Märker, Gesine (2020) *Spatial attention in cognitive healthy ageing.* PhD thesis.

Spatial Attention in Cognitive Healthy Ageing

Gesine Märker

A thesis submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy

Institute of Neuroscience and Psychology

College of Science and Engineering

University of Glasgow

August 2019

Author’s Declaration

I declare that this thesis represents my own work except unless indicated in the text and that it does not include work forming part of a thesis presented for another degree.

Gesine Märker

Abstract

In young adults, spatial attention typically manifests in a processing advantage for the left side of space ("pseudoneglect")(Bowers & Heilman, 1980), whereas older adults tend to display no strongly lateralised bias, or a preference towards the right side of space (Benwell, Thut, Grant, & Harvey, 2014; Schmitz & Peigneux, 2011). However in addition, in recent studies, pseudoneglect has also been found to be maintained into old age (Brooks, Darling, Malvaso, & Della Sala, 2016; Brooks, Sala, & Darling, 2014; Friedrich, Hunter, & Elias, 2018). This suggests that the traditional view of an attenuated spatial asymmetry bias with increasing age may be too simplistic and that the spatial biases observed could be sensitive to a range of influences besides age. In addition, the traditionally observed shifts in spatial asymmetry in older adults have been attributed to neuroanatomical changes in the right hemisphere (with age), however as yet, there is limited evidence linking neurophysiological results to such behavioural shifts.

To this end, for older adults, spatial attention research lacks systematic investigation of intra- and inter-task consistency. In the first of the four experiments of this thesis, I built on an earlier study which investigated young adults (Learmonth, Gallagher, Gibson, Thut, & Harvey, 2015, see 2018), and addressed this issue by investigating the magnitude and direction of spatial asymmetry in older adults aged between 60 to 86 years in five commonly used spatial tasks (line bisection, landmark, grey and grating scales and lateralised visual detection). I also compared the obtained spatial biases to a driving task. Results confirmed a stable retest reliability of all spatial tasks across two testing days in older adults. The line bisection and greyscales tasks elicited significant left spatial biases, in accordance with pseudoneglect, while the other tasks showed no significant biases to either side of space. Interestingly, in the driving task a right bias emerged for older adult and was stable across testing sessions. Yet, it failed to correlate with the other spatial measures. In comparison to the young adults' sample from Learmonth et al. (2015, 2018), only the landmark task was age sensitive. However, none of the task showed significant inter task correlations. This replicates the findings of Learmonth et al. (2015, 2018) for an older age group. So in view of my findings of no significant inter-task

correlations, as well as the inconsistent directions of the observed spatial biases for the older adults, I present supporting evidence that pseudoneglect is a multi-component phenomenon and highly task sensitive. Each task may reflect a distinct neural mechanism, likely to be impacted differently by age or other non-spatial modulators.

In fact, the influence of other non -spatial modulators on spatial attention was the central topic of the other three experiments presented in Chapters 3 and 4. I employed a dual task paradigm (Chapters 3 and 4) and electroencephalography (EEG) (Chapter 4 only) to investigate behaviourally as well as neurophysiologically if an increase in attentional load has a reducing effect on spatial asymmetry and whether this would be more pronounced with old age. Interestingly, for the last experiment including EEG (Chapter 4) in particular, results showed that although older adults perform similarly well to young adults on a behavioural level, changes are visible on a neuronal level. Specifically, I found that older adults showed an age related reduction in the right hemisphere, for right lateralized targets at the early stages of stimuli processing, indexed by the N1 component, which was absent in young adults. Moreover, the results suggest that older adults used additional neuronal recruitment in the later stages of stimuli processing (P3), to compensate for increased task difficulty and increased resource allocation, likely improving the behavioural results of the older adults so that they were similar to young adults. The work presented in this thesis thus suggest that ageing *per se* does not result in an attenuated spatial asymmetry (that would be seen as equal to a decline in spatial attention ability). Instead I would argue that, independently of age, a set of underlying non spatial factors (such as load for example) influence the magnitude and direction of spatial asymmetry. In addition, additional neuronal recruitment and intrinsic mechanisms are used in older adults to compensate for possible deficits and this results in maintained performance in this age group.

Published articles

The results presented in Chapter 2 have been submitted for publication:

Märker, G., Learmonth, G., Thut, G., Harvey M. (*submitted*). Intra- and Inter-Task Reliability of Spatial Attention Measures in Healthy Older Adults

A subset of the data presented in Chapter 2 have been published in:

Learmonth, G., Märker, G., McBride, N., Pellinen, P., & Harvey, M. (2018). Right-lateralised lane keeping in young and older British drivers. *PloS one, 13(9)*, e0203549.

The publication contains the data of the Landmark, Manual Line Bisection task and Lane Keeping task from testing day 1. We presented the data of all 40 participants tested (including 2 participants that were excluded from analysis in Chapter 2).

The findings presented in Chapter 2 and Chapter 3 have also been presented at the European Conference on Visual Perception, and have been published as an abstract:

Maerker, G., Learmonth, G., Thut, G., & Harvey, M. (2016, August). Spatial attention measures in healthy aging. Poster presented at 39th European conference on visual perception (ECVP), Barcelona, Spain.

Abstract published at:
https://journals.sagepub.com/doi/full/10.1177/0301006616671273

Maerker, G., Learmonth, G., Thut, G., & Harvey, M. (2017, August). Investigating interactions between spatial and sustained attention in young and older adults. Poster presented at 40th European Conference on Visual Perception (ECVP 2017), Berlin, Germany.

Abstract published at: http://journals.sagepub.com/page/pec/collections/ecvp-abstracts/index/ecvp-2017

Acknowledgement

I would like to thank Dr. Monika Harvey, Professor Gregor Thut and Dr. Gemma Learmonth for their support and expertise throughout this process.

In addition, I would like to thank every participant that took interest in my study and took part in the experiments.

A special thank you also goes to my family and friends who supported me throughout the PhD.

Table of Content

List of Figures

List of Tables

Chapter One

A general introduction to spatial attention and its changes throughout the lifespan

As visual input often exceeds our attentional capacities, adequate information processing is a challenge apparent across the lifespan. Spatial attention in particular, allows us to selectively attend relevant from irrelevant information in space, when navigating through our environment (Posner, 1980). With age, cognitive resources are thought to decline thus influencing the ability of cognitive processes such as spatial attention, due to changes in neuronal activity, as well as possible cortical decline. Some studies argue for a lower overall baseline performance with older age (above 50 years old), in contrast to young adults (Learmonth, Thut, Benwell, & Harvey, 2015; Madden et al., 2007), resulting in greater task difficulty for older adults at baseline (Benwell, Harvey, & Thut, 2014). Other studies suggest a faster depletion of attentional resources in older adults (Swan, Hutchinson, Everard, & Shimozaki, 2015), which are thought to be more susceptible to increased attentional load and increased task demands. Spatial attention is also posited to suffer from changes with age, reflected in changes of spatial asymmetry likely indicative of neuroanatomical changes throughout the lifespan.

With an increasingly aging population it becomes imperative to understand how healthy cognitive ageing is characterized, especially in the domain of spatial attention. In a wider context, understanding healthy ageing is beneficial for informing methods that hope to improve and maintain functionality throughout the lifespan. A better, systematic investigation could also identify ways to accommodate challenges in everyday life such as navigating through the environment or driving well into the late decades of life. A better understanding of the underlying neuronal mechanism of spatial attention with age is also beneficial in order to identify possible markers of cognitive decline. Yet, to date, little is known about the impact of ageing processes on spatial attention, and its progression over the lifespan. Our current understanding of spatial attention still lacks systematic investigation of its specific manifestation and the associated cortical activations, especially in context of healthy aging. This is specifically relevant for the completion of multiple tasks where a shift of attention is imperative, or attentional load is increased, as for example in driving a car. Older adults are thought to be more prone to accidents and an overall decline in attentional processes, however, it may be too simplistic to attribute these changes to aging effects alone.

Visuospatial attention in healthy adults (Pseudoneglect)

In the research literature on visuospatial attention, the emphasize is on a particular phenomenon called pseudoneglect, which was firstly reported by Bowers and Heilmann (1980). The name was intended to mirror the condition of hemispatial neglect, in which patients show inattention to the left side of space, due to brain damage to the, often, right hemisphere after stroke (Bowers & Heilman, 1980; Jewell & McCourt, 2000). Conversely in pseudoneglect, cognitive healthy adults show the opposite pattern, a preference for processing stimuli in the left visual field when orienting attention in space (for a review see Jewell & McCourt, 2000). For spatial tasks, pseudoneglect is characterised as a relatively consistent finding for young healthy adults to err to the left side of space when asked to identify the veridical centre of a line (i.e. as in the case of a Manual line bisection task). This spatial bias towards the left side of space is interpreted as resulting from an asymmetrical distribution of spatial attention resources, with a right hemisphere dominance over the left hemisphere that favours the left visual field of space when allocating spatial attention (Bowers & Heilman, 1980; Brooks et al., 2014; Jewell & McCourt, 2000). Interestingly, pseudoneglect appears across multiple components, as it has been found in different spatial task that require, apart from judgement of size as in the more classic tasks of line bisection or landmark task (McCourt & Jewell, 1999), luminance judgements (Nicholls, Bradshaw, & Mattingley, 1999), spatial frequency judgements (Niemeier, Stojanoski, & Greco, 2007), lateralized visual detection (Hilgetag, Théoret, & Pascual-leone, 2001) or emotion discrimination for chimeric faces (Failla, Sheppard, & Bradshaw, 2003; Luh, 1995). Moreover, pseudoneglect has been repeated in different modalities, in the absence of vision, such as in tasks based on auditory, and tactile judgements, as well as in mental representation (see Brooks et al., 2016), suggesting that this phenomenon is a manifestation of an attentional preference for the left side of space in young cognitive healthy adults *per se* and not purely visual.

Age related changes in spatial attention

A range of studies suggest that with age, this leftward spatial bias is reduced, indicating an attenuation of this lateralised spatial attention, resulting in either a reduced, or even reversed, spatial bias to the right side of space . However over recent years, mixed results of spatial bias manifestations in older adults have emerged, including studies arguing for the continuity of pseudoneglect into old age(Brooks et al., 2016, 2014). This suggests that a consistent bias to the right side with age may be too simplistic a view. As a more detailed review is discussed in Chapter 2, here I will give only a brief overview of the research into spatial attention in older adults leading to these mixed results.

An early study of a manual line bisection task showed that, across three different age groups (young, middle and older adults), attention shifts to the right side tended to increase with age (Fujii, Fukatsu, Yamadori, & Kimura, 1995), yet, this trend was not significant. Further studies in older adults and the use of other commonly used spatial attention tasks, such as a computerised version of the manual line bisection task i.e. Landmark task, have reported both reduced and reversed spatial biases (i.e. rightward shifts) in older adults (Benwell, Thut, et al., 2014; Failla et al., 2003; Fujii et al., 1995; Goedert, Leblanc, Tsai, & Barrett, 2010; Hatin, Sykes Tottenham, & Oriet, 2012; Jewell & McCourt, 2000; Learmonth, Benwell, Thut, & Harvey, 2017; Learmonth, Gallagher, et al., 2015; Loureiro-Silva, D'Almeida, Mateus, Oliveiros, & Castelo-Branco, 2010; Nagamatsu, Carolan, Liu-Ambrose, & Handy, 2011; Stam & Bakker, 1990; Veronelli, Vallar, Marinelli, Primativo, & Arduino, 2014) , as well as a stable leftward bias (pseudoneglect), which survived into old age (Brooks et al., 2016, 2014).These findings could be the result of asymmetrical aging of the brain but also a consequence of deficits of attentional modulations in elderly people, such as decreased sustained attention for example (Benwell, Thut, et al., 2014). It is thus important to investigate visuospatial biases throughout the lifespan, in order to assess possibly altered perception, as well as the underlying neural dynamics as these could be diagnostic of poor cognitive function.

In Chapter 2, I investigated spatial attention in older adults behaviourally, as the current research literature lacks systematic investigation: specifically my aim was to understand the direction of spatial bias in older adults on five commonly used spatial attention tasks, namely the Manual Line Bisection task, the Landmark task, Gratingscale task, the Greyscale task and a Lateralized Visual Detection task. I based this work on the study of Learmonth et al. (2015, 2018) who tested healthy young adults, and found that while these common measures of spatial bias offer a stable test-test reliability over testing days, they did not elicit the predicted leftward bias (pseudoneglect) in all the tasks. Only the Landmark and MLB task showed a significant deviation to the left side for young adults. In response to these findings and the mixed results for older adults reported earlier, I wanted to systematically investigate the direction and test-retest reliability of spatial bias over multiple testing days for older adults, and assess just how they differ from the collected young adults sample by Learmonth et al. (2015, 2018). I predicted that with age, there might be a greater degree of variability between testing days in that older adults might be more heavily influenced by external factors such as changes in alertness between testing sessions. In addition, I wanted to investigate the correlation between the spatial measures as repeatedly now, a lack of inter task correlation has been shown (2015, 2018) and this poses a limitation on translating bias changes into real life scenarios.

In fact especially for an ageing population, even though a change of asymmetry of spatial attention may indicate cortical changes virtually nothing is known of possible adverse effects to everyday life. Only a very limited amount of studies have investigated the relationship between spatial bias and everyday life scenarios such as navigation through the environment. Research suggest that people overestimate the left side of space, which results in a behavioural shift to the right side of space in a form of compensation during navigation, i.e. bumping into obstacles or doorways (Nicholls et al., 2010; Nicholls, Loftus, Mayer, & Mattingley, 2007; Thomas et al., 2017). Moreover, there appears to also be a link between increased right bias in older adults and increased risk of falling (Nagamatsu, Liu-Ambrose, Carolan, & Handy, 2009). This highlights the importance of investigating laboratory based spatial biases and ‘real life’ behaviour further. Therefore, in chapter 2 I was also interested in investigating possible existing relationships between a simulated driving task and the obtained measures of spatial attention. In particular I investigated whether a deviation from true centre in spatial measures to either side, translated into lane positioning in a simulated driving task.

Hemispatial Neglect

As briefly mentioned earlier, there has thus been an implicit assumption that pseudoneglect equates to healthy cognitive performance in spatial attention and that any deviation from the leftward bias, especially with age, may suggest changes in the neuroanatomy or neurophysiology, such as a reduction of right hemisphere activity with age. Yet, at present, the current research literature offers little insight into the neural correlates underpinning visual attention in the healthy ageing brain. Thus far, our understanding of visuospatial attention stems predominantly from young to middle aged healthy participants or clinical studies based on patients with hemispatial neglect (typically resulting from right hemisphere stroke (Heilman & Valenstein, 1979; Jewell & McCourt, 2000). Investigations into hemispatial neglect in particular, have influenced the development of cognitive models that attempt to explain spatial attention and pseudoneglect. From the phenomenon of hemispatial neglect, we know that (in most cases) damage to the right hemisphere after stroke leads to an inability for patients to attend to the space contralateral to the damage damaged part of their brain(Heilman, Bowers, Valenstein, & Watson, 1987; Heilman & Abell, 1980; for a review Rode, Pagliari, Huchon, Rossetti, & Pisella, 2017). This often translates into a large asymmetry bias towards the right side of space, as the left space is neglected (unattended) and patients are unable to respond, attend or report to stimuli in this neglected space unless their attention is directed towards it (see (Heilman et al., 1987). Unsurprisingly, this has dramatic effects on the patients' everyday life, including their ability to securely manoeuvre and navigate through their environment without collision to obstacles that they are not aware of, as well as social interactions or mundane everyday activities such as eating, resulting in i.e. not attending to/ eating one side of the plate(Nijboer, Kollen, & Kwakkel, 2013). Despite continuous research, there is, to date, no reliable therapy to rehabilitate hemispatial neglect (Bowen, Hazelton, Pollock, & Lincoln, 2013; K. P. Y. Liu, Hanly, Fahey, Fong, & Bye, 2019). In the same vein, understanding the neurological/physiological as well as behavioural patterns of spatial attention in healthy aging is vital also for uncovering critical markers of decline and also possible avenues for future therapies to rehabilitate disruption of spatial attention.

Models of spatial attention and cognitive ageing

So largely derived from patient studies of hemispatial neglect, several models of visuospatial attention have been suggested to explain pseudoneglect. A prominent model is the right hemisphere (RH) dominance model which suggests that spatial selective attention results from stronger activation of the RH over the left hemisphere (LH), which leads to an overestimation of features within the contralateral left space (Heilman & Van Den Abell, 1979).

Alternatively, the interhemispheric competition model of spatial attention (Benwell, Thut, et al., 2014; Kinsbourne, 1977) suggests that attentional asymmetries arise due to different activation of the LH and RH. Instead of a RH dominance, both sides compete in activation, leading to a relative imbalance of activity within the left and right hemispheres, giving rise to a spatial attention bias. In this model, attention is thought to be balanced across both hemispheres (J. Chen & Niemeier, 2017; Dolcos, Rice, & Cabeza, 2002; Kinsbourne, 1977). Yet, the right inferior parietal lobe is thought to be dominant in tasks involving bilateral allocation of attention, which links to the observation of greater impairment (Cicek, Deouell, & Knight, 2009), such as in neglect, after brain damage to the RH (Weintraub & Mesulam, 1987). According to this approach, damage to the RH, as typically observed in such neglect patients, would lead to a rightward attentional shift and reduced leftward attention due to an imbalance between the hemispheres. Thus, both models suggest a contribution of the two hemispheres to the contralateral visual field, although they differ in their precise involvement.

Another influential model of spatial attention describes shared networks that modulate and shift spatial attention and rely predominantly on a bilaterally activated dorsal fronto- parietal network (DAN) and a right hemisphere dominant ventral attention network (VAN) (Corbetta, Patel, & Shulman, 2008; Kinsbourne, 1977; Mesulam, 1999). Therefore, any observed asymmetries in spatial attention are mediated in the dorsal orienting network (DAN) which controls top down attention towards stimuli (location in space) (Chandrakumar et al., 2019;

Corbetta et al., 2008; Corbetta & Shulman, 2011). The dorsal network is bilaterally active across both hemispheres, anatomically connecting the intraparietal sulcus with the frontal eye fields, via the superior longitudinal fasciculus white matter tracts (Corbetta & Shulman, 2011; de Schotten et al., 2011; Ptak, 2012). In contrast, the ventral network is proposed to be lateralised towards the right hemispheres. Anatomically, it connects the temporoparietal junction (TPJ) and the ventral frontal cortex (Corbetta & Shulman, 2011; de Schotten et al., 2011). This VAN controls the interhemispheric competition of the bilateral dorsal orienting network (Corbetta et al., 2008). The ventral attention network is therefore more sensitive to changes that can influence spatial attention such as decreased attention, i.e. during prolonged time-on - task (Benwell, Thut, Learmonth, & Harvey, 2013; Nagamatsu et al., 2011, 2009; Nagamatsu, Munkacsy, Liu-Ambrose, & Handy, 2013; Newman, O'Connell, & Bellgrove, 2013) or possibly ageing (Benwell, Thut, et al., 2014; Schmitz, Dehon, & Peigneux, 2013; Schmitz & Peigneux, 2011). Such non-spatial factors are proposed to have a decreasing effect on the activation of the ventral network and are meant to result in decreased RH activation, which is reflected in attenuated spatial biases to the right side of space (Corbetta & Shulman, 2011; Newman et al., 2013; Takio, Koivisto, & Hämäläinen, 2014)

With respect to ageing, no neural model underpinning spatial processing has been proposed specifically as yet. The Hemispheric Asymmetry Reduction in Older Adults (i.e. the HAROLD) model(Cabeza, 2002; Cabeza, Anderson, Locantore, & McIntosh, 2002; Cabeza et al., 2004, 1997; Dolcos et al., 2002; Huang, Polk, Goh, & Park, 2012; Reuter-Lorenz et al., 2000) proposes that with age lateralized processes observed in young adults are more represented bilaterally, leading to a reduction of asymmetry between the hemispheres. Although the HAROLD model has been investigated predominantly with memory tasks (Bäckman et al., 1997; Cabeza et al., 2004; Grady, Bernstein, Beig, & Siegenthaler, 2002; Logan, Sanders, Snyder, Morris, & Buckner, 2002; Schmitz et al., 2013), such reduction in asymmetry could be the result of compensatory mechanisms to counteract processing deficits with age (Cabeza, 2002) and could also apply for spatial attention (see Cabeza, 2002; Cabeza et al., 2004; Dolcos et al., 2002).

Another newer model attempting to incorporate age related changes in attention is the ‘compensatory-related utilisation of neural circuits hypothesis’ (CRUNCH) Model (Reuter-Lorenz & Cappell, 2008), which suggests additional recruitment as a form of compensation of declining cognitive processes with age, via additional neural resources. While the HAROLD model differentiates between the 2 hemispheres, the CRUNCH model suggests that additional neuronal resources could be recruited from any part of the brain to compensate processes(Reuter-Lorenz & Cappell, 2008). The CRUNCH is therefore not limited to lateralization but could account for the observed shift to more anterior activity from posterior processes with age (Huang et al., 2012). At present, the field lacks a model that can fully account for possible healthy age related changes in spatial attention, yet the proposed models provide a good framework for investigating the underlying neuronal mechanism at play.

Attentional load modulates spatial attention

Past research has established already that the degree of spatial bias can be influenced by non-spatial modulators. Research in patients and participants with acquired deficits in sustained attention (ADHD) (Bellgrove, Eramudugolla, Newman, Vance, & Mattingley, 2013) have reported changes in spatial bias with increase and decrease of vigilance or alertness (Bellgrove, Dockree, Aimola, & Robertson, 2004). Generally, increased alertness leads to a shift towards the left side of space while a reduction of alertness can attenuate spatial bias towards the right side of space, even in healthy young adults, in a variety of tasks (Bellgrove et al., 2004; Fimm, Willmes, & Spijkers, 2006; Manly, Dobler, Dodds, & George, 2005; Matthias et al., 2009; Schmitz, Deliens, Mary, Urbain, & Peigneux, 2011) but see Chandrakumar et al. (2019)for a review. Modulating factors that impact on attention can also include extended time-on task (Benwell, Harvey, Gardner, & Thut, 2013) or increased task difficulty through cognitive load (Dodds et al., 2008; Peers, Cusack, & Duncan, 2006), in addition to possible age related factors with healthy aging.

In addition, O’Connell et al.(2011) and Bonato et al.(2015) suggest a modulating effect of increased attentional load on spatial attention, reflected in the attenuation of behavioural spatial bias as well as changes in the neuronal processing under increase of load (see O’Connell et al., 2011): Using a dual task paradigm in which attentional load was increased via three levels (no load, low attentional load and high load), O’Connell et al. (2011) investigated the perceptual processing of lateralized stimuli in healthy adults, and reported evidence for an asymmetrical effect of early visual orienting on a neuronal level, as indexed by changes in the P1 and N1 components due to changes in attentional load. In particular, they reported increased recruitment of attentional resources when attentional load was engaged the most (high attentional load condition), and reflected in enhanced P1 and N1 waveforms at the early visual processing stage of stimuli processing. Further, they found a slower processing of and response to the peripheral stimuli when central load was increased (from no load), reflected in reduced peripheral P2 and P3 components. In light of ageing, changes in the neuronal correlates may be more pronounced when attentional load is increased and tasks become more difficult. Perhaps, for older adults the results would show reversed effects in behavioural spatial bias as well as on a neuronal level indicating structural changes with age. Yet, until now this has not been investigated systematically.

So in Chapters 3 and 4 I aimed to investigate exactly this. Firstly, I studied the modulating effect of attentional load on spatial attention to see if attentional load had greater attenuating spatial bias effects in older adults. The results informed my final experiment where I employed EEG in order to investigate possible age related changes at the electrophysiological level. In the absence of behavioural differences between young and older adults, it is possible that age related changes are still present at the neuronal level, due to differences in resource allocations or internal motivation

Decline of hemispheric lateralization with age

The previously discussed (and also questioned) trend towards a behavioural attenuation of spatial bias, or a reversal into the right side of space for older adults (as well as models of neurocognitive aging such as the CRUNCH (Reuter-Lorenz & Cappell, 2008) and HAROLD model (Cabeza, 2002; Dolcos et al., 2002)) highlight the right hemisphere as a likely area for observing a decline of lateralized neural activity. In young adults, spatial attention tasks such as the landmark task have been found repeatedly to elicit greater right hemisphere activity when comparing the engagement of lateralised attention networks

(Benwell, Thut, et al., 2014; Foxe, McCourt, & Javitt, 2003; Longo, Trippier, Vagnoni, & Lourenco, 2015), with a particular emphasis on the right parieto-occipital cortex and the right temporoparietal junction (TPJ) (Benwell, Harvey, et al., 2014; Benwell, Thut, et al., 2014; Foxe et al., 2003; Learmonth, Benwell, et al., 2017) as the source location for the spatial bias.

Only a few studies have, at present, investigated age related reductions of asymmetric lateralization in spatial attention specifically. However, they confirm the notion of a lateralized reduction of the right hemisphere. For example, Nagamatsu et al. (2011) identified a reduction in the ability to allocate spatial attention in a top down manner for the left visual field in older adults, indicting a decline in activity for the right hemisphere. For the ‘anterior directing attentional negativity’ (ADAN) component, older adults showed an advantage for right targets in the contralateral hemisphere, but left targets elicited only a small advance in amplitude activity for the contralateral RH over the LH. In contrast, young adults showed much stronger ADAN amplitudes for both left and right targets in their contralateral hemispheres. This supports age related changes in lateralization.

A more recent EEG study by Learmonth et al. (2017) also confirmed this age related reduction of lateralization. They reported an absence of lateralization in older adults as compared to larger right parieto – occipital response in young adults for spatial bias in a landmark task. In Chapter 4, I thus aimed to investigate the neuronal mechanisms of spatial attention in older adults by manipulating attentional load. With the use of EEG, I aimed to investigate the following: does a change in attentional load modulate spatial attention and if yes, are such effects more pronounced in older adults? Moreover, I was interested in understanding how the modulating effects of attentional load were reflected in the neuronal activity in older adults, and if an increase in attentional load would be reflected in a greater reduction of RH lateralization or an absence of lateralization, in contrast to young adults.

Overview of Thesis

The present thesis presents results of four experimental studies investigating spatial attention in cognitive healthy older adults.

In the first study (Chapter 2), my focus was on the behavioural evidence of age related changes in visuospatial attention. I aimed to identify and understand the magnitude and direction of spatial attentional biases in an older adult sample and understand how they may differ from a sample of young adults, with respect to their robustness over different days of testing and across different tasks of spatial attention. I investigated the test-retest reliability of 5 commonly used spatial measures of spatial attention in healthy older adults and contrasted the findings with the earlier obtained young adults sample from Learmonth et al. (2015, 2018). I also investigated if and how, the obtained spatial biases translate into driving behaviour as measured in lane positioning in a driving simulation task.

In the following two experiments, I aimed to explore how an increase of attentional load (and therefore indirectly assessing the impact of task difficulty and/or sustained attention), modulates spatial attention. Again, with a special focus on the aging population, I wanted to map age related differences in spatial attention and how they might translate into the neuronal correlates, using electroencephalography (EEG).

Specifically, in Chapter 3 I investigated the direction of young and older adults' behavioural spatial bias in a spatial dual task while attentional load was increased in a low and high attentional load condition. The results of this study informed the final EEG experiment in Chapter 4, where I argue that age related changes in spatial attention might be absent in behavioural shifts of spatial attention, but visible in the neural mechanisms underlying spatial attention. I used EEG and investigated stimuli evoked event related potentials, to uncover age related differences as a result of cortical structural changes and possible resource distribution with healthy aging, and compared them to behavioural measures of possible spatial shifts.

In the final Chapter Five, I discuss the findings of the thesis in relation to the wider literature concerning healthy aging. I conclude by suggesting possible future directions for research into age related changes of spatial attention asymmetries in healthy cognitive ageing.

Chapter Two

Investigating intra-and inter task reliability of spatial attention measures in healthy older adults

As stated in chapter 1, with a growing senior population in our society, understanding healthy cognitive ageing is imperative for identifying possible markers of cognitive decline. Yet, to date, little is known about the impact of ageing processes on spatial attention, and its progression over the lifespan. Thus far, research investigating visuospatial attention in healthy, predominantly young to middle aged participants, describes an attention asymmetry towards the left visual space, termed “pseudoneglect” (Bowers & Heilman, 1980). In pseudoneglect, young adults show an attention asymmetry, typically displaying a leftward spatial bias, when asked to estimate the veridical centre of a centrally presented line in the line bisection task (Jewell & McCourt, 2000). In contrast, patients with neglect (typically resulting from right hemisphere stroke) show the opposite pattern: a large rightward spatial attention bias due to perception deficits in the contralesional side of visual space (K. M. Heilman & Abell, 1980). There has thus been an implicit assumption that the presence of pseudoneglect equates to healthy cognitive performance in the spatial attention domain. In addition, across the lifespan, older adults have been thought to show a reduction of this lateralised spatial attention, resulting in either a reduced or even reversed spatial bias to the right side of space, comparable to patients suffering from hemispatial neglect (Harvey, Milner, & Roberts, 1995; Olk & Harvey, 2002). However, the evidence paints a mixed picture, with some recent studies reporting maintained *leftward* biases into older age e.g. (Brooks et al., 2016; Friedrich, Hunter, & Elias, 2016). As such, the premise of a rightward shift occurring in all older adults, and across all spatial attention measures, is likely to be too simplistic.

Five commonly used spatial tasks

Recently Learmonth et al.(2015, 2018) investigated the inter- and intra- task reliability of five common measures of spatial attention in young adults; (Landmark task (LM), computerised Manual Line Bisection task (MLB), Greyscale task (GREY), Gratingscale tasks (GRA), Lateralised Visual Detection task (LVD). They reported moderate-to-strong correlations of the 5 tasks across different testing days, suggesting that each of them are reliable measures of spatial bias on their own. However, only the landmark and line bisection task displayed a leftward bias, (pseudoneglect) in young adults across both days. Moreover, they reported a lack of correlation between the spatial tasks. This is a problem across a variety of spatial tasks used in the current literature (Heber, Siebertz, Wolter, Kuhlen, & Fimm, 2010; Luh, 1995; Nicholls et al., 1999). Hence, to reliably assess and differentiate between age related changes in pseudoneglect, when testing older adults, and neurological deficits linked to neglect in older adults, it is important to understand spatial attention as a multi component phenomenon (see Learmonth, Gallagher, et al., 2015) and understand the components assessed when using different spatial measures

Spatial attention in older adults

It recently become apparent that the direction of the spatial biases in cognitively healthy older participants are even less consistent across the wider literature (Friedrich et al., 2018) and below I briefly present findings for the 5 most commonly used spatial tasks described above.

Manual Line Bisection Task

So far, line bisection tasks have yielded varied results, with some reporting a shift of bias towards *the right side of space* in older adults compared to young adults (Barrett & Craver-lemley, 2008; P. Chen et al., 2011; Failla et al., 2003; Fujii et al., 1995; Goedert et al., 2010). Specifically, an early study on a manual line bisection task showed that, across three different age groups (young, middle and older adults), older adults generally shifted towards favouring the right side of space, with the largest rightward biases in the oldest group (Fujii et al., 1995). In contrast, studies also report *a lack of spatial bias* , as well as a lack of age related differences in spatial bias between young and older adults, with older adults showing no directional bias at all (De Agostini, Curt, Tzortzis, & Dellatolas, 1999; Halligan, Manning, & Marshall, 1990; Hatin et al., 2012; Learmonth, Märker, McBride, Pellinen, & Harvey, 2018). Moreover, a more recent study by Brooks, Darling, Malvaso, and Della Sala (2016) identified a maintained leftward spatial bias in older adults, reporting pseudoneglect in both young and older groups. This was also true for tasks which did not allow visual involvement such as the rod bisection task, which uses tactile information for bisection, or the mental number representation which requires a mental visualisation to allow estimation of the median number between a pair of numbers.

Landmark task

Similarly, in the landmark task, results have spanned from reduced to reversed spatial biases (i.e. rightward shifts) in older adults(Benwell, Thut, et al., 2014; Learmonth, Benwell, et al., 2017; Schmitz et al., 2013; Schmitz & Peigneux, 2011) while others found no age differences for group level spatial biases despite a trend towards the right side of space in older adults compared to young adults (Learmonth, Benwell, et al., 2017; Learmonth, Märker, et al., 2018).

Greyscale task

Other tasks probing spatial lateralisation involving target features have been the Greyscale (Nicholls et al., 1999) and the procedurally similar Gratingscale (Niemeier et al., 2007) task. For both tasks, pseudoneglect has been reported in young adults (Nicholls et al., 1999; Niemeier et al., 2007). With regard to spatial lateralisation in older adults, results are sparse and tend to focus on patient groups with hemispatial neglect. So far, only two studies have reported on the performance of older adults on the greyscale task, both suggesting a reliable leftward bias in older adults (pseudoneglect) (Friedrich et al., 2016; Mattingley et al., 2004). Interestingly, investigating seven age groups, Friedrich et al. (2016) highlighted that all age groups showed a leftward bias, with the strongest leftward bias in the oldest age group (80-89 years), as compared to the youngest age group (18-29 years). This shows further evidence for leftward biases with increased age rather than a reduced pseudoneglect pattern.

Gratingscale task

Particularly, the Gratingscale task has not yet been investigated in cognitively healthy older adults. Based on the results from Niemeier et al.(2007), young participants are more likely to judge the left visual side of space as higher-frequency patterned if the side included a portion of “thin stripes”. However, Learmonth et al.(2015) reported no spatial bias in young adults when judging High spatial frequencies over multiple days.

Lateralised Visual Detection task

The same variation in spatial asymmetry was reported for the lateralised visual detection task, displaying a leftward bias in young adults (Hilgetag et al., 2001; Learmonth, Thut, et al., 2015), as well as an absence of bias in young adults when targets were not titrated (Learmonth, Gallagher, et al., 2015). Older adults showed no spatial bias to either side of space, even with titrated targets (Learmonth, Thut, et al., 2015), suggesting an attenuation of spatial bias.

Lane Keeping Task

Finally, the relationship between laboratory based measures of spatial bias and real life simulations of everyday navigation is still contentious, especially for the ageing population. Akin to the spatial attention tasks described, investigations tend to focus on young adults. Research suggest that people overestimate the left side of space, which results in a behavioural shift to the right side of space as a form of compensation during navigation, i.e. bumping into obstacles or doorways (Nicholls et al., 2010, 2007; Thomas et al., 2017). Moreover, visuo-spatial skills, like mental rotation (Turnbull, Carey, & McCarthy, Rosaleen, 1997), appear to correlate with manual line bisection tasks (Roberts & Turnbull, 2010), suggesting an underlying mechanism that influences both tasks. In Learmonth et al. (2018)the present sample of older adults was compared to young adults on a simulated driving task and the LM and MLB task. Results showed a negative correlation for young adults between a right lateralised lane positioning in the driving task and a leftward bias (pseudoneglect) in the landmark task. Whereas older adults also maintained a rightward bias in lane positioning during the driving task, the obtained spatial measures did not inter correlate between the tasks. This highlights the importance to investigate laboratory based spatial biases and ‘real life’ behaviour further in order to investigate whether a deviation from true centre in spatial measures translate into driving behaviour.

Aims and Hypotheses

Given this lack of consensus, it is thus important to investigate visuospatial biases across the lifespan in order to assess underlying neural dynamics in older age, as well as potentially identifying diagnostic markers of pathological visuospatial perception. This paper expected to achieve two aims: As the majority of spatial attention research focuses on young adults, there is a lack of understanding whether spatial biases in healthy older adults are 1) stable over time and 2) stable across different tasks. Taking previous findings into consideration (Learmonth, Gallagher, et al., 2015, 2018), I tested the inter-task and intra-task reliability for five commonly used measures for spatial attention: 1) Manual Line Bisection 2) Landmark, 3) Greyscales, 4) Gratingscales, and 5) the Lateralised Visual Detection task in an ageing population. It was predicted that older adults would show weaker correlations in terms of their spatial attention bias across different measures and across testing sessions, similar to previous results using the lateralised visual detection task (2015, 2018). Furthermore, I investigated whether the spatial tasks used here reflect a spatial bias in a more complex driving task. A maintained pseudoneglect with age should result into an overcompensation and drift to the right side of space in the driving task. A correlation between testing sessions of the spatial tasks in older adults would provide evidence that the employed measures are reliable and sensitive measures of spatial attention, even in an older population. As previous results have been mixed, this study is expected to give valuable insights into the accuracy and sensitivity (within and across) each of these measurements, and ultimately guide researchers and clinicians into choosing the most sensitive task to assess spatial bias across the life span.

