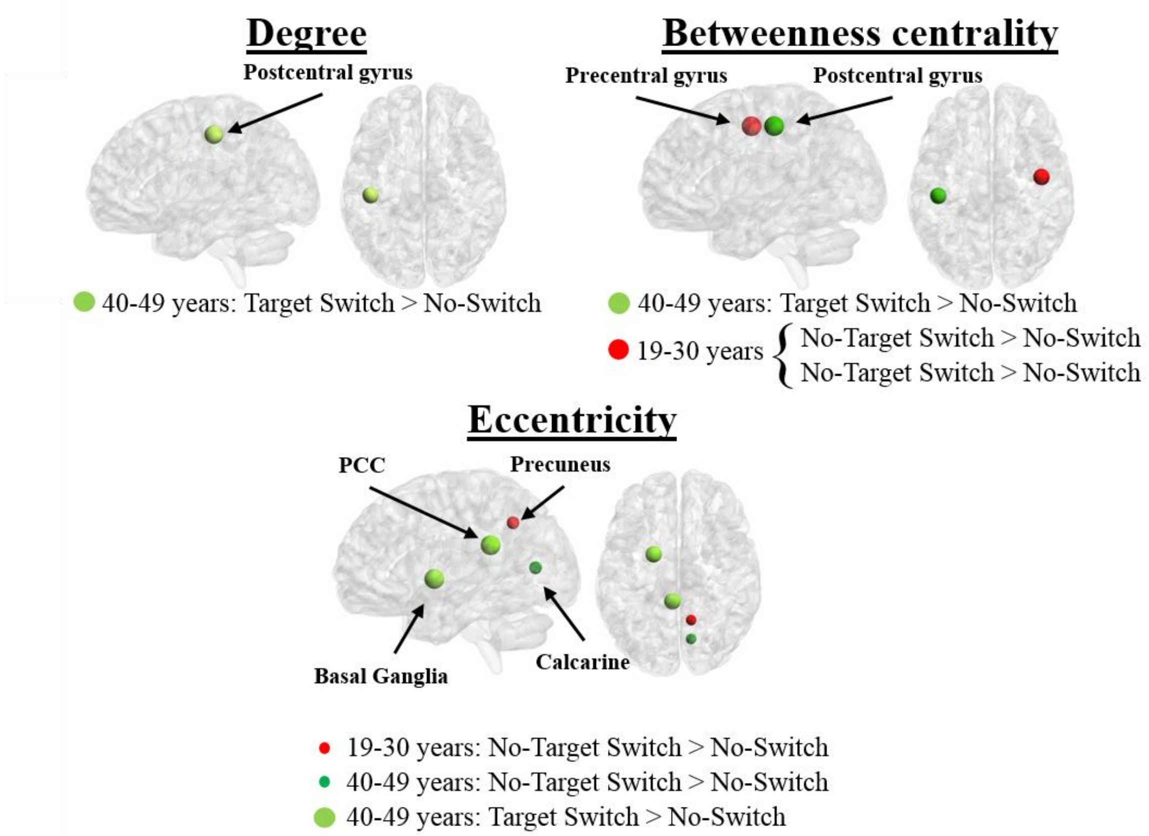

Figure A3.6.2. Alpha (10-14Hz, 0.45-.95s) MST comparisons (permutation t-tests) of degree (top left), betweenness centrality (top right) and eccentricity (bottom) across RSVP conditions: Nodes with differences in local measures the 19-30 years group (red), and 40-49 years group (green). Nodes are plotted in BrainNet on surface plots. Node sizes represent significance level, where larger nodes *p*<.05 and smaller nodes *p*<.10. There were no significant differences between the No-Switch and either of the Switch conditions in any local measure in the 60+ years group (*p*>.10).

