Flexible allocation of attention in time or space across the life span: Theta and alpha oscillatory signatures of age-related decline and compensation as revealed by MEG

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Abstract

In our recent behavioural research (Callaghan et al., 2017) we reported age-related changes in the speed of switching between temporal and spatial attention. Using magnetoencephalography (MEG), we now compared the neural signatures between three age groups (19-30, 40-49 and 60+ years) and found differences in task-related modulation and cortical localisation of alpha and theta oscillations as well as in functional network connectivity. Efficient (fast) switching between the temporal and spatial attention tasks in the youngest group was reflected by parietal theta effects that were absent in the older groups. Difficulties in refocusing attention in the older and middle-aged adults (slowed response times) were accompanied by reduced theta power modulation in occipital and cerebellar regions. Older and middle-aged adults seem to compensate for this posterior theta deficit with increased recruitment of frontal (both groups) and temporal (older group) areas, possibly reflecting a greater dependence on top-down attentional control. Importantly, rather than theta oscillatory connectivity becoming weaker with age due to increased neural noise, both older age groups displayed stronger and more widely distributed connectivity. However, differences in alpha-band modulations did not translate into enhanced connectivity patterns in the older groups. Overall we conclude that theta oscillations and connectivity reflect compensatory strategies in older and middle age that induce a posterior to anterior processing shift, while alpha oscillations might reflect increased neural noise but require further investigation.

Keywords: aging, cognitive decline, attention switching, brain oscillations, network connectivity, magnetoencephalography

Abbreviations: ACC, Anterior cingulate cortex; ACE-3, Addenbrookes cognitive examination 3; ANOVA, Analysis of variance; DICS, Dynamic imaging of coherent sources; EEG, electroencephalography; FFT, Fast Fourier Transform; (f)MRI, (Functional) magnetic resonance imaging; HPI, Head Position Indicator; ICA, Independent component analysis; IPS, Intraparietal sulcus; LCMV, Linearly constrained minimum variance; MEG, Magnetoencephalography; MFG, Middle frontal gyrus; MNI, Montreal Neurological Institute; MSR, Magnetically shielded room; MST, Minimum spanning tree; NBS, Network based statistics; NTVA, Neural Theory of Visual Attention; PASA, Posterior to anterior shift in ageing; PET, Positron emission tomography; PFC, Prefrontal cortex; RSVP, Rapid serial visual presentation; SFG, Superior frontal gyrus; SNR, Signal to noise ratio; STAC, scaffolding theory of aging and cognition; TFR, Time-frequency representation; VS, Visual search; wPLI, Weighted phase lag index.

1. Background

1.1. Age-related decline of attention

It has recently been found that switching between temporal and spatial attention becomes more difficult with increased age (Callaghan et al., 2017). Exploring the neural mechanisms that underpin this age-related difficulty in refocusing attention would further our understanding of age-related cognitive decline and could inform the development of interventions that may prevent or delay deterioration of performance on important daily activities such as driving (Callaghan et al., 2017). Age-related deterioration has been reported separately for temporal as well as spatial selective attention (Bennett et al., 2012; Foster et al., 1995; Humphrey and Kramer, 1997; Lahar et al., 2001; Lee and Hsieh, 2009; Li et al., 2013; Maciokas and Crognale, 2003; Plude and Doussardroosevelt, 1989), while the potential deficits in switching attention from one mode to the other has remained largely under-investigated (Callaghan et al., 2017).

Spatial attention is often quantified with a visual search (VS) task, in which participants' response times (RTs) to detect a predefined visual target among an array of distractors is recorded. It is well established that there are specific age-related declines in serial but not pop-out VS performance with increased age. Older adults' increased RTs on pop-out VS tasks, in which the target is distinct from the distractors and "pops out" of the VS display, remain constant with increasing numbers of distractors and have therefore been attributed to general slowing (Bennett et al., 2012; Foster et al., 1995; Humphrey and Kramer, 1997; Li et al., 2013; Plude and Doussardroosevelt, 1989). In contrast, VS performance is thought to decline with age when the target and distractors are visually indistinct and share certain features, and a serial search is required (Bennett et al., 2012; Foster et al., 1995; Humphrey and Kramer, 1997; Li et al., 2013; Plude and Doussardroosevelt, 1989). In serial VS task performance, the increase in RTs with increasing numbers of distractors becomes steeper with age, which has been interpreted as a deficit in the mechanisms specific to serial VS rather than a general slowing of RTs (Bennett et al., 2012; Foster et al., 1995; Humphrey and Kramer, 1997; Li et al., 2013; Plude and Doussardroosevelt, 1989).

There are also age-related declines in temporal attention. Older adults are not only slower at processing visual stimuli (Ball et al., 2006; Rubin et al., 2007) but also display an increased magnitude of the "attentional blink", which is commonly interpreted as a reflection of an attentional bottleneck (Lahar et al., 2001; Lee and Hsieh, 2009; Maciokas and Crognale, 2003; Shih, 2009; van Leeuwen et al., 2009). The attentional blink is where, for up to 500ms after detecting a target in a rapidly changing stream of visual stimuli - i.e. a rapid serial visual presentation (RSVP) stream - there is a reduced ability to detect a second target (Raymond et al., 1992). This effect is stronger and lasts for longer with increased age (Lahar et al., 2001; Lee and Hsieh, 2009; Maciokas and Crognale, 2003; Shih, 2009; van Leeuwen et al., 2009), which, again, cannot be explained by general slowing alone (Lee and Hsieh, 2009; Maciokas and Crognale, 2003).

It is widely acknowledged that older adults are impaired in inhibiting irrelevant visual information (Adamo et al., 2003; Gazzaley et al., 2008; Greenwood and Parasuraman, 1994; Hasher and Zacks, 1988; Lustig et al., 2007; Maciokas and Crognale, 2003). Difficulties in temporal and spatial attention may therefore be due to a decline in selective attention mechanisms resulting from impaired excitatory-inhibitory attention processes, where excitatory mechanisms fail to reach activation thresholds and inhibitory mechanisms fail to suppress interference from visual distractors (Shih, 2009). In other words, deficits in mechanisms sustaining a balance between excitation and inhibition could lead to a decline of selective attention efficiency in time or space. In a recent behavioural study (Callaghan et al., 2017), we investigated whether further costs are incurred with age when these selective attention mechanisms have to be re-tuned or switched from selectively attending to targets in time to selecting targets in space. We indeed observed increased "switch-costs" in older age groups. The current paper addresses the question of how the underlying neural mechanisms change to explain this reduced attentional flexibility.

1.2. Neural mechanisms of attention

The neural implementation of excitatory and inhibitory attention mechanisms has been outlined in influential neural competition models of visual attention, which postulate that numerous stimuli can be processed in parallel in perceptual networks, yet compete for access to conscious processing at the level of working memory (Beck and Kastner, 2009; Bundesen et al., 2005; Desimone, 1998; Scalf et al., 2013; Treisman, 1985; Treisman and Gormican, 1988). Attention would then be defined as a bias towards enhancing some competing excitation patterns over others. This proposition is supported by evidence from single cell recordings (Reynolds et al., 1999), which suggest that this early competition is carried out in separate cell assemblies for separate stimuli (Luck et al., 1997). Attention can therefore be conceived of as a set of mechanisms that bias processing in favour of salient and/or task relevant stimuli through bottom-up as well as top-down signal enhancement of certain neural assemblies (Dehaene et al., 2006). Similar to the “global neuronal workspace model” proposed by Dehaene and colleagues (1998; 2006), the Neural Theory of Visual Attention (NTVA; Bundesen et al., 2005) suggests that attention works to increase or decrease the number of neurons involved in processing each object and alters the firing rate of neurons coding for certain features. The authors further propose that as temporal expectation increases, temporal attention mechanisms increase the firing rate of neuronal populations that represent anticipated features. In contrast, spatial attention would alter the number of cell assemblies allocated to processing objects in specific (attended) parts of the visual field (Bundesen et al., 2005; Vangkilde et al., 2012; Vangkilde et al., 2013). Thus, it could be expected that switching between temporal and spatial attention requires adjustments to both firing rates and the allocation of feature-coding neuronal populations to receptive fields. Dehaene et al.’s (2006) framework of conscious visual processing proposes that frontal, parietal and anterior cingulate regions are crucial for conscious processing of visual stimuli. According to this framework, fronto-parietal networks would be crucially involved in top-down changes in selective enhancement during attentional flexibility, dynamically adjusting expectations in space and time by modulating the temporal and spatial dynamics of firing rates in posterior neuronal populations.

Overlapping networks across occipital, frontal, parietal and motor regions have been implicated in both, directing attention in time and space (Coull and Nobre, 1998; Fu et al., 2005; Gross et al., 2004; Li et al., 2013; Madden et al., 2007; Shapiro et al., 2002). In addition to finding overlapping activation for temporal and spatial attention in their functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies, Coull and Nobre (1998) found sub-patterns of activation that were distinct for the two types of attention. Regions found to be involved in both spatial and temporal orienting of attention in both the PET and fMRI results were bilateral premotor cortex, intraparietal sulcus (IPS), visual cortex and cerebellum. PET revealed that, compared to temporal attention, spatial attention involved more activity in the inferior parietal lobule, whereas temporal orienting triggered more activity in the left IPS, left cerebellum and left ventral premotor cortex, the latter of which was exclusive to temporal attention. Furthermore, the authors' fMRI results revealed right IPS and temporo-parietal junction activity specific to spatial orienting.

In addition to the distinct patterns of cortical activity across temporal and spatial attention, differences in cortical processing have been observed when comparing serial and pop-out VS or when comparing tasks with different attentional demands. For example, Imaruoka et al. (2003) found the right IPS was more strongly involved in pop-out than serial search, which the authors interpreted as an involvement of this region in bottom-up attention. In contrast, prefrontal regions have been implicated more generally in top-down executive control of attention (Badre and Wagner, 2004; Baluch and Itti, 2011; Bouvier, 2009; Kastner and Ungerleider, 2000; Kerns et al., 2004). In particular, the anterior cingulate cortex (ACC) has been associated with selective attention in more demanding tasks that require resolving conflict between incongruent or ambiguous information (Badre and Wagner, 2004; Kerns et al., 2004).

1.3. Inhibition, alpha oscillations and attention

Shih (2009) proposed that age-related decline of attention could be a result of impaired neural inhibition and/or increased neural noise. Both increased neural noise and impaired inhibition could result in increased activation thresholds to select visual stimuli, thus, resulting in enhanced difficulties in reaching these thresholds (Adamo et al., 2003; Aydin et al., 2013). The notion of increased neural noise is supported by increased age-related variability that affects signal-to-noise ratios in fMRI studies with older age groups (Huettel et al., 2001) as well as in studies using event related potentials (ERP), where increased variability results in reduced ERP amplitudes (Polich et al., 1985). The notion of inhibition has been strongly linked to alpha oscillations (8-12 Hz), including task-related modulations in amplitude and phase.

It is now widely believed that inhibition is at least partly achieved through increased alpha frequency amplitudes (or frequency power) over parieto-occipital cortex, whereas an alpha decrease typically reflects enhanced attention in space and time (Capotosto et al., 2009; Hanslmayr et al., 2007; Hanslmayr et al., 2005; Klimesch et al., 2007; Rohenkohl and Nobre, 2011; Sauseng et al., 2005; Thut et al., 2006; Yamagishi et al., 2003). In addition to inhibition of irrelevant sensory information, alpha increases are also typically present during sustained attention (Dockree et al., 2007; Rihs et al., 2007, 2009) and are likely to inhibit unattended locations and irrelevant sensory information (Rihs et al., 2007). Successful visual target discrimination can be predicted by the magnitude 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 et al., 2009; Busch and VanRullen, 2010; Dugué et al., 2011; Mathewson et al., 2009). It has therefore been proposed that posterior alpha oscillations suppress processing through sensory gating, where the processing of a stimulus is modulated by the phase of the alpha cycle (Bonnefond and Jensen, 2015; Busch et al., 2009; Dugué et al., 2011; Jensen and Mazaheri, 2010; Mathewson et al., 2009). The direct relationship between increased alpha power and suppression of processing has been corroborated by the manipulation (entrainment) of parietal alpha oscillations through transcranial magnetic stimulation (Gooding-Williams et al., 2016; Herring et al., 2015). All-in-all there is substantial evidence to suggest that inhibition is partly achieved through increased alpha power, whereas an alpha decrease appears to reflect enhanced attention, suggesting an implication of alpha modulation in selective attention.