Methods

Participants

Thirty-seven cognitively healthy older adults aged between 60 to 86 years were tested (19 Females, *M* = 71 years; S.D. = 6.05). The study received ethical approval from the University of Glasgow, College of Science and Engineering Ethics Committee, and participants gave written informed consent before participation.

Pre-screening measurements

All participants were right handed and had normal or corrected-to-normal vision, as per Snellen chart (280 cm viewing distance). Participants were pre-screened for possible visual field changes and detection accuracy of small stimuli with a short computerised assessment (see Learmonth, Benwell, et al., 2017): Over 36 different positions, a small black dot (10 x10 pixel) appeared for 150ms. Participants were instructed to press the spacebar if they perceived the dot anywhere on the screen, while fixating on the cross in the middle of the screen. The 36 locations extended to 12.0° visual angle (VA) from the fixation along the vertical axes and 16.06 ° VA along the horizontal axis (see Figure 3). A total of 72 trials were presented (36 locations x2) including 24 ‘catch’ trials where responses were withheld. No participants were excluded based on this visual acuity screening. Furthermore, participants were screened for mild cognitive decline with the Montreal Cognitive Assessment test (MOCA) (Nasreddine, Charbonneau, & Cummings, 2005) and all showed normal performance (*M* = 28.61; S.D. = 1.06).

Procedure

The procedure was identical to Learmonth et al. (2015), however a pilot phase in 3 older adults highlighted that the LVD task used in Learmonth et al. (2015) was too perceptually challenging for older adults, and was adapted for this study. The study was conducted over two separate sessions (a minimum of 24 hours apart) lasting around 1.5 hours (short breaks included). Participants were asked to rate their subjective alertness (from 0 = almost asleep to 100 = fully alert) on a linear scale before and after each session. They were seated in a dark room in front of a computer screen. The viewing distance was kept constant at 60cm from the screen using a chin rest. Each participant completed 5 common spatial tasks: 1) Manual Line Bisection (MLB), 2) Landmark task (LM), 3) Greyscale task (GREY) 4) Gratingscale task (GRA), 5) Lateralised Visual Detection Task (LVD). The test order was counterbalanced across the participants. On both testing days, the task order was kept identical for each participant. Each task was introduced with written and verbal instructions and a practice trial of around 20 trials. The blocks lasted roughly 5 minutes each and allowed for a break afterwards. The data of the total 40 participants for the MBL, LM and driving task on day one have been described in Learmonth, Märker, et al. (2018).

Stimuli

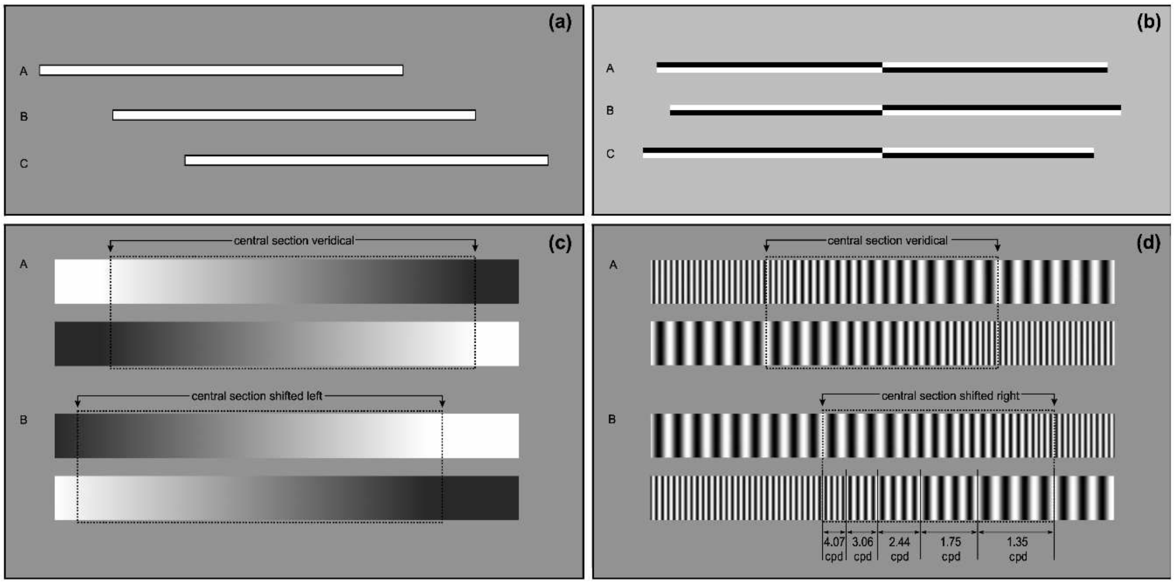

Figure 1 Schematic representation of the Stimuli
Examples of the (a) manual line bisection (MLB), (b) landmark (LM), (c) greyscales (GREY) and (d) gratingscales (GRA) stimuli. See Learmonth et al. (2015) PLOS ONE doi: https://doi.org/10.1371/journal.pone.0138379.g001 ,

The stimuli were presented using E-Prime 2.0 (Psychology Software Tools Inc., Pittsburgh, PA) and obtained measures of reaction time and accuracy. The study was executed on a Dell Precision 380 PC and a 19” Dell 1908FP Ultra Sharp LCD flat screen monitor, with a 1280x1024 pixel resolution. The five spatial tasks described in Learmonth et al. (Learmonth, Gallagher, et al., 2015)(and identical in method and measures) were used, with only the viewing distance shortened from 70 to 60cm to accommodate the older sample. The LVD task was also slightly modified to meet the requirements of this older adult sample (see task description below).

Manual Line Bisection task (MLB)

Participants were asked to indicate the horizontal centre of a line with the mouse cursor. They completed (108 trials) in which a horizontal white line (805x 15 pixels / 23. 5cm x 0.4cm with a 22.16 x 3.81° visual angle, (VA)) was presented for a maximum of 6 seconds on a grey background (Figure 1a). The position of the line varied laterally on a trial by trial basis, presented at 9 different positions repeated for 12 times along the horizontal axis to the left and to the right of veridical centre (0 = centred, and 40, 80, 120 and 160 pixels, 1.01, 2.02, 3.03, 4.04 ° VA). The mouse pointer appeared at the top centre of the screen (screen co-ordinates: X = 640, Y = 40 pixels; 16.06° above fixation) at the start of each trial and was dragged down by the participant to bisect the line using the left-click of the mouse as accurately as possible. A response triggered the onset of a new trial, with the stimulus appearing after 1000ms. If no response was given, the next trial started after 6 seconds had elapsed.

Landmark task (LM)

In each trial, participants were instructed to indicate which side of a pre-transected centrally presented line was shorter using the ‘v’ (left) or ‘b’ (right) keys (Jewell & McCourt, 2000; Learmonth, Gallagher, et al., 2015; Milner, Brechmann, & Pagliarini, 1992). The trial started with a central fixation cross (15x15 pixels; 0.38° VA) for 1000ms followed by a stimulus that appeared for 150ms. A forced-choice response was required in order to move to the next trial. The stimuli consisted of horizontal 100% black and white Michelson contrast lines (800 x14 pixels; 23.5cm x 0.4cm; 20.01 x 0.35° VA). The shading of the upper left and lower right was randomised, with half of the trials involving a dark upper left/lower right, and half lower left/upper right (see Figure 1b). The line was vertically transected at the veridical centre of the screen. The asymmetry of the line varied across trials, resulting in 17 different stimuli with 8 repetitions. The left and right sides of the most asymmetric lines differed by 24 pixels (0.6° VA). Stimuli varied in size, with a decrease of 3-pixels (0.08° VA) per stimulus. One final stimulus involved lines where both sides were equally long.

Greyscale task (GREY)

Participants were instructed to indicate which of two horizontally parallel rectangular bars were darker overall (Learmonth, Gallagher, et al., 2015; Mattingley et al., 2004). The bars were gradually shaded from black to white until 100% luminance in black on one side and white on the other side was reached, resulting in a steady luminance gradient. The upper bar was then flipped along the vertical axis so that the lower bar was shaded from black to white in the inverse direction relative to the upper bar (Figure 1c) To allow for an analysis method of psychometric curve widths, a “window of interest” which spanned 640 pixels (80% if the line length, 16.06° VA) was shifted along the horizontal axis to create the stimuli. A total of 17 different stimuli were used, were each window was moved in 10- pixel instalments (0.25 VA) to either side of space (800 x 100 pixels (approximately 23.5cm x 2.9cm; 20.01 x 2.53° VA) with a distance of 41 pixels (1.04°) between the bars. Prior to each trial, a fixation cross was presented for 1000ms, followed by the stimulus for 150ms, and a key press choice indicating if the upper or lower bar was darker overall, with participants using the “upwards arrow” or the “downwards arrow” with their right hand. The maximum deviation from symmetry differed by 80 pixels (2.02°; -10% or +10% of total length). The remaining part of the bar was completed with either white or black. The block entailed 136 trials with 17 Stimuli which were repeated 8 times, half of which showed black in the upper left and lower right and vice versa.

Gratingscale task (GRA)

Participants had to indicate via key press (up or down arrow) which horizontal rectangular had more thin stripes over all: the top bar or the parallel presented bottom bar (Learmonth, Gallagher, et al., 2015; Niemeier et al., 2007). One block entailed a total of 136 trials with 17 Stimuli which were repeated 8 times in a trial. A fixation cross appeared for 1000ms followed by the stimulus for 150ms, and a response which triggered the next trial. The stimuli were identical to Learmonth et al. (2015) (see for stimuli details). The rectangular bar was sine-wave grated with high-frequency grating (35 pixels per cycle; 1.15 cycles per degree of visual angle (cpd)) at one end and low-frequency (11 pixels per cycle; 3.49 cpd) at the other end (Figure 1d). Half of the stimuli had high frequency grating on the upper left and lower right side, and the other half had higher grating on the upper right and lower left side. A central segment of 400 pixels (50% of the total length, 10.08°) was shifted in 12-pixel (0.30°) instalments to either the left or right side to compile 17 different stimuli with the maximum deviation from symmetry at 96 pixels (2.43°; -12% or +12% of total length), and the rest filled with high or low frequency pattern to continue the gradient pattern. Identical to Learmonth et al.(2015, 2018), consisting of 5 spatial frequencies, the central segment included 4 sine wave cycles per frequency. The frequencies ranged from the lowest frequency at 35 to 26, 19, 14 and the highest frequency at 10 pixel per cycle (i.e. the number of pixels per cycle reduced by a factor of approximately x 0.74).

Lateralised Visual Detection task (LVD)

Participants were instructed to indicate whether they saw a small target appearing on their left or right side, with a key press (“v” for left, “b” for right) or no response when no dot appeared (catch trial) (Hilgetag et al., 2001; Learmonth, Gallagher, et al., 2015).A fixation cross appeared for 1000ms followed by the stimulus for 40ms. Participants had to make a response within 1750ms before the next trial started, in order to allow “catch trials” and false negatives. The stimuli consisted of a small target presented either to the left (-145mm; -13.78° VA) or right visual field (+145mm; +13.78° VA)., In contrast to the young sample, the current stimuli consisted of 10 different sizes (1x2, 2x2, 2x3, 3x3, 3x4, 4x4, 4x5, 5x5, 5x6, 6x6 pixels ; ranging from 0.03 x 0.05° VA to 0.13 x 0.15° VA), to accommodate the greater variability in detection sensitivity in the older adults (Learmonth, Thut, et al., 2015). The block consisted of 126 trials for the ten different dot sizes (6 left and 6 right for each of the 10 stimulus sizes, i.e. 60 total targets), plus 6 catch trials. In Learmonth et al.,(2015, 2018), young adults were presented with stimuli of 5 different sizes only (1x2, 2x2, 2x3, 3x3, 3x4 pixels yet 132 targets).

Lane -Keeping task (LK)

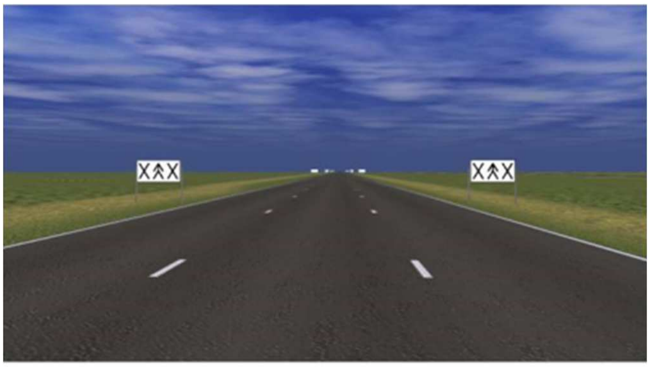

Figure 2: Lane Keeping –task
The screen shot displays the setup of the driving simulation.

The procedure and set up were identical to Learmonth et al. (2018) where I presented a small subset of the data (but see (Mattes, 2003) for technical details also). Older participants completed the task, in a different laboratory to the spatial tasks, on a Dell Precision T7400 PC with a Dell Ultrasharp 2408WFP 24” LCD computer screen (1680x1050 pixel resolution). Viewing distance was kept at approximately 1m to the screen, while participants operated a steering wheel and 3 pedals, focussing on the break and gas, simulating a realistic driving set up. They were instructed to keep a steady speed of (simulated) 60mph and to place themselves in the centre of the simulated street lane (before passing a yellow start sign), and to hold a central position throughout driving. Each participant completed 3 laps with the 1st lap as a practice trial. The parkour entailed a right bend curve which transitioned into a straight lane. Throughout the duration of one lap, participants had to keep to a centred position within the middle lane and where instructed to make adjustments via the wheel, when deviating from the centre of the lane. Furthermore, they were told to ignore any road signs displayed along the parkour (18 signs with an interval of 150ms) but instead focus on the task instructed. However, for each participant, 18 time points were extracted from these signs to calculate the mean lane position (in simulated meters) across the two laps, separately for testing Day 1 and Day 2. Participants took approximately 3 minutes to complete one lap (simulation of 3km x 3,85m per lap) (see (Learmonth, Märker, et al., 2018; Mattes, 2003).

Analyses

Analysis of PSE and Curve Widths

The point of subjective equality (PSE) was analysed for the five tasks in order to estimate the magnitude of a spatial bias. Results were then transformed into % of total line length, relevant to the stimuli. The Landmark (LM), Greyscales task (GREY) and Gratingscale (GRA) were analysed in a similar manner. A percentage score was calculated for each of the 17 stimuli separately, where the participants perceived the stimulus to be either longer (LM) / darker (GREY) / have more “thin stripes” (GRA) on the right side of space.

Following this, the data were plotted as psychometric curves (17 stimuli vs percentage of trials where target was judged to be on the right) per individual and per task, and psychometric functions were fitted to this data using the curve fitting toolbox for Matlab (Borgo, Soranzo, & Grassi, 2012) to calculate the point of subjective equality (PSE) and curve widths. The psychometric function used the cumulative logistic function described by the equation:

$$f(\mu, x, s) = 1/(1 + \exp\left(\frac{x - \mu}{s}\right))$$

In this function, μ is the point on the x-axis that equates to 50% left and 50% right-response rate, x represents the transector locations and s describes the psychometric curve width. The curve widths were then converted to percentage line length. Specifically, curve widths indicate an individual’s precision on the task. A narrow curve width can be interpreted as a good performance on the task.

For the MLB task, the subjective midpoint was calculated by subtracting the x-co-ordinate, obtained through the mouse click, from the co-ordinate from the veridical centre of the line. The mean bias and standard deviation on a subject by subject basis indicated the overall spatial bias for this task.

Analysis of D’Prime (d’) and PSE in the LVD Task

As per Learmonth et al. (2015) the LVD task was analysed in two ways: a) D-prime (d’) to determine the visual detection sensitivity, b) fitting a psychometric function to the data (PF 50%).

For the D-prime (d’) calculation I used visual detection sensitivity. *D’* was calculated using the function:

$$d' = z(Hits) - z(False\ Alarms)$$

where *z* represents the z-score for each side of space. “Hits” represent the percentage accuracy for each target side (i.e. dots correctly perceived to the left side or right side of space), subtracted by the number of “false alarms” in response to catch trials. Here, enhanced sensitivity to detected targets is represented in a greater *d*’ score. Subtracting the Left visual field (VF) *d’* from Right VF *d’*, created a *d’* lateralisation index (Learmonth, Gallagher, et al., 2015).

Similar to the analysis of the LM, GRA– and GREY tasks, a psychometric function was fitted to the 10 stimulus sizes of the LVD task separately for each visual field, and PSE and curve widths were calculated. The stimulus sizes were labelled 1-10, with 1 = the smallest (1x2 pixel) target up to 10 = the largest (6x6 pixel) target. Thus, a small PSE of 1.5 indicates a relatively good visual detection accuracy, placing the 50% accuracy (PF 50%) between the 1x2 and 2x2 target size.

Subtracting the Right VF PSE from the Left VF PSE calculated a lateralised spatial bias. Again, as reported by Learmonth et al. (Learmonth, Gallagher, et al., 2015, 2018) both measured of the lateralised visual detection task (The PF 50% and *d’* methods) correlate on both testing days with each other (Day 1: r= .88, p<.001; Day 2: r= .96, p<.001; Mean Days 1+2: r= .94, p<.001), confirming their reliability.

Analysis of the Lane- Keeping task

As per Learmonth, Märker, et al. (2018) the mean lane position was analysed to estimate the magnitude of the left or right side deviation. The deviation from the midpoint of the middle lane was recorded by the LCT software and indicated by either positive (right side deviation) or negative values (left deviation from centre). Over an interval of 150ms, time points were averaged to calculate the mean deviation from the midpoint across the last two laps of each participant. The final mean lane positions of Day1 and Day 2 were then averaged across both testing sessions.

Outlier detection and winsorized means

Rather than excluding participants due to individual outliers, the group-level spatial biases of each testing day were winsorized Firstly, the individual spatial biases per day and spatial tasks where screened for outliers that exceeded a spatial bias above 3 x standard deviation o the group level mean. Once a spatial task was identified to have outliers, the whole sample of this testing day (37 individual biases) was winsorized to adjust the spatial biases. The winsorized mean is calculated by replacing 20% of the complete 37 individual biases. The smallest and largest spatial biases are replaced with the values closest to them (Wilcox & Keselman, 2003).There were no outliers identified that deviated by 3 times from standard deviation in the LM and MLB tasks, and these remained untrimmed. For the GREY, GRA and LVD tasks 20% winsorized (modified) means were used. The average bias of both testing days for a spatial task was calculated on the original (unmodified) means and then winsorized by 20%. In addition, one participant was excluded from the LVD task due to perceptual difficulties despite the task modifications made (PSE= -22), but they were not excluded from the other 4 tasks. This resulted in 37 participants for LM, MLB, GREY and GRA tasks, and 36 participants for the LVD task, thus maintaining cross-task comparability as much as possible.

Results

Subjective alertness

Performance of a 2x2 analysis of variance (ANOVA) (TIME: pre- vs post-experiment x Day: Day 1 and Day 2) revealed that participants showed significantly reduced subjective alertness after the experiment (pre- test Day 1: M = 84.7 %; S.D. = 11.17 vs. Post-test Day 1: M = 77.97% ; S.D. = 13.09 and pre– test Day 2: M= 87.32%; S.D. = 10.13 vs. Post-test Day 2: M = 81.05%; S.D. = 10.31), Main effect of Time F(1, 36) = 44.11, p< .001. There was a main effect of Day also F(1,36)= 4.61, p = .04, with participants more alert overall in the second testing session (Day 1: M = 81.38% ; S.D. = 11.52 vs. Day 2: M = 84.18%; S.D. = 9.37).

Post Day1 vs Day 2 t(36) = -2.15, p= .04.

Importantly, there was no significant interaction between Time and Day of testing, with no indication of a larger deterioration of alertness on one day over the other.

Visual acuity screening

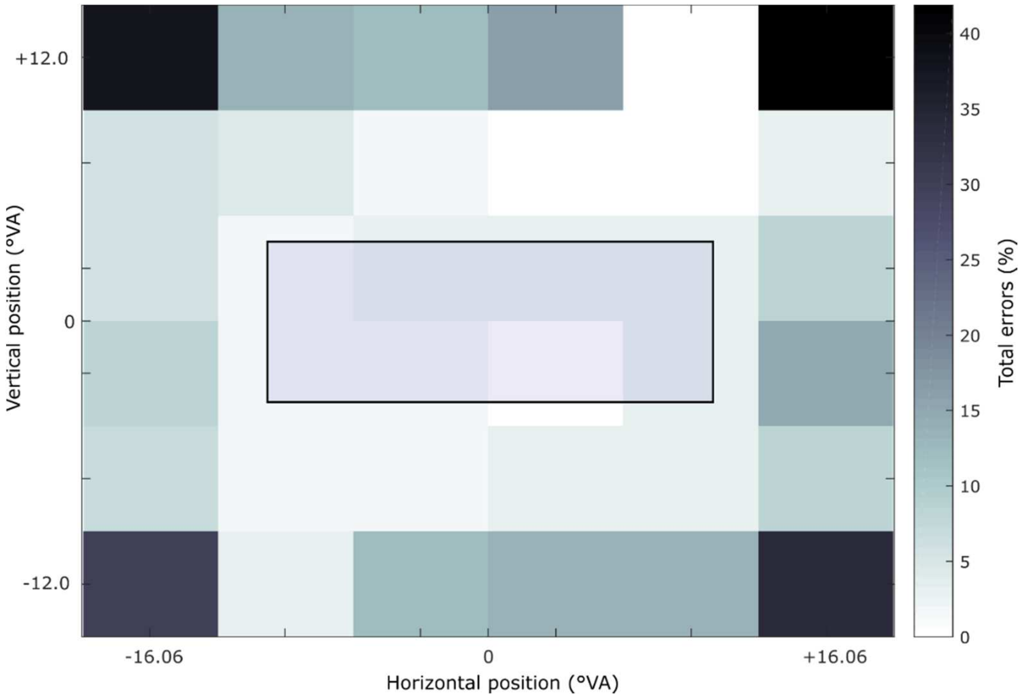

Figure 3 : Overall percentage of detection errors for visual acuity detection Task. Each of the 6x6 squares displays the error rate across participants made at this position equalling to the screen and visual field of the participant. A colour bar on the right side indicates the percentage of errors made (0-50% detection error rate). The blue square in the centre indicates the region of interest, where the spatial tasks were presented

Results of the visual acuity screening (Learmonth, Benwell, et al., 2017) showed that participants made most detection errors in the periphery.

The most extreme values were at the outer corners, ranging from 30% – 42 % (M = 35.8%; S.D. = 5.2) both within and between participants. Most importantly, in the middle of the visual field that corresponded to the area where the stimuli were presented had an accuracy detection rate of M = 98.2%; S.D. = 1.18 across 16 positions, excluding the outer positions. Detection accuracy was at an average of M = 91.25 %; S.D. = 10.91 collapsed across all 36 positions. No single participant fell below this. Detection accuracy was at an average of M = 91.2%; S.D. = 10.91, collapsed across all 36 positions.

Inter- Task Spatial Biases

Manual Line Bisection task (MLB)

Repeating the analysis per Learmonth et al. (See (Learmonth, Gallagher, et al., 2015, 2018), the average spatial bias across both testing days for the MLB task for older people was analysed. Each of the 9 different positions of the MLB stimuli were analysed separately and the one-sample t- tests against zero (i.e. no bias) revealed a significant leftward bias for the 5 most leftward positions (left120 t(36) = -2.68, p = .01, left80 t(36)= -2.76, p = .009, left 40 t(36)= -2.51, p = .02, veridical t(36)= -2.31, p= .03 , right160 t(36)= -2.11, p = .04. When the line was jittered to the left side of space, participant showed a greater spatial bias to the left side.

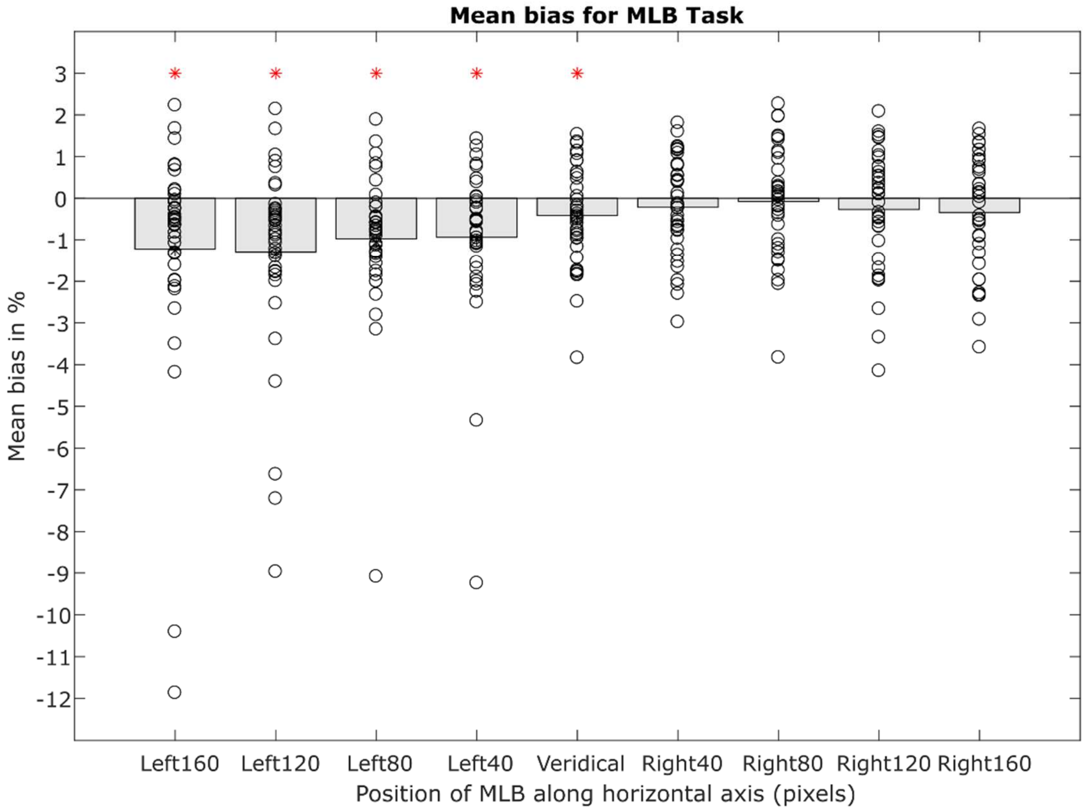

Figure 4: MLB task line positions jittered across the visual field.
The bars show the 9 different line positions from -160 to +160 pixel from the veridical centre of the screen. The individual Mean spatial biases are presented in % line length and overlaid on the group mean. A significant group bias per position is marked with a red asterisk (*).

A repeated measures ANOVA for the different positions showed a main effect for Position [F(1, 36) = 10.46, p = .003)]. In order to determine when leftward bias was lost, paired samples t-tests were performed on neighbouring line positions. A significant leftward shift of bias was found when the line was shifted 40 pixels left of centre compared to when positioned in the centre of the screen (the veridical position (0)): t(36) = -2.46, p = .02 (see Figure 4). There was a larger leftward bias when the line was positioned 40 pixels, compared to 80 pixels, to the *right* of centre: t(36) =-2.32, p =.03. Furthermore, a trend was found for a difference in bias for 0 - +40 right of centre: t(36)= -1.92, p = .06, and +80 – +120 at the right side of space t(36)= 1.93, p=. 06. No other pairs showed significant differences in bias.

A one-sample t-test over all positions and participants, displayed a significant leftward bias (pseudoneglect) t(36)= -2.73, p = .01 (*M* =-.64, S.D.= 1.42).
[Day 1: t(36)= -2.48, p = .02, M = -.65, S.D. = 1.59, Day 2: t(36)= -2.57, p= .01, M=-.63, S.D. = 1.48].

Landmark (LM), Greyscale (GREY) and Gratingscale (GRA) task:

The PSE for the LM task did not display significant biases, on either testing days or when collapsed together.
Day 1: t(36)= -.65, p = .52, M = -.08; S.D. = .78,
Day 2: t(36) = -.51, p = .61, M = -.05 ; S.D.= .64,
Average of testing days: t(36)= -.66, p = .51, M = -.07, S.D. = .65.
However, the GREY showed a significant leftward bias (pseudoneglect) on each testing day and when averaged across testing days.
Day1: t(36)= -2.23, p = .03, M = -1.05; S.D. =2.86,
Day 2: t(36)= -2.13, p= .04, M = -.92; S.D.= 2.62,
Average of testing days: t(36) = -2.65, p = .01, M =-.95, S.D.= 2.19.
The GRA task, showed no significant bias to either side across testing days.
Day 1: t(36)= 1.30, p = .20, M= .37, S.D.= 1.73;
Day 2: t(36)= 1.07, p = .29, M = .31, S.D.=1.75;
Average of testing days: t(36)= 1.27, p= .21., M = .31, S.D.= 1.49

Lateralised Visual Detection task (LVD)

D-Prime

Collapsed over both testing days, participants at a group-level correctly rejected 95% of catch trials and correctly identified an average of 40% of the presented targets in LVF and 37% in the RVF. The lateralisation index, which was collapsed over both testing days $d^{'}RVF - d^{'}LVF = d'(group\ bias)$ was M= -.05, and did not support a significant lateralisation bias in older adults when tested against zero
Day 1: t(35) = -1.04, p = .31, M = -.07, S.D. = .38,
Day 2: t(35)= -.23, p = .82, M = -.02, S.D.= .50,
Average of both days: t(35)= -.65, p = .52, M = -.05, S.D.= .42.

LVD (PF 50%)

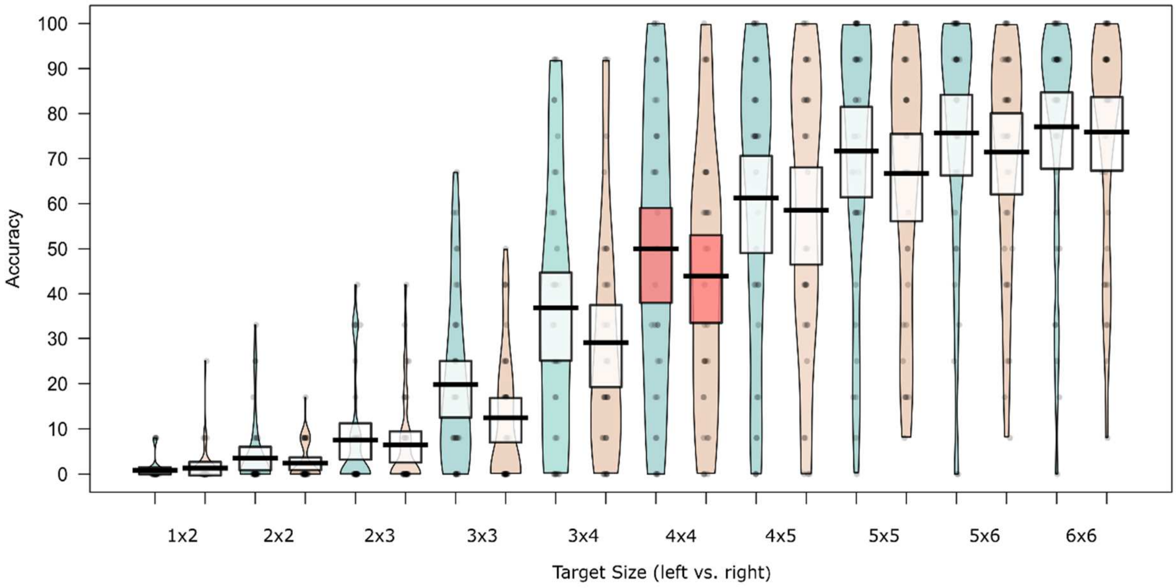

Figure 5 Performance on the LVD task.
The figure shows the detection accuracy in % for each of the 10 different stimuli sizes (in pixels) averaged over both sessions. Each violin plot shows the detection separated in left- (green bars) and right visual field (orange bars) presentation. Boxplots display the group level mean as a black bar within the box displaying 95% HDI. The group level PSE per target size is indicated with a red box, showing a 50% accuracy.

As per Learmonth, Gallagher, et al. (2015, 2018) a psychometric curve was fitted to the LVD data. In the first instance, separating the PSE of the mean group average (PF50%) per visual field revealed that averaged over both testing days, the 50% detection rate for a stimulus for the left visual filed was at M =6.7 and

at M= 7.1 for the right visual field. This is equivalent to a 50% detection rate at target size 4x4 to 4x5 (see red highlight in Figure 5). Thus, suggesting a slightly lower mean threshold for perceiving stimuli in the left visual field than the right. Yet, this difference was not significant
(LVF vs. RVF: t(35)= -.986, p = .33).

A one-sample t-test against zero on the lateralisation index
$RVF - LVF = PSE(group\ bias)$, did not support a significant lateralisation bias
Day 1: t(35) = 1.81, p = .08, M = .46; S.D.= 1.51,
Day 2: t(35)= 1.69, p = .10, M = .45; S.D. = 1.58,
Average of both testing days t(35)= 1.33, p = .19, M= .30; S.D. 1.36.
Furthermore, a 2 (Side) x 2(Day) Repeated Measures ANOVA PF(50%) revealed no differences across position LVF vs. RVF and testing days.
No main effect for day F(1, 35)= .18, p=.67 or side F(1, 35) = .97, p= .33, and no interaction F(1, 35)= .02, p= .90.

Overall task bias summary

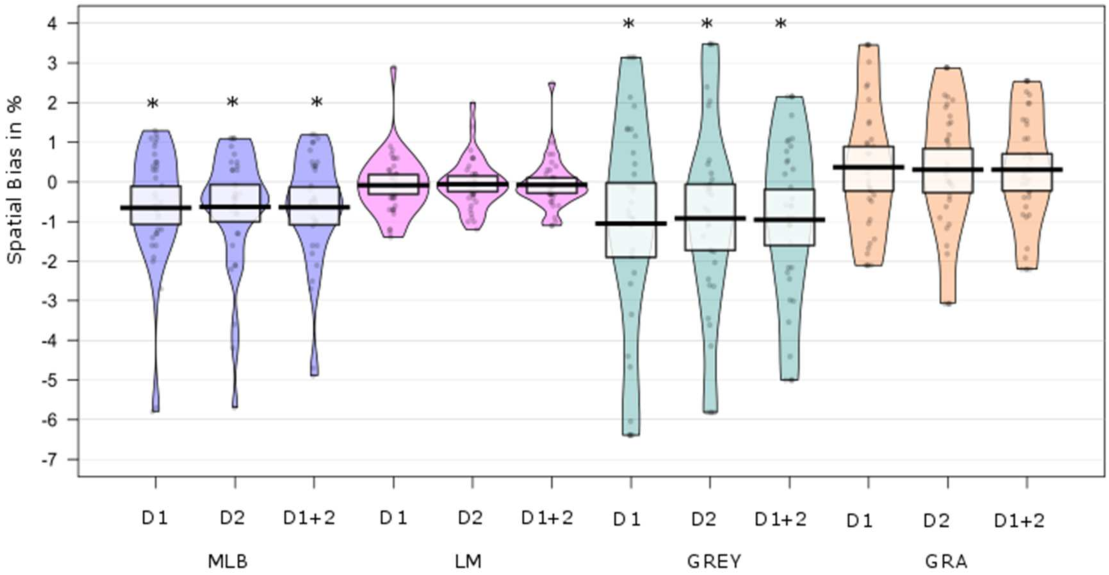

Figure 6 : Overall Spatial Bias for the MLB, LM, GREY and GRA task.
The spatial biases are shown for testing Day 1, Day 2 and collapsed over both testing days. The violin plots are overlaid with the raw data of the spatial biases per individual to show the distribution of PSE in % of total line length. Boxplots display the group level mean and 95% HDI. Significant values compared to 0 are marked with an asterisk (*). Only the MLB and GREY tasks displayed a significant bias.