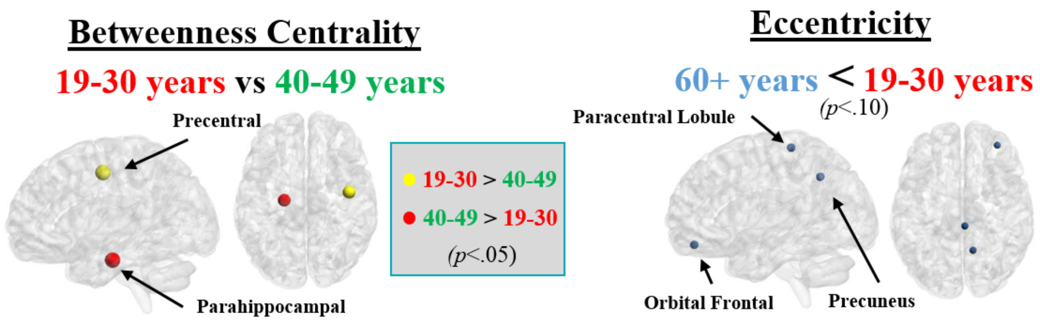

Figure A3.6.4. Alpha (10-14Hz, 0.45-0.95s) MST group comparisons (permutation t-tests): Nodes with age group differences in the difference between No-Target Switch and No-Switch conditions in local MST metrics betweenness centrality (left) and eccentricity (right). Nodes are plotted in BrainNet on surface plots. Node sizes represent significance level, where larger nodes *p*<.05 and smaller nodes *p*<.10.

Appendix 3.7

Correlations between MST local metrics and RT Switch-Costs

To explore the relationship between task performance and theta and alpha local MST metrics, Spearman's correlation analyses were carried out between Switch-Costs and local MST metrics in nodes that showed significant group differences. Correlations were computed separately for each age group. Correlations were computed between Target Switch-Costs and local MST metrics in the Target Switch and No-Switch networks, and between No-Target Switch-Costs and local MST metrics in the No-Target Switch and No-Switch networks. Correlations were exploratory and therefore multiple comparisons were not corrected for, however were related to current hypotheses, and only nodes that showed significant differences at *p*<.05 were entered into analyses.

Correlations between Target Switch-Costs and theta MST eccentricity

Correlations between Switch-Costs and theta MST local metrics degree and betweenness centrality were not explored because differences between age groups did not reach significance (*p*>.05). Theta MST local metric eccentricity in the Target Switch condition positively correlated with Target Switch-Costs in the 40-49 years group in eight nodes, labels of which are listed in Table A3.7.1 with their correlation coefficients. Positive correlations signify that as centrality within the network increased (i.e. eccentricity decreased), Switch-Costs decreased, supporting that the recruitment of these additional nodes that was seen in Figure A4.6.3 in the 40-49 years group is compensatory.

Table A3.7.1. Spearman's correlation coefficients exploring the relationship between Target Switch-Costs and node eccentricity in the Target Switch network in the 40-49 years group

Node Label	***r***
Inferior frontal gyrus, opercular part (L)	.49*
Median Cingulate (L)	.47*
Middle occipital gyrus (L)	.75***
Paracentral lobule (R)	$.43^{ns}$
Putamen (L)	.83***
Pallidum (L)	.84***
Middle Temporal pole (L)	.73***
Cerebellum_8 (L)	.68***

^{ns}p<.10, *p<.050, **p<.010, ***p<.001. Letters in brackets correspond to left (L) and right (R) hemispheres.

In the 40-49 years group, a negative correlation was found between Target Switch-Costs and eccentricity in the No-Switch condition in the left median cingulate that did not reach significance (*r*=-.40, *p*=.083). As centrality decreased (i.e. eccentricity increased), Switch-Costs decreased. There were no other significant correlations between eccentricity and Target Switch-Costs in any age group (*p*>.10).

Correlations between No-Target Switch-Costs and theta MST eccentricity

In the 40-49 years group, No-Target Switch-Costs significantly negatively correlated with eccentricity in the left median cingulate (*r*=-.56, *p*=.010) and left cerebellum (*r*=-.53, *p*=.017) in the No-Switch MST. Consistent with the pattern seen between the median cingulate and Target Switch-Costs, as eccentricity increased (i.e. centrality decreased), Switch-Costs decreased. The same pattern was seen in left cerebellum eccentricity.

In the 19-30 years group there was a non-significant positive correlation between No-Target Switch-Costs and eccentricity in the left pallidum in the No-Target Switch condition (*r*=.41, *p*=.076). As node centrality of the left pallidum increases (i.e. eccentricity decreases) Switch-Costs decrease.

In the 60+ years group there was a non-significant negative correlation between No-Target Switch-Costs and eccentricity in the left middle temporal pole in the No-Target Switch condition (*r*=-.40, *p*=.059). As left middle temporal pole centrality increases (i.e. eccentricity decreases) Switch-Costs increase. This is consistent with the increased temporal theta power modulation observed in the 60+ years group (Figure 3.3 in Chapter 3 main text). There were no other significant correlations between eccentricity and No-Target Switch-Costs in any age group (*p*>.10).