Accordingly, older adults fail to modulate alpha oscillations to the same extent as younger adults (Deiber et al., 2013; Hong et al., 2015; Pagano et al., 2015; Vaden et al., 2012) and consistently 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), which could be indicative of a failure to inhibit irrelevant visual distractors (Vaden et al., 2012). However, failure to modulate alpha oscillations does not seem to consistently result in impaired 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 was not associated with impaired 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 alternative 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 recruit different frequencies and/or brain areas to compensate for impaired posterior alpha modulation, a notion that requires further investigation.

1.4. Compensatory recruitment or neural noise?

The literature has consistently 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 et al., 2007). It has been debated as to whether this increase in activity spread reflects increased neural noise (Quandt et al., 2016; Welford, 1981) or compensatory recruitment (Fabiani et al., 2006; Madden et al., 2007; Park and Reuter-Lorenz, 2009; Quandt et al., 2016; Reuter-Lorenz and Cappell, 2008; Reuter-Lorenz and Park, 2014). In other words, is the wider spread of activity detrimental or beneficial to functioning?

The notion of increased neural noise assumes that activation thresholds become more difficult to reach and, in turn, the focality of neural activation is affected, resulting in a more wide-spread pattern of activity within and across brain areas (Shih, 2009; Welford, 1981). Similar to a neural noise hypothesis of neural ageing, Cabeza (2002) proposed a dedifferentiation hypothesis, where ageing results in a decreased specialisation of cortical processing. Enhanced neural noise or dedifferentiation with increased age (Cabeza, 2002; Huettel et al., 2001; Polich et al., 1985; Shih, 2009; Welford, 1981) characterises the wider spread of brain activity as detrimental, thereby providing an explanation for impaired selective attention (Shih, 2009).

On the contrary and in support of a compensatory recruitment hypothesis of more widely distributed brain activity in older age, there is cognitive evidence to suggest that older adults are indeed able to compensate for attentional deficits with top-down control of attention, such as utilising cues more effectively than younger people in selective attention tasks (McLaughlin and Murtha, 2010; Neider and Kramer, 2011; Watson and Maylor, 2002). As proposed by the “Scaffolding Theory of Aging and Cognition” (STAC; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014), successful compensatory cognitive strategies are likely to recruit additional neural resources, which could be reflected by a wider distribution of brain activity – prominently involving brain areas related to top-down control. Accordingly, 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 multiple cognitive paradigms have indeed reported 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 prefrontal cortex (PFC) and parietal regions (Cabeza et al., 2004; Grady, 2000; Madden, 2007). 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. The widely acknowledged decline in the structure of frontal regions with age makes the PASA hypothesis counterintuitive (Colcombe et al., 2005; Daigneault et al., 1992; West, 2000; West, 1996). However, in addition to the vast literature supporting a frontal lobe deterioration hypothesis of ageing (Colcombe et al., 2005; Daigneault et al., 1992; West, 2000; West, 1996), 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.

However, inconsistent with the simple formulation of the PASA hypothesis of ageing (Davis et al., 2008), theta modulations (3-7hz) along the frontal midline have been shown to deteriorate with increased age - in both resting state and task related conditions (Cummins and Finnigan, 2007; 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 cognitive control (Cavanagh et al., 2009; Cavanagh and Frank, 2014; Min and Park, 2010), target processing (Demiralp and Başar, 1992), working memory (Sauseng et al., 2010) and selective attention (Green and McDonald, 2008). Frontal midline theta is thought to reflect medial PFC and ACC activity (e.g. Asada et al., 1999) which are central to attentional control (Cavanagh et al., 2009; Cavanagh and Frank, 2014; Konishi et al., 1999; Pollmann, 2004). Functional connectivity mediated by theta oscillations has been shown to play an important role in attention, error monitoring and executive function (Cavanagh et al., 2009; Schack et al., 2005; Voloh et al., 2015; Wang et al., 2016b). For example, Voloh et al. (2015) found increases in theta-gamma phase-amplitude coupling between ACC and PFC in non-human primates before successful but not before unsuccessful attentional shifts.

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 and Finnigan, 2007; Reichert et al., 2016; van de Vijver et al., 2014). Although there is an overall reduction in frontal midline theta power with increased age, it could be that there is an increase in compensatory lateral PFC theta activation that has not been identified by previous EEG studies due to poor spatial resolution, or which may not be reflected in theta power modulation (but in alpha modulations, for instance). More consistent with a PASA hypothesis of ageing (Davis et al., 2008), Gazzaley et al. (2008) found an increase in frontal midline theta power in older adults when implementing a visual attention task, consistent with an increase in the implementation of top-down attentional guidance.

1.5. The current study

In the light of the aforementioned inconsistencies and competing theoretical accounts we set out to clarify the notion of age-related deficiencies and possible compensatory mechanisms of attention by investigating modulations of alpha and theta frequency bands during switches between temporally vs. spatially tuned attention. We used Magnetoencephalography (MEG) to increase spatial resolution over previous EEG studies, while achieving the necessary temporal resolution for frequency-specific analysis, thus, allowing for oscillatory analysis in source space.

The aim of the current study was to investigate the neural mechanisms that reflect age-related changes in the ability to refocus attention between time and space that has been reported in our previous behavioural work (Callaghan et al., 2017). Age groups were compared 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 to identify a target in a VS display. This reallocation of attention can be conceived of as a switch in attentional focus and we will refer to increased costs of refocussing (e.g. as reflected by increased RTs) as “Switch-Costs”, although the paradigm employed is not a traditional task-switching paradigm (Callaghan et al., 2017).

To manipulate the cost of switching (the 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. Conforming to our recent behavioural work (Callaghan et al., 2017), 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 youngest group. It is important to note that in Callaghan et al. (2017) we observed increased Switch-Costs already in the group aged 40-49 years, which informed our current hypothesis that both older groups would differ from the youngest group (aged 19-30 years). Furthermore, in our novel RSVP-VS paradigm pop-out, VS performance appeared to be more sensitive to age-related differences than serial VS performance, which was most likely due to the older adults' slowed RTs reaching ceiling point in the case of serial VS (for details see Callaghan et al., 2017). We therefore decided to employ pop-out VS only so as to optimise sensitivity to age-related changes in brain oscillations.

MEG was recorded while participants completed the attention switching task to enable the investigation of age-related changes in oscillatory neural mechanisms that may explain deficits in switching. Based on previous literature (Gazzaley et al., 2008; Hong et al., 2015; Reichert et al., 2016; Vaden et al., 2012), it was expected that there would be age-related changes in alpha and theta oscillations that would explain age group differences in attentional switching (as reflected by RT increases). It was hypothesised that there would either be an increase in frontal theta activity reflecting additional top-down compensatory processing (Davis et al., 2008; Fabiani et al., 2006; Gazzaley et al., 2008; Madden, 2007), or a reduction in theta power, particularly across the frontal midline as has been demonstrated in previous EEG studies (Cummins and Finnigan, 2007; van de Vijver et al., 2014), and which might result from increased activation thresholds due to increased neural noise as a consequence of age-related deterioration. 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).

Modulations of theta and alpha source power were hypothesised to correlate with behavioural measures of RT-Switch-Costs. We expected more widely distributed power modulations in the older groups compared to the youngest group (Adamo et al., 2003; Lague-Beauvais et al., 2013; Li et al., 2013; Madden et al., 2007). Correlations between Switch-Costs and power modulation in regions that form this wider distribution would support theories of compensatory recruitment (Cabeza et al., 2018; Fabiani et al., 2006; Madden et al., 2007; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014). Alternatively, more widely distributed power modulations without or with negative association with reduced Switch-Costs could suggest increased neural noise.

Finally, 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 (decreased neural precision) 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). Graph theoretical metrics were expected to reveal topologies with a more “star-like” structure in the younger adults, reflecting efficient local connectivity (e.g. in specialised cortical regions), whereas more “chain-like” topologies were expected to be seen in older adults, reflecting less efficient, longer range connectivity. Furthermore, graph theoretical metrics were expected to correlate with Switch-Costs, demonstrating a relationship between network topology and task performance.

2. Methods

2.1. Participants

Participants were recruited from Aston University staff and students and the community. Participants aged over 60 years were also recruited from the Aston Research Centre for Healthy Ageing (ARCHA) participation panel. Participants provided written informed consent before participating and were screened for contraindications to having an MRI or MEG scan and received standard payment according to local rules. The research was approved by Aston University Research Ethics Committee and complied with the Declaration of Helsinki.

Sixty-three participants in three age groups (19-30, 40-49, 60+ years; see Table 1 for details) were included in the final analysis. Note that we began by investigating 60-69 and 70+ years groups separately, however, given the lack of significant difference in behavioural data and similarity in neural signatures, it was decided to collapse these into a single 60+ years group (60-82 years). 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 that provide measures of language, memory, attention, fluency and visuospatial abilities. In total 73 participants were tested, but six participants were excluded from analysis due to low performance accuracy and/or too noisy MEG data resulting in fewer than 30 out of 80 trials remaining for one or more conditions after data pre-processing. These six participants included one individual aged 40-49 years and five participants aged 60+ years. Two participants withdrew from the study and in two 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 one 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 1.

Table 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

This table presents the demographics for each age group, including 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.

2.2. Materials and procedures

2.2.1. Attention switching task and MEG recordings

The attention switching paradigm from Callaghan et al. (2017) was adapted for use with MEG (see Figure 1). The major change to the MEG paradigm was to reduce the number of conditions while increasing the number of trials in each condition (for the required signal-to-noise ratio for MEG analysis), by focusing only on pop-out VS, since Callaghan et al. (2017) had reported performance ceiling effects for serial VS. On each experimental trial participants attended to an RSVP stream first before switching to a pop-out 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. E-Prime 2.0 Professional (Psychology Software Tool. Inc.) was used on a windows PC to present stimuli, record responses, and send triggers to the MEG through a parallel port (at the onsets of RSVP, target (if applicable), and VS display, as well as upon response to VS). Stimuli were back-projected onto a screen inside a magnetically shielded room (MSR) 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, namely a digit (1/2/3/4/6/7/8/9), which participants were expected to detect and memorise for report at the end of the trial (after the VS). The target could be either the first stimulus of the stream (removing the need to attend to the stream) or the seventh or ninth item in the stream of ten stimuli. In the remaining one third of the trials the RSVP contained only letters and no target digit. Due to its visual similarity to the letter S, ‘5’ was excluded from the pool of targets. Based on their visual similarity to certain numbers, letters I, O, and S were excluded from the stream. Letters K and Z were the pre-defined targets for the VS task and were therefore also not employed as distractors in the RSVP. It should be noted that the current RSVP task differs from a standard attentional blink paradigm as the RSVP stream could only contain a maximum of 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, conforming to effects observed by Callaghan et al. (2017; see Introduction for details). 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. Note that conforming to Callaghan et al (2017) this button press did not discriminate between K or Z, but merely indicated that the participant had identified the target on that trial. Participants’ RTs to press this button were recorded and allowed for a more accurate and less variable search time estimate than a discriminative response (for detailed discussion see Callaghan et al., 2017). For MEG it had the added benefit that this response did not trigger different neural motor patterns (e.g. for different finger taps). Subsequently, participants 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 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.