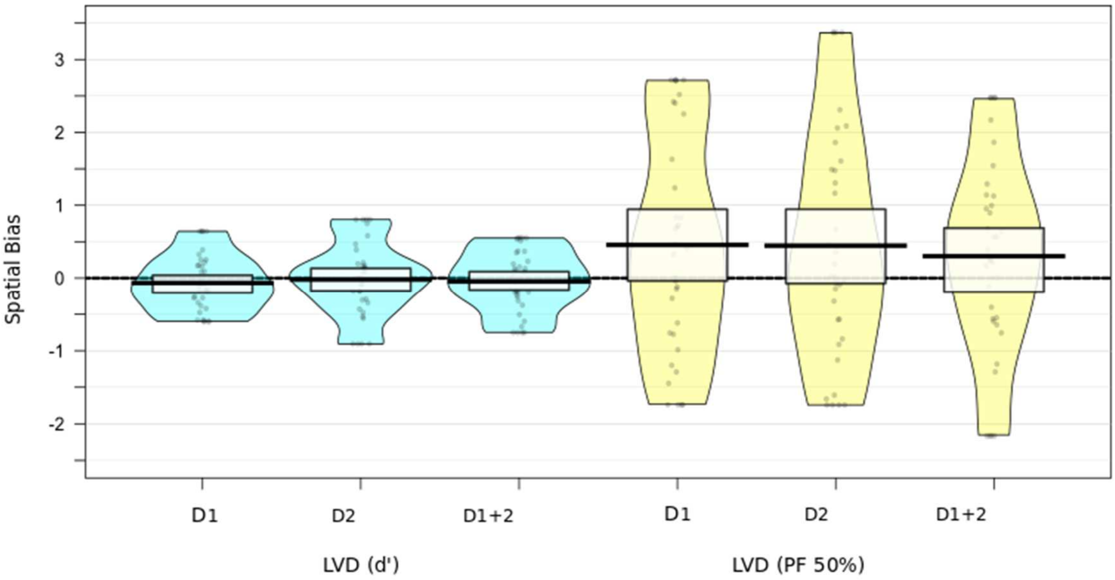

Figure 7: Overall spatial bias for LVD Task across testing Days
The violin bars show the mean spatial bias and the individual biases are overlaid for Day 1, Day 2 and mean of both testing days across the LVD task and its two analyses (D'Prime and PF50%). Group level means are displayed as black bar within a box displaying 95% HDI. None of the biases were significant.

Across the five common spatial measures, only the MLB and GREY task showed a significant leftward spatial bias (pseudoneglect) in older adults. The GRA, LM, and LVD tasks did not show a lateralised bias on either testing day in older participants.

Intra-task reliability

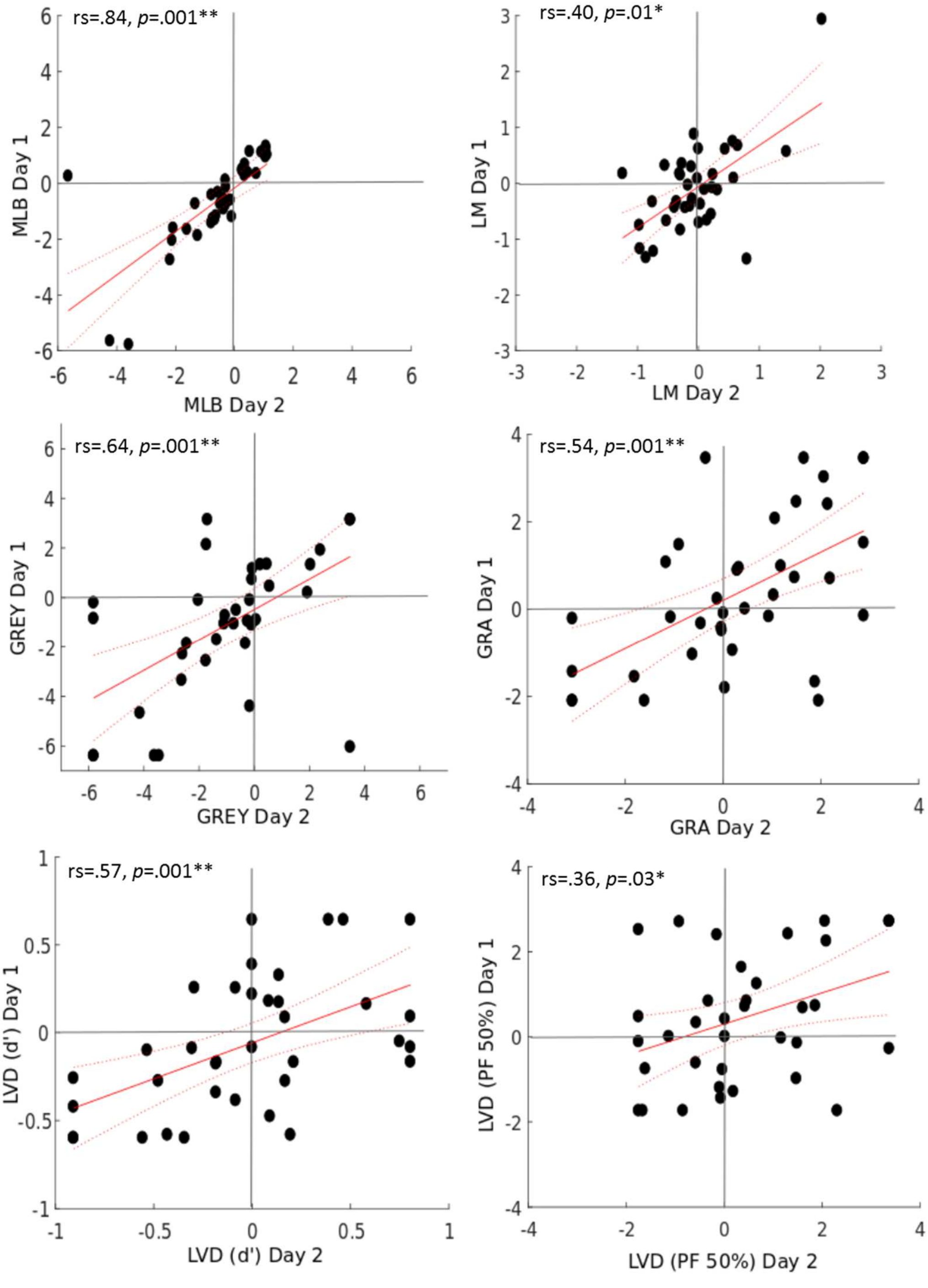

Figure 8: Intra-task correlation plots
Showing the MLB, LM, GREY, GRA and LVD tasks with D'Prime and PF50% analysis between Day 1 and Day 2. The red line displays the polynomial best fit and the dotted lines display the 95% confidence bounds.

In order to assess the test-retest reliability between both testing days, the five spatial tasks were analysed separately with a series of Spearman rho correlations on the biases obtained on Day 1 versus Day 2 (see Figure 8). Results showed significant correlations between both testing days on all tests (see Table 1).

Table 1 Intra-task correlation

	MLB	LM	GRA	GREY	LVD (d’)	LVD (PF 50%)
95% Confidence Interval	rs= .84	rs=.40	rs= .54	rs=.64	rs=.57	rs=.36
	p=.001**	p=.01*	p=.001**	p=.001**	p=.001**	p=.03*
Lower	.61	.06	.23	.32	.25	-.02
Upper	.96	.70	.78	.87	.80	.66

This table shows the results of the Spearman’s rho (rs) correlation and p- value for the 5 spatial tasks tested between two testing sessions. Significant correlations at p= .01, corrected for multiple comparison are marked with double asterisk (**), p = 0.05 with (*)

Inter- task reliability

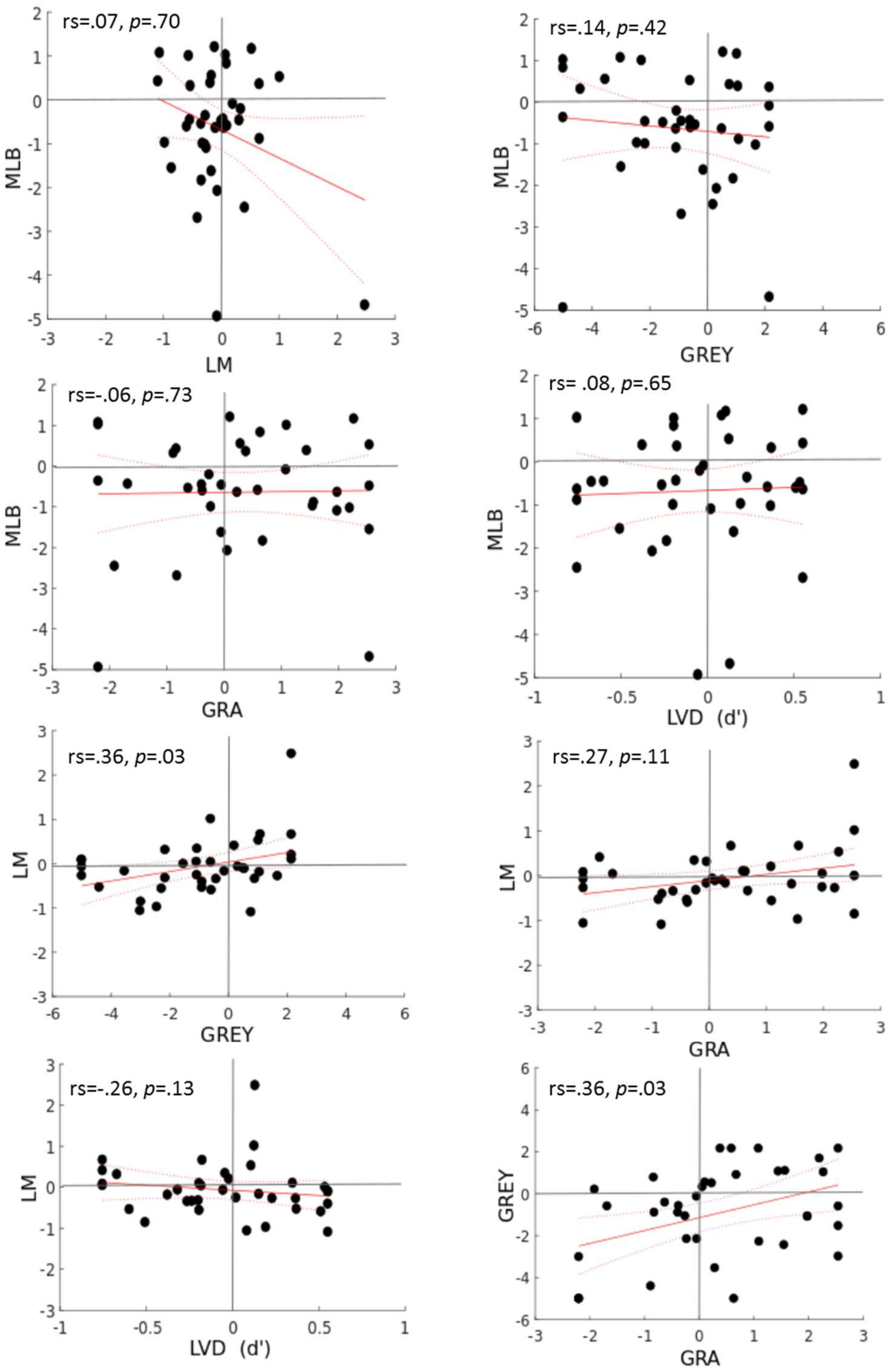

Figure 9: Inter- task correlation plots for MLB, LM, GREY, GRA and LVD task

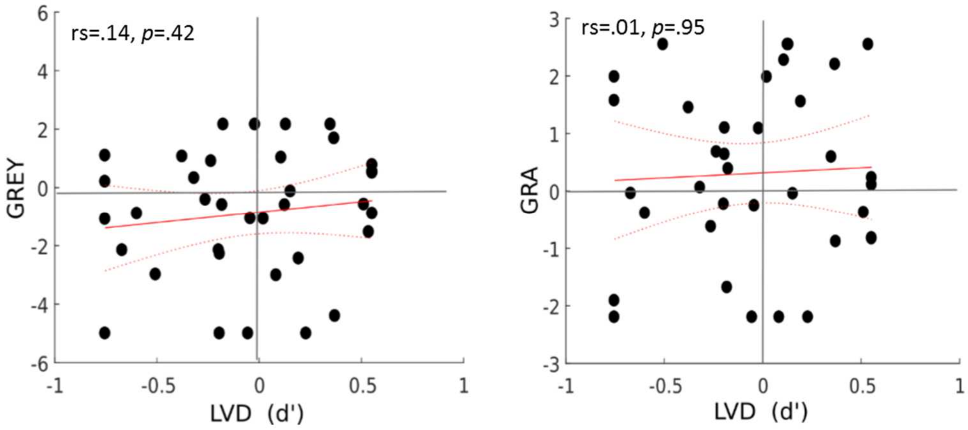

Figure 10: Inter- task correlation plots for LVD, GREY and GRA task.
Plots showing the correlation of the spatial tasks with each other MLB, LM, GREY, GRA and LVD task with D'Prime across the mean of both testing days. The red line displays the polynomial best fit and the dotted lines display the 95% confidence bounds.

Following on from the confirmed test-retest reliability of the tasks, Spearman's rho correlations were used to investigate whether the magnitude of spatial bias in one task was correlated with the magnitude of spatial bias in the other 4 tasks.

Table 2: Inter-task correlation

	LM	*GRA*	*GREY*	*LVD (d')*	*LVD (PF 50%)*
N=	37	37	37	36	36
MLB	rs = .07	rs= -.06	rs= -.14	rs= .08	rs= -.001
	p= .70	p= .73	p = .42	p= .65	p= .98
95% CI Lower	= -.31	= -.44	= -.44	= -.23	= -.30
95% CI Upper	= .42	= .31	= .26	= .40	= .32
LM		rs= .27	rs= .36	rs = -.26	rs= .19
		p= .11	p= .03	p= .13	p=.27
95% CI Lower		= -.12	= -.54	= -.54	= -.21
95% CI Upper		= .60	= .08	= .08	= .52
GRA			rs= .36	rs = .01	rs= .03
			p= .03	p= .95	p = .85
95% CI Lower			= .02	= -.35	= -.35
95% CI Upper			= .65	= .35	=.45
GREY				rs = .14	rs=-.004
				p =.42	p= .98
95% CI Lower				= -.16	= -.37
95% CI Upper				= .43	= .34
LVD (d')					**rs= -.71****
					p= .001
95% CI Lower					= -.92
95% CI Upper					= -.45

This table shows the results of the Spearman's rho (rs) correlation and p- value for the 5 spatial tasks tested. Significant correlations at p= .003, corrected for multiple comparison are marked with an asterisk (**)

Results showed that collapsed over both testing days, only the LVD task measures of D’Prime and PF 50% were strongly correlated (rs= .71, p = .001), confirming the reliability between the analysis methods The LM and GRA as well as the GRA and GREY task showed a small correlation, which did not survive Bonferroni correction. No other tests were correlated with each other.

Task precision (Curve Width)

Curve width was analysed for the tasks LM, Grating-, Greyscales and LVD tasks as a measure of precision of task engagement and sustained attention over both testing days. High task precision is reflected in a steep curve.

Correlating the intra-task curve widths (Spearman’s rho) over both testing days confirmed a consistency of precision between the testing sessions in older adults (LM *rs*= .62, p = .001, GRA *rs*= .63, p=.001, GREY *rs*=.67, p= .001, LVD Left visual field *rs*=.55, p =.001, Right visual field *rs*= .65, p= .001). Paired samples t-tests for Day 1 vs Day 2 showed that precision improved on the second day for the LM t(36)= -2.85, p = .007 (Day 1 M = -.89 , S.D. = .48, Day 2 M= -.71, S.D. = .47) and GRA task t(36)= -2.04, p = .05 (Day 1 M = -6.36, S.D.= 3.49, Day 2 M= -5.41), S.D. = 2.82, as reflected in a narrower curve on the second day.

Lane- Keeping task (LK)

The Lane keeping task showed a significant rightward bias on both testing days.
Day 1: t(35)= 5.24, p < .001 M= .22, S.D. = .25,
Day 2: t(35)=5.69, p < .001 , M = .23, S.D. = .25,
Average on both testing days: t(35)= 5.92, p< .001, M = .23, S.D. = 23,
Spearman's rho confirmed a significant correlation between both days, as a further example of a stable spatial bias over separate testing sessions *rs*=.70, p=.001 (see Figure 11). Against the predictions, none of the five spatial tasks showed a significant correlation with the driving task (see Table 3 for results).

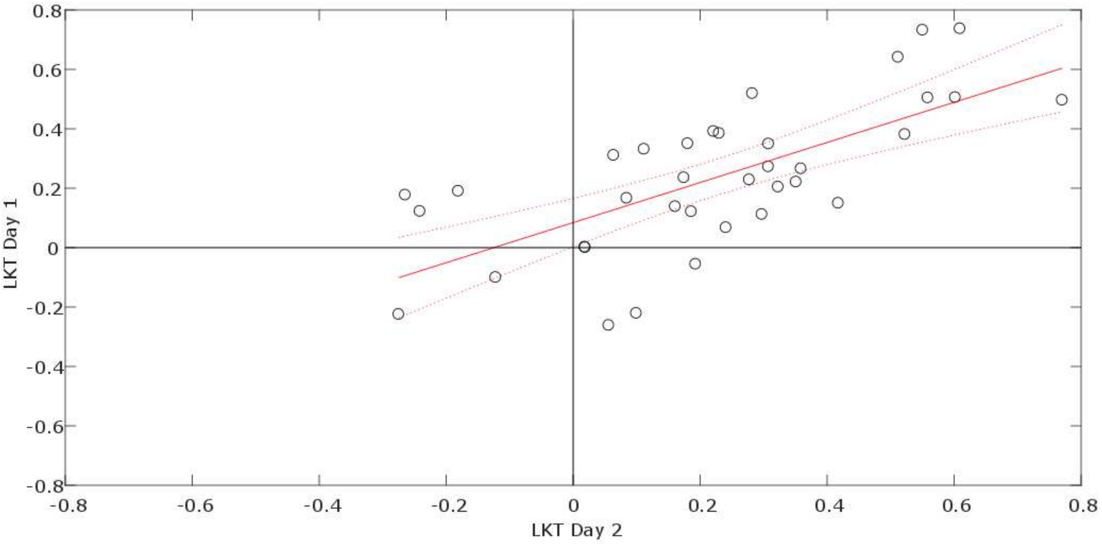

Figure 11 : Correlation of the LK task across testing days.
The red line displays the polynomial best fit and the dotted lines display the 95% confidence bounds. The figure shows the correlation between testing Day 1 and 2 for LKT

Table 3: Correlation with the LK task and the five spatial tasks

N= 36	***MLB***	***LM***	***GREY***	***GRA***	***LVD D'Prime) ** N= 35***
Lane Keeping Task	rs =.12	rs =-.08	rs = .01	rs = -.10	rs = -.11
	p = .47	p =.64	p =.95	p =.56	p =.54

The table shows the correlation between the Lane Keeping task and the other five spatial measures.

Comparison between young and older adults

Despite the slight difference in viewing distance between the two age group samples (present study vs. Learmonth, Gallagher et al.,(2015, 2018)), four of the five spatial tasks were procedurally identical in the older group (N = 37) reported here, relative to the young adult sample investigated by Learmonth et al. (Learmonth, Gallagher, et al., 2015, 2018)(N = 50). I therefore performed a direct, between-group comparison between the young and older adults to assess age-related differences in spatial biases across the 4 tasks. A one-way MANOVA on the mean data obtained on Days 1&2 revealed a significant effect of age on spatial biases. F(4, 82)= 3.58, p =. 01, ηp^2=.15, Wilks' Δ = .85. The ANOVA revealed an interaction between LM x Age = F(1, 85) =4.26, p = .04, ηp^2 = .05 but no other measures yielded a significant interaction. Welch's t-tests revealed that the Landmark task elicited significantly different biases in young and older adults, t(84,6)= -2.14, p = .04). While young adults showed a leftward bias (M = -.39) (pseudoneglect), older adults had no mean spatial bias for this task (M = -.08), thus not showing pseudoneglect. All other measures did not differ significantly between age groups (see Figure 12).

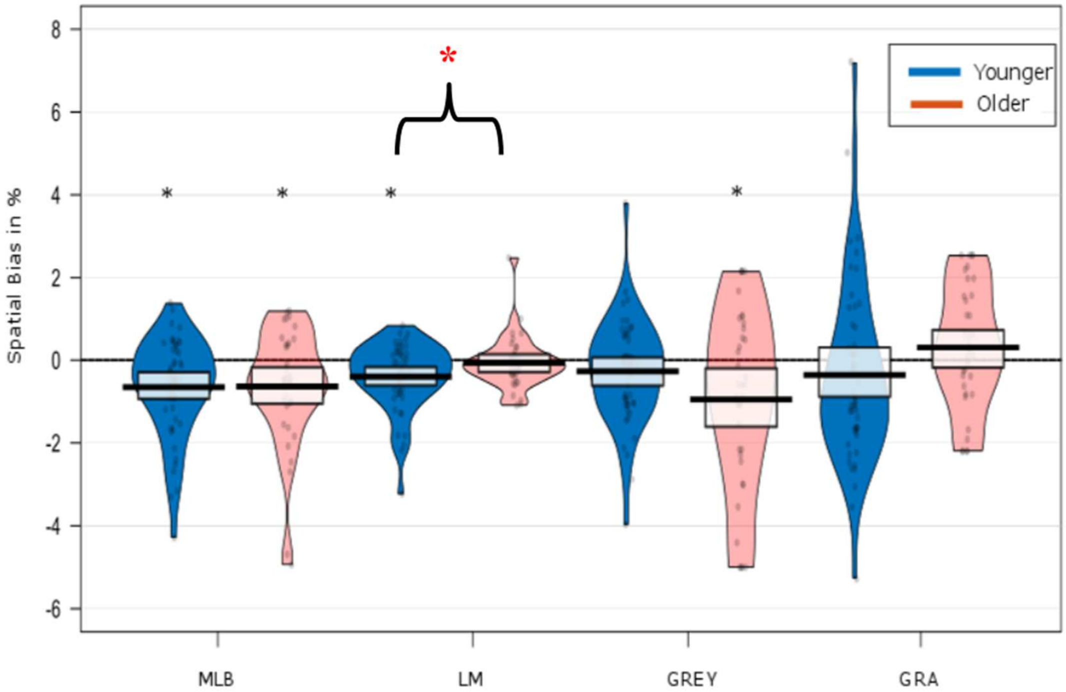

Figure 12 Spatial Biases of the younger and older Adults
The violin plots display the group mean spatial biases collapsed over both testing days for four spatial tasks. The individual spatial biases are overlaid. The boxplots display the mean per task with 95% HDI. A significant spatial bias is depicted with a black asterisk (*). A significant difference between age groups within a task is depicted with a bracket and a red asterisk (*).

Discussion

The present study investigated possible age related changes in spatial asymmetry and its impact on the intra and inter task reliability of five commonly used spatial tasks. Summing up the results of the older adults in the first instance, according to our hypothesis, the 5 tasks present here elicited consistent spatial biases in older adults when tested on different testing days. In contrast to reports of a higher variability in re-retest reliability(Manning, Halligan, & Marshall, 1990), the present tasks proved as reliable measures of spatial attention asymmetry with a good re-test reliability for an older age group. Overall, only the line bisection and greyscales tasks elicited significant, stable leftward biases (pseudoneglect), whereas the remaining tasks did not reveal a significant spatial asymmetry. Secondly, no relationship was found between any of the tasks, when investigating the inter- task correlation, replicating the results by Learmonth et al. (2015, 2018) in young adults. Most importantly, a direct comparison between the young and older adult datasets indicated that the landmark task separated the groups in terms of spatial bias, with young adults demonstrating pseudoneglect that was not present in the older group.

Intra-task correlations

Encouragingly, the stable test-retest reliability for each of the five measures of spatial attention that were previously reported for young adults (Learmonth, Gallagher, et al., 2015, 2018) were also found in the present, older age group. This seems to support the conclusion by Learmonth et al. (2015, 2018) that each of the five spatial measures that were investigated, activate a consistent property of the attention network, each dependent on the respective task-demands at hand.

Leftward biases in older adults

Interestingly, none of the tasks tested here displayed a critical rightward bias in older adults. On the contrary, in accordance with Brooks et al.(Brooks et al., 2016) I demonstrated that pseudoneglect remains present throughout the aging process when assessed using some spatial attention tasks. Here I have replicated the previously reported maintained leftward bias for the line bisection task (Beste, Hamm, & Hausmann, 2006; Brooks et al., 2016; Alice Varnava & Halligan, 2007), as well as the greyscales task, which has been found to elicit a strong leftward bias in very elderly adults aged 80 -89 (Friedrich et al., 2016). These findings support prior claims that right hemisphere attentional orienting can be retained into old age (e.g. Brooks et al., 2016).However, here I add to this literature by identifying that this may only hold true for certain visuospatial tasks. The current results are in line with previous work, where it has been argued that different spatial attention tasks place a unique set of cognitive and motor demands on the spatial attention networks (Learmonth, Gallagher, et al., 2015; Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, 2010). Here I have replicated this finding within a healthy older sample and suggest that the neural resources that are involved in the line bisection and greyscales tasks are less susceptible to age-related neural changes.

Presence of ageing effects on measures of spatial bias

In a direct comparison with the young adult sample of Learmonth et al. (Learmonth, Gallagher, et al., 2015, 2018), I found that only the landmark task was modulated by ageing (i.e. a leftward bias in young adults and no significant bias in the older group). The attenuated spatial bias in the older adults here could potentially reflect a selective age-related decline of right-hemispheric processes that are involved in undertaking this task (e.g. as described by the ‘Hemispheric Asymmetry Reduction in Older Adults’ (HAROLD) model of cognitive aging (Dolcos et al., 2002)). In fact, our group recently reported evidence for decreased right hemisphere activity in older adults when performing the landmark task in EEG recording (Learmonth, Benwell, et al., 2017). Similar to the present results, that sample of older adults also showed an absence of leftward bias in comparison to young adults. In addition, there was a time-window of right-sided lateralisation of neural activity in young adults, which was absent in the older group. It may be that, in line with the HAROLD model, the older participants recruited supplementary contralateral brain areas when dealing with this task to maintain their performance (for a discussion see (Dolcos et al., 2002; Learmonth, Benwell, et al., 2017; Reuter-Lorenz & Park, 2010). In fact, all of the current participants were within normal range on the MOCA test, which is further evidence that this observed shift is likely to be attributed to healthy neuronal mechanisms of aging, rather than cognitive decline. However, the difference in behavioural performance between the groups was subtle, with a substantial overlap in the range of biases in both young and older adults (see Figure 12). The specific mechanism, and indeed the relevance of this age-related shift in the landmark task must now be clarified.

Inter-task correlations

The spatial measures showed no significant correlation between each other, even if they were procedurally similar. Only the GREY and GRA and LM and GREY showed small between task correlations, however these did not survive Bonferroni correction. On the basis of the earlier results in young adults (2015, 2018), and findings in the past and current literature (Heber et al., 2010; Luh, 1995; Nicholls et al., 1999) this lack of between task correlations is independent of age. However, it poses a critical problem when assessing spatial attention, and generalising spatial biases across tasks should be treated with caution. This highlights the importance of understanding spatial attention as a multi component phenomenon as has been proposed by Learmonth et al.(2015, 2018). They previously suggested that the five commonly used spatial tasks in the current literature appear to measure subcomponents of spatial attention, in terms of: size judgement (MLB, LM), luminance judgement (GREY) and spatial frequency detection(GRA) (Learmonth, Gallagher, et al., 2015, 2018). To reliably assess and differentiate between age related changes in pseudoneglect and possibly also neurological deficits linked to neglect in older adults(Verdon et al., 2010) , it is important to understand these subcomponents of spatial attention in an ageing context, as they might be impacted differently by age, resulting in the observed spatial biases at present.

Specific task effects

Despite their procedural similarity, the LM and MLB task yielded different spatial biases, with leftward biases for the MLB and an absence of spatial bias for the LM task. Both measurements have been previously found to engage right lateralized brain activity and involve the right intra-parietal sulcus (IPS) and right lateral peristriate cortex (Cicek et al., 2009) and in our younger sample I found directional effects to be the same (Learmonth, Gallagher, et al., 2015, 2018). Nonetheless two studies have now reported a lack of correlation between these two tasks in young adults (Cicek et al., 2009; Learmonth, Gallagher, et al., 2015, 2018) and together with our reported findings in this older sample, equivalence between these tasks can no longer assumed to be a given.

For the first time, I tested older adults on the Gratingscale (GRA) task, which is procedurally similar to the Greyscale (GREY) task. Again, as for LM vs MLB, I report divergent spatial biases with significant pseudoneglect for the GREY task but no significant spatial asymmetry in the GRA task. Both results resemble the spatial bias observed in young adults in Learmonth et al.(Learmonth, Gallagher, et al., 2015, 2018), who reported no bias for the GRA task and also a significant leftward bias on day one for the GREY task, which then attenuated at re-test. These findings were somewhat contrary to findings of a robust preference in young adults for the left visual field in both tasks (GRA, GREY), as well as an intra-task correlation between them (Niemeier et al., 2007). It is worth noting that in the GRA task here, participants assessed the number of stripes, directing their attention to the largest amount of “thin stripes”. Low spatial frequencies (SFs) are processed in the left hemisphere, while high spatial frequencies (SFs) are more likely processed in the right hemisphere (Niemeier et al., 2007; Piazza & Silver, 2017). With the focus on the high SF (more “thin stripes”), the right hemisphere should be more involved in spatial judgements, leading to the observed leftward bias and confirming the claims made by Niemeier et al.(Niemeier et al., 2007) for a robust measure of spatial bias. Our finding of an absence of a leftward bias for older adults, could reflect the finding that older adults become less sensitive to spatial frequency processing (Costa, Nogueira, Pereira, & Santos, 2013; Elliott & Werner, 2010; McGrath & Morrison, 1981; Santos, Simas, & Nogueira, 2004), so while the task may not have been sensitive enough for young adults, it might have been sufficed to elicit a spatial shift in the older sample.

The results of the LVD task did not elicit a significant bias in older adults, confirming our earlier findings of an absent bias (Learmonth, Benwell, et al., 2017; Learmonth, Gallagher, et al., 2015) and poor consistency over testing days (Learmonth, Gallagher, et al., 2015, 2018). Despite adjustments in the design to ensure an adequate range for older participants to perceive a threshold of stimuli, which included 10 different stimulus sizes, the task difficulty varied vastly among older participants, with some perceiving the task as either very difficult (or others not challenging enough).

Finally, I tried to investigate a more ‘naturalistic’ spatial bias obtained from a Lane keeping driving simulation. While the Lane keeping task elicited a significant rightward bias, which again remained stable over testing sessions, I again failed to find a correlation with the five spatial tasks described above. The presence of a rightward bias (positioning to the right side), in the Lane keeping task makes sense, as in a more realistic setting, a rightward positioning would result from an overestimation of the left side of space (i.e. Pseudoneglect), as a compensative strategy. However, as would be expected if this were indeed the case, Learmonth, Märker, et al. (2018) found a correlation between Lane keeping task and LM in young adults, yet this correlation was absent in the older population. This absence of such a correlation could reflect a true shift of spatial asymmetry in older adults, elicited in this more complex driving task (see also (Benwell, Thut, et al., 2014), for a similar argument). Yet again, at present this is speculation only.

In accordance with Brooks et al.(2016) I demonstrated that pseudoneglect remains stable throughout the lifetime in some spatial attention tasks. However, I found the exact direction and magnitude of the spatial bias to be task as well as age sensitive. Several studies demonstrate that spatial asymmetry is present across different modalities and not confined to perception alone, i.e. tactile and mental representation (Brooks et al., 2016), or auditory representation (Eardley, Darling, Dumper, Browne, & Velzen, 2017). I replicated the reported retained leftward bias for the MLB task (Beste et al., 2006; Brooks et al., 2016) but report a loss of spatial bias in contrast to young adults in the LM task. None of the tasks tested here displayed a critical rightward bias but instead a stable leftward bias in the GREY and MLB task. The absence of spatial bias in any given task, such as the LM, GRA and LVD task is difficult to interpret: on the one hand such an absence of spatial bias could be a result of right hemisphere decline due to healthy ageing or possibly even unidentified presence of mild neglect in an otherwise healthy older adult. On the other hand it could be simply a task effect.

Limitations

In light of the present findings, the variability in the direction of spatial bias reported here and in previous studies suggest that the effects are task dependent rather than task general. Perhaps, there is another underlying factor such as changes in sustained attention or differences in task difficulty across the spatial measures that drives the observed leftward bias, rather than spatial attention. An increase in task difficulty could result in an attenuation of a leftward bias and this might be individual rather than driven by age effects. It should be noted, that it is possible that the tasks which elicited a leftward bias in the present older sample are in fact the better tasks to estimate spatial attention then the tasks which did not elicit a spatial bias (i.e LM GRA and LVD task). The mixed results of older adults' retained and attenuated spatial bias across the tasks tested, may also relate to differential vs overlapping brain regions required for each task demand. Ultimately only further in depth EEG, fMRI and meta-analyses will provide definite answers to characterize such possible modulators of pseudoneglect and the following chapters address these questions also.

Conclusion

Similar to earlier findings in young adults, I report good test- retest reliability of five spatial measures taken over different days, in a population of cognitive healthy older adults. I confirm that the direction of the spatial bias is task sensitive rather than task general. The MLB and GREY tasks showed a spatial bias to the left side of space, with older adults demonstrating pseudoneglect for these tasks. In a direct comparison to the young adults sample (Learmonth, Gallagher, et al., 2015, 2018), only the LM task showed an attenuated spatial bias in older compared to younger adults, possibly consistent with neuronal findings of an age-related reduction of the right hemisphere (Learmonth, Benwell, et al., 2017). As our participants did not score clinically on measures of early neurological decline, this is likely a result of healthy aging. Yet, the inconsistent bias results found here and in the more recent literature seem to point to other factors possibly driving these effects. An increase in task difficulty or sustained attention for example, could account for the absence of leftward biases described here (and these modulators could be age dependent or independent). Fitting with this assumption are the (now repeatedly observed) lack of inter-task correlations. This complicates generalisation and comparability of pseudoneglect effects across different tasks and age groups.

Chapter Three

Investigating the impact of attentional load on spatial attention in young and older adults with a behavioural paradigm

As described in the previous chapter 2, young adults typically show a preference for the left side of space (pseudoneglect), resulting in faster reaction or behavioural overestimation to the left side of space. Yet, results involving older adults have been mixed and lack clear consensus, so the view that spatial attention declines with age *per se* may be too simplistic. Results of my recent study (See chapter 2) have shown that older adults show both, a maintained leftward bias (pseudoneglect) as well as no bias to either side of space. Thus my data expand previous findings of mixed results for older adults, i.e. no spatial bias, or a trend towards the right side of space in the landmark task (see Benwell, Thut, et al., 2014; Schmitz et al., 2013; Schmitz & Peigneux, 2011), the MLB (compared to young adults (Barrett & Craver-lemley, 2008; P. Chen et al., 2011; Failla et al., 2003; Fujii et al., 1995; Goedert et al., 2010), as well as for lateralised visual detection tasks (Learmonth, Thut, et al., 2015; Nagamatsu et al., 2011, 2009, 2013). In contrast, there are also reports of maintained leftward bias across different tasks in older adults (Chapter 2, Brooks et al., 2016).

This variation in the directionality of the spatial bias appears to be highly task sensitive and an absence of a leftward bias for the MLB task and LM task (for young adults in previous studies), could be due to differences in stimuli size (Manning et al., 1990), as well as presentation differences in the horizontal plane (see Jewell & McCourt, 2000 for a review). Moreover, differences in viewing distances have shown to influence the magnitude of spatial bias, with greater leftward biases when stimuli are presented in peripersonal space and an attenuation the further stimuli are presented in the extra personal space (Dellatolas, Vanluchene, & Coutin, 1996; A. Varnava, McCarthy, & Beaumont, 2002). However, these factors could also have an influence on the task difficulty due to increased attentional demand, which in turn will have an impact on the allocation of spatial attention. Thus, instead of hemispatial decline of the right hemisphere with age (i.e. HAROLD) (Cabeza, 2002; Dolcos et al., 2002), changes in load capacity could be an underlying factor of changes in spatial biases that are observed in older adults.

Networks of dorsal (spatial) and ventral attention

Models of spatial attention describe a right-hemisphere dominance that is responsible for selecting and shifting spatial attention, entailing a ventral (VAN) and dorsal attentional network (DAN) (Corbetta et al., 2008; Kinsbourne, 1977; Mesulam, 1999). The characteristic attention bias towards the left side of space in pseudoneglect is linked to enhanced demands on the VAN in the right hemisphere (Coull, Frackowiak, & Frith, 1998; Newman et al., 2013). This VAN controls interhemispheric competition in the DAN (Corbetta et al., 2008; Corbetta & Shulman, 2011).When selectively attending across space and executing responses to task relevant or irrelevant stimuli, the bilateral DAN is activated. The right lateralised VAN however is associated to non-spatial attention capacities (Culham, Cavanagh, & Kanwisher, 2001; Newman et al., 2013; Schwartz et al., 2005) and alertness regulations (Paus et al., 1997; Sturm & Willmes, 2001).A decrease of activation in the VAN is suggested to result into a global decrease in the RH activation (Corbetta & Shulman, 2011; Newman et al., 2013) due to decreased attention i.e. through time on task (Benwell, Thut, et al., 2013; Nagamatsu et al., 2011, 2009, 2013; Newman et al., 2013) or aging (Benwell, Thut, et al., 2014; Schmitz et al., 2013; Schmitz & Peigneux, 2011). However, it is possible that the observed aging effects might be rather linked to changes in the ventral attention networks, rather than a right hemisphere decline with age alone (HAROLD) (Cabeza, 2002; Dolcos et al., 2002).