Correlations between Target Switch-Costs and alpha MST local metrics

Correlations between Switch-Costs and alpha MST local metrics degree and eccentricity were not explored because age group differences did not reach significance (*p*>.05; Appendix 3.6 Figure A3.6.4).

In the 40-49 years group, there was a significant positive correlation between Target Switch-Costs and betweenness centrality in the right precentral gyrus in the Target Switch network (*r*=.50, *p*=.026), as well as in the No-Switch network that did not reach significance (*r*=.39, *p*=.091). As network centrality of the right precentral gyrus increases Target Switch-Costs increase in the 40-49 years group only. There were no other significant correlations between Target Switch-Costs and betweenness centrality in the right precentral gyrus and the left parahippocampal gyrus in any age group (*p*>.10).

Correlations between No-Target Switch-Costs and alpha MST local metrics

In the 40-49 years group there was a negative correlation between No-Target Switch-Costs and betweenness centrality in the left parahippocampal gyrus in the No-Target Switch network that did not reach significance (*r*=-.40, *p*=.085). As network centrality of the left parahippocampal gyrus decreases, No-Target Switch-Costs increase in the 40-49 years group only. There were no other significant correlations between eccentricity and Target Switch-Costs in any age group (*p*>.10).

Appendix 4

Supplementary material from Chapter 4.

Appendix 4.1

UFOV

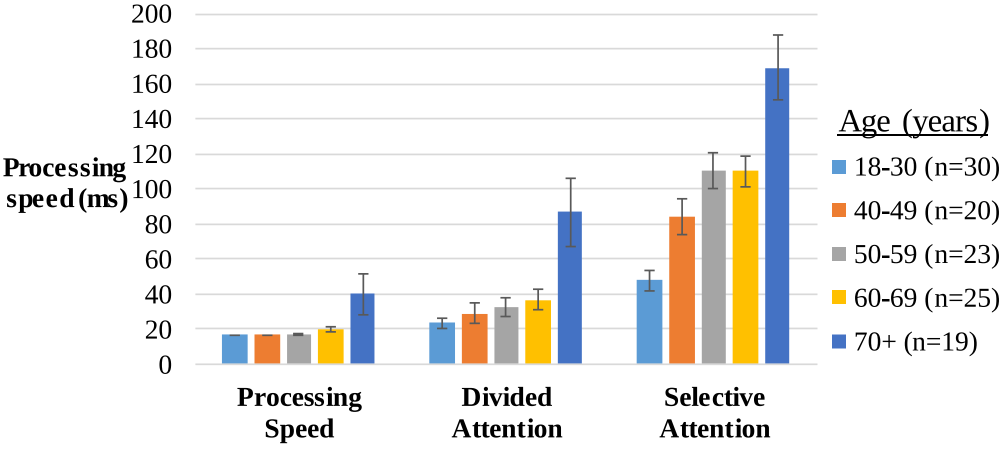

Figure A4.1.1. Mean processing speed threshold for each age group on the UFOV speed of processing task, divided attention and selective attention.

Three one-way ANOVAs were conducted to explore the effects of age on UFOV performance. There was a significant main effect of age on UFOV processing speed (*F*(4, 113)=4.69, *p*=.002), divided attention (*F*(4, 113)=8.85, *p*<.001) and selective attention (*F*(4, 113)=17.88, *p*<.001).

Post hoc comparisons revealed that the 70+ years group had significantly slower processing speeds than all other age groups on all three UFOV tasks (*p*<.001). Additionally, the 18-30 years group had significantly faster processing speeds on the selective attention task than the 50-59 and 60-69 years groups (*p*<.001).