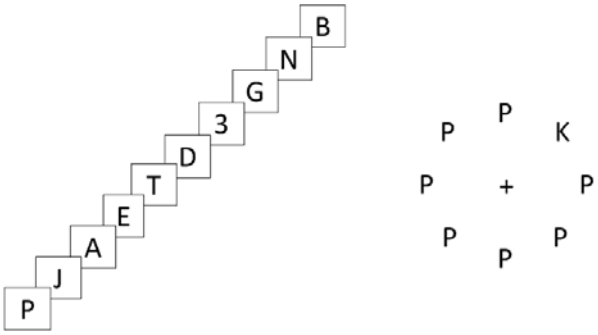

Figure 1. Illustration of examples of the stimuli set up. The RSVP stream illustration (left) displays a Target Switch RSVP stream. Each trial consisted of a fixation cross (2000ms) followed by an RSVP stream immediately followed by a pop-out VS display (right).

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.

2.3. Data analysis

2.3.1. Response times

Participants' median VS RTs (ms) on trials where both VS and RSVP responses were correct were extracted. 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), yet, there is evidence to support that ANOVA is robust to violations of 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 and 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.

2.3.2. MEG

MEG data were preprocessed in Elekta software using MaxFilter (temporal signal space separation (tSSS), .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 instead. 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 et al., 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 2.0s after the onset of the VS display. Trials were visually inspected for artefacts and any noisy trials were removed.

Sensor level analysis

For data cleaning independent components analyses (ICA) were implemented for each participant, across all conditions and components with eye blink or heartbeat signatures were removed from the data. Noisy MEG channels were interpolated with averaged signal from neighbouring sensors. Time-frequency analysis was carried out on signals 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).

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 using non-parametric cluster permutations (Maris and Oostenveld, 2007).

Second level analysis was carried out by pre-calculating Switch-Costs for each participant, by subtracting the No-Switch condition from each of the Switch conditions separately. Pre-calculated Switch-Costs were then compared at group level (Bögels et al., 2014; Wang, Callaghan, Gooding-Williams, McAlliste, & Kessler, 2016) by entering differences 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).

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 principle components analysis 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 (5mm voxels) were created from these coregistered MRIs. Head-models were normalised to MNI space (Montreal Neurological Institute template).

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 2.0s of data padding.

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 and Oostenveld, 2007).

Consistent with the sensor level analysis, second level analysis was carried out by comparing Switch-Costs at the group level (Bögels et al., 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 in power (at peaks of each significant cluster of the source analysis) between each of the Switch conditions and the No-Switch condition in theta and alpha power were entered into Spearman's correlation analysis with behavioural RT-Switch-Costs. An explanation of how RT-Switch-Costs were calculated is provided in Section 2.3.1. Correlation analyses were exploratory and so multiple comparisons were not corrected for, however analyses were related to hypotheses and will inform future research trajectories.

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 et al., 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 phase locking value, phase lag index 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). Spatial filters for each of the 116 regions were computed with a linearly constrained minimum variance (LCMV) beamformer (Van Veen et al., 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 0.0-2.0s 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.

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 et al., 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 et al., 2017; Verstraete et al., 2011; Ye et al., 2014; Zalesky et al., 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 2.1-5.0) to understand the implications of thresholding on resulting networks. The range of thresholds at which clusters were significant are reported in Figures 9-12.

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 et al. (2017) and Ye et al. (2014). 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.

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, 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, where most nodes would have at least two "neighbours", rather than a network characterised by chain-like, long range connectivity (Tewarie et al., 2014; Tewarie et al., 2015).

Global metrics, mean eccentricity and leaf fraction, were analysed in SPSS 21. To investigate the effects of age and RSVP condition on overall network topology, four 3×3 (age group × RSVP condition) ANOVAs were performed on leaf fraction and mean eccentricity for alpha and theta MSTs. 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 alpha MST mean eccentricity independent t-tests were implemented to compare age groups on mean eccentricity separately for each RSVP condition. Consistent with the RT analysis, Levene's test for equality of variance is not reported (Budescu, 1982; Budescu and Appelbaum, 1981). Where Mauchly's Test of Sphericity was significant, indicating that the assumption of sphericity has been violated, Greenhouse-Geisser corrected statistics were reported. Local MST metrics are reported in the SM.

Global MST metrics 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 related to hypotheses.

3. Results

3.1. 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 RSVP targets in both RSVP conditions. RSVP accuracy was unrelated to the aims and hypotheses of the current study and no further analysis was carried out on RSVP accuracy. The proportion of correct RSVP target identifications in the two Target conditions are presented in Figure SM1 in the SM. Group means of participants' median VS RTs are presented in Figure 2.

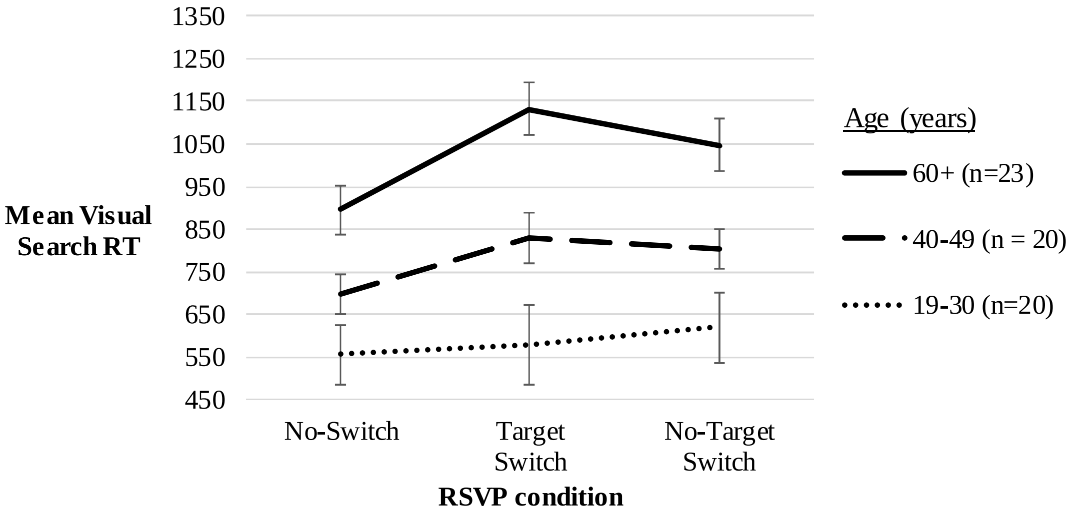

Figure 2. Group means of participants' median VS RTs. Vertical bars represent the SE.

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+ years 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. Please refer to Methods (Section 2) for a description of how Switch-Costs were calculated for each participant. Means and SDs of participants' Switch-Costs are presented in Table 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).

The RT results replicated findings from Callaghan et al. (2017) by demonstrating deficits in switching in both the 40-49 years and 60+ years groups in comparison to the 19-30 years group. Consistent with Callaghan et al. (2017), greater Switch-Costs in the older age groups were only significant when participants were required to process a target digit before switching. When there was no target in the RSVP stream older participants seem better able to cope with switching from temporal to spatial attention, suggesting either the availability of more processing resources and/or differences in strategies used to switch under this increased demand of target consolidation. To improve our understanding of the cognitive strategies used to switch between modalities of attention across the three age groups, in the following sections we will investigate group differences in task related oscillatory signatures, in both MEG power and functional connectivity analyses.

Table 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

3.2. MEG results

Frequencies from 2-30Hz were explored. From the TFRs presented in Figure 3, 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. Note that although group differences were also present in the beta frequency band (15-25hz), given the evidence for impaired inhibition (Adamo et al., 2003; Gazzaley et al., 2008; Greenwood and Parasuraman, 1994; Hasher and Zacks, 1988; Lustig et al., 2007; Maciokas and Crognale, 2003) and deficits in alpha modulation (Deiber et al., 2013; Hong et al., 2015; Pagano et al., 2015; Vaden et al., 2012) in older age, and the link between alpha oscillations and inhibition within selective 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), we focused only on alpha frequency throughout the analysis. 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.

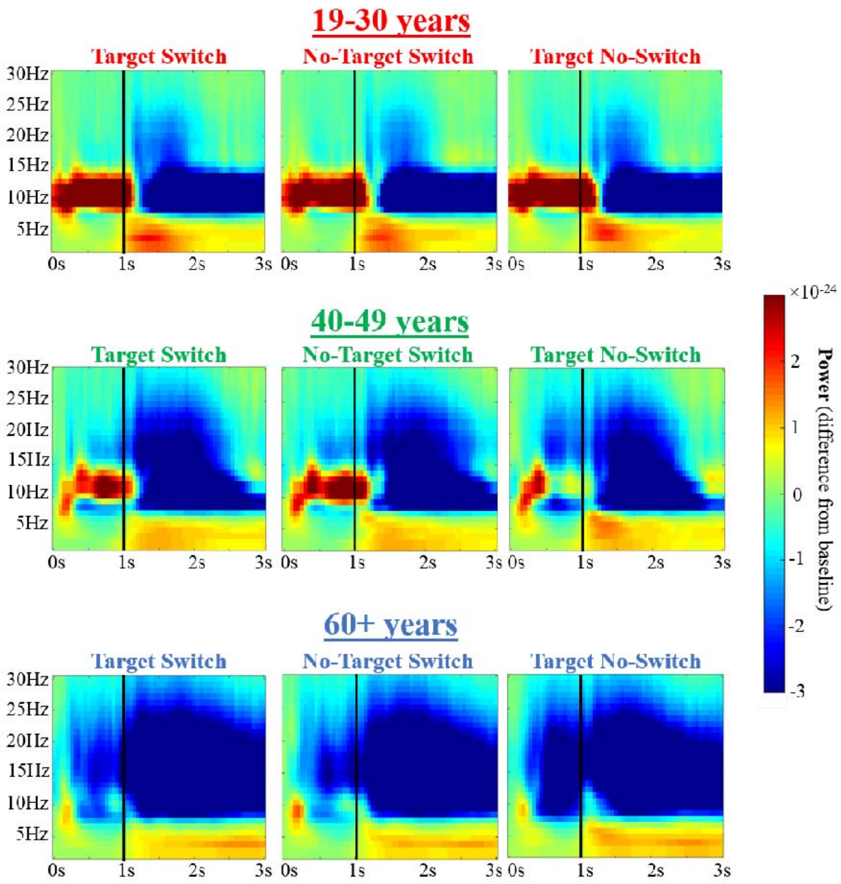

Figure 3. TFRs present power in relation to a baseline period of -0.6s - -0.01s in a group of four posterior gradiometer pairs. The onset of the RSVP stream occurred at 0.0s. Black lines placed over TFRs indicate the onset of the VS display, and RSVP target onset occurred at either 0.7 or 0.9s.

3.2.1. Theta power (in sensor and source space)

Target Switch vs No-Switch

Statistical results comparing theta power in Target Switch and Target No-Switch conditions in sensor and source space, and exploring the interaction between RSVP condition and age group, are presented in Figure 4 (at sensor level as topographies of significant clusters and in source space as significant clusters mapped onto an anatomical head-model. For details see Methods, Section 2).