Attentional load modulates spatial attention

This is plausible as it has been shown that the degree of spatial bias is modulated by non-lateralized processes, such as vigilance and alertness (Bellgrove et al., 2004) as well as spatial working memory, either to the left (with increased alertness) or the right side of space (reduced alertness) in a variety of tasks (see Chandrakumar et al., 2019 for a review). Moreover, in participants with chronic reduced alertness such as ADHD or right hemisphere damage after stroke, the right spatial bias has been linked to reduced alertness(see Bellgrove et al., 2013). In their studies, Bellgrove et al. (2013)

found reduced response to left visual stimuli with increased attentional load in both patients and children with ADHD. Other studies have found that the observed rightward bias in patients with hemispatial neglect was reduced when the level of awareness was increased i.e. via a warning tone (Dobler et al., 2005; Robertson, Mattingley, Rorden, & Driver, 1998). In contrast, a shift from a previous leftward bias towards the right side of space was observed in young children and healthy young adults, when alertness was decreased, i.e. through prolonged time on task exposure (Bellgrove et al., 2013; Benwell, Thut, et al., 2013).

As noted above, older adults show mixed results on spatial biases and in fact do not replicate the strong rightward bias observed in patients who showed extreme deviation to the right side of space as a result of hemispatial neglect. This suggests that advanced age does not equal to a decrease in attention. Instead, attentional capacities might be reached quicker and according to the HAROLD model (Cabeza, 2002; Dolcos et al., 2002), compensatory strategies might be employed, as well as additional neuronal mechanisms recruited to cope with attentional load, mirroring the same behavioural patterns observed in young adults, yet derived at through different processes. So far this has not been investigated systematically and I will address this with a dual task paradigm.

In patient studies, dual task paradigms have shown that increasing attentional load has an asymmetrical impact on spatial attention. Patients with right hemisphere damage have shown lateralized deficits in their spatial processing (i.e. extinction of the left side) as a result of load constraints on their attentional capacities (Bonato, 2015). Interestingly, this lateralisation towards the right side of space (neglect) was observed even in patients where neglect was not present in the classical clinical measurements or when patients had been found to have recovered from previous neglect (Bonato, 2015).

Similarly perceptual processing was found to be asymmetrically and directly influenced by non-spatial processes such as acquired poor attention due to brain damage after stroke (Bellgrove et al., 2013). Comparing patients with left visual extinction (after stroke) to healthy older adults, using a classical dual visual task paradigm to assessing attentional capacities, Bellgrove et al. (2013) found that the degree of spatial neglect (the extinction of the left side of space) was correlated with impairments in non-lateralised attention. Attentional load was altered in 3 conditions, no load, low load (pop out task) and high load (conjunction search task). Greater attentional load resulted in overall increased reaction times (RT) to peripheral targets, irrespectively of location. Patients further showed significantly decreased detection to left targets, if load was increased.

The same results of asymmetrical lateralization processing when load was increased were also found in children with ADHD and matched controls (Bellgrove et al., 2013), suggesting a similar pattern even if deficits in attention are developmental. With ADHD as an indicator of developmental attention disorder, a lateralized spatial bias emerged when load was increased and became more apparent with load difficulty (high attentional load), resulting in decreased detection of left targets in contrast to the "no attentional load" condition and control group. Thus, these findings suggest an overlapping of non-spatial attentional and spatial orienting networks (see conclusion by Bellgrove et al. (2013)) and that by depleting attentional resources, i.e. through acquired brain damage or developmental deficiencies, spatial re-orienting decreases in efficiency. Based on the HAROLD model that argues for an aging of the right hemisphere in older adults, such effects could be also observed as a result of healthy aging.

In healthy participants, such asymmetrical impacts on lateralization processes were found for cognitive rather than perceptual load. While both studies (See Bellgrove et al., 2013) reported no asymmetries for their healthy controls, Naert et al. (2018) reported a diminishing effect of processing advantages in healthy young adults when cognitive load was increased: employing a dual task with a cognitive load (an uncued working memory task), left peripheral targets were negatively impacted, and the left side processing advantage (pseudoneglect), reported in the low load condition, diminished. However, cognitive load did not affect the processing of the right peripheral targets (see Naert et al., 2018).

Other studies using multisensory integration (Chen & Spence, 2017) or secondary sound discrimination tasks (Peers et al., 2006) have also shown asymmetric spatial processing towards the right side of space when cognitive non-spatial load was increased in dual task paradigms in healthy participants. Thus, studying the effects of load on spatial attention could uncover asymmetries in lateralisation processes for healthy aging that might otherwise not be observed and thus give insight into structural and cortical changes with healthy aging.

Neuronal correlates of cognitive load and spatial attention

So despite some recent advances in uncovering the interplay of attentional capacity and spatial attention in dual tasks in healthy aging, the underlying neuronal correlates have been hardly been investigated and are not fully understood.

O'Connell et al. (2011) found supporting evidence for an asymmetrical effect of early visual orienting due to changes in attentional load. They measured EEG using a classic dual task which involved a lateralised visual detection task, and allowed an altering of attentional load in a rapid serial visual presentation (RSVP) stream. Attentional load was increased by changing the central target from no relevant target to a pop out task (low attentional impact) and a conjunction search task (high attentional load), while participants had to identify a lateralised peripheral target. Their results revealed a behavioural processing advantage for stimuli presented to the left hemifield in adults (resembling pseudoneglect). This was present across all conditions thus suggesting this bias to be unrelated to attentional load. However, in terms of neuronal activity, they found that higher attentional load led to increased recruitment of attentional resources as evidenced in enhanced P1 and N1 waveforms at early visual processing. Further, they found that this was related to a slower processing of and response to the peripheral stimuli when central load was increased (from no load), reflected in reduced peripheral P2 and P3 components. Age related effects might be more pronounced in similar components and might result in reversed effects in older adults. Yet, this has until now not been investigated systematically.

Aims

In their study O'Connell et al. (2011) did not differentiate between age groups and thus, age related effects were not investigated. Therefore, any inferences of attentional load effects on healthy cognitive aging nor changes of early visual processing as indexed by ERPs (with age) cannot be made from their results. Their testing sample had an average age of M= 24 years, with an age range 18-47 years, thus not including a senior population (+60 years) at all.

In the next two chapters I present work that aimed to extend this previous research on non-spatial attention modulations on asymmetric spatial attention to performance across the lifespan (O'Connell et al., 2011), by making a clear separation between young adults and cognitive healthy older adults.

The following presented behavioural investigations informed a follow up study (Chapter 4) where EEG was then employed to investigate the neuronal components of attentional load manipulations. Hence the design of the current study was adapted from O'Connell et al. (2011) to meet this overall research aim. With attentional load expected to impact on age, spatial attention performance was investigated in young as well as healthy cognitive older adults in a visuospatial dual task paradigm. The current design closely resembled the experimental set up of O'Connell et al. (2011). Attentional load was manipulated in two conditions to increase the task difficulty to a low and high attentional impact (See Method section). Based on the behavioural results by O'Connell et al. (2011), I expected to see spatial asymmetry effects when detecting peripheral targets. While O'Connell et al.(2011) reported these across all load conditions (faster responses for left targets), an increase of attentional load might result in different spatial effects in older compared to young adults.

Hypotheses

In the presented study, specific age related effects were thus expected. For the behavioural responses, I predicted a difference in asymmetry in older compared to young adults. When the task gets more difficult, older adults might show a right spatial bias, while young adults might continue showing pseudoneglect across all attentional load conditions. However, it is also possible that older adults recruit additional resources to compensate for the increased task demands and depleted attention capacities and that there will therefore be no differential behavioural change for the older age group.

Methods

Participants experiment 1

For the second experiment, two age groups were compared, consisting of a young adult age group and an older adult group. The young group consisted of twenty young adults between 19 and 25 years (4 males, M = 20.65, S.D. = 1.78). The other group consisted of fifteen cognitive healthy older adults (9 males) age range 62 – 83 years, M = 71, S.D. = 6.4). Exclusion criteria for participants where a history of stroke, colour blindness and dominant left handedness. All participants reported normal or corrected to normal vision. To confirm this, all participants were pre-screened for visual acuity using the Colenbrander Mixed Contrast Card Set (Colenbrander & Fletcher, 2005) and subjected to a computerised visual detection task (Learmonth, Benwell, et al., 2017) to screen for possible visual field deficits. Moreover, they all completed the colour blindness test with colour plates (Ishihara, 1918; Nakajima, Ichikawa, Nakagawa, Majima, & Watanabe, 1960). In addition, the older adults completed the MoCA (Montreal Cognitive Assessment (Nasreddine et al., 2005) to screen for possible mild cognitive decline. The experiment was carried out within the School of Psychology, at the University of Glasgow and obtained ethical approval from the University of Glasgow, College of Science and Engineering Ethics Committee.

Design

Participants completed a computer based task which involved repeated measures of a dual task of lateralised dot detection and a central rapid serial visual presentation (RSVP) stream containing alphanumeric stimuli (see O’Connell et al., 2011). Thus, the study thus had a 2 (Age: young vs. old) x 2 (Load: Low, High) x 2 (Side: Left vs Right) x 2 (Temporal Position: 3 vs 6) mixed measures design.

Stimuli and Procedure

Participants received written and verbal information about the experimental procedure prior to the study. They were informed that participation was voluntary and that they could withdraw from the study at any time. The experiment lasted approximately 1.5 hours including pre-screening measurements and breaks.

Pre-screening procedure

Upon arrival, participants were greeted by the researcher and completed a consent form and a brief questionnaire regarding their demographic information. They were screened for visual acuity with the Colenbrander Mixed Contrast Chard, which involved reading out letters placed in front of them. No participants were excluded based on this visual acuity screening. Furthermore, older participants were screened for mild cognitive decline with the Montreal Cognitive Assessment test (MOCA) (Nasreddine et al., 2005) and all participants for both experiments showed normal performance (M= 28.61, S.D.= 1.06).

Visual Acuity Measurement

Participants were assessed also for possible visual field changes and detection accuracy of small stimuli. This was done with a short computerised assessment (see Learmonth, Benwell, et al., 2017): Over 36 different positions, a small black dot (10 x10 pixels) appeared for 150ms. Participants were instructed to press the spacebar if they perceived the dot anywhere on the screen, while fixating on the cross in the middle of the screen. The 36 locations extended to 12.0° visual angle (VA) from the fixation along the vertical axes and 16.06 ° VA along the horizontal axis (see Figure 14). A total of 72 trials were presented (36 locations x2) including 24 ‘catch’ trials where responses had to be withheld.

Dual Task with Rapid Serial Visual Presentation (RSVP)

Participants were instructed to make:

1) speeded responses to a black asterisk if they perceived it either to the left or right side of space (peripheral target) while simultaneously:
2) monitoring a central alphanumeric RSVP stream for a central target, which could be a red letter or a green number (Central Target), depending on the attentional load condition. Attentional load was split into two conditions, "low attentional load" and "high attentional load". Participants made a speeded response once they perceived a peripheral target (i.e. a black asterisk) and then made judgements about the central RSVP at the end of each trial, i.e. about the absence or presence of a central target via key press. Each participant completed both load conditions, with a break between the first and the second condition. Conditions were counterbalanced across all participants.

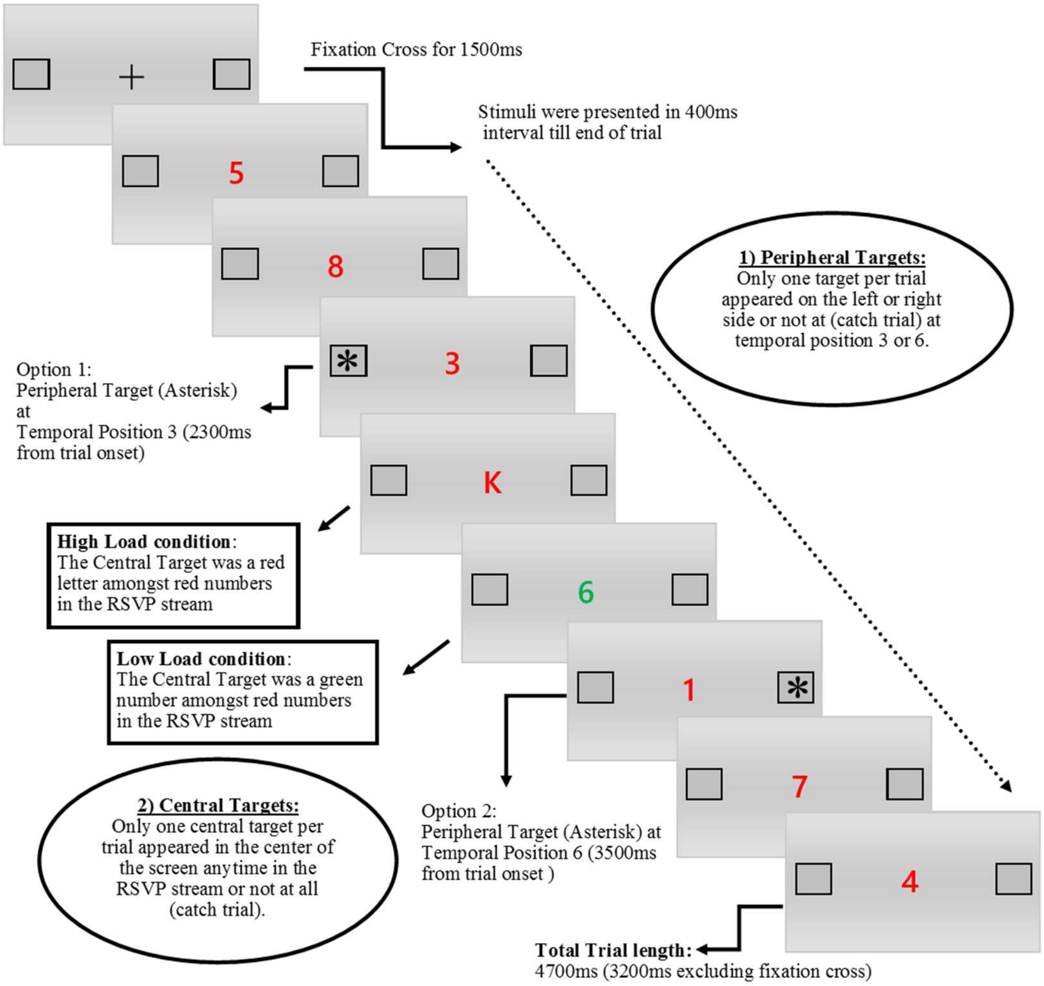

Figure 13: RSVP Dual Task (adapted from O'Connell et al. (2011)
Displayed is the RSVP with alphanumeric red central targets and a peripheral target to the right side.

Stimuli were presented using E-Prime 2.0 (Psychology Software Tools Inc., Pittsburgh, PA. The experiment was conducted on a Dell Precision T3400 PC and 19.5″ Sun Microsystems CRT monitor (33.8 x27 cm with 1280 × 1024 pixel resolution and 100Hz refresh rate) in a dark EEG chamber. The stimuli were presented on a grey background. The participants' midsagittal plane was aligned centrally to the computer, the viewing distance was fixed at 0.8m via a chinrest. At the beginning of each trial, participants fixated a fixation cross for 1500ms and were instructed not to blink during the length of a trial. At the beginning of each trial, the central fixation cross appeared for 1500ms and was followed by 8 presentation slides forming the RSVP. Each slide was presented for 400ms, with a total of 3600ms per trial after fixation. The load conditions consisted of 6 blocks with 50 valid trials each, totalling 300 trials.

One third of the trials contained no peripheral targets (catch trials), nor central targets, while the other half of the catch trials contained no peripheral target but included a relevant central target. Each peripheral target appeared in the middle of either left or right rectangular 2.5 x 2cm placeholder, positioned 16cm from the central fixation point. Peripheral targets never appeared simultaneously with the central target. Responses to peripheral targets were given bimanually, using the key board. Response hands were congruent with target side. The left hand responded to left peripheral targets seen and the right hand to right targets. Responses towards central targets (at the end of the trial) were also bimanual, indicating seen or unseen with either the left or right hand. Here, attribution to the response hand was counterbalanced across participants, so that a seen response did not always correlate with a right (dominant) hand response.

Peripheral Targets

The peripheral target was a black asterisk (Font size 30), appearing either to the left or right in rectangular placeholders. Responses were made by pressing either “v” for left asterisk or “b” for right asterisk (on the keyboard) and the response withheld for catch trials, if no peripheral target (asterisk) was present. Participants were instructed to respond as quickly as possible.

The peripheral stimulus appeared for 400ms randomly at either 800ms (position 3) or 2000ms after the fixation cross timed out. For every trial only one peripheral target was displayed in either the left or right visual field and only at one of the two possible time locked positions. Participants were naïve to the temporal location and the catch trials should have prevented expectancy effects.

Central Targets

For the “low attentional load” condition, the central target was a green target number within the RSVP stream of red numbers. This “pop out task” requires less attentional capacity (Treisman & Gelade, 1980). At the end of each trial, participants made judgements as to whether a central target was present or absent using the keyboard keys: x (with their left hand) or m (with the right hand). The meaning of the keys (present: yes, no) was counterbalanced across participants.

For the “high attentional load” condition, participants made speeded responses to peripheral targets, while monitoring the central RSVP stream of red numbers for *a red target letter*, essentially a conjunction search task (Treisman & Gelade, 1980). After each trial, they indicated if they had seen a central target or not identical to the other condition.

Experiment 1

Results

Visual acuity screening

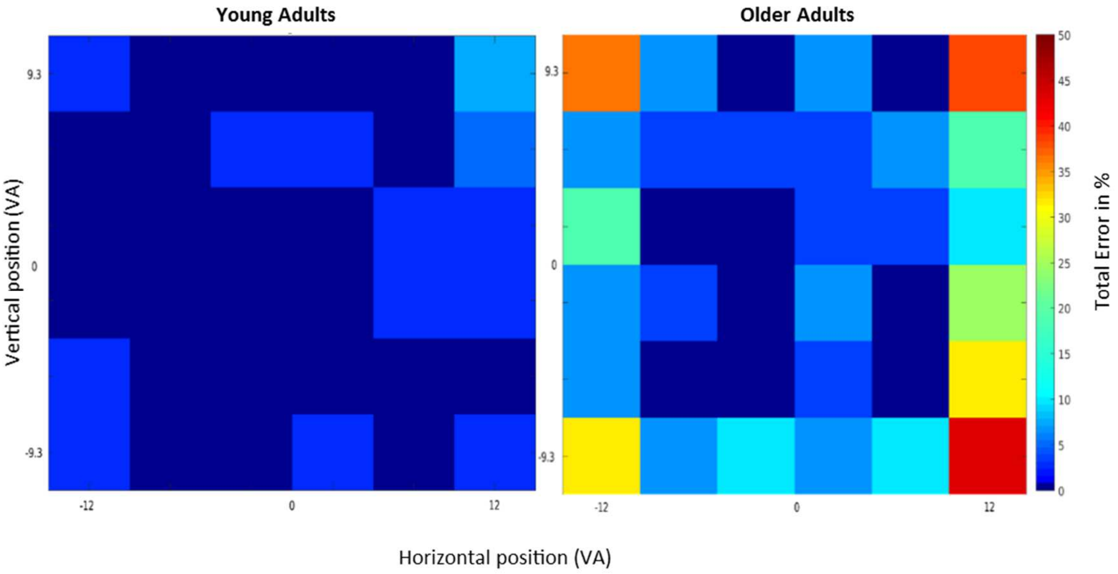

Figure 14: Overall detection errors for the visual acuity detection task for a) young adults and b) older adults at 80cm viewing distance. Each of the 6x6 squares reflect the screen and visual field of the participants. Different colours display the averaged error rate from all participants at this position. The colour bar on the right side reflects the error rate (0 - 50%).

For young adults, error rates were very low M = 1%, S.D.= 11.7% across all 6x6 fields, ranging from 0% to 7.5%. For older adults, most errors were made in the periphery: The total error range in the periphery ranged from 23% - 43%. However, as targets in this task were presented more centrally in a horizontal plane, the error rates in this area were low with an average of M = 5%, S.D.= 6% ranging from 0% - 23% (across the 24 positions, excluding the upper and lower horizontal positions) total error across the individual fields, suggesting no interference for the presented task.

Behavioural Results

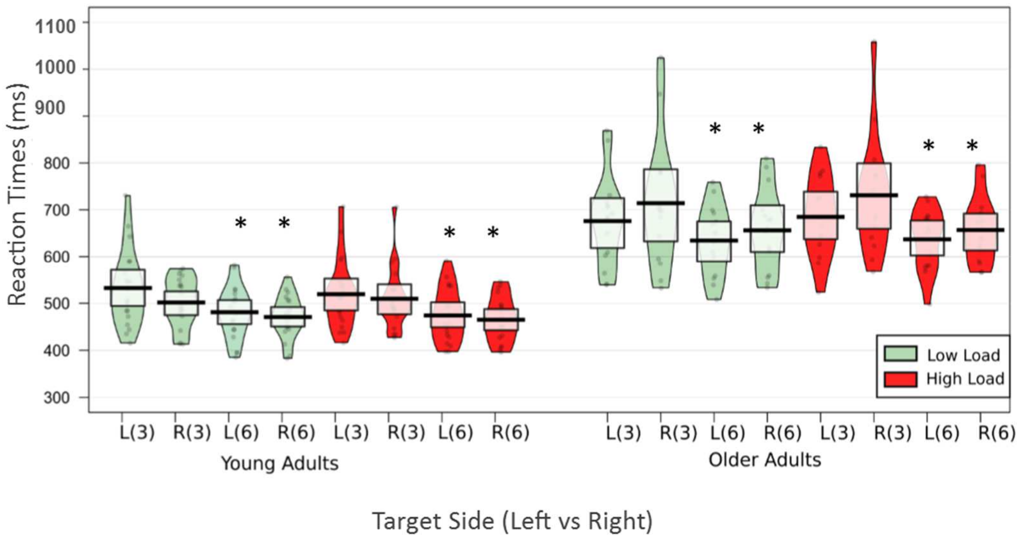

Figure 15: Overall Reaction times for young and older adults at all testing variables Reaction times towards peripheral targets are shown for the variables: target side, temporal position and attentional load, separately for young and older adults. The violin plots are overlaid with the raw data of the reaction times per individual to show the distribution from the group mean. Boxplots display the group level mean and 95% HDI. Targets at position 6 were significantly faster detected than at position 3. Faster reaction times are depicted with a black asterisk (*).

The results of the 2(age: young vs. old) x 2(load: LL, vs. HL) x 2(Side: Left vs. Right) x2(Position: 3 vs. 6) mixed model ANOVA revealed a main effect for temporal position in the first instance F(1, 33) = 63.99, $p < 001$ $\eta p^2 = .66$. Unsurprisingly, participants were faster to detect targets appearing later in the temporal RSVP stream if side was not considered [M: Position 3 vs. 6 = 608ms, S.D. = 12ms > 559ms, S.D.= 9.19 p = .001], this was independent of age. See Figure 15, faster reaction times for targets at position 6 are highlighted with a black asterisk in comparison to the targets at position 3.

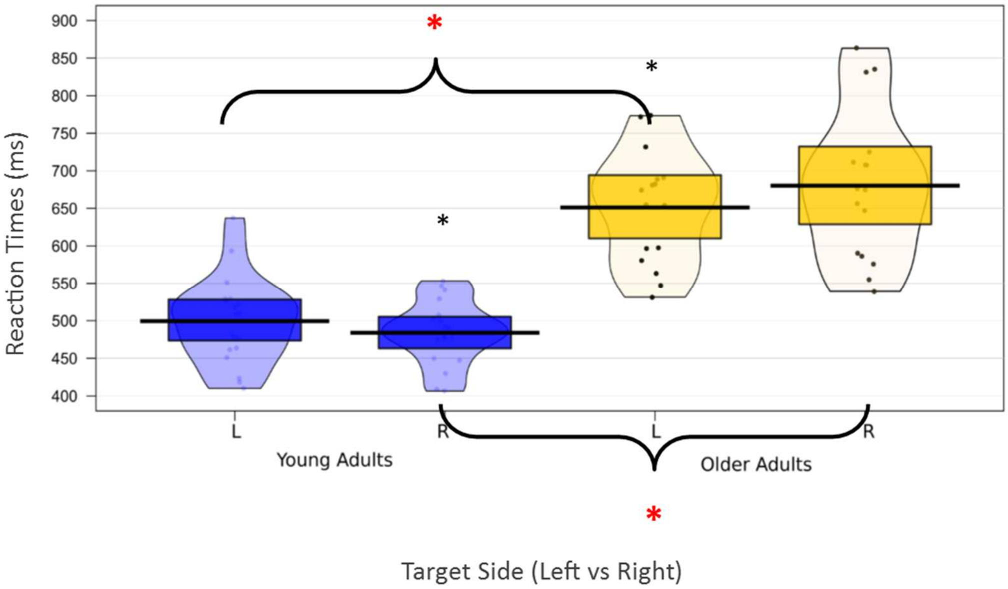

Figure 16: Reaction times separated by peripheral target side and age
The violin plots are overlaid with the raw data of the reaction times per individual to show the distribution across the whole sample of young (blue) and older (yellow) adults. Boxplots display the group level mean and 95% HDI. A significant difference in reaction times between target sides within age groups is depicted with a black asterisk (*). A significant difference between age groups within target side is depicted with a bracket and a red asterisk (*).

Moreover, there was a significant interaction between age and side F(1,33)= 5.24, p = .03, ηp^2 = .14. Further investigation revealed that, without the separation into temporal positions, younger adults responded faster to targets on the right side (M= 486ms, S.D.= 15) then left (M= 501ms, S.D.= 14). Older adults showed the opposite pattern and were faster on the left side (M= 658ms. S.D.= 18) then on the right (M= 689 ms, S.D.= 95). Between the age groups, young adults were faster than older adults for both target sides (see Figure 16, difference depicted with brackets and red asterisk).

Left Targets: Young adults M= 501ms, S.D.= 57< older adults M= 658ms, S.D. = 72 welches t test t(26)= -6.88, p< -.001.

Right Targets: Young adults M= 486ms, S.D.= 43< older adults M= 689ms, S.D.= 95 t(33)= -8.41, p<.001).

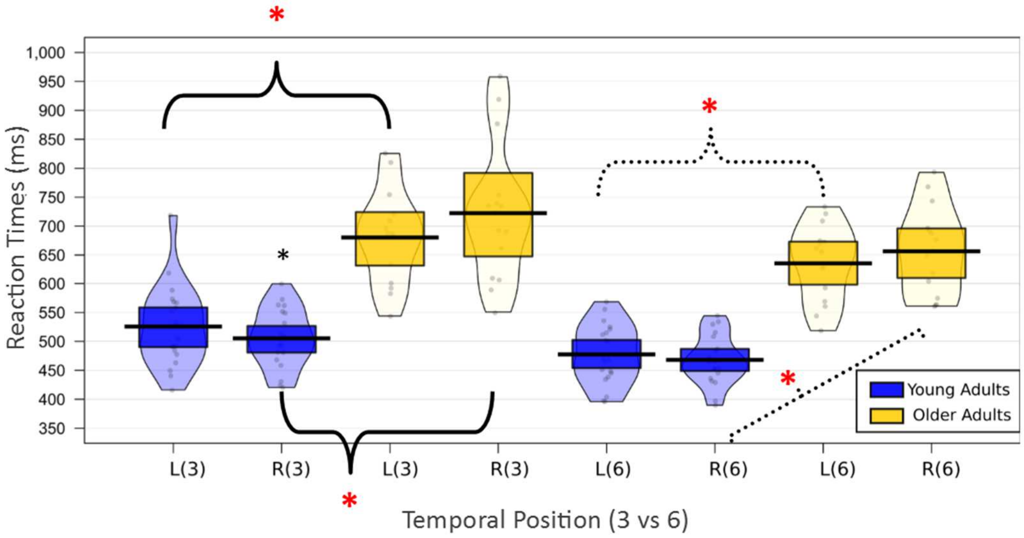

Figure 17: Reaction time towards peripheral targets separated into target side and temporal position by age.
The violin plots are overlaid with the raw data of the reaction times per individual to show the distribution across the whole sample of young (blue) and older (yellow) adults separated into target side (left, right) and temporal position (3 or 6).
Boxplots display the group level mean and 95% HDI. A significant difference in reaction times between target sides within age groups is depicted with a black asterisk (*). A significant difference between age groups within target side is depicted with a bracket and a red asterisk (*).

In addition, results revealed a significant three way interaction between Age, side and temporal position F(1, 33) = 4.22, p = .048, ηp^2= 113.
A follow-up 2 (Age) x 2 (Side) ANOVA revealed that, if separated into temporal positions, there were significant effects for targets earlier in the RSVP stream (temporal position 3), revealing an interaction between age and side F(1,33) = 5.65, p = .02, ηp^2 = .15 (See Figure 17). Independent samples t-test revealed that young adults were faster to react to both left and right targets compared to older adults (see Figure 17, difference between age groups is depicted with brackets and a red asterisk).

Left Targets: M (young) =525ms, S.D.= 70 < M (old) = 680ms, S.D. = 80, t(33) = -7.32, p<.001.

Right Targets: M (young) = 505ms, S.D.= 50 vs M (old) = 722ms, S.D.= 119, t(33)= -6.05, p< .001

Within age groups, young adults detected right targets faster than left targets (see Figure 17, significant difference between target sides is depicted as black asterisk for young adults).

Left Targets M = 525ms, S.D. 70 < **Right Targets** M = 505ms, S.D. = 80

t(19)= 2.13, p = .046.
Older adults were not significantly different.
Left Targets M = 680ms, S.D. 80 < **Right Targets** M= 722ms, S.D. = 119,
t (14)= -1.52, p= .15.

For temporal position 6, there were no significant main effects nor interactions. However, when comparing the reaction times at temporal position 6, young adults were again faster than older adults when reacting to peripheral targets (see Figure 17, difference between age groups is depicted with dotted brackets and a red asterisk).
Left Targets: Young adults M= 477ms, S.D.= 51 < older adults M= 635ms,
S.D. = 66, t(33)= -7.95, p< .001,
Right targets: Young adults M= 467ms, S.D.= 42ms < older adults M= 656ms,
S.D. = 75, t(33) = 9.33, p< .001.
Reaction times between left and right targets were not significantly different within age groups.

Experiment 2

Participants experiment 2

Twenty young adults (11 of them females, between 19 to 25 years old M= 21.3, S.D. =1.28), and 18 older adults (*11* of them females, between 60 and 86 years of age (M= 66, S.D. = 8.3) completed the modified study. Participants were naïve to the study's predictions and had not taken part in the previous study (Experiment 1, Chapter 3). The study received ethical approval from the University of Glasgow, College of Science and Engineering Ethics Committee, and participants gave written informed consent before participation.

Design

I modified the design in line with scientific feedback from the first pilot study. Now, viewing distance was decreased from 80 cm to 50 cm to try and elicit a more pronounced spatial bias. In previous studies, especially those investigating perceptual judgement tasks, presentations in peri-personal space (i.e., closer to the participant) have elicited a stronger leftward biases compared to presentation in extra personal space. (Heber et al., 2010; Longo & Lourenco, 2006, 2007, 2010; Longo et al., 2015; Lourenco & Longo, 2009). In additon, a decreased viewing distance to 50cm ensured that the current design was identical to O'Connell et al. (2011) who used the same viewing distance. This enhanced compareability of the results across both studies. The overall design of the experiment was kept identical to experiment 1 (See Figure 13). Participants completed again the pre-screening measures from experiment 1 before the experiment.

Results

Visual acuity screening

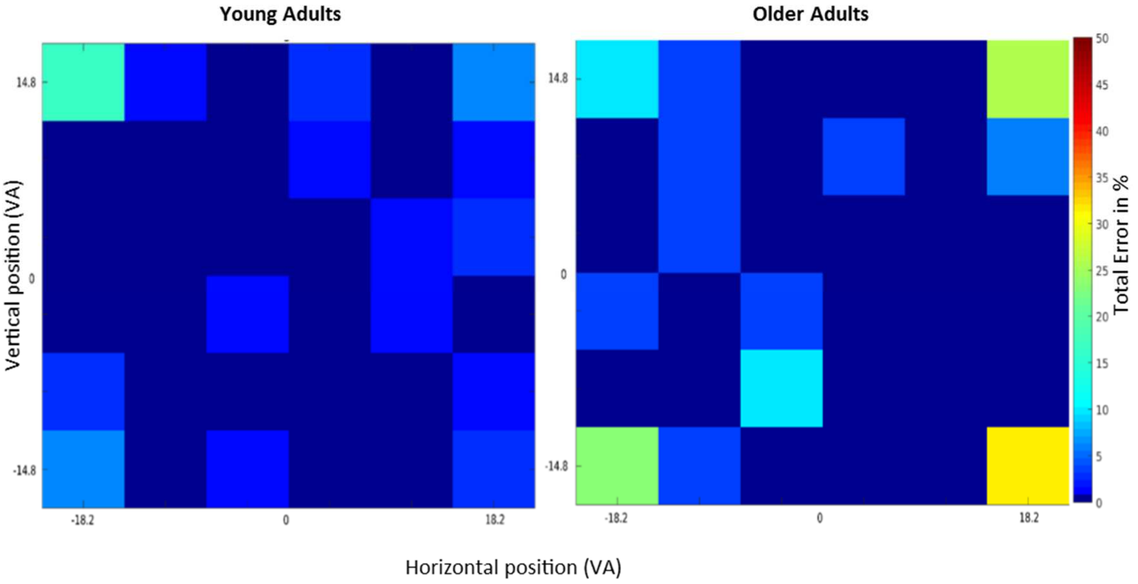

Figure 18: Overall detection errors for the visual acuity detection task of experiment 2 in a) young adults and b) older adults at 50cm viewing distance.
Each of the 6x6 squares reflect the screen and visual field of the participants. Different colours display the averaged error rate from all participants at this position. The colour bar on the right side reflects the error rate (0 - 50%).

Results of the visual acuity screening (Learmonth, Benwell, et al., 2017) showed that young participants had nearly perfect scores, with an overall error rate of M= 1.8%, S.D.= 2.8% ranging from 0 -7.5% across all 36 positions (see Figure 18). Older adults made most detection errors in the periphery, with most extreme values again at the outer corners ranging from 9 – 24%. Excluding the upper and lower horizontal positions, older adults had an error rate of M = 1.3%, S.D. = 2.4% collapsed over 24 positions. There were no visual deficits detected in the area the current task was presented. The reduced viewing distance very likely yielded these improved detection scores.

Behavioural Results Experiment 2

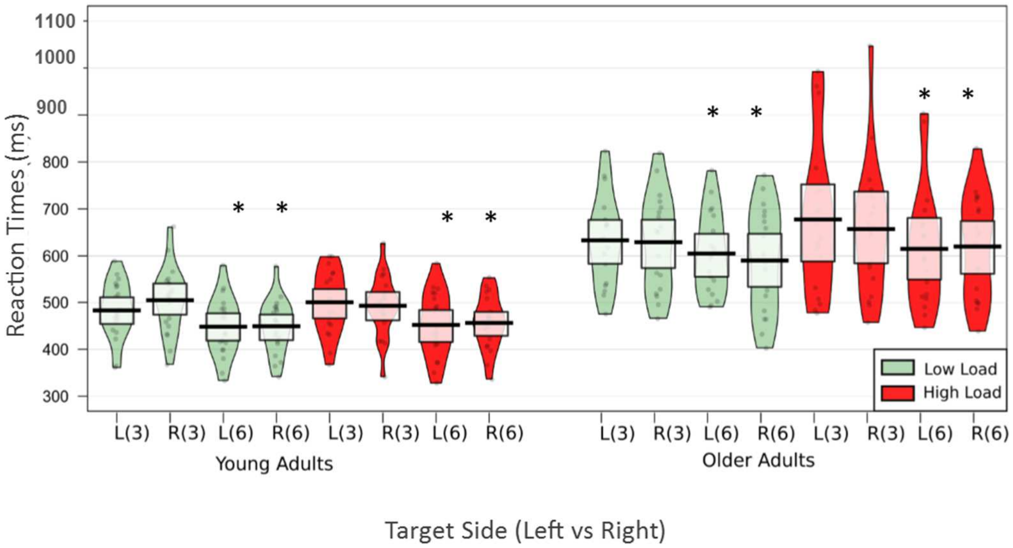

Figure 19: Overall Reaction times for young and older adults for all testing variables Reaction times towards peripheral targets are shown for the variables: target side, temporal position and attentional load, separately for young and older adults.
The violin plots are overlaid with the raw data of the reaction times per individual to show the distribution from group mean. Boxplots display the group level mean and 95% HDI. Targets at position 6 were significantly faster detected than at position 3. Faster reaction times are depicted with a black asterisk (*).