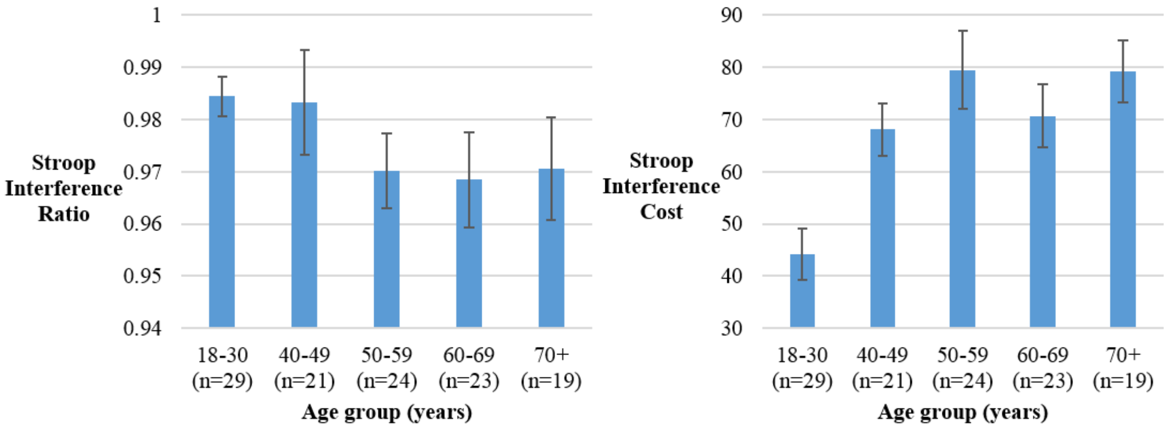

Figure A4.1.2. Group means of Stroop measures “interference ratio” (left) and “interference cost” (right).

A one-way ANOVA illustrated that there was a significant main effect of age on Stroop indexes interference cost (*F*(4, 115)=6.73, *p*<.001) but not interference ratio (*p*>.10). Post hoc comparisons demonstrated that the 18-30 years group had a significantly lower interference cost in comparison to all other groups, including the 40-49 (*p*=.043), the 50-59 (*p*<.001), the 60-69 (*p*=.012) and the 70+ (*p*<.001) years groups.

Complete data sets were present for both the driving simulator and the Stroop tasks for 29 participants from the 18-30 years group, 21 from the 40-49, 24 from the 50-59, 23 from the 60-69 years group and 19 from the 70+ years groups and so were entered into Spearman’s correlation analysis to explore the relationship between Dual-Task Switch-Costs and executive function, as measured by the Stroop.

Spearman’s correlation analyses highlighted that in the 18-30 years group there were negative correlations between Immediate Dual-Task Costs and Stroop interference costs (*r*=-.45, *p*=.015) and between Delayed Dual-Task costs and Stroop interference ratio (*r*=-.32, *p*=.089), although the latter did not reach significance. There was a significant positive correlation between Delayed Dual-Task costs and Stroop interference ratio in the 40-49 years group (*r*=.46, *p*=.047). There was a positive correlation between Delayed Dual-Task Costs and interference costs in the 60-69 years group that did not reach significance (*r*=.39, *p*=.078). There were no other significant correlations between Dual-Task Costs and Stroop indexes in any age group (*p*>.10).

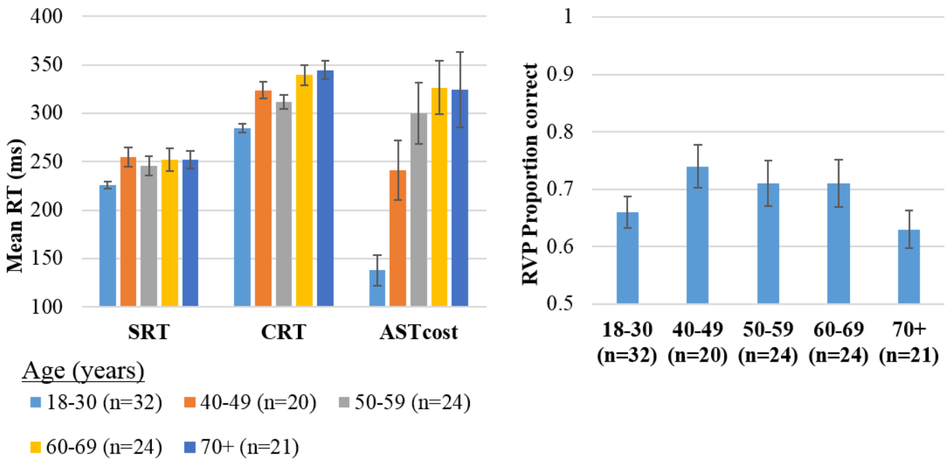

Figure A4.1.3. Group means of four CANTAB measures, including median simple response time (SRT), median choice response time (CRT), and attention switching task switch-costs (AST cost) (left) and the proportion of correct RVP responses (right). The proportion of false positives in each age group is not shown as all age groups displayed less than 1.5% false positive responses.

A one-way ANOVA illustrated that there was a significant main effects of age on CANTAB measures SRT (*F*(4, 120)=2.22, *p*=.071), CRT (*F*(4, 120)=10.11, *p*<.001) and AST cost (*F*(4, 120)=9.33, *p*<.001), but not on the proportion of correct RVP response or RVP false positives (*p*>.10). Note that the main effect of age on SRT did not reach significance.