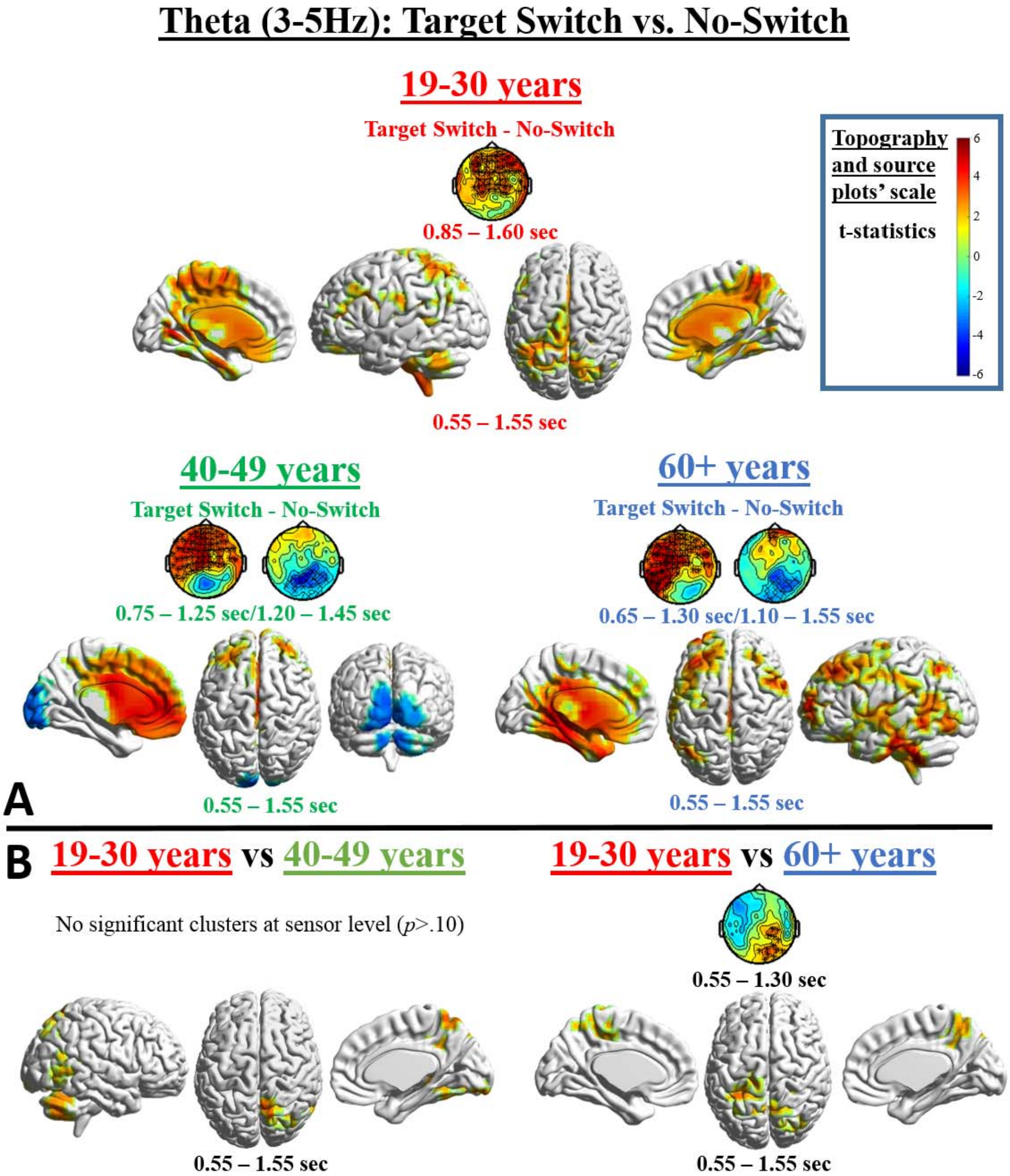

Figure 4. Effects in lower theta (3-5Hz) when contrasting Target Switch and No-Switch conditions in each age group (panel A) and when exploring the Target Switch condition × age interaction (panel B). Topographical (sensor level clusters) and source plots present *t*-statistics of significant clusters (*p*<.05 in sensor plots, indicated by asterisks and *p*<.025 in source plots).

The TFRs in Figure 3 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 (Figure 4A). 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 the limited sensitivity of cluster permutation analyses when localising both positive and negative clusters in source space.

Age group comparisons of differences between Target Switch and No-Switch conditions, which are presented in Figure 4B, 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 5.

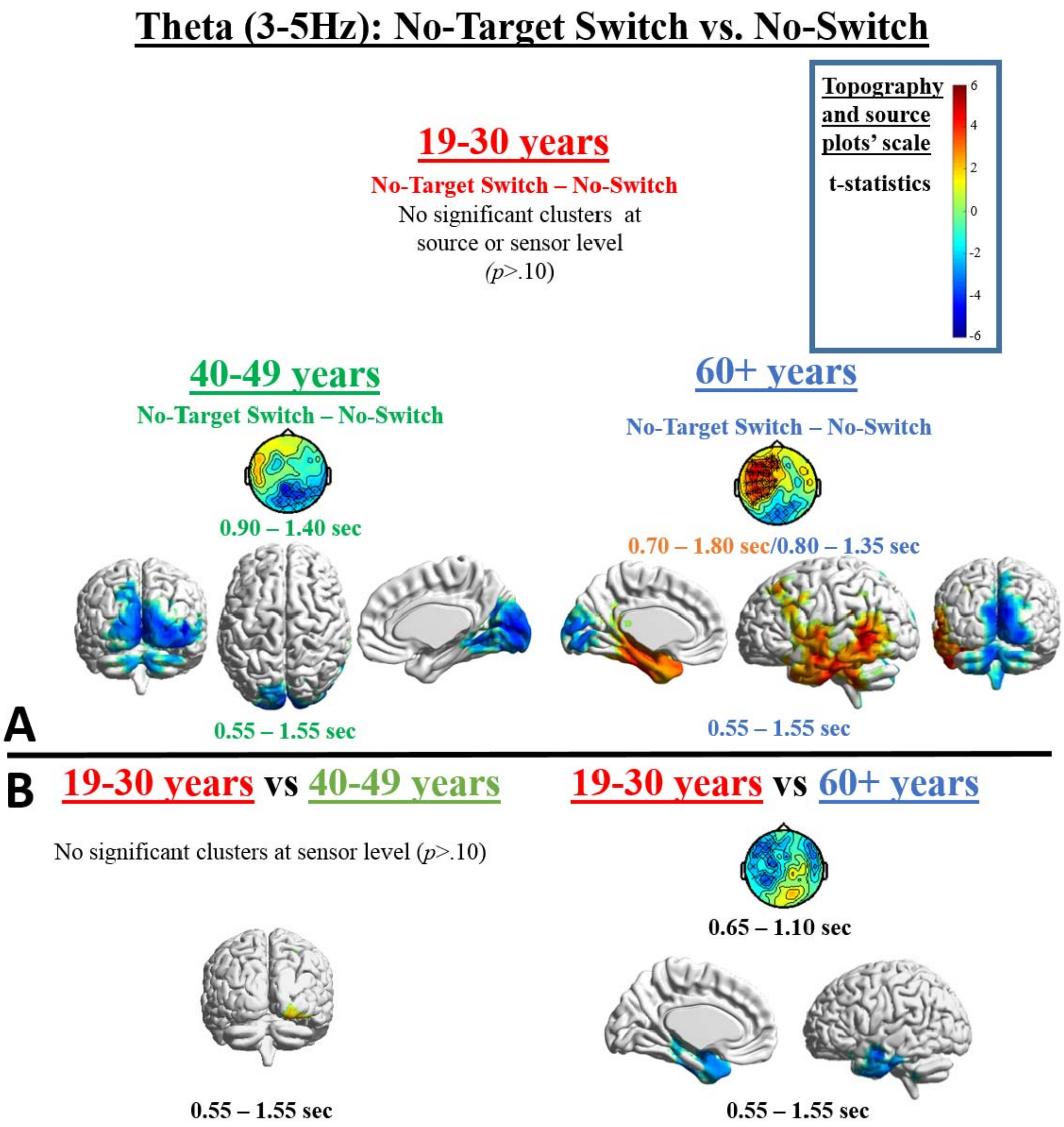

Figure 5. Effects in lower theta (3-5Hz) when contrasting No-Target Switch and No-Switch conditions in each age group (panel A) and when exploring the No-Target Switch condition × age interaction (panel B). Topographical (sensor level clusters) and source plots present *t*-statistics of significant clusters ($p<.05$ in sensor plots, indicated by asterisks and $p<.025$ in source plots).

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 theta power related to a Target Switch 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 IPS 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 to the No-Switch condition), which was contrary to the 19-30 years group. It could be that occipital theta deficits in the two Switch conditions are a reflection of deficient attentional guidance, where attention fails to modulate the temporal and spatial dynamics of activity in feature-coding neuronal populations (Bundesen et al., 2005), possibly contributing to the increased VS RTs observed in the two older groups after switching. Within the Dehaene et al. (2006) framework, this deficient attentional guidance in visual processing regions could be related to parietal theta deficits (Figure 4B).

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 recruiting additional resources and relying more on top-down attentional control (McLaughlin and Murtha, 2010; Neider and Kramer, 2011; Watson and 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 and Wagner, 1999) or silent vocalisation (Graves et al., 2007; Hickok and Poeppel, 2007; Hocking and Price, 2009; Smith et al., 1998).

3.2.2. Alpha power (in sensor and source space)

<u>*Target Switch vs No-Switch*</u>

Figure 6 presents the statistical results that compare alpha power in Target Switch and No-Switch conditions in sensor and source space (panel A), as well as the interaction between RSVP condition and age group (panel B).

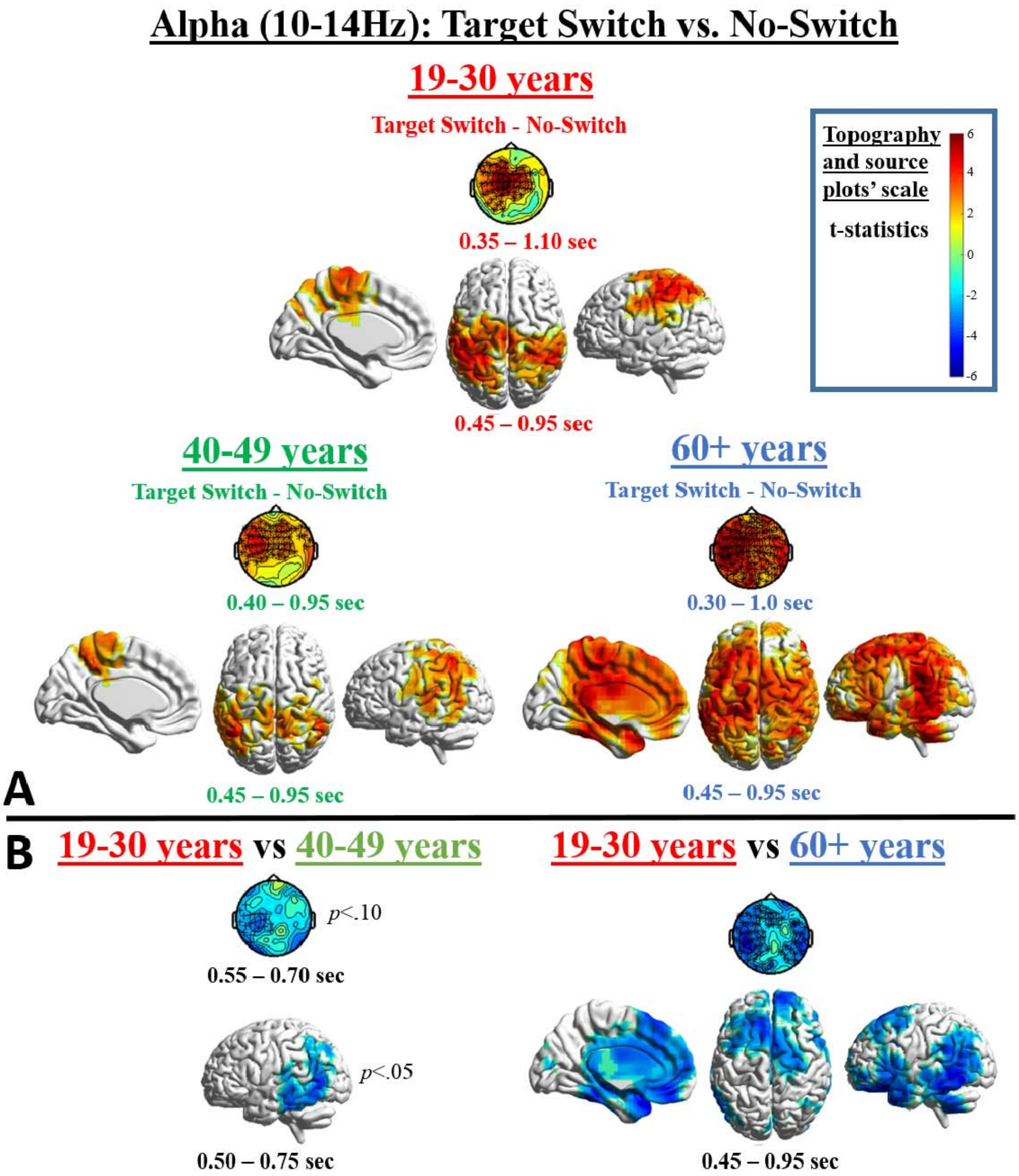

Figure 6. Effects in alpha (10-14Hz) when contrasting Target Switch and No-Switch conditions in each age group (panel A) and when exploring the Target Switch condition × age interaction (panel B). Topographical (sensor level clusters) and source plots present *t*-statistics of significant clusters ($p<.05$ in sensor plots, indicated by asterisks and $p<.025$ in source plots, or as indicated in the respective sub-plot).