For the 2(Age: young vs. old) x 2(Load: low, high) x 2(Target Side: left, right) x 2 (temporal position: 3, 6) ANOVA, results revealed again, a main effect for temporal position F(1, 36)= 97.67 p< .001, ηp^2= .73. Reaction times were faster for targets presented later in the stream. M (position 6) = 529 ms, S.E.= 13.20 ms < M (position 3)= 572 ms, S.E.= 14.49 ms, p= .001.

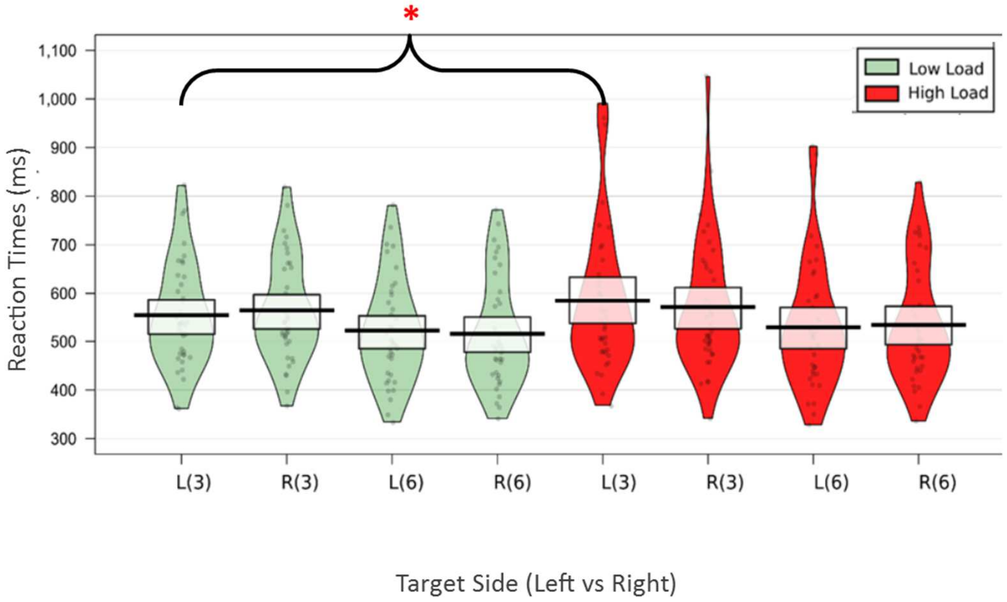

Figure 20: Reaction times separated by target side and temporal position.
The violin plots are overlaid with the raw data of the reaction times per individual to show the distribution across the whole sample (young and old combined) in either the low attentional (green) or high attentional (red) load condition. Boxplots display the group level mean and 95% HDI. A significant difference between load conditions for left targets at position 3 is depicted with a bracket and a red asterisk (*).

There was also a three way interaction between Load x Side x Position, (independent of age) F(1, 36)= 11.6, p= .002, ηp^2= .24. No other main effects or interactions reached significance.

To investigating the three way interaction, the follow up 2x2 ANOVA between Load and Side, revealed a significant interaction at position 3 for load and side F (1, 37)= 6.88, p = .01, ηp^2= .16 . Paired samples t-test showed that left targets were detected faster in the low attentional load compared to the high load condition. M (Low Load) = 554 ms, S.D. = 108, M (High) = 584ms, S.D. = 149ms, t (37) = -2.22, p = .03 (See Figure 20, the difference between the load condition for left targets at positon 3 is depicted with a bracket and red asterisk). No other pairs were significantly different.

For position 6 there were no significant main effects or interactions. Reaction times did not differ significantly.

Accuracy data for experiment 1 and 2

Accuracy rates towards both the peripheral and central targets were high in both experiments, suggesting that participants of both age groups were able to complete the task. In experiment 2, young participants detected the peripheral targets at a rate of 95% and the central targets (across both conditions) at 94%, while older adults detected 93% of both the peripheral and central targets.

Interim discussion of the results from experiments 1 and 2

In two experiments I investigated the modulating effects of central attentional load on spatial attention, with a particular focus on cognitive healthy aging. The aim of the presented studies was to extend the findings by O'Connell et al. (2011), by differentiating participants into two age groups, comparing young adults and cognitively healthy older adults on a dual spatial task. I predicted age related differences in the detection of the peripheral targets, with an asymmetrical processing advantage to the left visual side of space in young adults and a possible attenuation in older adults. Moreover, I predicted that increasing the attentional load to high attentional load would impact on the spatial bias of the older adults in particular, possibly leading to a processing advantage to the right side of visual space.

Results experiment 1:

In the first instance, results of experiment 1 are reported. While there were no modulating effects of load observed in this experiment, results revealed an interaction between age groups and target side, as well as a three way interaction with age group, target side and temporal position.

Overall young adults detected peripheral stimuli faster than older adults, when targets where collapse over both conditions. Yet, when target detection results were separated into peripheral target sides, results indicated a difference in spatial bias between both age groups. Young adults demonstrated significantly faster detection to targets on the right side. In contrast, older adults showed a preference towards the left side of space (in accordance with pseudoneglect).

When splitting the peripheral targets into temporal positions (i.e. targets appearing earlier or later in the RSVP stream unsurprisingly, younger adults were still overall faster to detect targets than older adults.

In young adults, right peripheral targets appearing earlier in the RSVP stream (position 3, 800ms after fixation) were detected faster than left targets. However, this advantage disappeared when targets appeared later in the RSVP stream (position 6, 3200 ms after fixation), and no difference in reaction times was apparent. In contrast, older adults did not show significant differences between target sides and thus no preference for any visual space at either temporal position. These effects were present independent of load conditions.

Overall, participants responded faster to peripheral targets when they appeared later in the trial as in contrast to earlier presentation. This replicates the findings of O’Connell et al. (2011) and makes sense as this is most likely a result of a greater expectancy to encounter a relevant peripheral target, thus resulting in faster reaction times.

Contrary to our predictions, changes of attentional load did not lead to changes in spatial bias in experiment 1.

Results experiment 2:

The design of experiment 2 was kept identical to experiment 1, except for a decrease in the viewing distance from 80cm to 50cm. I predicted that moving presentation closer into the peri- personal space would enhance possible lateralised processing advantages (Heber et al., 2010; Longo & Lourenco, 2006, 2007, 2010; Longo et al., 2015; Lourenco & Longo, 2009). This was also driven by the finding of O'Connell et al. (2011) who reported a spatial bias towards the left side in space, with a viewing distance of 50cm.

Similarly to experiment 1, participants responded faster to targets appearing later in the trial, thus replicating the findings from experiment 1, as well as the results by O'Connell et al. (2011). Interestingly, this time attentional load showed a modulating effect. When separated into temporal positions, left targets presented earlier in the RSVP stream were detected faster when attentional load was low, compared to high attentional load. No difference was found for right targets. However, reaction times were not significantly different between loads and target side when they were presented later in the RSVP stream (position 6).

This suggest that attentional load was a modulating factor for the detection of left targets. The processing advantage for left targets in the low attentional condition was attenuated when attentional load was increased. However, this was only observed early in the trial at position 3.

Results of experiment 2 revealed no significant effects between age groups and therefore, did not replicate the observed effects of side and age reported in experiment 1. This could suggest similar behavioural results for young and older adults. Very likely due to the reduced viewing distance, as this was the only parameter changed in this design, older adults appeared to benefit from this shift into a closer peri personal space in experiment 2 in comparison to experiment 1. The age differences in detecting peripheral targets disappeared in experiment 2 and reaction times were overall faster in experiment 2 than 1. Reaction times were faster by an average of 20ms in young adults and 45 ms in older adults collapsed over both target types in contrast to experiment 1, suggesting that older adults reacted faster when viewing distance was reduced to 50 cm. Moreover, visual acuity was enhanced for older adults with a reduced error rate from 5% to 1.5 % in experiment 2 at the relevant presentation area. As viewing distance was also kept at 50cm for the EEG experiment, the results of experiment 2 are more informative for the expected behavioural results of the EEG experiment.

General discussion

In two experiments I replicated a processing advantage for targets presented later in the RSVP, a finding also reported by O’Connell et al (2011). It is likely, that this effect drove the other interactions too. Yet, with respect to investigating differences in the lateralized detection and age related differences, results of experiment 1 confirmed that younger adults responded faster toward targets than older adults, yet this effect was attenuated when stimuli were presented closer to the participants (as evidenced in experiment 2, where no differences between age groups were reported). Encouragingly also, there was a processing advantage for left peripheral targets in experiment 2, which is in accordance with pseudoneglect. Moreover, this advantage appeared to be independent of age. Yet, this effect was only revealed when attentional load was low and in targets presented in the beginning of the RSVP stream. It is possible that this left processing advantage may have been attenuated through adding load (through the central load manipulation). In order to confirm this, an additional third condition with no attentional load manipulations will be added to the follow up EEG study, in order to measure baseline performance and investigate the direction of the spatial bias under no attentional load.

Spatial attention and load in aging

Although I had predicted age related differences in responses towards peripheral targets and a stronger lateralized effect when attentional load was increased, the present results tie in to the findings of earlier studies which investigated central load as a modulating factor on spatial attention. For example, Bellgrove et al. (2013) reported no lateralization effects in their healthy controls (older adults and young children) only in patients and children with ADHD as a function of poor sustained attention. Yet, the absence of a behavioural spatial bias between the age groups may mask age related cortical changes. According to the HAROLD model, the right hemisphere declines in activity with age (Cabeza, 2002; Dolcos et al., 2002). Through increasing task difficulty with attentional load, it is possible that other attentional resources are activated in order to compensate for attentional resources that are depleted by increased attentional load. This may not be reflected in spatial bias changes. Studies on titrated lateralized visual detection task have also shown no spatial bias for older adults, even if task difficulty ensured a 50 % detection rate for older adults (Learmonth, Felisatti, et al., 2017). Thus, it is important to further investigate the neurological underpinning and cortical activities when young and older participants carry out these tasks.

In fact O'Connell et al.(2011) found evidence that increased attentional load, in contrast to no additional attentional load, led to asymmetrical processing in the early stage processing of the lateralized stimuli, supporting the view of an enhanced activity in the right hemisphere during visual orienting. This lateralized activity was attenuated when attentional load was increased (from no load), thus suggesting that overlapping neural circuits in the right hemisphere facilitate an interplay between non spatial attention (manipulated via central load) and spatial attention. Moreover, they confirmed that increased attentional load at the centre of an RSVP stream, identical to the present design, lead to increased recruitment of attentional resources, reflected in enhanced P1 and N1 in early visual processing (O'Connell et al., 2011). Also, the processing advantage for left peripheral targets reported in the right hemisphere, was decreased with the increase of attentional load (from no load) (O'Connell et al., 2011), reflecting the view, that increased non spatial attention can result in a rightward shift in spatial attention (Benwell, Harvey, et al., 2013; Dodds et al., 2008; Manly et al., 2005; Peers et al., 2006). However, it is also possible that the absence of the spatial bias reflects an intrinsically lower alertness (as a result of the addition of attentional load), as it has been suggested also that reduced alertness facilitates a spatial shift towards the right side of space (Bellgrove et al., 2004; Matthias et al., 2009; Paladini et al., 2016). Thus, I think for my EEG experiment, a baseline condition is necessary to uncover any behavioural changes as a function of load.

Other modulating factors affecting spatial attention and aging

Although I focus on possible differential effects of attentional load on spatial bias changes across young and older age groups, there are other modulators that may distinguish the two age groups:

One such moderating factor could be differences in strategies between young and older adults. Some studies suggest that in contrast to young adults, older adults prioritize accuracy over speed (Starns & Ratcliff, 2010, 2012) and perform tasks more conservatively (Hertzog & Rypma, 1991; Nagamatsu et al., 2011; Smith & Brewer, 1985).

Another non spatial attribute benefitting older adults could be their increased intrinsic motivation to complete a task well (Hess, Emery, & Neupert, 2012; Staub, Doignon-Camus, Després, & Bonnefond, 2013; Tomporowski & Tinsley, 1996) or simply an interest in the study and the wish to contribute to research (in contrast to younger adults). Such intrinsic motivation could benefit reaction times and accuracy (Hess et al., 2012; Staub et al., 2013; Tomporowski & Tinsley, 1996)and could account for an absence of age differences in the present task performance.

Predominantly, it is thought that older adults' performance is inferior to that of young adults as a result of cortical and neuronal changes. Some research suggests that attentional resources are depleted faster and that attention is decreased more when attentional load is added to a task, with a resulting greater negative impact for older than for young adults (Swan et al., 2015). Other studies however suggest that a lower baseline performance for visual attention tasks in older adults (Learmonth, Thut, et al., 2015; Madden et al., 2007) might mask any beneficial or adverse effects of increased attentional load with cognitive ageing. There is also evidence showing better performance in older compared to young adults or similar performance on a variety of tasks (Brache, Scialfa, & Hudson, 2010; Carriere, Cheyne, Solman, & Smilek, 2010; Jackson & Balota, 2012; McVay, Meier, Touron, & Kane, 2013; Tomporowski & Tinsley, 1996), but see (Staub et al., 2013) for a review on sustained attention in cognitive aging. Mind wandering is a failure of attention and older adults appear to engage less in task unrelated thoughts (i.e. mind wandering) (Giambra, 1989;

Jackson & Balota, 2012; Krawietz, Tamplin, & Radvansky, 2012; McVay et al., 2013) and in everyday life (Maillet et al., 2018), which benefits performance and sustains attention in time on task settings. One example of this are Go/No Go paradigms in which older adults have been found to sustain vigilance and attention over the course of the respective task and thus maintained performance compared to young adults who showed a decrease and less accurate performance overall (Jackson & Balota, 2012; McVay et al., 2013; Staub, Doignon-Camus, Bacon, & Bonnefond, 2014). This type of paradigm is similar to a dual task paradigm in the sense that attention needs to be switched and decisions made between task response and withheld response, akin to my present paradigm of withholding the response to a central target until the end of task. It is thus possible that such beneficial effects have been present in the current experiments, leading to the absence of age related differences.

Limitations and methodological considerations.

Finally, there have been numerous studies on the effects of handedness and response hand on spatial attention (See for a review Chandrakumar et al., 2019). The current study investigated right handed participants only, yet I asked participants to make use of both hands in response to the peripheral targets. Although some studies suggest no significant effect of response hand on spatial bias if presented congruently (i.e. left hand for left target response) (Peers et al., 2006), others suggest an enhancing effect on left spatial bias when only the left hand is used, and a reduction in the right side bias with the use of the right hand only (Bradshaw, Bradshaw, Nathan, Nettleton, & Wilson, 1986; Brodie & Pettigrew, 1996; Fukatsu, Fujii, Kimura, Saso, & Kogure, 1990). This may have been a confounding factor. It has been found repeatedly that handedness plays an important role in the relationship between alertness and spatial bias (Chandrakumar et al., 2019). In recent fMRI studies, results for the ventral attentional network have shown clear cortical differences between right handed and left handed participants, and that these cortical differences drive spatial biases (H. Liu, Stufflebeam, Sepulcre, Hedden, & Buckner, 2009). In right handed participants, the ventral attentional network is lateralised towards the right side but left and right hemispheres are activated equally for left hand participants (H. Liu et al., 2009). In addition, the dorsal front parietal network (DAN) has been found to predominantly activate the right hemisphere in left handed participants, instead of a bilateral activation for in right handed participants (Petit et al., 2015).This difference in cortical structure may possibly influence the behavioural spatial bias. Moreover, for my experiments, the use of bimanual responses might explain the observed preference for the right targets in young adults. It could be explained by the use of the dominant right hand rather than a processing advantage. In order to decrease any impacting effect of motor activity on the neuronal correlates and reduce confounding factors, the responses to the peripheral stimuli will be changed to right hand response only in the following EEG experiment.

Conclusion

Taken together, the behavioural results of the current studies present promising findings for the follow up EEG study. Both experiments showed different results and were only uniform in the finding of a processing advantage for targets presented later in the RSVP. This was also reported by O'Connell et al (2011), likely reflecting a higher expectancy for targets appearing later in the trial. Encouragingly, there was a processing advantage for left peripheral targets in experiment 2, which is in accordance with pseudoneglect. This was found to be independent of age, suggesting that older adults were indeed able to perform the dual task and did not perform significantly worse than young adults (also indexed by reaction time and accuracy performance). Yet, this processing advantage to the left side of space was only revealed when attentional load was low and in targets presented at the beginning of the RSVP stream. It is possible, that this processing advantage was attenuated with increased attentional load or time in the trial, as a result of depleted attention. In order to confirm this, an additional third condition with no attentional load manipulations will be added to the follow-up EEG study. This will enable me to investigate the direction of the spatial bias under no attentional load influences and establish baseline performance. In this final EEG study (Chapter 4), I aim to investigate the neuronal underpinnings of central load and its influence on spatial attention, as indexed by ERPs, with a particular focus on the senior population. I aim to compare these findings to current models of attentional networks and the models of healthy cognitive aging (i.e. HAROLD) (Cabeza, 2002; Dolcos et al., 2002) and investigate how and if lateralisation changes when non spatial attention processes are taxed in older adults specifically.

Chapter Four

Investigating impact of attentional load on spatial attention and the neuronal correlates in young and older adults with the use of EEG

The experiments described in chapter 3 informed the design of the EEG experiment presented here: although the two experiments showed different results, encouragingly, there was a processing advantage for left peripheral targets in experiment 1 (chapter 3), in accordance with pseudoneglect. This was found to be independent of age, yet revealed only when attentional load was low and when targets were presented at the beginning of the RSVP stream. As it is possible, that this processing advantage was attenuated with increased attentional load or time in the trial, possibly as a result of depleted attentional resources, I added a third, no attentional load manipulation to this EEG study. This enabled me to investigate the direction of the spatial bias under no attentional load influences and establish the baseline performance of the participants. So in this final EEG study, I investigated the neuronal underpinnings of central attentional load (at fixation) and its influence on spatial attention, as indexed by ERPs, with a particular focus on the senior population. I compared these findings to current models of attentional networks and models of healthy cognitive aging (i.e. HAROLD (Cabeza, 2002; Dolcos et al., 2002) and investigated how and if lateralisation changes, when non- spatial attention processes are taxed in older adults specifically.

In the following, I will describe now, current electrophysiological findings on the effects of attentional load on spatial attention as well as the few studies that have focused on age-related differences.

Attentional load modulates neuronal correlates

As discussed in chapter 3, attentional load has been suggested to play a modulating factor in visuospatial orienting (Bonato et al., 2015; Dodds et al., 2008; O’Connell et al., 2011; Peers et al., 2006; Pérez et al., 2009) and O’Connell et al. (2011) were the first to report an asymmetrical processing in the first stages of visual orienting, as indexed in the electrophysiological P1 and N1 components. They stated that under the influence of attentional load, the right hemisphere showed reduced activity in response to lateral stimuli in comparison to no attentional load (where there was greater RH activity) (see O'Connell et al., 2011). This suggests that there are overlapping neural circuits in the right hemisphere that facilitate an interplay between non-spatial (possibly sustained) attention and spatial attention. Specific effects of load were seen in the N1 components predominantly. The processing advantage for left peripheral targets reported behaviourally and at for the right hemisphere was decreased with an increase in attentional load. For the baseline condition (no additional attentional load), elicited by contralateral stimuli, N1 was enhanced over both hemispheres. With the addition of load (for both low and high attentional load), activity in the RH for N1 was attenuated for left stimuli (contralateral to the orienting response). This reported RH reduction in relation to the left stimuli can be seen as possible support for the model of Corbetta et al. (2008).

In O'Connell et al.(2011) the later positive P2 and P3 components were also affected by increased load. P2 was enhanced in low and high load in contrast to no load, but equally over both hemispheres. P3 instead was reduced when load was increased. The later P3 component is interpreted predominantly to reflect resource allocation, as well as stimulus categorization and response decision : (Anderer, Semlitsch, & Saletu, 1996; Falkenstein, Hoormann, & Hohnsbein, 2002; Picton, Stuss, Champagne, & Nelson, 1984; Polich, 1996, 2007; Polich & Kok, 1995). An increase in load thus seemed to lead to decreased allocation of attentional resources (reflected in the increased reaction times with load).

Although there were methodological differences, load effects on the early components of target processing have also been reported by Bonato et al. (2015). Bonato et al. (2015) investigated increased load on spatial attention from a single to a dual task paradigm across modalities, either increasing visual or acoustical load in the dual task. They also reported load effects on the early components of target processing. For visual duals tasks, they found increased P1 amplitudes for the high load condition, while O'Connell et al. (2011) found the same effect at fixation when participants were assessing central targets. Bonato et al. (2015) conclude that the increase in P1 activity reflects the greater impact of high load on attentional orienting, and thus enhances recruitment of the RH posterior activity during early target processing. Moreover, the negative N2 component was found to be influenced by high attentional load. Right lateralized targets evoked contralateral activation of premotor areas and left target activated the contralateral SMG (supramarginal gyrus), thus supporting a load impact on the RH and early visual orienting which was disrupted by increased load.

Age related differences

Focusing on the neurophysiological effects of aging, healthy aging has been identified to impact on later components, such as the N2 and P2 and also significant age differences in the late P3 component (see Staub et al., 2014). Age related differences in the P300 are typically shown as enhanced amplitudes and interpreted as either reflecting enhanced resource allocation as compensatory mechanisms in older adults (Staub et al., 2014), or reflecting stimulus categorization and response decision in Go No Go paradigms: (Anderer et al., 1996; Falkenstein et al., 2002; Picton et al., 1984; Polich, 1996, 2007; Polich & Kok, 1995). In a Go/ No go task, Staub et al. (2014) found that behaviourally, older adults maintained sustained attention during the time course of the task, as indexed by accuracy and reaction time, leading older adults to perform equally well as younger adults on the task. This maintained level of sustained attention in the older adults was matched in the neuronal results and reflected in larger P2 and P3 (here for GO targets) amplitudes in contrast to young adults.

Studies investigating age related differences in spatial attention further suggest a right hemisphere decline pointing towards a reduction of hemispheric lateralisation with age (Learmonth, Benwell, et al., 2017; Nagamatsu et al., 2011). This is again accompanied with neuronal activity differences in the late P3 components. For example, Nagamatsu et al. (2011) reported evidence for possible age related change in RH function using a cued spatial orienting task and EEG. In contrast to young adults, older adults showed a reduced top down attention allocation for the left side of space as evidenced in a reduction of amplitudes in the late component (375 – 430ms post cue for their older adult sample) anterior directing attentional negativity (ADAN), which is assumed to reflect visual attentional control (Green, Teder-Sälejärvi, & McDonald, 2005; Jongen, Smulders, & Van der Heiden, 2007; Seiss, Gherri, Eardley, & Eimer, 2007). Behaviourally, this was supported by greater left visual field errors shown for the older adults. Nagamatsu et al (2011) conclude that age related differences are even visible in processes involved with executive attentional control, likely derived from cortical differences in the aging brain (See Nagamatsu et al., 2011).

In a landmark paradigm, Learmonth et al. (2017) report again a reduction of hemispheric lateralisation that was age related but also stimulus driven. Behaviourally, older adults showed no spatial bias to either side of space at group level, in contrast to young adults who displayed a left bias for long line stimuli. At the neuronal level, Learmonth et al.(2017) reported greater right parieto occipital ERP response for their long as opposed to short landmark lines in young adults, that was absent in the older adults. Older adults further showed no lateralised clusters while young adults showed a phase of right lateralisation elicited by the long line stimuli, thus suggesting an age related attenuation of such a lateralization. Older adults further showed a reduced P300 component. In both studies (Learmonth, Benwell, et al., 2017; Nagamatsu et al., 2011), age related differences were therefore apparent in the P300 component, with older adults showing a reduction in the P300 amplitude in contrast to young adults, likely reflecting an increased recruitment of resources in the older adults to achieve task completion.

Topographic shifts reported for older adults

Interestingly, for the P3 component specifically, age related differences appear to be correlated also with a topographic shift in cortical activity. A variety of studies have reported a shift of peak P300 amplitudes from posterior electrodes towards more anterior electrodes with old age (Fjell & Walhovd, 2004; Friedman, 2003; O'Connell et al., 2012; Polich, 1997; West, Schwarb, & Johnson, 2010). A frontal P3 activity in a sustained attention context for example, is generally interpreted as reflecting an increased recruitment of frontal regions in order to compensate and counteract possible processing deficits that arise in the posterior areas. For interpretation see (Learmonth, Benwell, et al., 2017; Lucci, Berchicci, Spinelli, Taddei, & Di Russo, 2013; O'Connell et al., 2012; Reuter-Lorenz & Park, 2010).

Aims

So in the final experimental study I aimed to assess how attentional load (as a non-spatial attentional factor) impacts on spatial attention. I focussed on differences between young and older adults in particular as I intended to uncover neuronal mechanisms that underlie the behavioural differences observed sometimes with spatial attention. Building on the research conducted by O'Connell et al.(2011), the current design resembled their experimental set up closely (see O'Connell et al., 2011) yet adapted to accommodate EEG analyses in an older adult sample (see Method section).Employing electroencephalography measurement, continuous EEG activity was recorded to investigate post stimulus (peripheral targets) event related potentials (ERPs) and compare these between attentional loads and age groups in order to answer the following research questions:

I investigated: 1) if increased attentional load modulated spatial attention and if such effects were more pronounced with healthy ageing. 2) how the modulating effects of attentional load were reflected in the neuronal correlates in an ageing context (i.e. a reduction in RH lateralization for older adults?). 3) if possible age related spatial asymmetry changes observed in the behavioural results were reflected in the neuronal correlates.

Specific hypotheses

Based on the current literature and my own pilot behavioural data I predicted the following results:

As described in chapter 3, behaviourally the two age groups did not show significant differences in reaction times and accuracy between low and high attentional load. With the addition of a no load condition, I thus predict any age related differences in responses towards peripheral targets to be visible in the no load condition, with the possibility of these being attenuated with additional attentional load. As such, young adults might display a preference for left peripheral targets (see O'Connell et al. (2011)but this may be attenuated in the low and high load conditions. Older adults might not show a preference for either side of space in the baseline condition and although attentional load may slow down reaction times, I think it unlikely that load would lead to a shift to the right side of space (rightward bias).

Derived from previous studies on the neuronal correlates using EEG, I will also investigate the typical ERP components of N1, P1, N2, P2 and P3 O' Connell et al.(2011) showed decreased processing of right hemifield stimuli at N1, when load was high. This was seen predominantly at the occipital and inferior parietal regions of the RH. Moreover, at P1 (90ms- 140ms) perception was enhanced for left side stimuli with increased load, when attention was allocated toward the target (fixation) (in contrast to slower processing of stimuli on the right side of space, with decreased amplitudes in the left but increased amplitudes in the right hemisphere). Thus, in the present study, ERP differences between the age groups were expected. Specifically, it is possible that older adults recruit additional neuronal resources to compensate for increased task demands and depleted attention capacities. This may result in similar behavioural results to the young adults but should be reflected in the ERPs, especially in the late P3 component.

Method

Participants

Forty cognitively healthy adults were tested in two age groups. The young age group consisted of 20 (15 female) participants, between 18-25 years of age (M= 22, S.D. = 2.35). The majority were undergraduate students and were sampled through the Psychology subject pool. The older adult group consisted of 20 (15 female) participants aged 63-76 years (M =70, S.D. = 3.89), who were opportunistically recruited. The exclusion criteria for participants were the same as described in chapter 3: a history of stroke colour blindness and dominant left handedness. The study received ethical approval from the University of Glasgow, College of Science and Engineering Ethics Committee, and participants gave written informed consent before participation.

Pre-screening Measurements

As for the previous experiments, each participant was right handed and had normal to corrected to normal vision as per Colenbrander Mixed Contrast Card Set (Colenbrander & Fletcher, 2005) for mid and close range vision. All participants were pre-screened for visual acuity using the computerised visual detection task to screen for possible visual field deficits (see chapter 3 and Learmonth, Benwell, et al., 2017). Again they completed the colour blindness test with colour plates (Ishihara, 1918; Nakajima et al., 1960) and older adults completed the MOCA (Montreal Cognitive Assessment (Nasreddine et al., 2005) to screen for mild cognitive decline. As for the previous experiments. all participants showed normal cognitive performance (*M*= 28.56, S.D.=1.24) (with scores greater than 26 defined as normal in the MOCA test (See Nasreddine et al., 2005)).

Design

Participants completed a behavioural task with a 2 (age: young vs. older) x 3 (load: no load, low load, high load) x 2 (target side: left vs. right) mixed measures design, closely adapted from O'Connell et al (see O'Connell et al., 2011), while EEG was recorded. Reaction times to the peripheral targets (left asterisk, right asterisk) as well as accuracy were measured. Responses towards the central targets (alphanumeric targets in low and high condition) were unspeeded and only accuracy was measured.

Procedure and Stimuli

The study was conducted over two separate sessions (a minimum of 24 hours apart) lasting around 1.5 to 2.5 hours (short breaks included). This included the time needed for preparing and setting up the EEG equipment. The first session typically included pre-screening measures, the EEG set up and two experimental conditions. EEG recordings were collected using a 64- electrodes BioSemi system, sampled at 1000Hz. In between the two experimental conditions, participants took a break. On the second day, participants completed the third condition in a shorter session (~ 1.5 h), also using EEG.

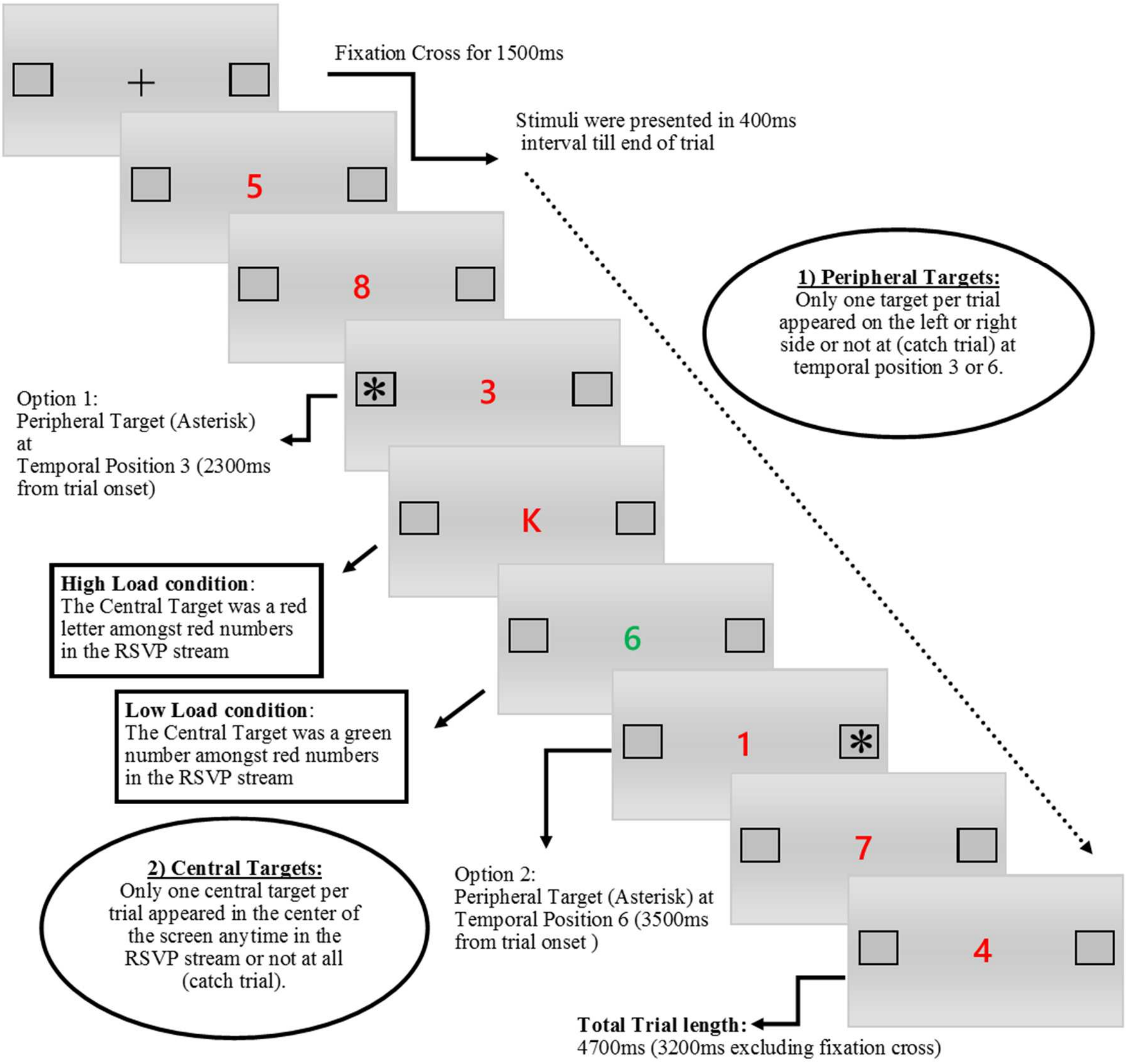

Figure 21: Schematic display of an experimental trial (adapted from O'Connell et al. (2011) Displayed is the RSVP with alphanumeric red central targets and a peripheral target to the right side.

Participants were seated comfortably in a dark room in an EEG chamber 50 cm away from the computer. Their midsagittal plane was centrally aligned to the computer via a chinrest. The task involved a 2 (Age: Young, Old) x 3 (Load: Neutral, Low, High) x 2 (Side: Left vs Right) repeated measures dual task. It comprised of a lateralised target detection task and a central RSVP stream which contained alphanumeric stimuli (O'Connell et al., 2011). The stimuli were presented using E-Prime 2.0 (Psychology Software Tools Inc., Pittsburgh, PA) on a Dell Precision T3400 PC and 19.5″ Sun Microsystems CRT monitor (33.8 x27 cm with 1280 × 1024 pixel resolution and 100Hz refresh rate) in a dark EEG chamber. The stimuli were presented on a grey background.

Participants made a speeded response once they perceived a peripheral target (i.e. a black asterisk, Font size 30), followed by an unspeeded response towards a central probe event at the end of each trial. Participants fixated a fixation cross for 1500ms at the beginning of each trial, and were instructed to withhold blinking during the length of a trial. Each trial consisted of 8 consecutive slides of alphanumerical stimuli forming a RSVP stream (See Figure 21). Within this stream, peripheral targets could appear to either the left or right side within rectangular place holders (2.5 x 2cm), 16cm away from the central fixation point. Peripheral targets never appeared simultaneously with the central target. The peripheral stimulus appeared for 400ms randomly at either 2300ms (Slide 3) or 3500ms (Slide 6) after trial onset (See Figure 21). Participants were not informed of this time-locked event. In every trial only one peripheral target was displayed to either left or right visual field, or was absent in the event of a catch trial.

In the presence of the researcher (to confirm participants understood the instructions), participants completed 24 practice trials per condition, before completing the condition on their own. The results of the practice trial were not analysed and only the completed conditions were submitted to further analyses. Each participant completed 300 trials (50 trials across 6 Blocks) per attentional load condition. Each block contained a total of 16 peripheral targets per side. As for the previous experiments, one third of the trials were catch trials, half of which contained no peripheral targets (asterisk) but central targets corresponding with the load condition. The other half contained neither peripheral nor central targets. Between conditions, participants took a break of ~10-20 minutes to rest before continuing the experiment.

Load conditions

Attentional load was manipulated by altering a central target in the alphanumeric RSVP stream. Instructions for each of the 3 conditions were given verbally and presented on the computer screen, omitting the label of the attentional load only. Instructions for the peripheral target were identical throughout the conditions, only the task for the central target responses changed.

No attentional load:

Participants were instructed to pay attention to the peripheral targets (black asterisk, font size 30), while keeping their eyes fixated in the centre. Using only their right hand, responses were ‘v’ key for left asterisk and ‘b’ for right asterisk. They were asked to monitor the central RSVP stream but no central target was presented and no decision had to be made at the end of a trial. This condition was used as a baseline measure to assess any changes of load on the brain activity measured with EEG.

Low attentional Load:

Participants were instructed to make a speeded response to the peripheral target, identical to the no attentional load condition. In addition, they were instructed to monitor the central stream for a central target and make judgements if the central target was present or not at the end of each trial, using the same response keys (‘v’ for yes or ‘b’ for no; the response keys were counterbalanced between participants). For the low load condition, the central target was always one green number (from a range of 1-8) that appeared amongst the stream of red numbers in a given trial. This manipulation is considered to impact on attention with a low load, due to the pop out characteristic of the salient colour change (Treisman & Gelade, 1980).