Post hoc group comparisons displayed no significant differences between any age groups in SRTs (*p*>.10). The 18-30 years group had significantly faster CRTs than the 40-49 (*p*=.008), 60-69 (*p*<.001), and 70+ (*p*<.001) years groups and the 70+ years group displayed a trend towards slower CRTs than the 50-59 years group that did not reach significance (*p*=.065). The 18-30 years group displayed significantly lower AST costs compared to all other groups apart from the 40-49 years group (*p*<.001). There were no other age group differences in CANTAB measures SRT, CRT or AST costs.

Complete data sets were present for both the driving simulator and the CANTAB tasks for 32 participants from the 18-30 years group, 20 from each of the 40-49, 50-59 and 70+ years groups and 23 from the 60-69 years group and so were entered into Spearman's correlation analysis to explore the relationship between Dual-Task Switch-Costs and cognitive performance, as measured by the CANTAB tasks SRT, CRT, AST and RVP. There were significant correlations in certain age groups between SRT, CRT and AST measures, reflecting increases in Dual-Task Costs while driving as RTs and AST switch-costs increase.

In the 18-30 years group there was a positive correlation between SRT and both Immediate (*r*=.51, *p*=.003) and Delayed (*r*=.43, *p*=.015) Dual-Task Costs, and between CRT and Immediate Dual-Task Costs (*r*=.46, *p*=.009). As CRTs and SRTs increase, Dual-Task Costs increase. Consistent with the correlation between CRTs and Immediate Dual-Task Costs, in the 18-30 years group, there was a positive correlations between Immediate Dual-Task Costs and both AST RTs (*r*=.44, *p*=.011) and AST switch-costs (*r*=.32, *p*=.076), although the latter did not reach significance.

In the 50-59 years group there was a significant positive correlation between Immediate Dual-Task Costs and CRT (*r*=.48, *p*=.033) and between Delayed Dual-Task Costs and AST RT.

In the 70+ years group there were significant negative correlations between SRT and both Delayed (*r*=-.46, *p*=.042) and Immediate (*r*=-.43, *p*=.058) Dual-Task Costs, although the latter did not reach significance. In the 70+ years group there were significant negative correlations between CRT and both Immediate (*r*=-.53, *p*=.016) and Delayed (*r*=-.39, *p*=.092) Dual-Task Costs, although the latter did not reach significance.

In the 18-30 and 50-59 years groups increased RTs in CANTAB tasks were associated with increased switch-costs as one would expect, whereas the oldest group showed the opposite pattern, where there was a decrease in Dual-Task Costs as RTs increased. This could reflect driving task performance gradually reaching ceiling level with increased RTs. As participants become slower at SRT and CRT, the difference between switch and no-switch conditions becomes smaller due to slow indicator RTs reaching ceiling in both conditions.

There were no other significant correlations between Dual-Task Costs and SRT, CRT or AST in any other age group (*p*>.10). There were no significant correlations between RVP performance and Dual-Task Costs in any age group (*p*>.10).

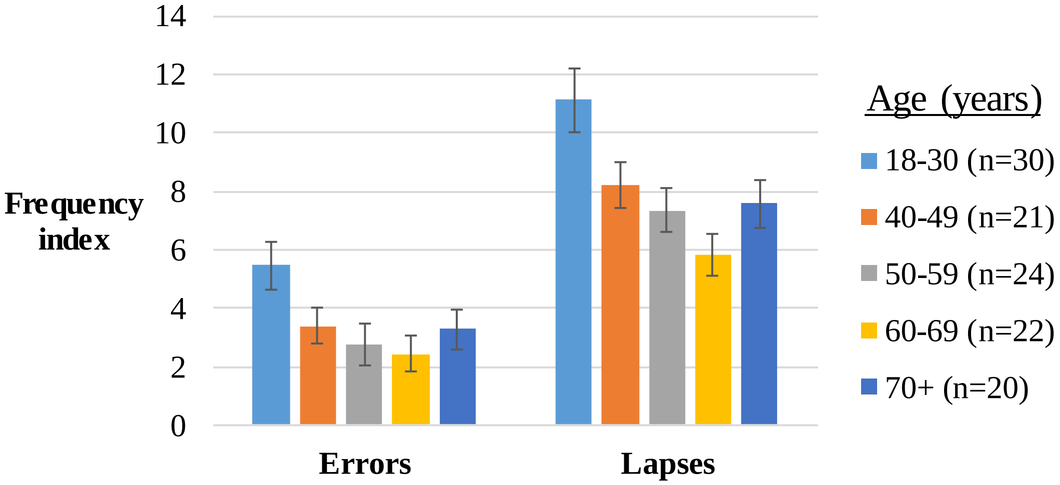

Figure A4.1.4. Group means of Driving Behaviour Questionnaire (DBQ) measures "Errors" (left) and "Attention Lapses" (right).