All age groups show significantly higher alpha power in the Target Switch condition in comparison to the No-Switch condition which localised primarily to parietal regions in all age groups but was widely distributed across the cortex in the 60+ years group. The TFRs in Figure 3 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 in Figure 6B. These negative clusters were confined to temporal and parietal areas in the 40-49 years group and were only marginally significant at the sensor level, while the 60+ years group revealed more widely distributed clusters compared to the 19-30 years group, encompassing frontal, parietal, and temporal areas.

No-Target Switch vs No-Switch

Statistical results comparing alpha power in No-Target Switch and No-Switch conditions in sensor and source space are presented in Figure 7A, and analysis of the interaction between RSVP condition and age group is displayed in Figure 7B.

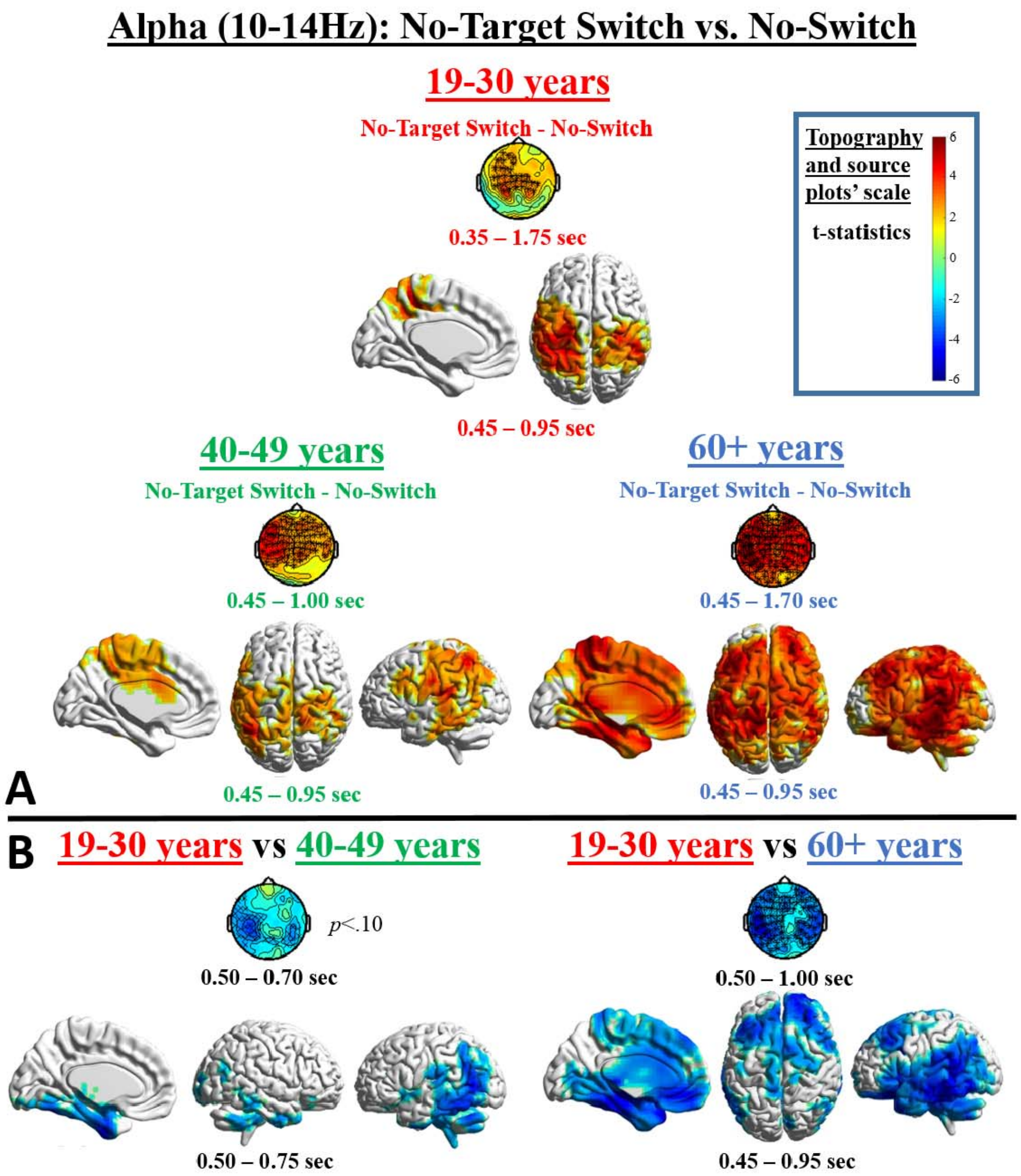

Figure 7. Effects in alpha (10-14Hz) when contrasting No-Target Switch and No-Switch conditions in each age group (panel A) and when exploring the No-Target Switch condition × age interaction (panel B). Topographical (sensor level clusters) and source plots present *t*-statistics of significant clusters ($p<.05$ in sensor plots, indicated by asterisks and $p<.025$ in source plots, or as indicated in the respective sub-plot).

Similar to the Target Switch vs. No-Switch contrast, 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 but was more 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 6, 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 (see also Figure 3).

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 in Figure 7B. 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 frontal and prefrontal areas.

3.2.3. Correlations between (theta and alpha) power and Switch-Costs

In this section we explore the potential relationships across age groups between theta and alpha power differences (between Switch and No-Switch conditions) on the one hand and behavioural Switch-Costs in RTs on the other. This could help us to understand whether some of the power differences we observed within and between age groups might reflect compensatory strategies (power modulations in the older groups might be related to <u>de</u>creasing Switch-Costs) or rather increased neural noise (power modulations in the older groups might be unrelated to behaviour or might even contribute towards <u>in</u>creasing Switch-Costs) or deficient neural processing (deficiencies in power modulation in the older groups might contribute towards <u>in</u>creasing Switch-Costs). We were therefore primarily interested in understanding how power effects in the two older groups would relate to Switch-Costs in RTs and pursued the following two-step logic. Firstly, for each older age group we related RT-Switch-Costs to source power effects at specific coordinates found in the analyses within the respective age group. Secondly, we related RT-Switch-Costs in each older group to source power effects in that group but taken from coordinates identified in the youngest group. For the latter we reasoned that residual activation in older participants in sources identified to be involved in efficient processing in the young participants might still be beneficial for processing in the older participants. This would corroborate the notion that processing deviations of the ageing brain from the “young” brain are indeed related to decreased processing efficiency. Specifically, we expected that residual power in older groups at coordinates reflecting “young” processing could contribute towards reduced behavioural Switch-Costs.

To analyse the relationship between theta and alpha power modulation and RT-Switch-Costs, for each participant differences in 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 RT-Switch-Costs. RT-Switch-Costs were correlated with power differences between Target Switch and No-Switch and between No-Target Switch and No-Switch conditions, respectively, for each of the two older age groups (40-49, 60+ years) and each of the frequency bands (theta, alpha) separately. MNI coordinates for each age- and frequency-specific correlation were selected based on the peak *t*-values of significant clusters that compared Switch and No-Switch conditions in the respective age group as well as in the youngest group. Selected MNI coordinates (and corresponding atlas labels) are provided in the SM, in Tables SM1 - SM4. Correlation analyses were exploratory and were not corrected for multiple comparisons.

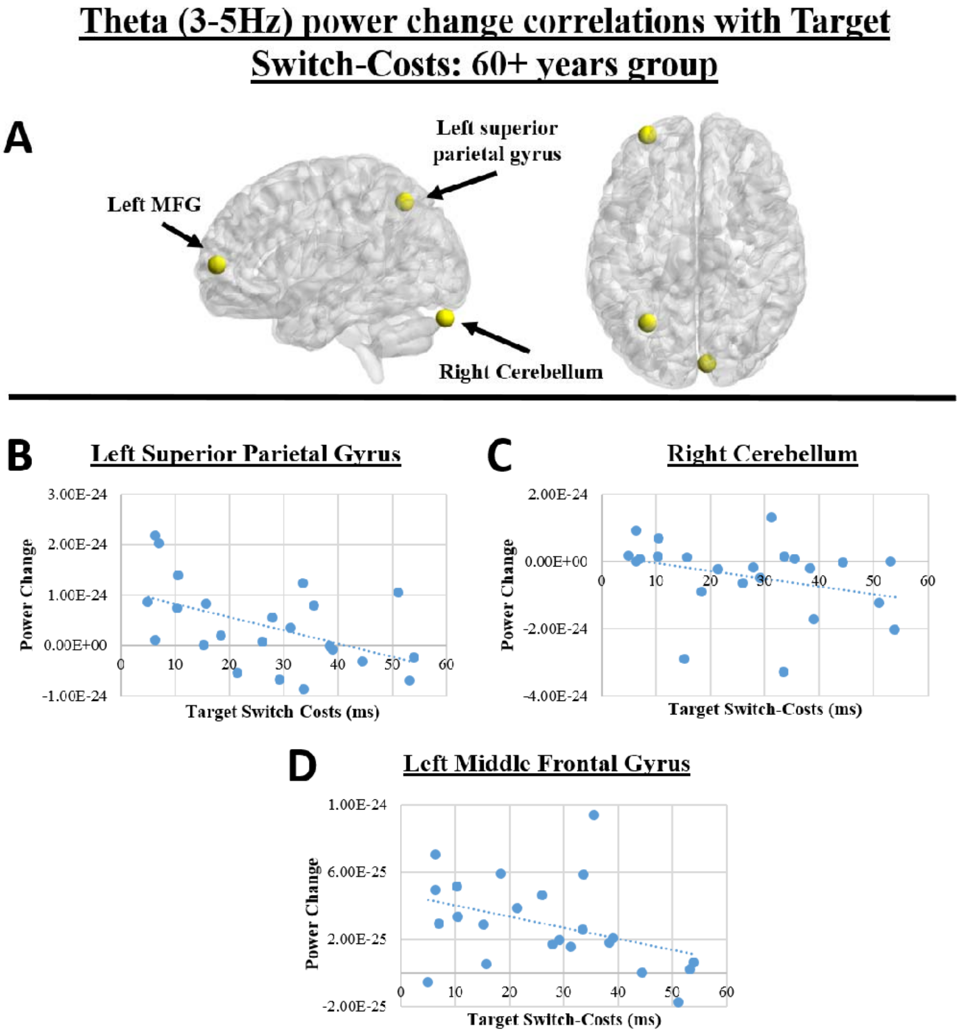

Figure 8. MNI coordinates of significant correlations between theta (3-5Hz) power change and Target Switch-Costs in the 60+ years group (panel A), and scatter-plots illustrating these correlations in the left superior parietal gyrus (panel B), right cerebellum (panel C) and left middle frontal gyrus (panel D).