High attentional load condition:

In addition to detecting peripheral targets in the left or right visual field, participants monitored the central stream for a central target consisting of one red letter amongst a stream of red numbers in a given trial. The response keys used were identical to the low load condition. This condition was intended to increase the level of attentional load due to its characteristic to a conjunction search task, requiring more attentional resources to complete the task at hand (Treisman & Gelade, 1980).

EEG acquisition and pre-processing

The neurophysiological data was recorded using a 64 channel BioSemi EEG system. Additionally, 2 external ocular electrodes (EOG) were placed on the outer side of the left and right eye and used to record eye movements and blinks during a trial. Continuous EEG was acquired using ActiveView. The data was re sampled at a rate of 1000Hz. Pre-processing and analyses of the data were performed in MATLAB using the EEGLAB toolbox (Delorme & Makeig, 2004) including customised scripts.

Only valid trials, in which both peripheral targets and central targets were correctly detected or rejected, were analysed. During the pre-processing, the EEG data was resampled to 1000 Hz and re-referenced offline to an average signal across all of the scalp electrodes. The data was first epoched around trial onset (-100 to 4.500ms) with invalid trials deleted manually based on the behavioural data (due to incorrect responses) and visual inspection for abnormalities in the recorded signal. The data was then re-epoched in -100ms to 600ms segments around the peripheral target onset. The data was high pass filtered to 0.3 Hz and low pass filtered to 40 Hz and baseline corrected (-100 to 0ms) and again visually inspected for noisy epochs. The data was then combined across all conditions per individual and submitted to independent component analysis (ICA), including all 64 electrodes and the external eye electrodes (to filter out systematic eye movements). ICA was used to reject abnormal trends in the data. After components were removed, the data was de-trended and again re-epoched in segments around the peripheral trial onsets (-100 to 600ms). ERPs were generated for trials with peripheral targets, separated into left and right peripheral targets for each attentional load condition, collapsed over both temporal positions (3 and 6).

Total trials

A series of independent t -tests showed that between both age groups, there was *no significant difference* between the total of trials submitted to the EEG analysis per load condition.
Mean trials:
No Load Young: 295, S.D.= 4.2 vs Older: 293, S.D. = 6.3, t(38)=-1.18, p= .24
Low Load Young: 288, S.D.=4.3 vs Older: 287, S.D. = 6.2, t(38)= .71, p= .48
High Load Young: 288, S.D.= 4.5 vs Older : 288, S.D.= 6.1, t(38)= -.03, p= .97

A series of paired t-tests compared the amount of total trials across load conditions. Results revealed that the amount of trials were reduced in both, the low load condition and high load condition in comparison to the no load condition. No Load = 294, S.D.= 5.3 > Low Load= 287, S.D.= 5.3,
t(39)= 7.31, p <.001 and High Load = 288, S.D. = 5.3, t(39)= 6.93, p <.001.
However, the amount of total trials were not different in the low and high condition p = .54

Results

Visual acuity screening

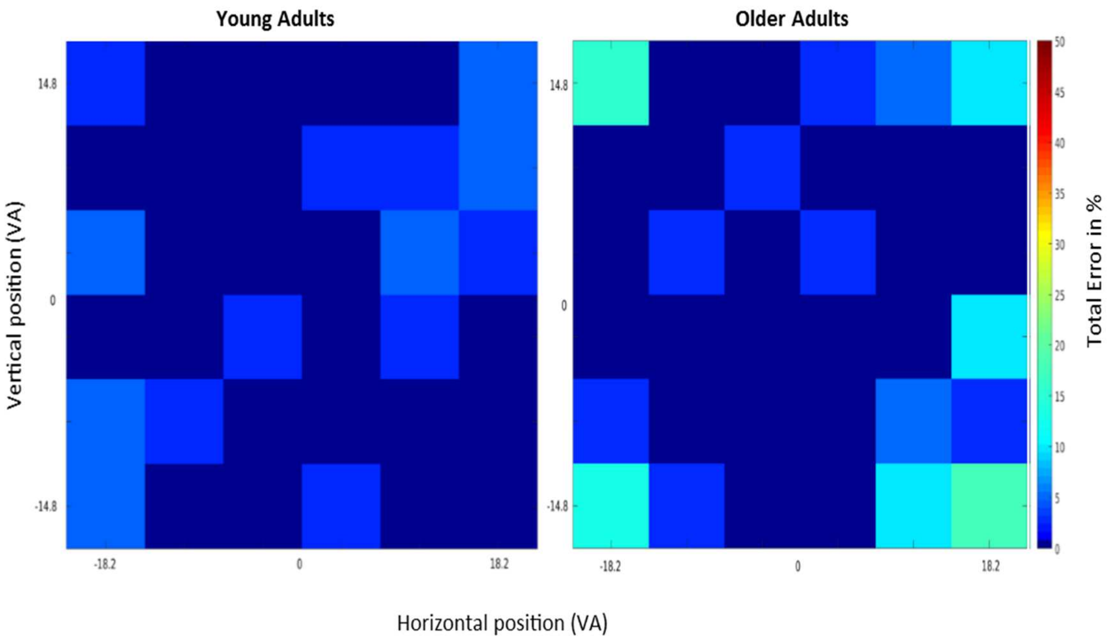

Figure 22 : Overall percentage of detection errors for visual acuity detection task for a) young and b) older adults.
Each of the 6x6 squares displays the error rate across participants made at this position equalling to the screen and visual field of the participant. A colour bar on the right side indicates the percentage of errors made, ranging from no errors to a 50% detection error rate.

Results of the visual acuity screening (Learmonth, Benwell, et al., 2017) showed that participants made most of their detection errors in the periphery, with most extreme values at the outer corners, ranging here from 30% – 42 % (M = 35.8%, S.D.= 5.2) both within and between participants. Most importantly, for the middle of the visual field that corresponded to the area where the stimuli were presented, the accuracy detection was at a rate of M= 98.2%, S.D. = 1.18 (across the 16 positions, excluding the outer positions). Detection accuracy was at an average of M = 91.25 %, S.D. = 10.91 collapsed across all the 36 positions. No single participant fell below this. (See Figure 22).

Behavioural results

Accuracy

1) **Central Target:**

The 2(Age) x2 (Low and high Load only) ANOVA for central target accuracy revealed no main effects of load nor age. Overall, there were no accuracy differences in detecting central targets in either the low or high load condition and accuracy was high for both conditions Low M = 93%, S.D. = 3.8,
High M= 94% , S.D. = 6.1. However, there was a significant interaction between load and age F(1, 38)= 11.58, p= .002 ηp^2 = .23. Independent samples t-tests to further investigate the direction of this interaction revealed that between the age groups, there was a difference for high but not low attentional load targets. Interestingly, for the high load condition, older adults were significantly more accurate in detecting central targets (a red letter) than young adults
t(38)= -2.97, p = .005, M (young) = 92%, S.D. = 7.3 < M (older) = 97% , S.D.= 3.03. For the low load condition, both young and older adults identified the central target similarly well M (young) = 94%, S.D. = 2.87, M (older) = 92% S.D. =4.58.

2) **Peripheral Targets:**

A 2 (Age) x3 (Load) x 2 (Side) ANOVA with age as a between factor revealed no main effect for age but there was a main effect for load
F(2, 76)= 25.99, p = <.001, ηp^2 = .41.
The baseline condition (No attentional load) was significantly higher in detection accuracy M = 97,5%, S.E. = .32 than both low load M = 94, S.E. = .57 and high load condition M = 94%, S.E. = .33 p <.001, suggesting a significant effect of load on peripheral detection accuracy when any additional type of load was added. There was no difference between low and high attentional load.

Interestingly, although there were no differences between the age groups there was a significant interaction between load and side
F(2, 76)= 219.74, p< .001 ηp^2= .85.
For low attentional load, left targets were more accurately detected than right targets. This pattern was reversed in the high attentional load condition.
Low Load: Left Target (M= 97, S.D. = 3.85) > Right Target (M = 91, S.D. = 3.71)

High Load: Right Target (M= 97%, S.D. = 2.3) > Left Target (M= 92%, S.D. = 2.51). In addition for left targets, accuracy was significantly reduced from no load condition compared to high load condition t(39)= 8.22, p<.001 and low load to high load condition t(39)= 11.06, p <.001.

For right targets, accuracy was significantly reduced from no load to low load t(39)= 10.73, p < .001. Accuracy increased from low load to high load conditions t(39)= -10.76, p < .001.

3) Reaction Times for Peripheral Targets

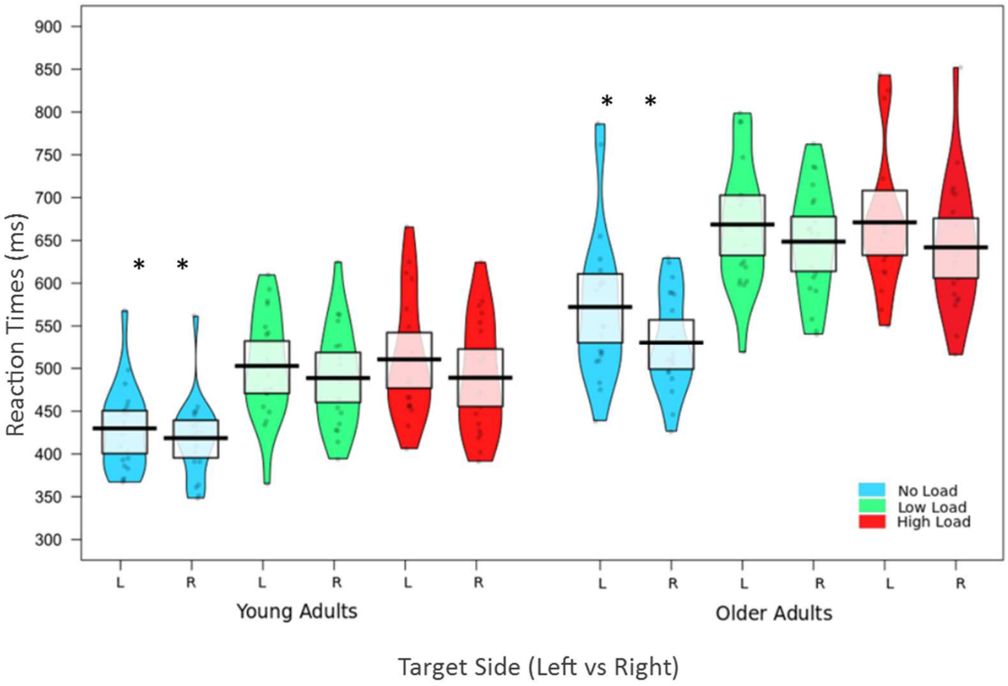

Figure 23: Reaction Times for peripheral Targets
Violin plots depicting reaction times across load conditions for left and right targets in young and older adults. Individual RTs are overlaid as scatterplots. The box depicts the 95% HDI with the group level mean as a black bar. Faster reaction times for peripheral targets in the no load condition are depicted with a black asterisk (*).

In order to investigate differences in reaction times between the age groups across the three load conditions, I performed a 2 (Age) x 3 (Load) x 2 (Side) mixed model ANOVA, with age as the between group variable. The results again revealed no main effect of age but this time only main effects for load and side, not an interaction (see Figure 23).

The main effect of load was F(2, 76)= 71.59, p< .001, ηp^2= .65 and a series of paired samples t- tests revealed that there were significantly faster reaction times for the No load condition (M= 487 ms, S.D.= 13.84) than both the Low load condition (M= 557 ms, S.D. = 16.37), t(39)= -9.86, p< .001 and the High load condition (M= 578 ms, S.D.= 16.70) t(39)= 8.53, p= .001. However, the reaction times of the low load condition and high load condition did not differ significantly t(39)= -.15, p= .88.

The main effect of Side was F(1, 38)= 19.01, p< .001, ηp^2= .33 and paired samples t-test comparing the left versus right side collapsed over all load conditions revealed that overall, participants reacted quicker towards targets on the right side (M= 536 ms, S.D. = 89.18) of space then the left side
(M = 559 ms, S.D. = 101), t(39)= 4.33, p .001.
No other effects or interactions were significant.

EEG statistical analysis:

The peripheral targets elicited standard visual –evoked potentials at P1, N1, P2, and P3 (see Figure 24). Peak amplitudes and latencies for these components were analysed using, similar to O'Connell et al. (2011) and Learmonth et al. (2017), a left and right region of interest (ROI).
Left ROIs included the 8 electrodes: P1, P3, P5, P7, P9, PO7, PO3, O1 (20 – 27) and right ROIs: P2, P4, P6, P8, P10, PO8, PO4, O2 (57 – 64).

Firstly, the electrophysiological data were averaged across all trials associated with either the left or right peripheral target per condition per person. This created an averaged waveform for the left hemisphere and an averaged waveform for the right hemisphere per person and condition. Individual peak amplitudes and latencies were calculated for the LH and RH separately. They are referred to as raw data in the results section, depicting the raw peak amplitudes and latencies on a group level and are depicted in the tables (see Table 4- Table 6). The obtained peak components for the LH and RH were then subtracted from each other on a subject-by-subject basis (RH – LH) in order to analyse the lateralization difference between peaks per individual and per component. The lateralization difference between peak latencies and amplitudes were calculated for left and right targets across all conditions and analysed using SPSS in a 2(Age) x 3 (Load) x 2 (Side) design. This method allowed me to interpret the results in terms of changes in the lateralised activity across the two hemispheres for the peak components P1, N1 and P2.

The P3 component was analysed regarding a possible topographic shift from parietal to more frontal activity with age, instead of a lateralization between the RH and LH. I used a similar approach to the above but focussed on the contrast between parietal and frontal ROI. The data was averaged across all relevant trials per condition on a subject-by-subject basis, creating an averaged waveform for the frontal ROI, which included the electrodes F3, Fz, F4 and an averaged waveform for the parietal ROI including the electrodes P3, Pz, P4. Peak latency and amplitude for the P300 were calculated for the frontal and parietal ROI separately. Again, raw group level peak amplitudes and latencies for the two ROI are presented in the tables (see Table 4 till Table 6).
The obtained peak amplitudes and latencies for the parietal and frontal ROI were then subtracted from each other on a subject-by-subject basis (parietal – frontal), calculating the difference between peaks per individual and per condition between parietal and frontal ROI. This difference was computed for left and right targets and analysed using SPSS in a 2(Age) x 3 (Load) x 2 (Side) design.

The selected component windows were kept identical between the young and older adults and were derived from the grand average waveforms and preliminary peak amplitude detections for the young and older adults (see Figure 24 and Figure 25). Figure 24 shows the grand average EEG waveforms for 64- channels illustrating the grand average waveforms of young (black) and older adults (red). They are overlaid with the scalp topographies of the mean component peaks (P1, N1, P2) collapsed over all conditions for young and older adults. The topographic plots show a similar distribution across the scalp for P1 and N1 between young and older adults and are in accordance with the predictions for the respective components. However, the scalp topographies for P2 are deviating from my expectations and concerns will be mentioned below. Figure 25 depicts the grand average ERP waveforms generated from the averaged ROI (Left and Right electrodes) for young and older adults, illustrating the amplitude and latency for the peak components (P1, N1, P2). While the magnitude of the waveforms show differences between young and older adults, they follow a similar time course. Thus, the following time windows were used to calculate peak latency and amplitudes in all conditions (see Figure 25);
P1 (80 – 150ms), N1(150 - 250), P2 (190 - 260), P3 (280 – 400ms).

A preliminary peak analysis for young and older adults for the N2pc(190 - 260) component did not elicit a distinct peak amplitude and this component was therefore not analysed any further.

P2 (cautionary comment):

Based on the topographies derived from the grand average waveforms (see Figure 24), the later positive P2 component should be interpreted with caution. I decided to select the window for this component based on the results by Learmonth et al.(2017) with a range of 190ms -260ms, yet on a group level (see topographical plots) older adults showed not the expected pattern of a positive activation in the posterior region when collapsed over all conditions, but a negativity. This could hint that the latency range for this component was not ideal and in fact maxed out for both age groups.

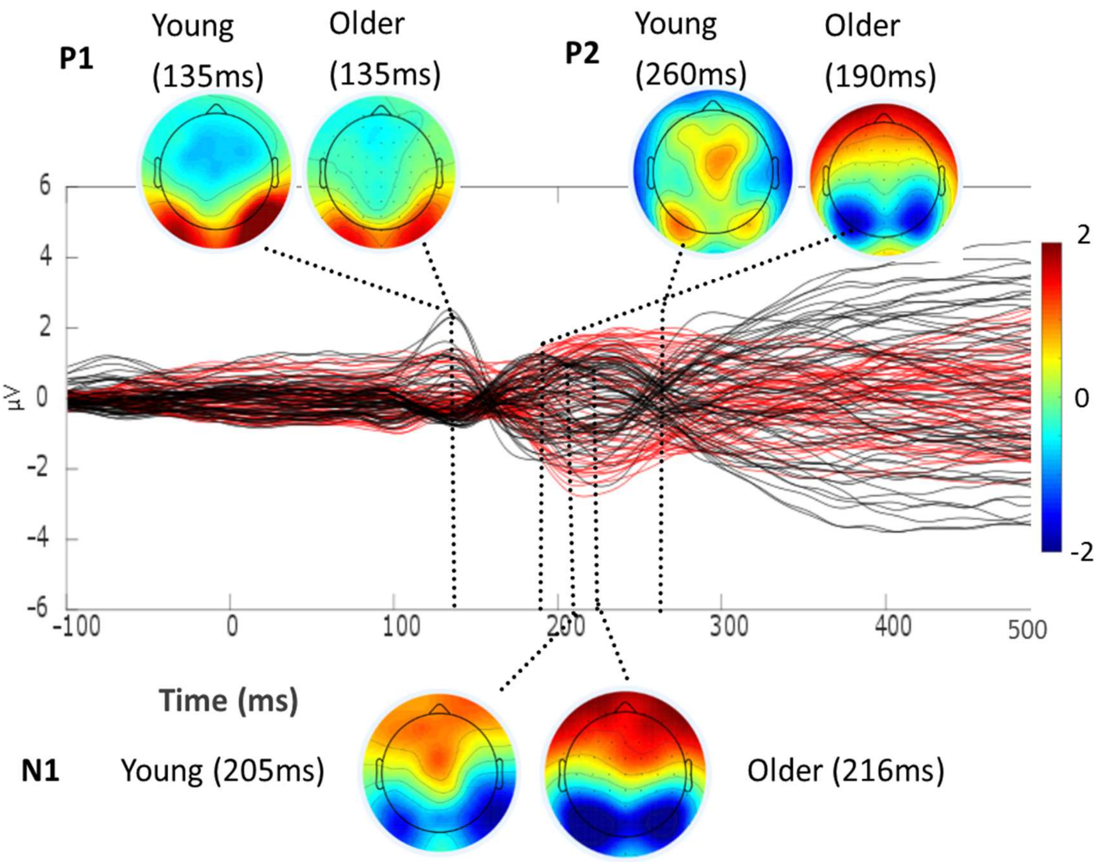

Figure 24: Butterfly plots showing the grand average EEG waveforms for 64- channels. illustrating the scalp topographies of the mean component peaks (P1, N1, P2) collapsed over all conditions, contrasting the grand average waveforms of young (black) and older adults (red).

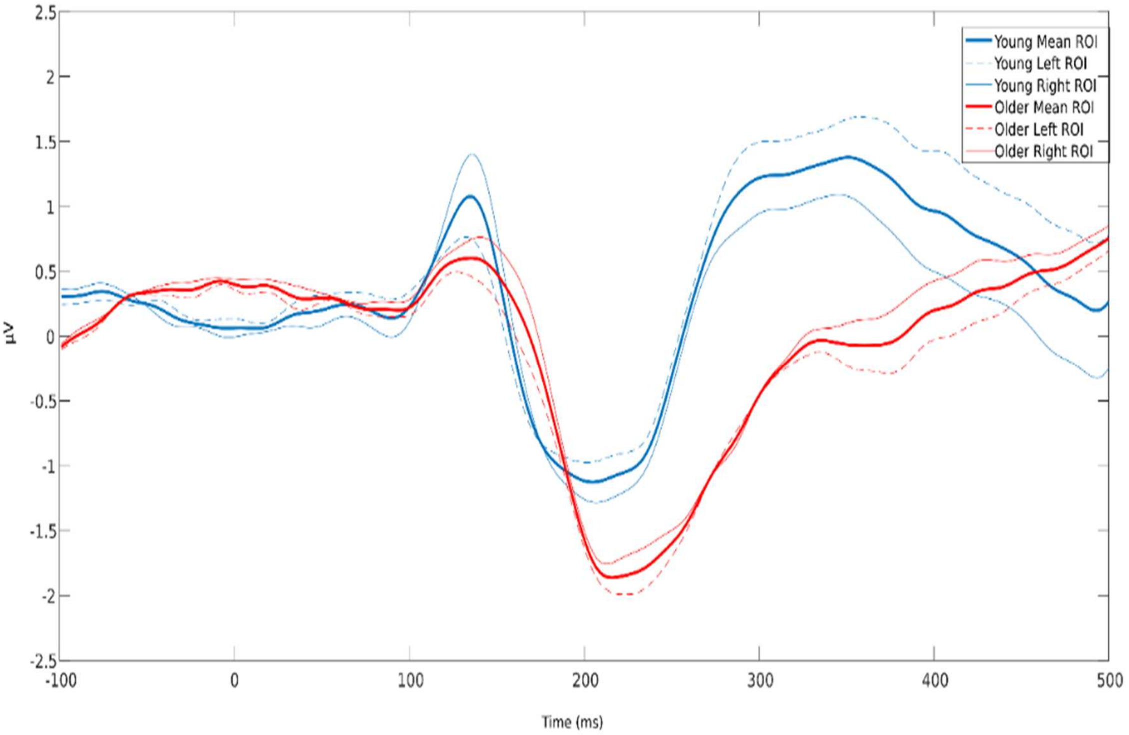

Figure 25: Grand average ERP from the averaged ROI (Left ROI and Right ROI electrodes). The waveform illustrates the amplitude and latency of the peak components (P1, N1, P2) for young (blue) and older adults (red), averaged across all trials and conditions.

ERP results

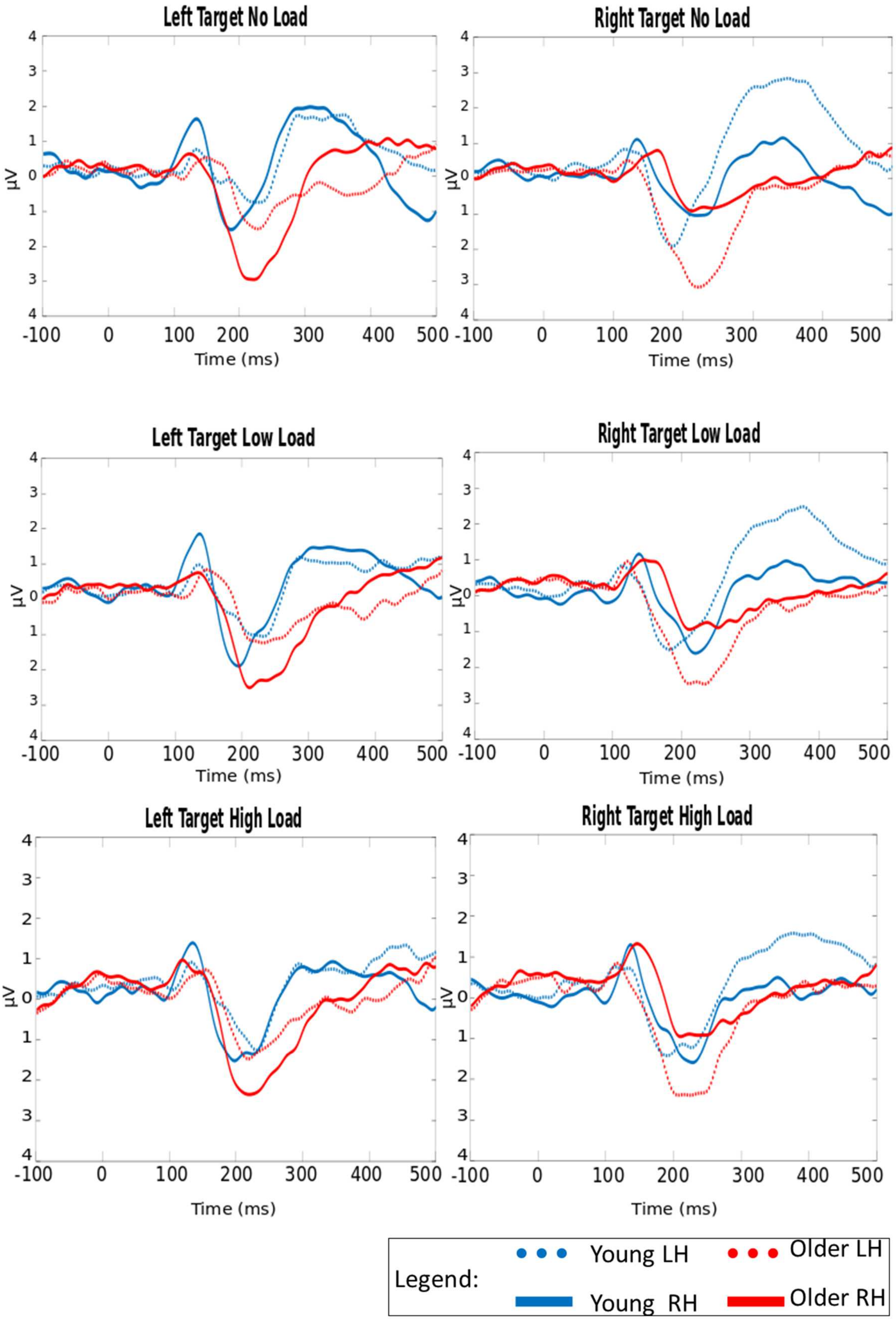

Figure 26: Mean ERPs for young and older adults showing the lateralization between LH and RH for left and right targets in the load conditions.
Mean ERPs are presented for left and right hemispheres for young adults (blue) and older adults (red).

Table 4: Raw data of mean amplitudes and latencies per target side and across the load conditions

	No Load		**Left Target**		**Right Target**	
	ROI		**LH**	**RH**	**LH**	**RH**
P1	Amplitude	YA	1.30	2.33	1.61	1.52
		OA	0.93	1.15	1.05	1.01
	Latency	YA	122.45	127.10	122.95	124.30
		OA	128.35	125.00	118.20	130.60
N1	Amplitude	YA	-1.77	-2.33	-2.68	-2.33
		OA	-1.95	-3.60	-3.56	-1.56
	Latency	YA	203.55	199.95	193.15	213.20
		OA	220.75	217.10	219.05	216.70
P2	Amplitude	YA	0.96	1.41	1.48	0.74
		OA	0.06	-1.19	-1.41	0.31
	Latency	YA	228.45	242.80	250.10	227.65
		OA	221.45	225.45	225.10	215.35
			Frontal	**Posterior**	**Frontal**	**Posterior**
P3	Amplitude	YA	0.83	4.69	0.94	5.03
		OA	1.72	1.88	1.78	1.73
	Latency	YA	337.35	360.15	338.70	361.50
		OA	338.85	389.55	343.50	391.85
	Low Load		**Left Target**		**Right Target**	
			LH	RH	LH	RH
P1	Amplitude	YA	1.47	2.30	1.55	1.61
		OA	1.14	1.28	1.25	1.27
	Latency	YA	128.25	127.35	116.05	134.60
		OA	138.75	125.40	122.15	137.85
N1	Amplitude	YA	-1.99	-2.58	-2.50	-2.35
		OA	-1.82	-3.16	-3.06	-1.57
	Latency	YA	205.70	205.55	195.50	221.70
		OA	227.05	218.55	221.75	213.10
P2	Amplitude	YA	0.50	0.50	0.86	0.34
		OA	0.13	-0.76	-1.11	0.39
	Latency	YA	231.70	244.70	237.00	230.85
		OA	210.00	222.70	220.15	215.55
			Frontal	**Posterior**	**Frontal**	**Posterior**
P3	Amplitude	YA	1.12	3.16	0.87	3.47
		OA	1.58	0.73	1.61	0.59
	Latency	YA	326.45	373.25	320.40	369.10
		OA	335.95	374.60	338.75	379.35

	High Load		**Left Target**		**Right Target**	
			LH	**RH**	**LH**	**RH**
P1	Amplitude	YA	1.44	1.92	1.61	1.72
		OA	1.06	1.35	1.05	1.52
	Latency	YA	132.30	129.80	119.25	129.45
		OA	133.65	124.30	117.60	138.00
N1	Amplitude	YA	-1.91	-2.57	-2.35	-2.20
		OA	-2.02	-2.99	-3.15	-1.69
	Latency	YA	216.35	206.35	203.45	218.95
		OA	220.50	214.55	219.80	220.30
P2	Amplitude	YA	0.34	0.30	0.21	0.22
		OA	-0.02	-0.83	-0.98	0.36
	Latency	YA	228.00	238.50	240.50	224.60
		OA	218.70	226.40	222.20	212.50
			Frontal	**Posterior**	**Frontal**	**Posterior**
P3	Amplitude	YA	1.07	2.31	1.02	2.27
		OA	1.22	0.54	1.32	0.51
	Latency	YA	326.10	364.90	328.10	370.85
		OA	312.70	370.40	328.60	381.05

The table shows mean amplitudes and latencies for young and older adults at each target side and within and across load conditions. The raw data of the peak components were analysed separately for LH and RH as well as frontal and posterior ROI.

Table 5: Mean peak amplitudes and latencies per load conditions averaged across target sides.

			No Load		**Low Load**		**High Load**	
	ROI		LH	RH	LH	RH	LH	RH
P1	Amplitude	YA	1.46	1.92	1.51	1.95	1.52	1.82
		OA	0.99	1.08	1.20	1.27	1.05	1.44
	Latency	YA	122.70	125.70	122.15	130.98	125.78	129.63
		OA	123.28	127.80	130.45	131.63	125.63	131.15
N1	Amplitude	YA	-2.23	-2.33	-2.25	-2.46	-2.13	-2.38
		OA	-2.76	-2.58	-2.44	-2.36	-2.58	-2.34
	Latency	YA	198.35	206.58	200.60	213.63	209.90	212.65
		OA	219.90	216.90	224.40	215.83	220.15	217.43
P2	Amplitude	YA	1.22	1.07	0.68	0.42	0.27	0.26
		OA	-0.68	-0.44	-0.49	-0.19	-0.50	-0.23
	Latency	YA	239.28	235.23	234.35	237.78	234.25	231.55
		OA	223.28	220.40	215.08	219.13	220.45	219.45
			Frontal	Posterior	Frontal	Posterior	Frontal	Posterior
P3	Amplitude	YA	0.89	4.86	0.99	3.32	1.05	2.29
		OA	1.75	1.81	1.59	0.66	1.27	0.52
	Latency	YA	338.03	360.83	323.43	371.18	327.10	367.88
		OA	341.18	390.70	337.35	376.98	320.65	375.73

The table shows the mean amplitudes and latencies for young and older adults at each attentional load condition, averaged across target sides. The raw data of the peak components were analysed separately for LH and RH as well as frontal and posterior ROI.

Table 6: Mean peak amplitudes and latencies per target side

			Left Target		Right Target	
	ROI		LH	RH	LH	RH
P1	Amplitude	YA	1.40	2.18	1.59	1.62
		OA	1.04	1.26	1.12	1.27
	Latency	YA	127.67	128.08	119.42	129.45
		OA	133.58	124.90	119.32	135.48
N1	Amplitude	YA	-1.89	-2.49	-2.51	-2.29
		OA	-1.93	-3.25	-3.26	-1.61
	Latency	YA	208.53	203.95	197.37	217.95
		OA	222.77	216.73	220.20	216.70
P2	Amplitude	YA	0.60	0.73	0.85	0.43
		OA	0.06	-0.93	-1.17	0.35
	Latency	YA	229.38	242.00	242.53	227.70
		OA	216.72	224.85	222.48	214.47
			Frontal	**Posterior**	**Frontal**	**Posterior**
P3	Amplitude	YA	1.01	3.39	0.94	3.59
		OA	1.51	1.05	1.57	0.94
	Latency	YA	329.97	366.10	329.07	367.15
		OA	329.17	378.18	336.95	384.08

The table shows mean amplitudes and latencies for young and older adults for the left and right peripheral target collapsed across the load conditions. The raw data of the peak component were analysed separately for LH and RH as well as frontal and posterior ROI.

All statistical results are presented below. As they are complex I present a short table listing the main findings for each component at the start of each section (see Table 7 - Table 10). The raw amplitude and latency data separated by LH and RH as well as frontal and posterior ROI are presented for young and older adults in the Table 4 till Table 6 above for reference.

P1:

Table 7 : P1 Summary of significant results with aging effects in bold

Amplitude	
Main effect: Target side	F(1, 38)= 7.25, p = .01, ηp^2 = .16
Interaction: Target side x Age	**F(1, 38)= 5.15, p = .03, ηp^2 = .12**
Interaction: Load x Target Side	F(2, 76)= 4.05, p = .02,
Latency	
Main effect: Target side	F(1,38)= 14.63, p < .001 ηp^2=.28
Interaction: Load x Target side	F(2, 76)= 3.41, p = .04, ηp^2= .08

4) P1 Amplitude

Effect of Side:

There was a main effect of Side F(1, 38)= 7.25, p = .01 ηp^2 = .16. Based on the raw data, left targets elicited a greater amplitude over the right hemisphere M= 1.7 S.D. = 1.18 than the left hemisphere M = 1.22, S.D. = .78. Importantly, there was a significant greater lateralization for left than right targets, with a difference of M = .50, S.E = .156 between the RH and the LH, rather than M= .09, S.E. = .158 p = .01 for the right targets.

This effect was qualified by the age and side interaction F(1, 38)= 5.15, p = .029, ηp^2 = .12. Paired samples t-test revealed that within age groups, young adults showed a significant difference in lateralization between left and right targets. They had a greater lateralization between the hemispheres for left targets with a difference of M = .77, S.D. = 1.26 between left and right ROI peak amplitudes, compared to right targets M= .02, S.D. = 1.17, t(19)= 2.79, p = .01.
The raw amplitude data showed that left targets had higher amplitudes over the RH M = 2.18 S.D. = 1.49 than LH M= 1.4, S.D. = .98 (see Table 6). This lateralization difference was not significant for older adults.

Effect of Load:

In addition there was a significant interaction between load and side F(2, 76)= 4.05, p = .02. Paired samples t –test revealed a significant difference between left and right targets for the No load and Low Load conditions. Separating the results into load conditions the following results were revealed:

No Load

For the no load condition results showed a greater lateralization for left targets M = .62, S.D. = 1.28 than for right targets M= -.06, S.D. = 1.09, t(39)= 3.07, p = .004. The raw peak amplitude data revealed that left targets elicited greater P1 amplitudes over the RH M = 1.74 S.D. = 1.34 than the LH M= 1.12, S.D.= 0.75. In contrast, right targets showed a smaller difference between the hemispheres and elicited a greater amplitude over the LH M = 1.33, S.D.= 0.9 than the RH M = 1.27, S.D.= 0.95 (see Figure 26, panel 1 and 2).

Low Load

For the low load condition, paired t-tests also revealed a greater lateralization for the left target M= .48, S.D= 1.28 than the right targets M= .03, S.D.= 1.05, t(39)= 2.15, p = .037. The raw data confirmed greater peak amplitudes for left targets over the RH M = 1.79, S.D.= 1.33 than the LH M= 1.30, S.D.= 0.94. In contrast, amplitudes in the LH and the RH for right targets were similar LH M= 1.40, S.D.= 1.00 vs. RH M= 1.44, S.D.= .96 (see Figure 26, panel 3 and 4).

Right Target and Load

Focussing only on the right targets between the three load conditions, revealed that there were significant differences in lateralization between the No load and High attentional load conditions, as well as between the Low and High attentional load condition (see Figure 26, right panels). Right targets elicited greater lateralization in the High load condition than the No load condition M= .29, S.D.= 1.19 > M= -.06, S.D.= 1.09, t(39)= -2.16, p = .04.

Based on the raw data P1 amplitudes for right targets in the High load condition were enhanced over the ipsilateral RH M= 1.62, S.D.= 1.15 in contrast to the contralateral LH M= 1.22, S.D.= 1.09.

Right targets in the no load condition showed enhanced P1 amplitudes over the contralateral LH M= 1.33, S.D= .09 over the RH= 1.27, S.D. = .95 but the lateralization difference was smaller.