A one-way ANOVA illustrated that there was a significant main effect of age on DBQ subscales errors (*F*(4, 116)=3.14, *p*=.017) and lapses (*F*(4, 116)=5.31, *p*<.001). Post hoc comparisons demonstrated that DBQ error scores were significantly higher (signifying more frequent self-reported errors) in the 18-30 years group compared to the 60-69 years group (*p*=.027) and there was a trend for a higher error score in the 18-30 years group compared to the 50-59 years group that didn't reach significance (*p*=.056). Post hoc comparisons demonstrated that DBQ lapses scores were significantly higher in the 18-30 years group compared to the 50-59 (*p*=.020), 60-69 (*p*<.001) and the 70+ (*p*=.056) years groups, although the latter did not reach significance. There were no other significant age group differences in either DBQ indexes errors or lapses (*p*>.10).

Complete data sets were present for both the driving simulator task and the DBQ self-report for 30 participants from the 18-30 years group, 19 from the 40-49, 20 each from the 50-59 and 60-69 years group and 19 from the 70+ years groups and so were entered into Spearman's correlation analysis to explore the relationship between Dual-Task Switch-Costs and self-reported driving behaviour, as measured by the DBQ subscales errors and lapses.

Spearman's correlation highlighted a significant negative correlation between Immediate Dual-Task costs and DBQ errors in the 50-59 years group only (*r*=-.48, *p*=.034). As errors increased, Dual-Task Costs decreased. There were no other correlations between Dual-Task costs and DBQ scores (*p*>.10).