Scatter-plots and source plots illustrating significant correlations are presented in Figure 8. In comparison to the younger adults, the two older groups had displayed greater theta power increases in frontal regions but weaker theta power increases in parietal regions for Target RT-Switch-Costs (Figure 4). Accordingly, in the 60+ years group, greater theta power increases in the left superior parietal gyrus (*r*=-.53, *p*=.010) and left MFG (*r*=-.40, *p*=.057) were associated with decreased Target RT-Switch-Costs. The left MFG coordinates were based on the theta power effect observed for the 60+ years group (Figure 4A) that indicated stronger frontal theta in this group. Importantly, due to deficient parietal theta in the 60+ years group overall (Figure 4B), the coordinates for the parietal correlation effect were adopted from the 19-30 years group, in order to specifically investigate whether residual theta power in the oldest participants would be beneficial for attention switching. This indeed seems to be the case and the overall pattern supports the notion that the additional frontal recruitment in the oldest group reflects compensation rather than increased neural noise and it further suggests that deficits in parietal theta could be related to impaired switching. However, no effects were observed for the 40-49 years group that could corroborate this conclusion.

The two older groups also displayed posterior negative theta power clusters that localised to occipital regions and the cerebellum. A negative correlation between Target RT-Switch-Costs and theta power modulation in the right cerebellum region (*r*=-.44, *p*=.035) in the 60+ years group may therefore reflect increased RT-Switch-Costs with increased posterior theta deficiencies, in concordance with previous findings (e.g. PASA hypothesis Davis et al. 2008; see Introduction for details). Note that in the Target Switch comparison (with No-Switch) the posterior negative cluster seen in sensor analysis failed to reach significance in the 60+ years group (Figure 4A). To reiterate, this is likely due to the limited sensitivity of cluster permutation analyses in localising both positive and negative clusters in source space. As a deterioration in task-related posterior activity was related to out hypothesis, we wanted to explore whether such changes were related to behavioural performance. Power change in this posterior negative cluster was therefore taken from coordinates based on the 40-49 years group's cluster peak. There were no further significant correlations between Target RT-Switch-Costs and theta power change in any age group (*p*>.05) and there were also no significant correlations between No-Target RT-Switch-Costs and theta power changes in any age group (*p*>.10).

Although the two older age groups displayed significantly stronger alpha modulations in comparison to the younger adults (Figures 6B, 7B), these modulations do not appear to have a clear relationship with Switch-Costs in RTs, since none of the calculated correlations reached significance (*p*>.10). The absence of a correlation between RT-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 alpha modulation in the two older groups across conditions implies that alpha oscillations are still task-related in older age, despite the seemingly weak benefits on performance. This was further strengthened by a lack of correlation between MFG theta (that had been related to reduced Switch-Costs) and posterior alpha. Rather than compensation it could therefore be that this strong modulation of alpha power reflects increased neural noise (Shih, 2009). This suggestion, however, will require specific further testing as it is based on the interpretation of a null result.

3.2.4. Network connectivity (NBS) analysis

Having observed age-related changes in both theta and alpha power, age-related changes in functional connectivity were explored. This analysis was based on the assumption that task-related frequency-specific connectivity requires a certain amount of neural precision to enable two brain regions to synchronise their neural activity in a manner beneficial to the task at hand. Therefore, if more extensive neural activation (power) is due to increased neural noise, functional connectivity should 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 the extent of precise communication across the cortex increases.

Functional connectivity between 116 AAL atlas regions was estimated with wPLI (see Methods Section 2). To investigate whether there were any changes in functional connectivity between Switch and No-Switch conditions and between age groups, non-parametric NBS was applied (Zalesky et al., 2010). NBS analysis of the main effects of RSVP condition for each age group are reported in the SM (Figures SM2 - SM5), as it was primarily the interactions between age group and RSVP condition that were most relevant to our hypotheses. Specifically, interactions were examined to establish whether older age groups presented with more extensive task-related connectivity, to compensate for difficulties in switching between attentional modalities, or weaker task-related connectivity, which would reflect that synchronisation between cortical regions is reduced with age.

To identify interactions between RSVP condition and age, age groups (19-30 vs 40-49 years; 19-30 vs 60+ years) were compared on the differences between Switch and No-Switch conditions, consistent with the analysis implemented for sensor and source power in Section 3.2.1 and 3.2.2. A description of how this was implemented can be found in the Data analysis section (Section 2.3).

Significant networks are presented in Figures 9 - 12. 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 9 - 12 illustrate the number of connections between each of the eight regions within each network. 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 differences should be interpreted with caution. A more detailed discussion of NBS can be found in Section 2.3.2.

Theta network connectivity

NBS results (theta network connectivity) investigating the RSVP condition Target Switch/No-Switch × age interaction are presented in Figure 9, and investigating the RSVP condition No-Target Switch/No-Switch × age interaction are presented in Figure 10.

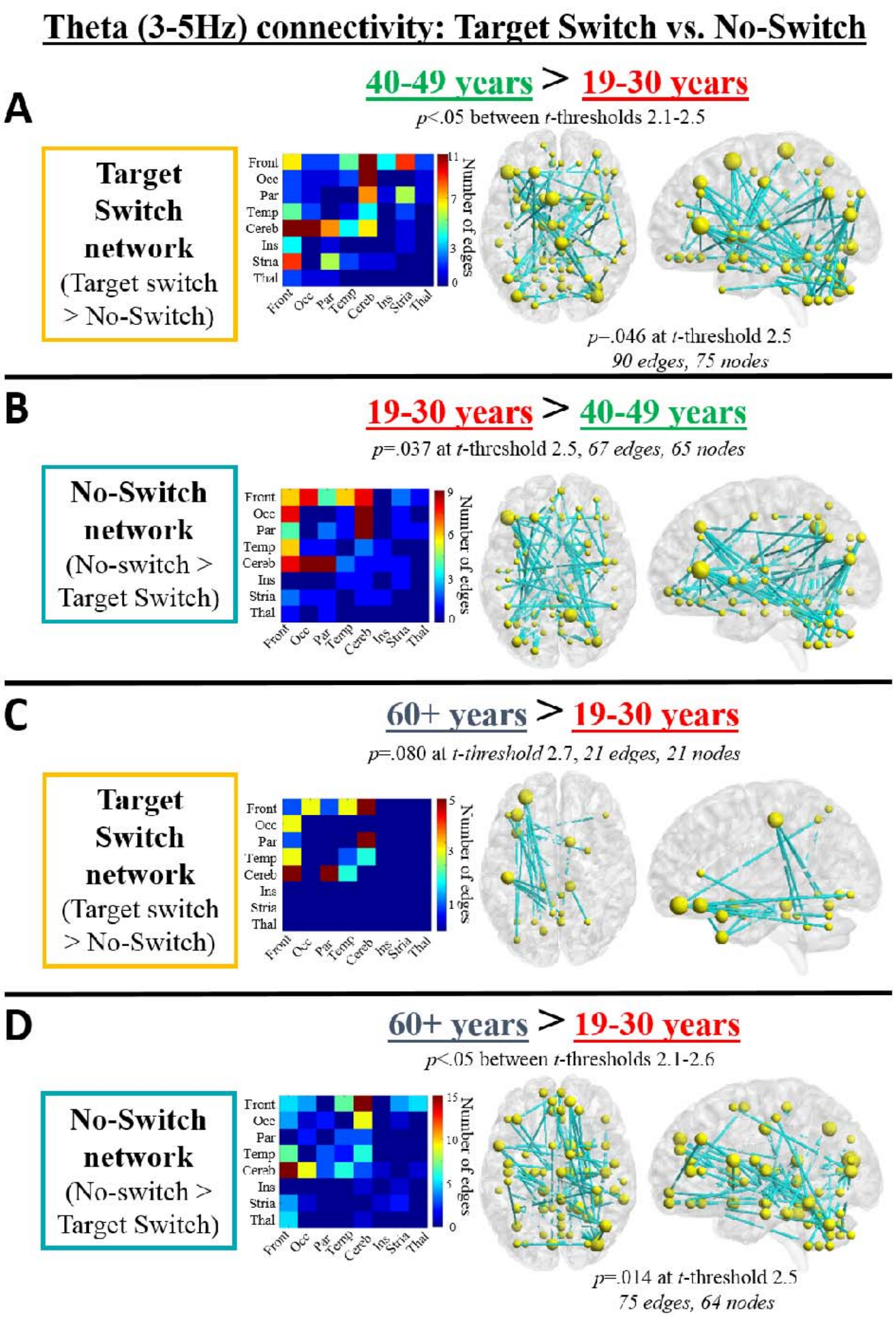

Figure 9. NBS results exploring the interaction between Target Switch condition and age group in theta (3-5Hz) connectivity (wPLI) between 0.55-1.55s. Group comparisons of Target Switch (Target Switch > No-Switch) networks (panels A and C) and No-Switch (No-Switch > Target Switch) networks (panels B and D). 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.