High load

The high load condition elicited greater lateralization than the low load condition also M= .29, S.D= 1.19 > M= .04, S.D. = 1.05, t(39)= -2.14, p = .038. The raw data showed enhanced amplitudes for right targets in the High load condition over the RH M= 1.62, S.D.= 1.15 in contrast to the LH M= 1.22, S.D.= 1.09.The enhanced amplitude over the RH was repeated in the Low Load condition but with a smaller lateralization difference LH M= 1.4, S.D.= 1.00 vs RH = 1.44, S.D= .96.

5) P1 Latency

Effect of Side

For the P1 latency, there was again no effect of age but there was a main effect of side F(1,38)= 14.63, p < .001 ηp^2=.278. There was a significant difference between latencies for the left and right targets p= .001. Right targets showed a greater lateralized difference in latencies between the LH and the RH M= 13.1, S.E. = 2.4 compared to left targets which only had a difference of M = - 4.1, S.E.= 2.4 . The raw data revealed that according to predictions, peak latencies for both target types were apparent earlier in the contralateral hemisphere. Right targets elicited earlier peak amplitudes in the contralateral LH M= 119.37ms, S.D= 20.4 over the RH M= 132.47ms, S.D= 18.2, which peaked before left targets, which elicited earlier peak amplitudes over the contralateral RH M= 126ms, S.D. = 18. 4 over the LH M= 130ms, S.D. 21.

Effect of Load

Furthermore, the P1 latency revealed an interaction between load and side F(2, 76)= 3.41, p = .038 ηp^2= .083.

Subsequent paired samples t-tests revealed a significant difference between left and right target latencies in the Low load and High load condition.

Low Load

For the low load condition, right targets showed greater difference in latencies between the LH over the RH than left targets.

M = 17.12, S.D. = 23.08 vs M= -7.12, S.D. = 28, t(39)= -3.65, p = .001.

The raw data of the P1 peak amplitude latency revealed that right targets elicited earlier amplitudes over the LH M= 119ms, S.D.= 21.74 than the RH M=

136ms, S.D.= 14.17. Left targets in contrast elicited earlier amplitudes over the RH M= 126ms, S.D= 18.41 vs the LH M= 133ms, S.D. = 21.69
(see Figure 26, panel 3 and 4).

High Load

For the high load condition, this pattern was repeated with greater differences for right targets over left targets
M= 15.3, S.D. = 20.8, vs M= - 5.9, S.D. = 27.54, t(39)= -4.45, p< .001.
The raw data revealed that right targets elicited earlier latencies over the contralateral LH M= 118ms, S.D. = 20.09 than over the RH = 133ms, S.D. = 18.06. In contrast, left targets elicited earlier peak amplitudes over the contralateral RH M= 127ms, S.D. = 20.12 vs the LH = 132ms, S.D. = 18.45 although with an overall smaller difference between both hemispheres compared to the right targets (see Figure 26, panel 5 and 6).

N1:

Table 8: N1 Summary of significant results with aging effects in bold

N1 Amplitude	
Main effect: Target side	F(1, 38)= 39.98, p< .001, ηp^2= .51
Interaction: Target side x Age	**F(1,38)= 12.77, p = .001 ηp^2= .23**
Interaction: Load x Target side	F(2, 76)= 4.46, p = .01, ηp^2= .10
Latency	
Main effect: Target side	F(1,38)= 7.64, p = .009, ηp^2= .17.
Interaction: Target side x Age	**F(1, 38)= 5.09, p = .03, ηp^2= .12**

6) N1 Amplitude

Effect of Side:

There was a main effect of side F(1, 38)= 39.98, p<.001, ηp^2= .51. Overall, there was a greater lateralization to the right hemisphere for left targets
M = -.96, S.E. =.20, versus right targets M= .94, S.E. = .22.
The raw data revealed enhanced negative N1 amplitudes for left targets over the RH M= -2.87 S.D. = 1.87 compared to the LH M= -1.91, S.D. = 1.34.
For right targets, negative N1 amplitudes were enhanced in the contralateral LH M = -2.88, S.D. = 1.64 over RH M = -1.95, S.D. = 1.46.

This main effect was qualified by the interaction between age and side F(1,38)= 12.77, p = .001, ηp^2= .23. Investigating this interaction further with a series of independent t-tests revealed that:

Between Age groups

Right targets showed a significant difference in peak amplitudes between the LH and the RH. Older adults showed a greater difference M= 1.65, S.D. = 1.25 than young adults M= .22, S.D.= 1.54, t(38)= 36.43, p< .001. Investigating the distribution between the hemispheres further, the raw data revealed that older adults had enhanced negative N1 amplitudes in the LH M= -3.26, S.D. = 1.41 with fewer negative peaks in the RH M= -1.6, S.D. = 1.58. Young adults also showed more negative peak amplitudes over the LH but with less of a difference in magnitude between the LH and the RH.

LH M= -2.51, S.D. = 1.80, RH M= -2.29, S.D. = 1.26 (see Table 6)

Within Age groups

Within age groups, paired samples t-tests revealed a significant difference between left and right targets in the older adults.

There was a greater difference between the hemispheres for right targets M= 1.65, S.D. = 1.25, than left targets M= -1.32, S.D.= 1.32, t(19)= -8.59, p< .001.

For right targets, older adults showed enhanced negative N1 peak amplitudes over the LH M= -3.26, S.D. = 1.41 than RH -1.61, S.D. = 1.58.

Left targets elicited greater negative N1 peak amplitudes over the contralateral RH M= -3.25, S.D.= 2.10, LH M= -1.9, S.D.= 1.45 (see Table 6).

Effect of Load:

There was also an interaction between load and side

F(2, 76)= 4.46, p = .01. ηp^2 = 105.

Subsequent paired samples t-tests to investigate the direction of the interaction revealed significant differences between left and right targets for all three load conditions. According to the predictions, targets elicited more negative N1 peak amplitudes in the contralateral hemispheres.

No Load

As expected, left and right targets showed a pattern of contralateral lateralization for N1 peak amplitudes. Peak N1 amplitudes were more negative over the RH M= -2.96, S.D.= 1.8 than the LH M= -1.8, S.D.= 1.5 for contralateral left targets. In contrast, right targets elicited greater negative amplitudes over the LH M= -3.12 S.D. = 1.9 than the RH M= -1.94, S.D.= 1.5

(see Figure 26, panel 1 and 2).

Low load

This pattern was repeated in the low load and high load condition. Results revealed a difference in lateralization between left M= -.96, S.D. = 1.57 and right targets M= .82, S.D. = 1.65, t(39)= -4.63, p< .001 pointing towards greater negative amplitudes over the contralateral hemispheres. For left targets, the raw data revealed greater negative N1 over the RH M= -2.87, S.D. = 1.96 than the LH M= -1.91, S.D. = 1.37. For right targets, N1 amplitudes were more dominant in the contralateral LH M= -2.78, S.D. = 1.53, than
RH M= -1.96, S.D. = 1.50 (see Figure 26, panel 3 and 4).

High load condition

There was again a greater difference in lateralization for left targets
M= -.82, S.D. = 1.37 than right targets M= .80, S.D. = 1.44, t(39)= -4.90, p <.001.
The raw data revealed the same pattern as above, negative amplitudes in the contralateral hemispheres.
Left Targets: RH M= -2.78, S.D. = 1.76 vs. LH M= -1.96, S.D. = 1.18.
Right Targets: RH M= -1.94, S.D. = 1.36 vs LH M= -2.75, S.D. = 1.53.
There was no significant difference for left or right targets between loads (see Figure 26, panel 5 and 6).

7) N1 Latency

Effect of Side:
There was a main effect for side F(1,38)= 7.64, p = .009, ηp^2= .17.
Collapsed over both age groups, the differences between the hemispheres was greater for right targets than left targets
(left target M= -5.30, S.D. = 23 <right target M= 8.54, S.D.= 26.98, p = .012)
Right targets elicited earlier negative N1 amplitudes over the contralateral
LH M= 208ms, S.D. = 26.17 than the RH M =217ms, S.D. = 27.411.
Left targets elicited earlier negative N1 amplitudes over the
RH M= 210ms, S.D. = 25.54 than the LH M= 215ms, S.D. = .27.32

This main effect was qualified by the interaction between age and side
F(1, 38)= 5.09, p = .03 ηp^2= .12 for the N1 latency.
Further analyses revealed that, within age groups, only young adults revealed differences between target sides.

Within age groups

Young adults showed greater latency differences in right over left targets.
L M= -4.58, S.D. = 26.37, R M= 20.58, S.D.= 26.31, t(19)= -3.19, p= .005 , with earlier latencies over the contralateral hemispheres.
Based on the raw latency data, N1 amplitudes peaked earlier for right targets in the LH M= 193ms, S.D. = 25.44 over the RH M= 217ms, S.D. = 25.97.
Left targets showed earlier latencies in the contralateral RH M = 203ms, S.D. = 28.22 over the LH M= 208ms, S.D. = 30.18 (see Table 6).

Between age groups

Independent samples t-tests revealed that between age groups, right targets showed significant differences in latency between the hemispheres, with a greater difference between the LH and the RH in
Young M= 20.59, S.D.= 26.31 over older adults M= -3.5, S.D.= 22.38, t(38)= 3.12, p = .003.
The raw latency data revealed that right targets in young adults elicited earlier N1 amplitudes in the contralateral LH.
LH M= 197ms, S.D. = 25.44 over the RH M= 217ms, S.D. = 25.97.
For older adults, this pattern was reversed with earlier amplitudes in the RH M = 216ms, S.D. = 29.08 over the LH M= 220ms, S.D. = 21.76 although the difference between the LH and the RH in the older adults was small (see Table 6).

P2

Table 9: P2 Summary of significant results with aging effects in bold

P2 Amplitude	
Main effect: Target side	F(1,38)= 11.44, p = .002, ηp^2= .23
Interaction: Target side x Age	**F(1,38)= 28.12, p< .001, ηp^2= .43**
Interaction: Age x Load x Target Side	**F(2, 76)= 6.02, p =.004, ηp^2= .14**
Latency	
Main effect: Target side	F(1,38)= 11.43, p = .002, ηp^2 = .23

8) P2 Amplitude

Effects of Side:

There was a significant main effect for side F(1,38)= 11.44, p = .002, ηp^2= .23, with greater difference in the lateralization of the P2 amplitudes between the hemispheres for right targets M= .55, S.D.= 1.6 than left M= -.42, S.D.= 1.49. The activity was stronger in the opposite direction to the previous components, showing enhanced amplitudes in ipsilateral rather than contralateral hemispheres.

The raw data revealed that for right targets, P2 amplitudes were surprisingly more enhanced over the RH M= .39, S.D. = 1.36 with smaller in activity in the LH M= -.16, S.D. = 1.80. For left targets, P2 amplitudes were also more enhanced over the ipsilateral LH M= .033, S.D.= 1.26 and smaller in the RH M= -.10, S.D. = 2.04.

There was also an interaction between age and side F(1,38)= 28.12, p< .001, ηp^2= .43 .

Right Targets:

Independent samples t-test revealed that between age groups, right targets showed significant differences in lateralization, with a larger difference for the older adults M= 1.5, S.D.= 1.17 than young M= -.41, S.D.= 1.46., t(38)= -4.63, p< .001.

Moreover, the two groups revealed dominant activation in opposing hemispheres: based on the raw data (see Table 6), right targets in older adults showed larger peak activity over the ipsilateral RH M= .35, S.D. = 1.23 and a smaller, negative amplitude over the LH M= -1.17, S.D. = 1.38.

Young adults in contrast showed enhanced peak P2 amplitudes over the contralateral LH M= .85, S.D. = 1.59 vs. the RH M= .43, S.D. = 1.50.
This could suggest an age related lateralization shift.

Left Targets:

Again, for left targets, older adults showed a greater difference between the hemispheres than the young adults.
Older M= -.98, S.D. = 1.45 > Young M= .13, S.D.= 1.35 t(38)= 2.52, p = .016.
Based on the raw P2 amplitude data (see Table 6), older adults showed again more positive P2 amplitudes over the ipsilateral LH M= .06, S.D. = 1.2 and a negative amplitude over the contralateral RH M = -.93, S.D. = 1.68.
Young adults in contrast showed the expected enhanced P2 amplitudes over the contralateral RH M= .73, S.D. = 2.03 and a smaller amplitude over the LH M = .60, S.D. = 1.27.

Within age groups

Within age groups only older adults showed significant differences in asymmetry between left and right targets (left target M= -.98 S.D. = 1.45 vs right target M= 1.52), pointing towards a greater difference for right targets between the hemispheres t(19) = -5.66, p < .001.
The raw data revealed that older adults showed more positive P2 amplitudes in the ipsilateral hemispheres, while contralateral hemispheres showed negative peaks.
Left Targets LH M= .06, S.D. = 1.2 vs. RH M=-.93, S.D. = 1.68,
Right Targets LH M= -1.17, S.D. = 1.38 vs. RH M= .35, S.D. = 1.23 (see Table 6).

Effects of Load:

Finally, there was a three way interaction between age, load and side F(2, 76)= 6.02, p =.004 ηp^2= .14.

Left Targets :

A follow up 2 Age x 3 Load ANOVA for the left targets revealed no significant effects or interactions.

Right Targets:

A follow up 2 Age x 3 Load ANOVA for the right targets revealed no significant main effect but a significant interaction between Load and Age $F(2, 76)= 4.19$, $p=.019$ $\eta p^2= .10$.

In order to investigate the direction of the interaction a series of t-tests were calculated. Between age groups, there were significant differences in all three load conditions (see Figure 26).

No Load

NL Young M= -.74, S.D.= 2.28 , Old M= 1.772, S.D.= 1.42, t(38)= 4.09, p< .001

There was a greater difference between the hemispheres in older adults compared to the young adults. Young adults showed enhanced peaks over the LH M= 1.48, S.D. = 2.01 than the RH M= .74, S.D. = 1.94.

Older adults showed enhanced peak amplitudes over the RH M= 0.31, S.D. 1.40 and a negative amplitude over the LH M= -1.4, S.D. = 1.58 (see Table 4).

Low Load

The same pattern was repeated for Low load young M= -.52, S.D.= 1.25, Older M= 1.5, S.D.= 1.11, t(38)= -5.15, p< .001, with the raw data showing the following amplitudes for young adults:

LH M= 0.86, S.D. = 1.58 > RH M= 0.34, S.D. = 1.41.

Older adults:

LH M= -1.11, S.D.= 1.33. < RH M= .39, S.D.= 1.20 (see Table 4).

High Load

In the High load condition, older adults also showed significantly greater differences between the hemispheres than the young adults.

Young M= .01, S.D.= 1.31, Old M= 1.33, t(38) = -3.26, p= .002.

Older adults showed a lateralization to the RH M=.36, S.D.= 1.09 > LH M= -.98, S.D. = 1.22, while young adults showed minimal differences in lateralization LH M= 0.21, S.D. = 1.17 < RH M= 0.22, S.D.= 1.14 (see Table 4).

Within age groups

Within age groups, paired samples t-tests revealed a significant difference for young adults between low load and high load right targets

Low M= -.52, S.D.= 1.36 vs High M= .01, S.D.= 1.31 t(19)= -2.30, p = .03.

No other pairs were significant. The raw peak data revealed that in the low attentional load, RH lateralization was more pronounced and a difference between the hemispheres nearly absent in the High load condition.

Low Load: Young adults LH M= 0.86, S.D. = 1.58 > RH M= 0.34, S.D. = 1.41.

High Load: LH M= 0.21, S.D. = 1.17 < RH M= 0.22, S.D. = 1.14 (see Table 4).

9) P2 Latency

Effect of Side:

There was a main effect of Side F(1,38)= 11.43, p = .002 ηp^2 = .23, with a larger difference between the hemispheres for right targets M= -11.42, S.D.= -14.83 than left targets M = 10.37, S.D.= 12.6, p= .002, again with asymmetry going in different directions: The raw latency data revealed that for right targets, P2 amplitudes peaked earlier in the ipsilateral RH M= 221ms, S.D. = 29.78 than in LH M= 232ms, S.D. = 30.13. For left targets, P2 amplitudes peaked earlier in the LH M= 233ms, S.D. = 32,04 than RH M= 233.4ms, S.D.= 30.84

P3

Table 10: P3 Summary of significant results with aging effects in bold

P3 Amplitude	
Main effect: Load	F(2, 76)= 12.10, p< .001 ηp^2 = .24
Interaction: Load x Age	**F(2, 76)= 3.42, p= .04, ηp^2 =.08**
Latency	No effects

10) P3 Amplitude

Effect of Load

A 2(Age) x 3 (Load) x 2 (Side) x 2 (ROI: frontal vs. posterior ROI) ANOVA revealed a main effect of load F(2, 76)= 12.10, p< .001 ηp^2 = .24.

No attentional load condition elicited a greater lateralization in the posterior ROI than the low load condition

(No Load M= 2.01, S.D. = 0.46 > Low Load M = .69, S.D. = .78, p = .004).

The raw data revealed that for the no load condition, the posterior ROI elicited enhanced P3 amplitudes in comparison to the frontal ROI

(frontal ROI M= 1.32, S.D. = 2.35. < posterior ROI M = 3.34, S.D. = 2.81).
For the low load condition, the posterior ROI also elicited higher amplitudes than the frontal ROI, although the difference was smaller than for the No load (frontal ROI M= 1.29, S.D. = 1.57 < posterior ROI M= 1.99, S.D. = 2.36).
Moreover, the difference in the No load condition was larger than for the high load condition. p= .001. NL M= 2.01, S.D. = 0.46 > HL M= .25, S.D. = .51.
An enhanced P3 amplitude was observed over the posterior ROI for the high load condition. Frontal ROI M= 1.16, S.D. = 1.62, posterior ROI= 1.41, S.D. = 2.12

There was also an interaction between age and load
F(2, 76)= 3.42, p= .04, ηp^2 =.08.
Subsequent independent t-tests revealed that there were differences in asymmetry for the no load and low load conditions but not the high load condition between both age groups. Unsurprisingly, there was a larger difference between posterior and frontal peak amplitudes in young adults than in older adults.

<u>No Load</u>
There was a greater difference for young adults than older adults between the ROI Young M= 3.9, S.D. = 4.59, Old M= .05, S.D. = 3.43 t(38)= 3.05, p = .004. The raw data revealed that for young adults, enhanced P3 amplitudes were elicited over the posterior ROI rather than the frontal ROI.
Young Frontal ROI =0.89, S.D. = 2.58 < Posterior ROI = 4.86, S.D. = 2.80.
Older adults showed a smaller difference between frontal and parietal ROI, although with higher peaks for the parietal ROI.
Frontal ROI = 1.75, S.D. = 2.08, Posterior ROI = 1.81, S.D. = 1.86 (see Table 5).

<u>Low Load</u>
In the Low Load condition, young adults showed a greater difference than the older adults.
Young M= 2.32, S.D. = 3.64, Old M= -.936, S.D. = 2.14, t(38)= 3.44, p = .001.
The raw data revealed that while young adults showed enhanced peak amplitudes over the posterior ROI, older adults showed higher activity over the frontal ROI.
Young Frontal ROI = 0.99, S.D. = 1.72 < Young Posterior ROI = 3.32, S.D. = 2.37.

Older Frontal ROI= 1.59, S.D. = 1.38 > Older Posterior ROI = .66, S.D. = 1.44
(see Table 5).

Young adults confirmed the prediction that posterior electrodes would elicit enhanced P3 amplitudes rather than frontal electrodes. Paired samples t-tests revealed that differences in asymmetry were only present in young adults but in all three load conditions, while asymmetry between the frontal and posterior ROI showed *no significant difference* in older adults. For young adults, differences were reduced with increase of attentional load, likely driven by a reduction of activity in the posterior ROI. Comparing the attentional load conditions with each other for young adults, differences between the ROI were greatest in the no load conditions and reduced in the low load and high load conditions.

Young adults:
No Load M = 3.97, S.D.= 4.59 > Low Load M= 2.32, S.D.= 3.6, t(19)= 2.88, p = .01,
Low Load M= 2.3, S.D. = 3.64> High Load M = 1.25, S.D.= 3.3, t(19)= 2.5, p = .02,
No Load M= 3.97, S.D.= 4.6 > High Load M=1.25, S.D.= 3.3, t(19)= 4.42, p< .001.
The raw data revealed that enhanced P3 amplitudes were elicited over the posterior ROI rather than the frontal ROI in all three conditions.
No Load: Frontal ROI M= 0.89, S.D. = 2.58 < Posterior ROI M= 4.86, S.D. = 2.80,
Low Load: Frontal ROI = 0.99, S.D. = 1.72 < Posterior ROI = 3.32, S.D. = 2.37,
High Load: Frontal ROI = 1.05, S.D. = 1.6< Posterior ROI= 2.29, S.D. = 2.00
(see Table 5).

Based on these results, the P3 amplitudes elicited over the posterior electrodes were investigated further with a 2(Age) x (Load) x (Side) ANOVA and revealed an interaction between age and load F(2, 76)= 5.4, p = .007 ηp^2 = .12. As expected, young adults had higher P3 peak amplitudes for the posterior electrodes than older adults in all three load conditions.
No Load: young M =4.8, S.D. = 2.7 > older M=1.8, S.D.= 1.8, t(38)= 4.17, p< .001,
Low Load: young M =3.3, S.D.= 2.3 > older M=.65, S.D.= 1.4, t(38)= 4.47, p<.001,
High Load: young M =2.29, S.D=1.9 > older M= .52, S.D.=1.8 t(38)= 3.00, p=.005.

Moreover, according to the predictions posterior activity was reduced with increased attentional load. Separated into age groups, young adults showed the highest activity in the no load condition

No Load M= 4.9, S.D= 2.7 > Low Load M= 3.31, S.D.= 2.28 t(19)= 5.43, p <.001,
Low Load M= 3.31, S.D.= 2.28 >High Load M= 2.29, S.D.= 1.91, t(19)= 3.42,
p=.003.

For the older adults, posterior activity was also reduced with the addition of attentional load:

No Load M= 1.8, S.D. = 1.8 > Low Load M=.66, S.D. = 1.35, t(19)=4.65, p< .001,
No Load M = 1.8, S.D. = 1.8 > High Load M =.52, S.D. = 1.8 , t(19)= 3.49, p = .002,
however the difference between low and high attentional load was non – significant but amplitudes were reduced in the high attentional load.
Low M=.65, S.D. = 1.3 >High M= .52, S.D. = 1.8 (see Table 5).

11) P3 Latency

For the P3 latency, there were, against my predictions no main effects of age, side or load and no interactions.

Discussion

My aim was to investigate if increased attentional load modulated spatial attention and if such effects were more pronounced with healthy ageing. Moreover, I aimed to investigate just how the modulating effects of attentional load were reflected in the neuronal correlates in an ageing context. In view of the reported absence of any age related differences in the behavioural results, the neuronal correlates provide an intriguing insight in the processing of the presented task.

My findings show some evidence for age related differences on how attentional load effects the processing of peripheral targets. Although attentional load did not lead to a spatial bias shift in neither the behavioural nor the neurophysiological data, the increase in reaction times between the different task conditions (no load to high load) confirmed that the manipulation worked and this also reflected in the ERPs of the peak components. Interestingly, while attentional load had an effect on the lateralization between left and right visual targets, there were no specific age load effects differentiating young from older adults in the early visual processing components. I had predicted a decrease of lateralization with increase of load that may have been more pronounced in older adults. Yet, the results revealed that older adults matched the performance of young adults behaviourally as well as for the neurophysiological data in all three load conditions. Solely in the late P3 components were age related differences observable, showing a reduction of parietal amplitudes in older adults and hinting at a possible age related topographical shift towards more frontal electrodes. In addition, the present results revealed age related differences that suggest a reduction of right hemisphere activity with age, which was independent of attentional load. These effects were seen predominantly over the early positive components P1 (80 – 150ms) and N1 (150 - 250) where I observed a shift towards the right spatial side as well as an increase of LH lateralization for older adults.

Influence of attentional load on spatial attention

Summing up the behavioural results in the first instance, it was revealed that there were no significant age related difference in performance between older and younger adults. Comparing the processing of peripheral targets between young and older adults revealed no significant differences in reaction times between the age groups. Collapsed across participants, reaction times increased exponentially with load with high attentional load resulting in the longest reaction times. This supports the premise that increased task demand through increased attentional load resulted indeed in a slower processing of peripheral targets. However, the difference between low and high attentional load was non-significant. It is possible that these two manipulations required similar effort despite the argument of a higher task demand for a conjunction search for the “high load” condition (O’Connell et al., 2011; Treisman & Gelade, 1980). Secondly, between peripheral targets, reaction times were significantly faster for right over left targets. This was reported for all three load conditions and again, was found to be independent of age.

In fact one of the more surprising results of this study is the absence of a spatial bias towards the left visual field, as was reported by O’Connell et al. (2011) who had found, although small, a stable left spatial bias in their study. Instead, my study revealed both a behavioural and electrophysiological processing advantage for right sided stimuli for both age groups. I had predicted to find a left or no spatial bias between target sides based on the results of the behavioural pilot studies, which closely resembled the present set up (See Chapter 3). The current results might support the findings that an increase of non-spatial attention leads to a rightward shift of attention in behaviour (Dodds et al., 2008; Peers et al., 2006). However, I did not find a leftward bias in the no load (baseline) condition, which would have been expected if increased task demand had led to a shift of attentional bias. Despite the procedural similarity between the behavioural pilot study and the current EEG set, I have found a preference for the right sided stimuli.

Yet, this preference of the right visual field targets appeared to be reflected in the reaction times only and not in the neurophysiological data which instead suggested a preference for the processing of left over right visual targets, at least in the first stages of stimuli processing.

I also measured percentage accuracy in response to both central and peripheral target detection. Similarly to O'Connell et al. (2011) and the pilot study (See Chapter 3), detection was again high (> 90 % allowing) for an adequate amount of trials to be analysed. Although accuracy plays a minor role in the measure of spatial bias, a more detailed analysis of the accuracy measures revealed an interesting pattern: first of all investigating the percentage accuracy towards the central targets revealed high detection accuracy and no significant differences between low and high attentional loads, suggesting equally strong detection of targets in both conditions (and further) reflecting the results of the reaction times. This suggests also that while both load conditions that included attention towards a central target were more taxing than the baseline condition (no load), the difference in task difficulty from low to high appeared to be less than may have been expected. This was likely driven by the result of older adults who outperformed young adults in the high attentional load condition, showing significantly higher accuracy, another interesting finding that has been reported before in a variety of tasks (Brache et al., 2010; Carriere et al., 2010; Jackson & Balota, 2012; McVay et al., 2013; Tomporowski & Tinsley, 1996).

The detection of peripheral targets was similarly high, ranging from 94-97%. Here, older adults performed as well as young adults, with no difference between the age groups, yet an increase in load led to slightly reduced accuracy, confirming the increase in task demand. Furthermore, there was a change in spatial bias in accuracy between the load conditions: while at baseline there was no difference between left and right targets, results showed higher accuracy for left than right targets in the low load condition and the reversed pattern in the high load condition. This is very similar to the effect I had predicted for young adults for reaction times, yet, as said already, reaction times proved to be faster for right over left targets throughout. It thus hard to interpret this effect, especially as accuracy was virtually at ceiling.

Electrophysiological evidence for attention load modulations on spatial attention

The electrophysiological data revealed that attentional load modulated the early positive P1 amplitude and N1 significantly, yet there were no age related reductions of hemispheric lateralization between or within attentional load conditions. Collapsed across all participants, the current data revealed differences in lateralization between both hemispheres for left and right targets. The P1 amplitudes in particular, were more lateralized for left targets than for right ones, showing a RH dominance. This suggests a processing preference for stimuli in the left visual field that is in accordance with pseudoneglect. I found this for both the no load baseline and the low load conditions. Yet, when attentional load was high and the task thus most difficult there were no significant differences in lateralization between left and right targets, which may suggests a possible increase of RH activation for both targets in order to deal with increased task demand at the high attentional level at an initial stimuli processing stage(Clark & Hillyard, 1996; Luck, 1995; Natale, Marzi, Girelli, Pavone, & Pollmann, 2006).

Focussing on the right targets only, the electrophysiological data revealed that for the P1 amplitudes there were significant differences in lateralization between the load conditions, which were absent for the left targets. While the lateralization between the LH and the RH for left targets did not change significantly, increase of attentional load lead to a significant change in lateralization for right targets. The LH dominance observed in the no load condition shifted to a more balanced activation over the LH and the RH for the low load condition, although this difference between the hemispheres was non-significant. Finally, for the high load condition, lateralization shifted to a significant RH dominance compared to the LH, with an enhanced P1 amplitude over the RH in contrast to the other two load conditions. This suggest that with increase of attentional load, processing of right targets became more lateralized to the right hemisphere during the early stages of visual processing, as a function of increased attentional demand. High task demand lead to an increase of P1. This suggests an increase in the allocation of spatial attention in a top down manner, (Taylor, 2002) similar to the findings of O’Connell et al.(2011). Interestingly, when comparing young and older adults at P1 amplitudes directly, the activity was not significantly different, suggesting no decline with age but instead similar patterns of activity during early visual processing.

For the N1 amplitudes, my results showed a pattern of contralateral lateralization for both left and right targets. There were no differences between load conditions, suggesting an absence of significant attenuation of the dominant hemisphere with increase of attentional load. However, within load conditions, right targets showed greater lateralization towards the contralateral LH and an enhanced negative N1 amplitude in the no load condition compared to left targets. In the other load conditions, left targets showed greater lateralization over right targets, with enhanced negative N1 amplitudes over the contralateral RH in the low and high load condition. Therefore, my findings of the lateralization of the N1 component are somewhat different to the findings of O'Connell et al.(2011) who reported a processing advantage for left stimuli over the RH that was attenuated with task demand via central load.

My findings with increased attentional load are similar to O'Connell et al (2011) and Bonato et al. (2015), in terms of an increased commitment of attentional resources at a low level early visual processing (as indexed in the P1 and N1 components) (Bonato et al., 2015; O'Connell et al., 2011). I also found an increase in reaction times that was associated with increase of load. The enhanced P1 amplitude with load repeats, in the main, the findings of Bonato et al. (2015) who also found an enhanced P1 amplitude with an increase in task demand as represented with a dual task characterized by a simultaneous multitasking design in their healthy adult sample: In my study, introducing an additional multitasking component with the instruction to pay attention to a central target in the central stream, in addition to detecting peripheral targets, shifted activity towards the RH for both types of lateralized targets. In the high load condition, this increase of attentional resource allocation was reflected in a shift and increase of RH activity for right targets at an early processing level.

The results of the P2 component should be interpreted with caution (see result section). Unfortunately, based on the topographies derived from the grand average waveforms, the mean peak amplitudes for the P2 component with a range of 190ms -260 ms, appeared to be maxed out for both young and older adults. The obtained results showed the most positive peak at the beginning of the interval for older adults and at the end for young adults and despite adaptation from Learmonth et al. (2017), the P2 peak amplitudes were not well defined across participants. Hence, while the obtained results might suggest an age shift in lateralization from a contralateral dominance towards a more ipsilateral activation, it is more likely that the results are skewed due to an artificial definition of the latency for this component. Moreover, the ROI for both hemispheres, in the grand average waveforms, showed negative activity for older adults, reflecting the current results of negative activity in the contralateral hemispheres for older adults. Based on the grand average and scalp topographies, the analysis of the P2 component would likely benefit from an analysis in separate time windows (for young and older adults), instead of my current approach of a combined window.

Similarly to O'Connell et al.(2011) who did not report on the N2pc component, my results also failed to elicit a separate second negative component (based on the grand average waveforms and preliminary peak detection on the group level). Therefore, I will not further discuss the P2 and N2pc component but instead focus on the later P3 component.

To sum up this far, the present results suggest that older adults were similarly able to process targets and the task at hand, under the dominant recruitment of the RH when discriminating between lateralized and central targets in the increased load conditions (low and high load) during the early stages of processing targets. Yet, there were age-related changes in the later stage of stimuli processing. My results revealed a significant influence of attentional load, were attentional load influenced the P3 component differently between the age groups:

Overall, the increase of attentional load lead to a reduction of the posterior ROI activity in the P3 (280 – 400ms) component, likely reflecting an increase in resource allocation as the tasks became more difficult. Particularly, the parietal P3b is thought to reflect the allocation of attentional resources in a 'top down manner that benefits the evaluation of stimuli see (Donchin, 1981; Nieuwenhuis, Aston-Jones, & Cohen, 2005; O'Connell et al., 2012; Polich, 2007; Verleger, 2008). This replicates and corroborates the findings by O'Connell et al. (2011), who reported a reduction of P3 components with attentional load. I found that greater attentional load lead to greater resource allocation and the attenuation of the amplitude possibly indicating compensation mechanisms for the decreased ability for stimulus categorisation. This became more apparent in older adults who showed a reduction of the posterior ROI P3 amplitude for all conditions, in contrast to the young adults, suggesting an age related decline in activity. This fits well with earlier studies who have linked a reduction in the P3 component to normal aging (Friedman, 2003; Polich & Criado, 2006; Rossini, Rossi, Babiloni, & Polich, 2007; Sutton, Braren, Zubin, & John, 1965).

In view of an age related topographical shift towards the frontal electrodes, the present findings indicate that while older adults showed less activity in the parietal electrodes compared to young adults, additional recruitment of frontal electrodes possibly served as a compensatory mechanism that benefitted the target processing, so that older adults were able to match the behavioural performance in young adults. Compensatory recruitment in older adults is thought to be reflected in additional recruitment of neuronal resources. For the late positive P3 component, this has been specifically found in an increased neuronal recruitment of frontal electrodes to compensate parietal decline with age. Earlier studies have repeatedly reported a posterior- anterior shift of P300 with healthy aging (Fjell & Walhovd, 2004; Friedman, 2003; Learmonth, Benwell, et al., 2017; O'Connell et al., 2012; Polich, 1997; West et al., 2010). In addition, it is also possible that factors such as higher intrinsic motivation in older adults or compensatory strategies were employed in older adults benefitting performance and attenuate disadvantages with increased load.

Age- related effects on spatial attention

As pointed out above, behaviourally, my results showed no difference between the age groups as all participants responded faster to right over left peripheral targets. However, the electrophysiological data revealed age related differences on spatial attention during the early stages of visual processing (indexed by the P1 (80 – 150ms) and N1(150- 250 ms) components) which suggest changes in lateralization with age. Particularly for the negative N1 component, older adults showed a processing preference for right visual targets and a shift of lateralization towards the contralateral LH that was absent in young adults:

Collapsed over both age groups, my results showed a processing advantage for targets in the left visual field during early stimuli categorization and processing (as indexed by P1 component). Left targets were more lateralized to the contralateral RH than right targets, which also showed a RH dominance yet a smaller difference between the peak amplitudes over both hemispheres. However, when I compared the lateralization of the P1 peak amplitudes in both age groups, there were age related differences apparent in this early processing stage. Young adults showed greater lateralization to the RH for left targets and a smaller difference between the hemispheres for right targets (possibly driving the overall effect of a left visual field preference in the P1 component observed when age was discarded). In contrast, older adults showed no significant difference in lateralization for left and right targets, with both targets eliciting similar P1 amplitudes in the dominant RH thus showing reduced amplitudes over the RH in comparison to young adults. This suggests a preference for left visual stimuli and a RH dominance in the early processing stage for young adults that is attenuated with age. This finding fits well with earlier studies which reported an attenuation of the P1 component in an older population in contrast to young adults(Gilmore, 1995; Kutas, Iragui, & Hillyard, 1994; Nagamatsu et al., 2009). The observed age related differences in the sensory aspects of attention, as evident in the P1 and N1 components, confirm changes in early sensory processing and orienting of attention towards attended stimuli (Mangun, Hillyard, & Luck, 1993) , where the P1 indexes the low level sensory processing and the N1 the discriminative processing (Vogel & Luck, 2000).

Here, age related effects of spatial attention became even more prominent for the N1 component. Again to recap, across all participants left targets were more lateralized than right targets at the N1 peak amplitudes showing an enhanced negative N1 over the contralateral RH. Right targets also showed an enhanced N1 over the contralateral LH but with less lateralized difference between the hemispheres.