Appendix 4.2

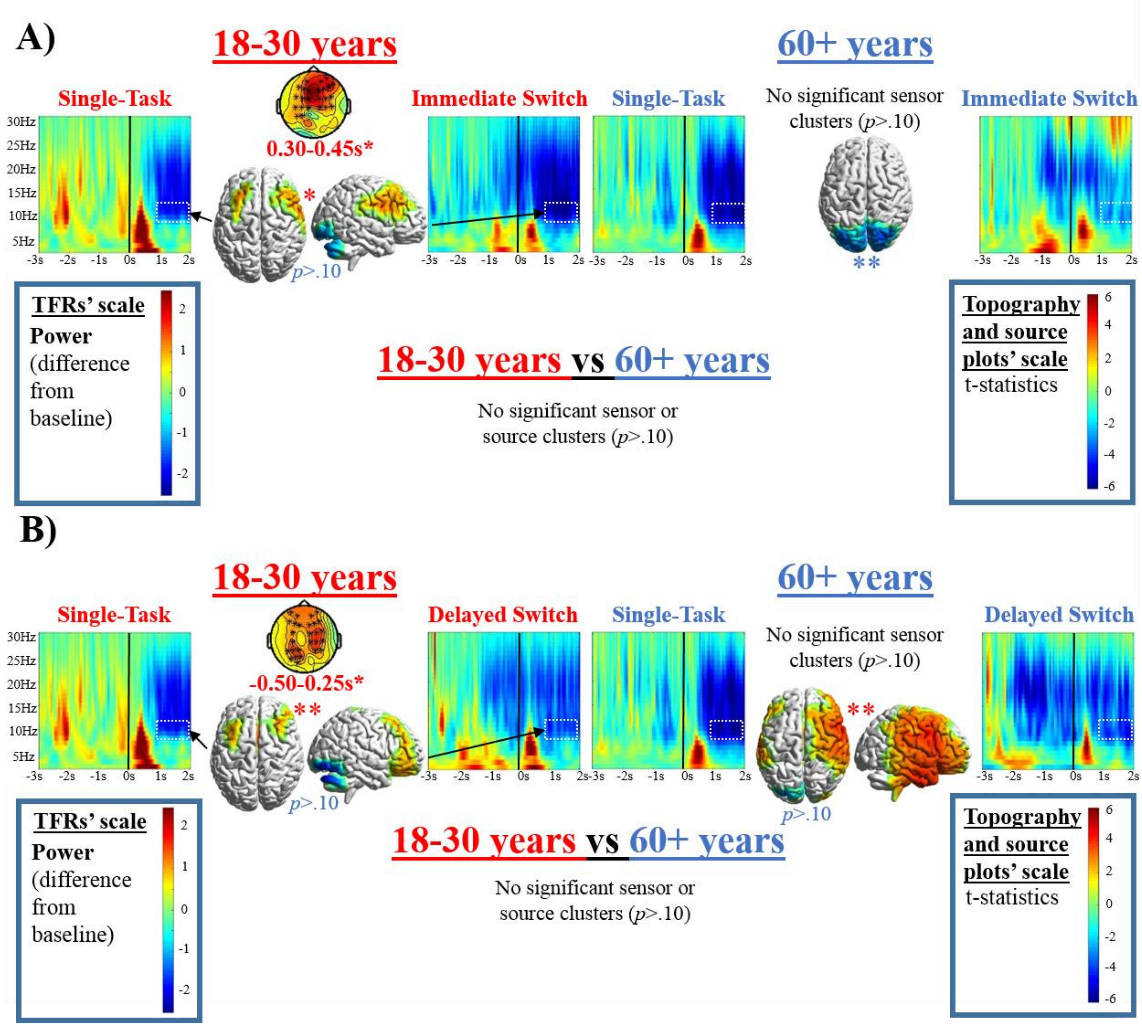

Figure A4.2.1. Effects in alpha (8-12Hz) EEG power when A) contrasting Immediate Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Immediate Switch/Single-Task) × age interaction (bottom row), and B) contrasting Delayed Switch and Single-Task conditions in each age group (top row) and when exploring the event condition (Delayed Switch/Single-Task) × age interaction (bottom row). TFRs present power in relation to a baseline period of -5.5s - -3.5s in a group of 10 anterior electrodes (AF3, AF4, F1, F2, F3, F4, FC1, FC2, FC3, FC4). Black lines placed over TFRs signify the onset of the road sign VS display at 0.0s. In the Switch conditions the car pulled in front of the participant at either 3.04m (~0.14s; Immediate Switch) or 30.48m (~1.42s; Delayed Switch) prior to the onset of the road sign. Topographical and source plots present *t*-statistics of significant clusters. Rectangles placed over TFRs highlight the time-frequency tile entered into source localisation. Note that the Single-Task TFRs for each age group are presented in both A and B. Significance levels are indicated as (ns)p<.10, *p<.050, **p<.025.

Appendix 4.3

Table A4.3.1 MNI coordinates and atlas labels from which theta power (3-7Hz) differences between Single-Task and Immediate Switch conditions were extracted for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
18-30	+	0.6 -3.8 0.0	Right lingual gyrus
18-30	+	1.4 1.8 4.0	Right median cingulate and paracingulate gyri
60+	-	-2.6 -7.8 -4.8	Left cerebellum crus2

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A4.3.2 MNI coordinates and atlas labels from which theta power (3-7Hz) differences between Single-Task and Delayed Switch conditions were extracted for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
18-30	+	-1.0 -3.8 -1.6	Left Hemispheric lobule IV, V
18-30	+	3.8 -3.8 4.8	Right inferior parietal
18-30	+	1.4 -1.4 6.4	Right supplementary motor area
18-30	+	1.4 2.6 -2.4	Right superior frontal gyrus, orbital part
60+	-	-5.8 2.6 0.8	Left inferior frontal gyrus, triangular part
60+	-	2.2 -2.2 -2.4	Right parahippocampal gyrus
60+	-	-5.0 -6.2 -3.2	Left cerebellum crus1

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A4.3.3 MNI coordinates and atlas labels from which beta power (15-25Hz) differences between Single-Task and Immediate Switch conditions were extracted at an early time window (0.0-0.5s) for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
18-30	+	0.6 1.8 2.4	Right anterior cingulate and paracingulate gyri
18-30	+	-0.2 -1.4 3.2	Left median cingulate and paracingulate gyri
18-30	+	2.2 -2.2 8.0	Right precentral gyrus
18-30	+	-2.6 1.8 6.4	Left middle frontal gyrus
18-30	+	-4.2 -3.8 3.2	Left supramarginal gyrus
60+	-	-3.4 -4.6 -4.8	Left Hemispheric lobule VIII