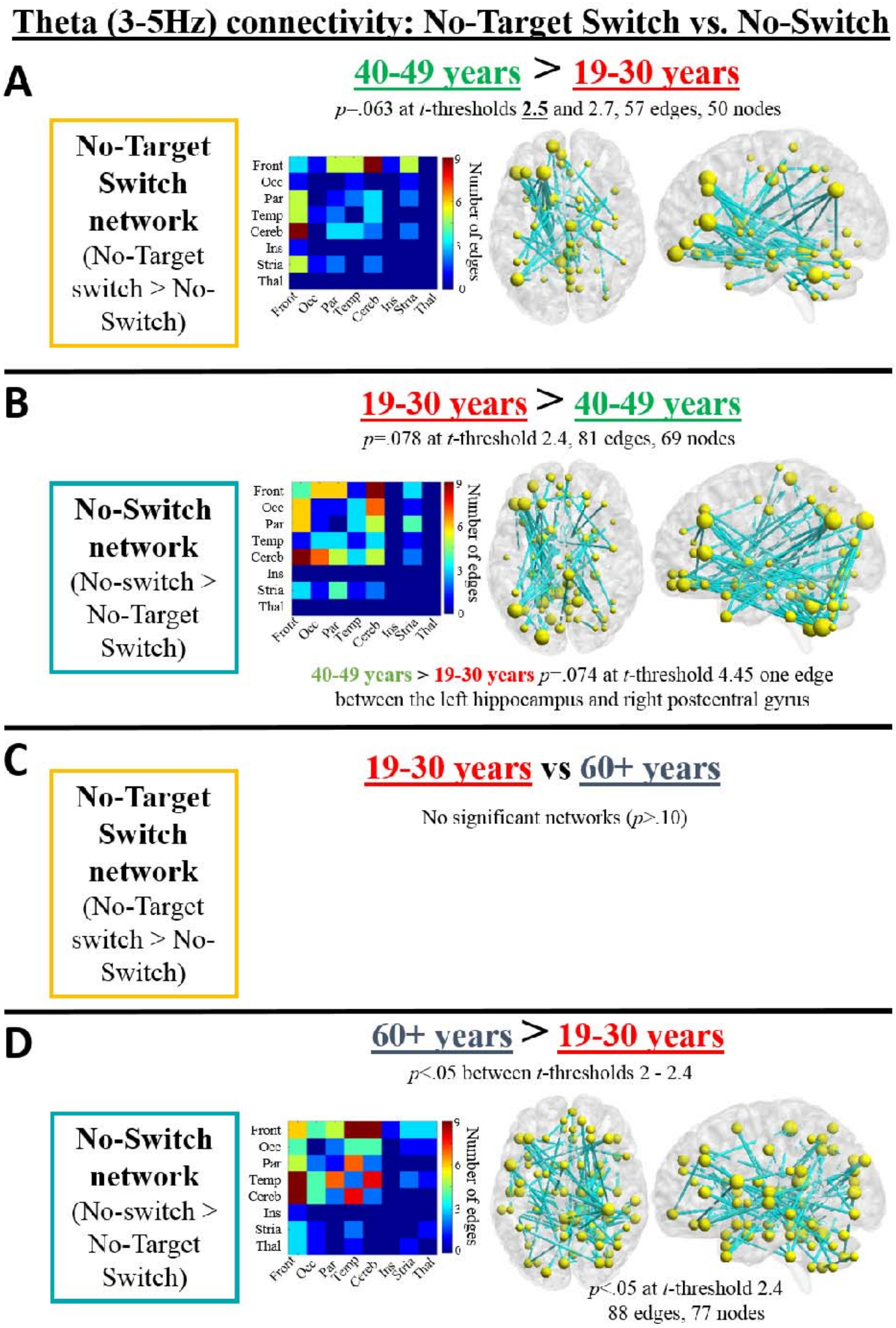

Figure 10. NBS results exploring the interaction between No-Target Switch condition and age group in theta (3-5Hz) connectivity (wPLI) between 0.55-1.55s. Group comparisons of Target Switch (No-Target Switch > No-Switch) networks (panels A and C) and No-Switch (No-Switch > No-Target Switch) networks (panels B and D). 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 40-49 years group showed more widely distributed theta networks than the 19-30 years group when there were increased attentional demands in the two Switch conditions, as can be seen in Figures 9A and 10A, particularly between frontal nodes and temporal and parietal regions and between the cerebellum and frontal, parietal and temporal regions. These findings are consistent with the additional theta power activity that we identified in frontal regions with source analysis in Section 3.2.1. Again, it could be that more extensive connectivity is reflecting compensatory recruitment, as participants utilise additional resources to cope with increased attentional demands. In the No-Switch networks, however, the 40-49 years group showed weaker connectivity in comparison to the 19-30 years group (Figures 9B and 10B). 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 in the network related to the easier task condition (No-Switch) is reflecting an initial decline in attentional networks in the 40-49 years group that is not yet seen in behaviour, and therefore not yet compensated for with an increase in top-down attentional control.

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, parietal 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 and Wagner, 2004; Baluch and Itti, 2011; Bouvier, 2009; Kastner and Ungerleider, 2000; Kerns et al., 2004), e.g. by supporting parietal regions that we found to be theta-deficient (see Figure 4B). Increased synchronisation between cortical regions supports 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, as variability in the firing rate of neuronal populations would prevent more precise synchronisation of distributed cortical regions. On the contrary, we found stronger synchronisation in the older group. Interestingly, the No-Switch networks that were greater in the 60+ years group compared to the youngest group (Figures 9D, 10D) were more pronounced and widely distributed than Switch networks (Figures 9C, 10C, the latter revealing no significant age group differences). This pattern could be taken to suggest that brain networks in older participants might already require compensatory recruitment to perform well under easy conditions, and in turn have limited additional resources to recruit under truly challenging conditions. This contrasts with the 40-49 years group who displayed more extensive connectivity than the youngest group (implying compensatory recruitment) when there were higher cognitive demands in the Switch conditions, not not in the No-Switch conditions (Figures 9A, 9B, 10A and 10B).

Alpha network connectivity

Figures 11 and 12 present alpha network connectivity NBS results, which investigate the RSVP condition × age interaction for the Target Switch condition (Figure 11) and No-Target Switch condition (Figure 12).

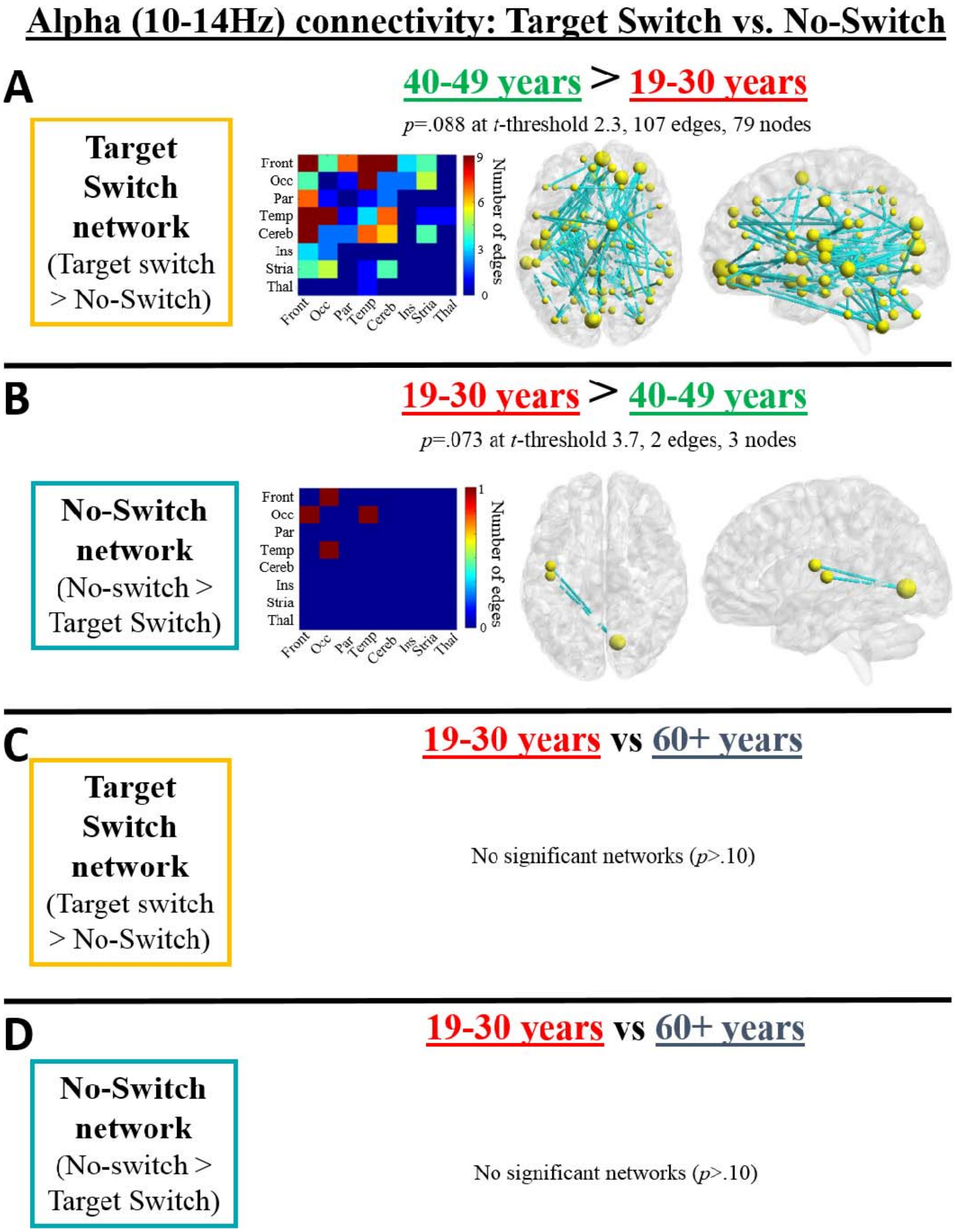

Figure 11. NBS results exploring the interaction between Target Switch condition and age group in alpha (10-14Hz) connectivity (wPLI) between 0.45-0.95s. Group comparisons of Target Switch (Target Switch > No-Switch) networks (panels A and C) and No-Switch (No-Switch > Target Switch) networks (panels B and D). 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.

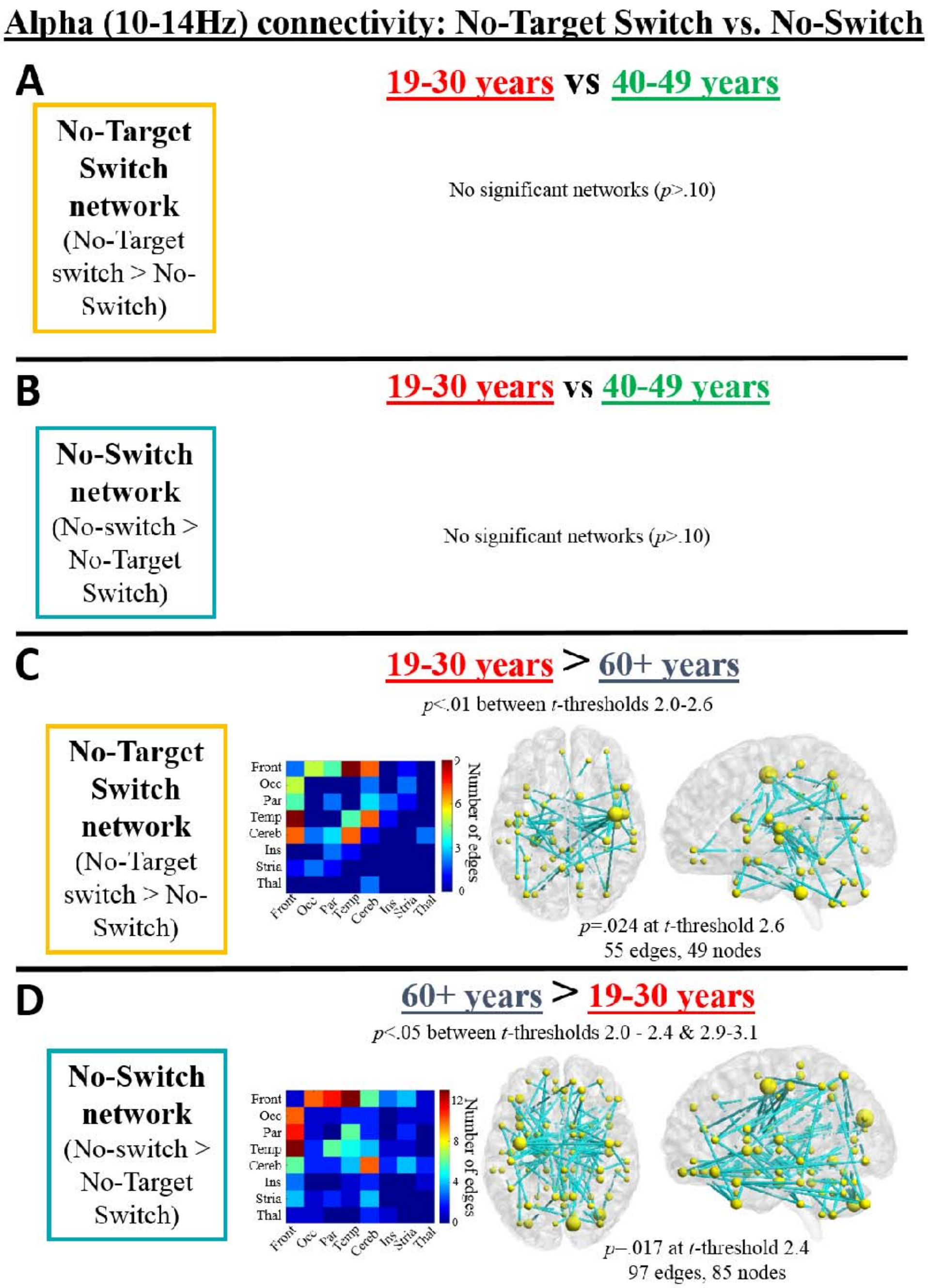

Figure 12. NBS results exploring the interaction between Target Switch condition and age group in alpha (10-14Hz) connectivity (wPLI) between 0.45-0.95s. Group comparisons of No-Target Switch (No-Target Switch > No-Switch) networks (panels A and C) and No-Switch (No-Switch > No-Target Switch) networks (panels B and D). 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 11B), but a more widely distributed network than the 19-30 years group when there was increased attentional demands in the Target Switch network (Figure 11A). 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 specifically under higher demands on processing. There were no significant differences between the 19-30 and 40-49 years groups when contrasting No-Target Switch and No-Switch networks (*p*>.10).

There were no significant differences between the 19-30 and 60+ years groups when contrasting Target Switch and No-Switch networks (*p*>.10). However, 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 (Figure 6) 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). On the other hand, 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, which demonstrates a certain level of functionality in increased alpha power modulation, rather than neural noise alone. Again it could be that brain networks in older participants already require compensatory recruitment to perform well under easy conditions, and have fewer additional resources available to recruit under harder conditions. It therefore seems that more extensive alpha power modulation in the oldest age group (Figures 6B and 7B) is not reflected in increased functional connectivity.

3.2.5. 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 comprised of 116 nodes corresponding to the 116 AAL atlas regions. Local MST metrics, degree, betweenness centrality and eccentricity were computed for each node in each MST. Results can be found in Figure SM8-SM11 in the SM.

Global MST metrics leaf fraction and mean eccentricity were computed separately for theta and alpha MSTs and submitted to two 3×3 (age group × RSVP condition) ANOVAs, respectively. 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) for the theta MSTs, which indicates that the global 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 SM7 in the SM. In contrast, alpha MSTs revealed significant effects described below (see Figure 13).

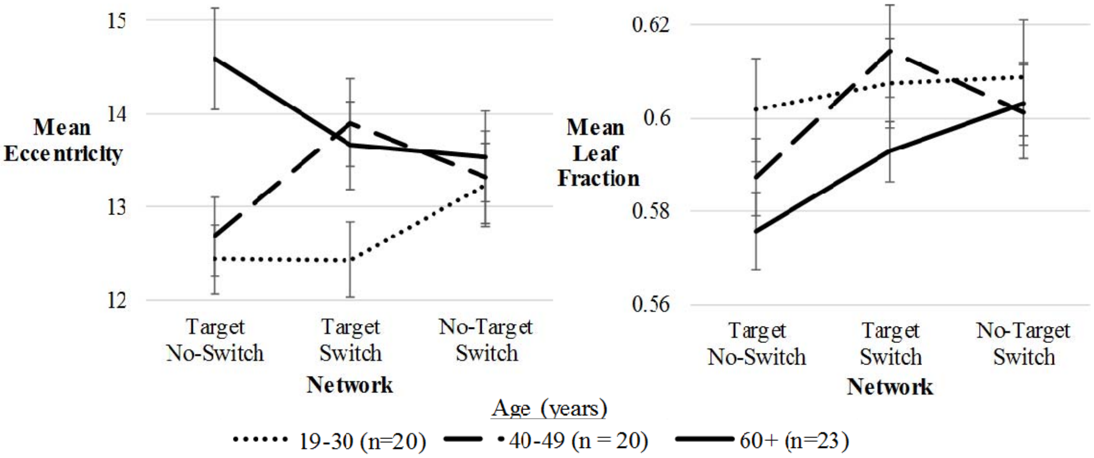

Figure 13. Group means of global alpha MST metrics mean eccentricity (left) and leaf fraction (right) for networks in each RSVP condition. Vertical bars represent the SE.

Mean eccentricity (alpha MST)

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, η^2_p=.11) and a significant interaction between age and RSVP condition (F(4,120)=2.73, p=.032, η^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), which corroborates the notion of recruitment of longer range networks in the oldest group for attempting compensatory strategies.

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 (see Figure 2). 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 RT-Switch-Costs (see Section 3.1). In the No-Target Switch condition the 40-49 years and 60+ years groups show no significant differences in RT-Switch-Costs in comparison to the 19-30 years group, and show no significant difference in mean eccentricity (p>.10). Despite alpha MST eccentricity mirroring mean RTs across age groups and RSVP conditions, there were no significant correlations between participants' mean eccentricity and Switch-Costs for any age group (p>.10).

Leaf fraction (alpha MST)

As shown in Figure 13 (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).

There were no significant correlations between participants' leaf fraction and Switch-Costs for the 19-30 or 60+ years group (p>.05). There was a significant positive correlation between No-Target Switch-Costs and leaf fraction in the No-Switch condition in the 40-49 years group (r=.55, p=.012). As the No-Switch MST presented more characteristics indicating local network connectivity, Switch-Costs increased.

4. Discussion

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

Also consistent with Callaghan et al. (2017), RTs of the 60+ years group were overall slower in comparison to the 19-30 years group. On the other hand, RTs of the 40-49 and 19-30 years groups did not significantly differ, implying that the 40-49 years group found the baseline No-Switch condition no more demanding than younger adults. However, the 40-49 years group again 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 SM in regards to local MST metric eccentricity.

Conforming to our hypotheses based on previous reports (Cummins and Finnigan, 2007; Deiber et al., 2013; Gazzaley et al., 2008; 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 (Figures 3-7). The hypothesis that there would be reduced theta power with increased age was partially 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. However, instead of a reduction in frontal midline theta power, as indicated by several previous reports (Cummins and Finnigan, 2007; Reichert et al., 2016; van de Vijver et al., 2014), frontal midline theta was increased for the attention Switch conditions in the two older age groups, particularly in the 40-49 years group in relation to a Target Switch. An increase in frontal midline theta with increased age is in line with the findings of Gazzaley et al. (2008). The 60+ years group presented with a more widely distributed theta increase in frontal regions across both Switch conditions. Theta power findings were therefore 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) that proposes a posterior to anterior shift with increasing age.

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 (Figure 3, 6B and 7B). 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. Alpha MST metrics confirmed our hypothesis that networks would display a more “star-like” structure in the younger adults, reflecting efficient local connectivity compared to the older adults who displayed more “chain-like” topologies, reflecting less efficient, longer range connectivity. 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. However, alpha modulations did not reveal significant correlations with behavioural Switch-Costs, possibly supporting an interpretation in terms of increased neural noise (Shih, 2009; Welford, 1981). In the following sections we will discuss various aspects of our results in more detail, before reaching final conclusions.

4.1. Theta power and network connectivity

As shown in Figure 4B, 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, increased parietal theta in the current task 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 (Figure 5A). It appears 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 parietal theta power related to target processing, 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 Figure SM9 for details). Reduced activity in the occipital lobe is consistent with previous findings of age-related reductions in visual cortex activity during visual processing and more generally with the PASA hypothesis (Davis et al., 2008; Huettel et al., 2001; Madden et al., 2002; Ross et al., 1997).

Current findings were consistent with the compensatory recruitment of additional cortical regions with increased age (Davis et al., 2008; Fabiani et al., 2006; Madden, 2007; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014). 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 4 and 5). Importantly, higher theta in the MFG and parietal cortex in the Target-Switch condition (compared to No-Switch) correlated with reduced RT-Switch-Costs in the 60+ years group, implying a compensatory role of the MFG (Cabeza et al., 2018; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014). The correlation between the parietal theta effect and Switch-Costs in this group is of particular importance as the parietal source coordinates were adopted from a theta effect in the youngest group. Thus, it appears that stronger residual parietal theta activity in older individuals, which resembles parietal theta activity in the young group, is beneficial to attentional switching in these older individuals and reflects the *maintenance* of attention mechanisms (Cabeza et al., 2018; Nyberg et al., 2012; Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014). This then seems to be complemented by compensatory MFG recruitment in theta.

Our interpretation of the current theta power findings as compensation rather than neural noise was further 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 (Figures 9 and 10). 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. The additional recruitment of frontal regions could reflect compensatory recruitment of top-down mechanisms to bias attention (Hopfinger et al., 2000). The additional temporal lobe activity in the 60+ years group on the other hand could indicate further compensatory strategies to complete the task, such as episodic memory encoding (Schacter and Wagner, 1999) or silent vocalisation (Graves et al., 2007; Hickok and Poeppel, 2007; Hocking and 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 EEG electrodes, and instead supports compensatory models of ageing such as STAC (Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014) and 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). Based on the assumption that task-related, frequency-specific connectivity requires higher neural precision, 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. The latter, however, does not appear to be the case (Figures 9 and 10). 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 (Cabeza et al., 2018), as reported in the SM, suggesting that those participants with stronger connectivity to the temporal pole have lower Switch-Costs. This further complements our observation that as theta power in the frontal and parietal lobe increased, Switch-Costs decreased in the 60+ years group.

The “middle-aged” group (40-49 years) provided 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 the 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 (Figures 9B and 10B). 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 (Figures 9A and 10A). Weaker connectivity in the easiest condition 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 Figure SM9). Importantly, as the network centrality of these nodes increased across individuals, Switch-Costs in the 40-49 years group decreased (see correlations reported in the SM), 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 9 and 10) and node centrality measures reported in the SM in Figure SM9. 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 et al., 2001), especially when timing is required (Keren-Happuch et al., 2014; O'Reilly et al., 2008). 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.

4.2. 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 6 and 7). Although alpha MST mean eccentricity seemed consistent with these power changes, by presenting "chain-like", long range connectivity in the 60+ years group, rather than "star-like", local connectivity, NBS revealed no significant differences between the 19-30 and 60+ years groups in alpha connectivity for the Target Switch network (Figure 11). Furthermore, the 19-30 years group recruited a more widely distributed No-Target Switch network than the 60+ years group (Figure 12) at alpha frequency. These two results seem inconsistent with source power and could suggest that the widely distributed alpha power effects in the 60+ years group reflect increased neural noise and dedifferentiation rather than compensation (Cabeza, 2002; Huettel et al., 2001; Shih, 2009; Welford, 1981). 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. However, the TFRs in Figure 3 clearly indicate that the older groups exhibited greater alpha power decreases in comparison to the younger group. Furthermore, the older group displayed stronger alpha network connectivity than the 19-30 years group in the No-Switch networks (No Switch > No-Target Switch; Figure 12D). 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.

Previous literature has shown that pre-stimulus 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 and Mazaheri, 2010) and enhance attention to visual stimuli (Capotosto et al., 2009; Hanslmayr et al., 2007; Hanslmayr et al., 2005; Klimesch et al., 2007; Rohenkohl and Nobre, 2011; Sauseng et al., 2005; Thut et al., 2006; Yamagishi et al., 2003) if these are no longer relying on 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 more widely distributed alpha network than the 19-30 years group in the Target Switch network (Figure

11A), but a weaker alpha network than the 19-30 years group in the No-Switch network (Figure 11B). 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 RT-Switch-Costs. From these findings it therefore seems that there is no effect of age on RTs or 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, which mirrors the pattern of increased RTs.

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 13). 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 measures of node centrality corroborate the recruitment of compensatory networks despite age group comparisons of alpha connectivity reflected in NBS (60+ vs 19-30 years; Figure 12) potentially suggesting increased neural noise.

5. Conclusions

We have replicated the findings of 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 theta power modulation 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. Efficient (low) Switch-Costs in the youngest group were reflected by parietal theta effects that were absent in both older groups. However, residual parietal theta in the oldest group was related to reduced Switch-Costs, thus, resemblance with efficient processing in the young brain appears to be beneficial for older brains. 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 modulation 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, indicating 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.

Overall our results demonstrate that older adults partially compensate for declines in attentional flexibility with the recruitment of additional neural mechanisms. These findings have important implications for future work, as they raise the question as to whether this compensatory recruitment can be enhanced with cognitive training programmes. Although we have shown that older adults compensate for functional decline, this compensation is only partially successful, and both middle and older age groups displayed poorer switching performance compared to younger adults. Improving older adults attentional flexibility could improve their performance in everyday functions such as driving, where one is required to quickly switch between fast changing events in multiple surrounding locations.

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