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A4.3.4 MNI coordinates and atlas labels from which beta power (15-25Hz) differences between Single-Task and Delayed Switch conditions were extracted at a late time window (1.0-2.0s) for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
18-30	+	-0.2 -1.4 4.0	Left median cingulate and paracingulate gyri
18-30	+	-1.8 0.2 7.2	Left superior frontal gyrus
18-30	+	3.0 -3.8 7.2	Right postcentral gyrus
18-30	+	-4.2 -6.2 5.6	Left inferior parietal gyrus
60+	+	-5.8 -3.8 0.8	Left middle temporal gyrus
60+	+	4.6 -4.6 -2.4	Right inferior temporal gyrus
60+	+	3.8 -1.4 6.4	Right precentral gyrus
60+	+	0.6 4.2 4.8	Right superior frontal gyrus medial part
60+	+	0.6 0.2 3.2	Right median cingulate and paracingulate gyri

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A4.3.5 MNI coordinates and atlas labels from which beta power differences between Single-Task and Immediate Switch conditions were extracted at a late time window (1.0-2.0s) for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
18-30	+	-1.0 -0.6 4.8	Left median cingulate and paracingulate gyri
18-30	+	-1.0 0.2 5.6	Left supplementary motor area
18-30	+	-2.6 1.8 6.4	Left middle frontal gyrus
18-30	+	-2.6 -2.2 7.2	Left precentral gyrus
18-30	-	4.6 -7.8 2.4	Right middle occipital gyrus
18-30	-	1.4 -8.6 -0.8	Right lingual gyrus
18-30	-	3.0 -6.2 0.8	Right calcarine fissure and surrounding cortex
60+	-	4.6 -7.8 0.8	Right occipital gyrus 2
60+	-	1.4 -8.6 2.4	Right cuneus
60+	-	-1.0 -6.2 4.8	Left precuneus
60+	-	-1.0 -7.0 -0.8	Left lingual gyrus2

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Table A4.3.6 MNI coordinates and atlas labels from which beta power differences between Single-Task and Delayed Switch conditions were extracted at an early time window (0.0-0.5s) for correlation analyses.

Age group (years)	Positive(+)/ Negative(-) cluster	MNI coordinates	Label
18-30	-	1.4 -5.4 -0.8	Right lingual
18-30	-	0.6 -4.6 -0.8	Vermic lobule IV, V
18-30	-	3.8 -7.8 1.6	Right middle occipital gyrus
60+	+	-3.4 -3.0 0.8	Left heschl
60+	+	-5.0 -5.4 2.4	Left angular gyrus
60+	+	4.6 -3.0 0.8	Right superior temporal gyrus

MNI coordinates of cluster peaks and their standardised anatomical labels based on the AAL atlas, the direction of the cluster (positive or negative) and the age group in which the cluster was observed in.

Appendix 4.4

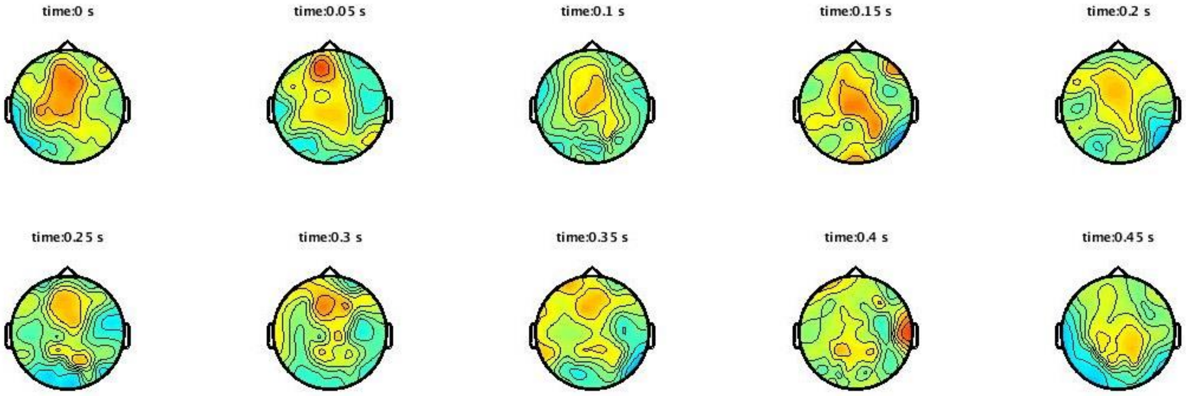

Figure A4.4.1. Topographical plot displaying t-statistics (*p*<.10) when comparing EEG beta frequency (15-25Hz) across Single-Task and Delayed Switch conditions in the 60+ years group. The plot displays a non-significant positive cluster from 0.0-0.45s.