Yet when investigating the N1 component within age groups, older adult showed a preference for processing right targets over left. Although for right targets only, I found a shift in the N1 amplitude activation from a dominant RH to the LH for older adults. I think this reflects a decrease in right hemisphere dominance towards a lateralization in favour of the LH with age. It supports the claim of a reduction in a processing advantage for left visual stimuli (pseudoneglect) that has been observed for young adults in these electrophysiological components, as well as a spatial attention orienting towards the right side of space with age (Benwell, Thut, et al., 2014; Failla et al., 2003; Fujii et al., 1995; Learmonth, Thut, et al., 2015; Nagamatsu et al., 2011, 2009, 2013; Schmitz & Peigneux, 2011; Stam & Bakker, 1990). In the absence of a behavioural effect, the present finding represent an age related shift of spatial attention on a neuronal level. On this basis, the present results accord well with the HAROLD model (hemispheric asymmetry reduction in older adults) (Cabeza, 2002; Cabeza et al., 2004; Dolcos et al., 2002; Huang et al., 2012; Reuter-Lorenz et al., 2000): It is thought that RH lateralized cognitive functions decreases in lateralization with age and in turn a more bilateral recruitment is used as a compensation for a reduction in the activation of the RH in older adults (to maintain cognitive performance (Cabeza, 2002)). This model has been supported by PET and fMRI studies showing an increase of bilateral activation when task difficulty was increased for older adults (Cabeza, 2002; Cabeza et al., 2004; Dolcos et al., 2002; Huang et al., 2012; Reuter-Lorenz et al., 2000). My results thus add to the present research literature arguing for a reduced preference for left visual space (pseudoneglect) with age that is also observed in neurophysiological correlates in the later negative N1 component (and underpins the preserved behaviour).

Furthermore, source localization of the right lateralization of activity in previous studies has identified a reduction of RH resources for attentional processing and highlighted the right temporo parietal junction (TPJ) in the ventral attention network as a vital area for generating spatial bias at an early processing stage (Benwell, Harvey, et al., 2014; Benwell, Thut, et al., 2014; Foxe et al., 2003; Learmonth, Benwell, et al., 2017). The TPJ has been linked also to visuospatial attention orienting as well as maintenance of arousal (Benwell, Thut, et al., 2014; Corbetta & Shulman, 2011) and has been found to map on to the timing of the N1 component (Benwell, Harvey, et al., 2014). TPJ activity likely plays an important role in explaining the present findings of a shift towards the LH in older adults. With age, it is possible that the RH TPJ activity reduces and thus impacts on the regulation of bihemispheric dorsal frontoparietal network which then results in shifts of spatial bias to the right side (Benwell, Harvey, et al., 2013) (but note I did not find this behavioural effect). This might also lead to a reversal of the RH dominance towards the LH in older adults, which in turn leads to a possible reduction of left visual field preference with age (attenuated pseudoneglect). It has been suggested that the sometimes observed behavioural rightward shift of spatial attention in older adults is linked to a more general diminished alertness in older adults and a reduction of RH dominance (Benwell, Thut, et al., 2014; Buysse, Monk, Carrier, & Begley, 2005; Goedert et al., 2010; Nebes, Buysse, Halligan, Houck, & Monk, 2009; Robinson & Kertzman, 1990), possibly in addition to a decrease in the interaction between the VAN and DAN of the RH, which supports visuospatial attention (Benwell, Harvey, et al., 2013; Benwell, Thut, et al., 2013; de Schotten et al., 2011).

Intriguingly, the study by Learmonth et al. (2017) also showed evidence for a right hemisphere lateralisation of the N1 and P2 components. Investigating spatial attention in a landmark paradigm their study was distinctively different as their analyses were based on clusters of lateralised activity, instead of a comparison of peak amplitudes at specific components as I did in the present study. However, this technique allowed them to identify age related differences that were not illuminated with the standard peak component analysis. They observed age related differences since no lateralised clusters were present for older adults for either stimuli type (lines of varying lengths), yet young adults showed a right lateralisation for long lines (Learmonth, Benwell, et al., 2017). In addition, they reported a stimulus dependent right parieto occipital activation in the right TPJ for long lines that was absent in older adults (no significant lateralization) and therefore possibly represents age related changes in hemispheric asymmetry. Moreover, they reported a reduction of the parietal P300 in the older adults, indexing an age related shift from posterior towards anterior activity (Fjell & Walhovd, 2004; Friedman, 2003; Learmonth, Benwell, et al., 2017; O'Connell et al., 2012; Polich, 1997; West et al., 2010), also observed in the present study. I would thus argue that the age-related differences in spatial attention in the N1 component I found, reflect a shift of spatial attention that is due to an age- related decline in RH lateralization.

Limitations and methodological considerations

I have to concede that it is also possible that the observed right target reaction time advantage found across both age groups may be an effect of time on task, as it has been shown in previous studies that prolonged time on monotonous tasks shifts spatial attention towards the right side of space. This is deemed to be a result of decreased arousal that has been linked to a reduction of activity in the right ventral network (Bellgrove et al., 2004; Benwell, Harvey, et al., 2013; Benwell, Thut, et al., 2013; Dodds et al., 2008; Dufour, Touzalin, & Candas, 2007; Manly et al., 2005; Newman et al., 2013). For my results it is possible that this rightward shift was induced because of the additional prolonged EEG setup on both testing days, in addition to the pre-screening regimes prior the first session, which always entailed 2 out of 3 attentional load conditions. It is possible that this decrease of arousal lead to less lateralised EEG signals for both groups as all trials (of one condition) were combined for analyses. Another consideration could be that the EEG set up in itself lad to a greater depletion of attention, as participants were instructed to reduce blinking, and may have focussed on blinking strategies in addition to task demands. Previous research has stated a trade-off between reaction times and accuracy with older adults favouring accuracy in particular (Starns & Ratcliff, 2010, 2012)(and central target accuracy data). The instructions to control and reduce eye movements could have added this as a further factor. However all this is speculation and needs to be investigated systematically.

Conclusion

I aimed to investigate the influence of non-spatial attentional modulation on spatial asymmetry and neural activity as indexed by ERPs. In particular I was interested in possible age related differences in both, the processing of peripheral lateralized targets and the effect of increased attentional load in healthy aging. The results of the behavioural data revealed an absence of age related differences, showing that older adults were able to match young adults in performance (as indexed by fast reaction times and high accuracy) and thus suggesting that (for spatial attention), they did not suffer from age related cognitive decline. Instead I found a preference for right over left targets that was independent of age group and attentional load condition.

Investigating the neuronal underpinnings with EEG, first of all again revealed an absence of apparent age differences with the increase of attentional load (on the peak components of P1 and N1). Nonetheless, older adults showed differences in the magnitude and direction of the peak amplitudes, suggesting underlying compensatory mechanism: in direct contrast to young adults, older adults showed a processing advantage for right instead of left targets for the N1 component, as well as an increase of resource allocation for left stimuli at early processing stages. This was further corroborated by a reduced activity in the parietal P3 component (in contrast to young adults across all test conditions) and an age related topographical shift of activity towards the frontal electrodes; indicating possible additional recruitment of neuronal circuits in order to compensate for possible cognitive deficits in the parietal area. So although behaviourally older adults showed no significant decrease in performance compared to young adults, these physiological differences suggest age related differences in lateralisation that might be associated with RH decline in healthy aging in line with the HAROLD model (Cabeza, 2002; Dolcos et al., 2002).

A reduction of RH activity with age has been interpreted as a form of compensation against age related cognitive decline in order to preserve performance when tasks get increasingly difficult (Cabeza, 2002; Dolcos et al., 2002). I thus expected to see more age related differences with an increase of attentional load. Instead, the presented results revealed an overall larger lateralization towards the RH for left targets in comparison to right targets, which was apparent in the early stages of visual orienting and processing. Yet there was no shift in lateralization to the other hemisphere with an increase in task demand. Further research investigating age-related RH changes are necessary in order to determine how such changes in lateralization with age are impacting on the everyday life and navigation of older adults. There are some studies linking real life experiences to changes in spatial bias (i.e. higher risk of falls with deficit in processing left visual hemispace (Nagamatsu et al., 2009) so it should be possible to estimate possible negative consequences of such neuronal changes on healthy aging.

Chapter Five
General discussion

With the work presented in this thesis, I aimed to investigating age related differences in spatial attention between cognitively healthy young and older adults and how such changes with age might translate into differences in neuronal correlates. Moreover, I attempted to address the question of if and how non spatial factors impact on spatial attention. I assessed this through changes in attentional load and therefore resource commitment in order to further understand healthy cognitive ageing and to possibly uncover markers of cognitive decline.

To address this wider research aim, I carried out four experiments, which employed a combination of behavioural as well as electroencephalography (EEG) methodology as this allowed me to investigate the neuronal correlates associated with shifts of spatial attention. I will summarize the key findings of the experiments in the first instance.

As described in Chapter 2, I found that older adults, similarly to young adults, showed reliable spatial biases over two separate testing sessions (for young sample see Learmonth et al. (2015, 2018)), contrary to my predictions of greater variability in this age group. Moreover, older adults showed similar patterns of spatial bias to young adults, where only the landmark task revealed an age related decline in bias. Again like Learmonth et al. (2015, 2018). I replicated the findings of a consistent lack of inter- task correlations. I argued that general assumptions gained from different spatial tasks are not merited anymore and that such generalizations should be viewed with caution.

In chapters 3 and 4, I further explored the influence of non-spatial modulators on spatial attention. Again, with particular interest in the aging population, I investigated how increases in attentional load, which impact on task difficulty and sustained attention, modulated spatial attention at both a behavioural (Chapter 3) and neuronal level (Chapter 4). The findings of the two behavioural experiments in Chapter 3 informed the follow up study described in

Chapter 4 and confirmed that older adults were engaged in the task and performed similarly well to young adults.

Finally in Chapter 4, employing EEG to investigate the neuronal correlates associated with spatial shifts in attention, I found that older adults did not differ from young adults behaviourally but that they showed a reduction of right hemispheric activity for both target sides at the P1 component in comparison to young adults. Moreover, for right targets older adults showed at the N1 component a shift towards increased LH activity over RH, possibly indicating an age related reduction of lateralization. Moreover, non-spatial factors such as the increased attentional load influenced both behavioural results (via reaction time increases) and early visual processing of stimuli (indexed by the P1 and N1 component). Although I did not observe a shift in asymmetry with increased attentional load, as right targets elicited faster reaction times in all conditions, attentional load increased reaction times and reduced P3 amplitudes which is indicative of greater taxing on the attentional resources. In comparison with young adults, older adults showed reduced posterior P3 amplitudes in all conditions, possibly indicating age related decline in this area. Moreover, the results suggest that older adults used additional neuronal recruitment in the later stages of stimuli processing (P3), to compensate for increased task difficulty and increased resource allocation, likely improving the behavioural results of the older adults so that they were similar to young adults.

I will now reflect on the obtained results in view of the wider literature and their possible implications for future research. Based on the presented results, I will suggest possible future directions in spatial attention research that could guide our understanding of healthy cognitive ageing further.

Spatial attention in older adults show presence and absence of asymmetry.

The results of the experiments provide an insight into the magnitude and direction of spatial bias in older adults. Based on the previous literature, I expected a lack of spatial asymmetry or a reduction towards the right side of space, as well as a clear difference in spatial attention behaviour between young and older adults (see Barrett & Craver-lemley, 2008; Benwell, Thut, et al., 2014;

Failla et al., 2003; Fujii et al., 1995; Goedert et al., 2010; Hatin et al., 2012; Jewell & McCourt, 2000; Learmonth, Benwell, et al., 2017; Learmonth, Gallagher, et al., 2015; Loureiro-Silva et al., 2010; Nagamatsu et al., 2011, 2009, 2013; Schmitz & Peigneux, 2011; Stam & Bakker, 1990; Veronelli et al., 2014). Perhaps most strikingly, in all four experiments, older adults did not show strong spatial biases that would suggest cognitive impairments. Instead, in experiments 1, 3 and 4, performance between young and older adults did not differ, suggesting no outperforming of young adults or inferior performance of the older age group.

In Chapter 2, I aimed to understand the direction and stability of spatial biases across testing session in healthy older adults, as opposed to healthy young adults studied previously by Learmonth et al.(2015, 2018). The results offer insight into the behavioural patterns of older adults in five spatial tasks but also highlight important limitations that will be addressed in the following:

Firstly, describing the magnitude and direction of bias in older adults, the results of chapter 2 offer a systematic overview of five common tasks and best reflect the variability between spatial tasks. Building on from the study by Learmonth et al.(2015, 2018), my results revealed that older adults showed a preference for the *left side of space* in two tasks (Manual Line Bisection and Greyscale task), while they showed a lack of bias in the other three measures. This corroborates findings from other studies who also investigated older adults in the lateralised visual detection task (Learmonth, Thut, et al., 2015) or the landmark task (e.g. Learmonth, Benwell, et al., 2017), as well as the study by Brooks et al. (2016), who used a form of the visuospatial line bisection and found a maintained leftward bias in older adults, leading to the argument of a maintained pseudoneglect into old age. Moreover, older adults also showed a reliable and stable bias across testing days, similar to the young adults, although I had predicted a greater variability with age.

Interestingly, in direct comparison to young adults (2015, see Learmonth et al. 2018) only the landmark task showed an attenuation in spatial bias for older adults that may reflect a selective age-related decline of right-hemispheric processes. The other tasks did not reveal a difference with age, reflecting the overall findings of the other presented experiments, which who suggested that older adults were able to perform the tasks akin to young adults, although possibly through different means such as differences in strategy or neuronal activity. The observed behavioural rightward shift with age in the landmark task presented here, may offer an insight into possible age related changes in the neuroanatomy for older adults. The finding fits with the assumptions of the HAROLD (e.g. as described by the Hemispheric Asymmetry Reduction in Older Adults) model of cognitive aging (Cabeza, 2002; Dolcos et al., 2002). The behavioural shift in spatial bias might be a result of additional recruitment of supplementary contralateral brain areas in order to maintain performance in this task (for a discussion see (Dolcos et al., 2002; Learmonth, Benwell, et al., 2017; Reuter-Lorenz & Park, 2010) and reflect compensatory mechanisms involved in healthy cognitive ageing. Learmonth et al. (2017) also reported an absence of a leftward bias in older adults in a landmark task, followed by a decreased in right hemisphere activity in older adults in the EEG recording (Learmonth, Benwell, et al., 2017), further supporting the claim of an association between a spatial rightward shift as a consequence of reduced lateralization and RH decline with age. Yet, the relevance of such shifts in the context of adapting and navigating in the real world remain elusive and further investigations here are necessary especially as the other tasks and experiments revealed no age related behavioural effects.

Other important findings gained from the results from Chapter 2 are the now repeatedly found results of variability in both the direction and magnitude of spatial biases across tasks, as well as a repeated lack of task correlations; see young adults sample by Learmonth et al.(2015, 2018) and also across different tasks in the spatial research literature (Heber et al., 2010; Luh, 1995; Nicholls et al., 1999). The present results of an absence of a uniform spatial bias (and instead task specific variations in spatial bias) suggest that while the tasks share aspects of spatial attention, they each also measure different components of spatial attention and a direct comparison between tasks should be cautionary. This is in agreement with Learmonth et al. (2015, 2018) who also proposed this argument and suggested pseudoneglect to be a ‘multi component phenomenon’ based on their earlier results.

Non spatial modulators influence spatial attention more than age

In light of the directional variability of the spatial biases reported in Chapter 2 and in recent studies (which also seem largely independent of age), the current results again highlight the importance of task choice, especially when testing for age related differences in older adults. In addition, it has been found that spatial attention asymmetries are modulated by non-spatial factors such as changes in sustained attention likely driven by time on task and reduced alertness, increased task difficulty or participant dependent variables (for a review see Chandrakumar et al., 2019).Therefore, an observed spatial bias might not simply reflect a fixed measure of asymmetrically spatial attention *per se but* might change across tasks and testing time, reflecting changes in other non-spatial components. The leftward spatial bias that is often observed in young adults has long been interpreted as a healthy norm and any deviation from it suggested to imply deficits, especially with older age. However, in view of the findings of other modulating factors, this view is too rigid and age *per se* might in fact not be influencing the shifts of attention.

The absence of inter- task correlations in Chapter 2 also reveals the limitation of making predictions for the natural environment, as a particular bias in one task does not predict the same behaviour for a different task. Moreover, while I found that older adults were similarly able to perform the tasks across different days I could not estimate which task, in comparison to the other 4, was more taxing on the participants as I did not control for task difficulty. Differences in task difficulty across the spatial tasks could account for the absence or presence of leftward biases in spatial attention. This complicates generalisation and comparability of pseudoneglect effects across different tasks, age-groups and studies.

The experiments in Chapters 3 and 4 attempted to address this issue and investigated the influence of attentional load on spatial attention in a dual task paradigm, while employing EEG (see Chapter 4). The design was adapted from O' Connell et al. (2011), who found modulating effects of attentional load on both spatial bias and early visual processing, as indexed in the P1 and N1 components. With the three experiments of Chapters 3 and 4, I extended their research by investigating if such modulations would be more pronounced in older adults.

Moreover, in contrast to the experiment in Chapter 2, this design allowed me to increase attentional load systematically from a baseline visual detection task in which participants did not monitor a RSVP steam for a target, to an increased attentional impact design. Attentional load was increased via an alphanumerical central target that participants were required to detect in a RSVP stream of red numbers while simultaneously reacting to lateralized peripheral targets. Attentional load was defined as either low: a green number as central target required low attentional resources due to it being a pop out task or high: a red letter within a stream of red numbers, as additional discrimination between central target and distracters became necessary (O'Connell et al., 2011; Treisman & Gelade, 1980) (see Methods in Chapters 3 and 4).

The behavioural results of experiments 2 and 3 (see Chapter 3) served as pilot studies and informed the design of the EEG experiment, were EEG was employed in addition, and the obtained results allowed a refinement of the testing parameters (see method section Chapter 3). In short, they deviated in methodology from the final study, as only low and high attentional loads were measured and the viewing distance was decreased to a closer peri- personal space (80 to 50cm), which was identical to the viewing distance of the study design by O'Connell et al.(2011) and enhancing comparability to the results of the previous study. Finally for the EEG study, hand response was limited to the right hand only. Spatial preferences between left and right targets shifted between experiments 1 and 2 (Chapter 3) based on the changes in viewing distance, supporting the argument that spatial biases become stronger at closer range (see Dellatolas et al., 1996; A. Varnava et al., 2002). Moreover, this finding also ties into the earlier argument that changes in non-spatial factors have a strong influence on the spatial biases observed.

Interestingly, as mentioned above, across experiments 2 (Chapter 3) and the EEG experiment (Chapter 4), older and younger adults showed similar behavioural results in terms of reaction times and accuracy detection towards the central targets in the attentional load manipulation conditions. This suggests that older adults were suitably engaged in the task and were able to perform it similarly well when compared to young controls. Focussing on the EEG study in particular (see Chapter 4), I found supporting evidence that changes in attentional load modulated spatial attention, as indexed by increased reaction times with increased attentional load. However, against my predictions this effect was not more pronounced in older adults but independent of age. Moreover, in view of spatial asymmetry, I found no separation by age but instead all participants showed faster reaction times to right over left targets. The observed preference of the right visual target is perhaps one of the more surprising results and I have discussed possible influencing factors in Chapter 4. Yet, as I did not find a decline with age in either visual field, and both reaction times and accuracy were good for both target types, this preference does not suggest a decline in ability with age. The electrophysiological data suggest instead that during early visual processing, left targets were processed better with increased additional attentional load (low and high load) as indexed by the greater lateralization and enhanced peak amplitudes over the contralateral RH for the N1 component. However, this advantage attenuated in the later processing stages, possibly driving the behavioural response for the faster right targets. I conclude that there was an absence of age related differences, specific to increased attentional load, in both the behavioural data and during the early spatial processing stages as indexed in P1 and N1 components.

Age-related reduction in lateralization is visible at a neuronal level only

In Chapter 4, I did report an age related shift in lateralization that was independent of attentional load manipulations. The biggest effect was for the N1 component were older adults showed a shift in N1 amplitude activation from a dominant RH to a LH. Even though I found this shift for right targets only, I think it reflects a reduction of right hemisphere dominance with age.

So in the absence of a behavioural preference for stimuli in the left visual field for both age groups with participants responding (on a group level) faster to right sided stimuli, the presented finding represents an age related shift of spatial attention at a neuronal level. On this basis, it accords well with the HAROLD model (hemispheric asymmetry reduction in older adults) (Cabeza, 2002; Cabeza et al., 2004; Dolcos et al., 2002; Huang et al., 2012; Reuter-Lorenz et al., 2000). It is thought that RH lateralized cognitive functions decrease in lateralization with age and in turn, a more bilateral recruitment is used as a compensation for a reduction in activation of the RH in older adults (Cabeza, 2002). The compensatory mechanisms are meant to be driven by increased task difficulty in order to maintain performance, and have been supported by PET and fMRI studies (Cabeza, 2002; Cabeza et al., 2004; Dolcos et al., 2002; Huang et al., 2012; Reuter-Lorenz et al., 2000). The current results thus add to the present research literature arguing for a reduced preference for left visual space (pseudoneglect) with age that is observed in neurophysiological correlates in the later negative N1 component. They also provide further supporting evidence for an age related reduction of RH activity for spatial attention orienting that has been reported in previous studies of spatial attention (Benwell, Thut, et al., 2014; Learmonth, Benwell, et al., 2017; Nagamatsu et al., 2009). Nevertheless, I had predicted this reduction in lateralization to be more distinct in older adults, and related to an increase in task demand (load) in particular. Therefore, in order to reliably conclude that older adults show changes of neurophysiology that reflect shifts of spatial attention, further research is necessary.

Methodological considerations and future directions

The sample size of the presented experiments were driven by previous studies rather than based on power analysis. In chapter 2, I aimed to match the young adults sample of N = 50 (Learmonth, Gallagher, et al., 2015) to ensure comparability between older and younger adults in experiment 1 (Chapter 2). From the successful recruitment of 40 older adults, I had to exclude 2 participants in the final analysis due to changes in the design of the LVD task to accommodate changes in older adults' performance.

In chapter 3 – 4 the sample size was driven by the study of O'Connell et al. (2011) who had a final sample size of 45 participants (aged 18 to 47 years (*M* = 24 years, standard deviation = 7.3) (O'Connell et al., 2011). I aimed to collect 40 naïve volunteers in all three experiments, split even in two age groups to adequately address the research questions.

Despite the advantages of EEG to allow the investigation of temporal event related potentials in a non-invasive manner, which is suited especially for investigating older adults, its ability to localise the neuroanatomical source of activity is limited. With the present approach, the observed right hemisphere reduction was associated with the activity of pre-defined posterior ROIs for the left and right hemisphere. In order to further uncover the differences in right lateralized activity and the precise activation of brain areas in the healthy aging brain, more studies using fMRI could be beneficial. These could give further insight into the additional neuronal recruitment of other brain areas that are not restricted to hemispheric lateralization, in accordance with the CHRUNCH model (Reuter-Lorenz & Cappell, 2008), which suggests that compensatory recruitment of additional resources in older adults can be generated from any part of the brain. Moreover, it is possible that such sources of activity change at different stages of stimuli processing. My EEG results showed that older adults had, at a later processing stage (at the P3 component), a reduction of activity with increased attentional load. This could be interpreted as a greater resource allocation as the task became more difficult and possibly taxed the participants' ability to sustain attention. This was more pronounced in older adults and activity deceased exponentially with attentional load. In accordance with the CRUNCH model, I found that while older adults did not shift towards an overall increased activity in the frontal electrodes (as is proposed for posterior- anterior shift in P3 with healthy ageing (Fjell & Walhovd, 2004; Friedman, 2003; O'Connell et al., 2012; Polich, 1997; West et al., 2010)), older adults did show an additional recruitment of frontal electrodes that was absent in young adults (to possibly compensate a parietal decline present with increased task demand). In fact Huang et al.(2012) reported that both sides of the posterior parietal cortex showed activation to counteract for age related decline (in contrast to young adults) and to improve performance in older adults. While Huang et al. (2012) conclude that activation in the prefrontal cortex is task independent and indicative of healthy ageing, they emphasize that the involvement of the left and right parietal contributions for compensatory recruitment is task specific (see Huang et al., 2012). With additional fMRI investigations, it would be possible to pinpoint whether other areas of the ageing brain further contribute to this compensatory resource recruitment in my paradigm and if the left parietal contribution would increase with increasing attentional load. Moreover, it would be interesting to investigate if this was visible at a group level or if individual differences might be more influential.

Pupillometry and saccades as measures of cognitive load

The idea that older adults show greater cognitive decline, lower baseline and earlier/ faster reduction of alertness (Learmonth, Thut, et al., 2015; Madden et al., 2007; Swan et al., 2015) stands in contrast of the current results reported. Therefore, my predominant focus on reaction times as a measure for the impact of attentional load on spatial attention, as was the case in Chapters 3 and 4, might have masked possible ageing effects in performance in the presence of increased attentional load. Especially when investigating age related effects reaction times could suffer from a speed / accuracy trade off, towards a greater emphasis on correct detection of trials than fast response in older adults (Starns & Ratcliff, 2010, 2012), and conservative response strategies (Hertzog & Rypma, 1991; Nagamatsu et al., 2011; Smith & Brewer, 1985).

A promising avenue for future research in terms of mapping cognitive changes would be therefore the addition of pupillometry and saccade measurements, as a valuable addition to investigate top down processing and possible impacts by attentional load. Pupillary responses have been shown to reflect increased mental load and to be sensitive to cognitive load and decreased sustained attention in visual detection tasks (Beatty, 1982; Hoekstra, Morey, Rouder, & Wagenmakers, 2014; Lisi, Bonato, & Zorzi, 2015; Partala & Surakka, 2003). In a lateralized dual detection task in particular, pupil dilation revealed increased task demand in the participants (with an increase of load) and thus evidence for a decrease of visuospatial awareness and task engagement (Lisi et al., 2015). In addition, monitoring saccades has revealed asymmetries in attention as well as differences in screening strategies in healthy young adults (Thomas, Loetscher, & Nicholls, 2014). These approaches might be especially beneficial in older adults who might rely more on strategies to perform well in a task that requires higher attentional demand. Therefore, replicating the experiment presented in Chapter 4 with pupillometry or saccade monitoring as an indicator of spatial asymmetry may give valuable insight into how attentional load influences older adults' performance in absence of conscious reaction and differences in mental strategy in particular.

Individual differences as influential factors on spatial asymmetry

Another promising avenue for future research would be to investigate individual differences and how non-spatial modulators such as attentional load impact on them. Previous research has established already that there are sub types of participants showing a consistent and stable rightward bias, estimated to cover 30 to 50% of the general population (for a review see Jewell & McCourt, 2000) but see also (Benwell, Harvey, et al., 2013; Braun & Kirk, 1999; Cowie & Hamill, 2011; Dellatolas et al., 1996; Manning et al., 1990). Moreover, participants with good versus poor sustained attention show different results (Bellgrove et al., 2004, 2013; Staub et al., 2014). As argued before this suggests that a shift to the right side of space does not necessarily equate to a reduction of spatial ability. In my results, aging differences were predominantly absent and individual spatial biases in the older adults group (Chapter 2) as well as asymmetric preferences of peripheral targets (Chapter 4) overlapped with measures in young adults showing individuals who performed faster than the group mean.

Cognitive reserve and education

So for older adults in particular, an enriching environment is thought to preserve or enhanced cognitive reserve, which in turn possibly modulates age related cognitive decline (Brosnan et al., 2018; Stern, Alexander, Prohovnik, & Mayew, 1992). Such enriching environments might support, at least in part, a greater activation of the fronto parietal network (FPN) with age, which in turn has been shown to support better performance in visual processing speed and storage capacity, in contrast to peers with less activation of the FPN (Brosnan et al., 2018; Robertson, 2013, 2014; Wiegand et al., 2014). Moreover, education has been identified as prominent factor that supports cognitive reserve (Robertson, 2014) and allows the aging brain to adapt better to degeneration or disease (Stern et al., 1992).

The older population in the presented studies were recruited from various social clubs and had been in higher education predominantly. They were likely benefitting from such an enriching environment and therefore possibly a higher cognitive reserve. In a more recent study, findings of higher right hemisphere activation have been linked to greater cognitive reserve (Brosnan et al., 2018).

Moreover, Brosnan et al. (2018) reported an asymmetry in processing targets in the left visual field in healthy older adults at baseline, supporting a greater activation of the right hemisphere for adults with high cognitive reserve. Akin, a higher level of education could result in similar results, benefitting right hemisphere activation and therefore processing in the left side of space.

Focussing on such individual differences in the context of ageing and visual spatial attention in the future would give greater insights into the diversity of ageing and how cognitive reserves are related to spatial attention. The present cohort represent an older generation that is highly active and also predominantly highly educated, with a majority of participants that have been in higher education. A wider range of participants with different social and educational backgrounds would be beneficial to investigate spatial abilities with age. This could possibly show a reduction of right hemisphere activity as a consequence of reduced cognitive reserve and be reflected in a more rightward shift of spatial attention. Moreover, it would be interesting to compare possible changes in spatial attention throughout the lifespan, particularly into the late decades of life. With a mean age of approximately 70 years the present older adults might have been not old enough in order to detect changes in cognitive processes due to age related neuronal decline. This could further guide our understanding of what factors preserve spatial ability and possibly uncover markers of decline.

Inferences for real life applications

Interestingly, none of the tasks tested here displayed a critical rightward bias in older adults that would suggest cognitive decline (see Chapter 2) or inability of spatial attention akin to neglect (Chapter 3 till 4). An absence of spatial bias could be seen as a result of right hemisphere decline due to age or possible falsely identified as the presence of mild neglect in an otherwise healthy older adult, when in reality the underlying mechanisms of the different tasks might be differently affected by age. It remains a vital question to define how healthy aging is reflected in spatial measures, for which the experiment in Chapter 2 present a framework. It is now necessary to define what the spatial measures commonly used are assessing under the term of spatial attention. The current results are in line with previous work, where the authors have argued that different spatial attention tasks place a unique set of cognitive and motor demands on the spatial attention networks (Learmonth, Gallagher, et al., 2015, 2018; Verdon et al., 2010). As the participants did not score clinically on measures of early neurological decline, the reported spatial biases are likely a result of healthy aging, therefore the results tentatively recommend the Landmark task as the most reliable perceptual spatial measure in older populations as none of the participants had to be excluded from the experiment in contrast to the Greyscale or Gratingscale task, which could be more sensitive to changes in task difficulty on an individual level. However, adopting the view of pseudoneglect as a multicomponent phenomenon, the issue remains to select a suitable spatial task to measure the particular component in question.

Finally, at present, it remains an open question if shifts in spatial attention and age related reduction of right hemisphere activity translate into navigation changes and different adaptation to the environment in everyday situations. Only a few studies have found correlations between left visual space deficits and real life situations (Nicholls et al., 2010, 2007; Thomas et al., 2017). Particularly, Nagamatsu et al. (2009) found supporting evidence for a possible negative impact that is associated with left special bias decline. They reported an increased risk of falls that were associated with left visual field processing deficits. In the present study, I did not find a correlation with driving simulation in older adults and the five spatial measures (see Chapter 2), suggesting at present that spatial asymmetries measured in spatial tasks does not give a predictive insight into declining driving behaviour.

Therefore, future research investigating the relationship between lab based spatial measures and driving simulations could focus on individuals who show a rightward spatial bias in order to answer if a shift to the right side of space really translates into cognitive and performance decline or if it is a result of old age and reflects healthy cognitive ageing of spatial attention throughout the lifespan, or indeed just simply reflects a task effect with no further wider implications. Further investigation into healthy ageing and if and how this is reflected in the neurophysiology and neuroanatomy and behavioural patterns of spatial attention thus still remains an important undertaking to find ways to prolong and improve the cognitive wellbeing in healthy ageing and to identify markers of decline.

References

Anderer, P., Semlitsch, H. V., & Saletu, B. (1996). Multichannel auditory event-related brain potentials: effects of normal aging on the scalp distribution of N1, P2, N2 and P300 latencies and amplitudes. *Electroencephalography and Clinical Neurophysiology*, *99*(5), 458–472. https://doi.org/10.1016/S0013-4694(96)96518-9

Bäckman, L., Almkvist, O., Andersson, J., Nordberg, A., Winblad, B., Reineck, R., & Långström, B. (1997). Brain activation in young and older adults during implicit and explicit retrieval. *Journal of Cognitive Neuroscience*, *9*(3), 378–391. https://doi.org/10.1162/jocn.1997.9.3.378

Barrett, A. M., & Craver-lemley, C. E. (2008). Is it what you see, or how you say it? Spatial bias in young and aged subjects. *Journal of the International Neuropsychological Society*, *14*(4), 562–570. https://doi.org/10.1017/S1355617708080764

Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychological Bulletin*, *91*(2), 276–292. https://doi.org/10.1037/0033-2909.91.2.276

Bellgrove, M. A., Dockree, P. M., Aimola, L., & Robertson, I. H. (2004). Attenuation of spatial attentional asymmetries with poor sustained attention. *NeuroReport*, *15*(6), 1065–1069. https://doi.org/10.1097/00001756-200404290-00027

Bellgrove, M. A., Eramudugolla, R., Newman, D. P., Vance, A., & Mattingley, J. B. (2013). Influence of attentional load on spatial attention in acquired and developmental disorders of attention. *Neuropsychologia*, *51*(6), 1085–1093. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2013.01.019

Benwell, C. S. Y., Harvey, M., Gardner, S., & Thut, G. (2013). Stimulus- and state-dependence of systematic bias in spatial attention: Additive effects of stimulus-size and time-on-task. *Cortex*, *49*(3), 827–836. https://doi.org/10.1016/j.cortex.2011.12.007

Benwell, C. S. Y., Harvey, M., & Thut, G. (2014). On the neural origin of pseudoneglect: EEG-correlates of shifts in line bisection performance with manipulation of line length. *NeuroImage*, *86*, 370–380. https://doi.org/10.1016/j.neuroimage.2013.10.014

Benwell, C. S. Y., Thut, G., Grant, A., & Harvey, M. (2014). A rightward shift in the visuospatial attention vector with healthy aging. *Frontiers in Aging Neuroscience*, *6*(JUN), 1–11. https://doi.org/10.3389/fnagi.2014.00113

Benwell, C. S. Y., Thut, G., Learmonth, G., & Harvey, M. (2013). Spatial attention: Differential shifts in pseudoneglect direction with time-on-task and initial bias support the idea of observer subtypes. *Neuropsychologia*, *51*(13), 2747–2756. https://doi.org/10.1016/j.neuropsychologia.2013.09.030

Beste, C., Hamm, J. P., & Hausmann, M. (2006). Developmental changes in visual line bisection in women throughout adulthood. *Developmental Neuropsychology*, *30*(2), 753–767. https://doi.org/10.1207/s15326942dn3002_6

Bonato, M. (2015). Unveiling residual, spontaneous recovery from subtle hemispatial neglect three years after stroke. *Frontiers in Human Neuroscience*, *9*, 413. https://doi.org/10.3389/fnhum.2015.00413

Bonato, M., Spironelli, C., Lisi, M., Priftis, K., & Zorzi, M. (2015). Effects of Multimodal Load on Spatial Monitoring as Revealed by ERPs. *PLOS ONE*, *10*(9), e0136719. https://doi.org/10.1371/journal.pone.0136719

Borgo, M., Soranzo, A., & Grassi, M. (2012). *MATLAB for Psychologists*. *MATLAB for Psychologists*. New York, NY: Springer New York. https://doi.org/10.1007/9781461421979

Bowen, A., Hazelton, C., Pollock, A., & Lincoln, N. B. (2013). Cognitive rehabilitation for spatial neglect following stroke. *Cochrane Database of Systematic Reviews*, *2013*(7). https://doi.org/10.1002/14651858.CD003586.pub3

Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: effects of hemispace on a tactile line bisection task. *Neuropsychologia*, *18*(4–5), 491–498. https://doi.org/10.1016/0028-3932(80)90151-7

Brache, K., Scialfa, C., & Hudson, C. (2010). Aging and Vigilance: Who Has the Inhibition Deficit? *Experimental Aging Research*, *36*(2), 140–152. https://doi.org/10.1080/03610731003613425

Bradshaw, J. L., Bradshaw, J. A., Nathan, G., Nettleton, N. C., & Wilson, L. E. (1986). Leftwards error in bisecting the gap between two points: Stimulus quality and hand effects. *Neuropsychologia*, *24*(6), 849–855. https://doi.org/10.1016/0028-3932(86)90084-9

Braun, J. G., & Kirk, A. (1999). Line bisection performance of normal adults: Two subgroups with opposite biases. *Neurology*, *53*(3), 527–527. https://doi.org/10.1212/wnl.53.3.527

Brodie, E. E., & Pettigrew, L. E. L. (1996). Is left always right? Directional deviations in visual line bisection as a function of hand and initial scanning direction. *Neuropsychologia*, *34*(5), 467–470. https://doi.org/10.1016/0028-3932(95)00130-1

Brooks, J. L., Darling, S., Malvaso, C., & Della Sala, S. (2016). Adult developmental trajectories of pseudoneglect in the tactile, visual and auditory modalities and the influence of starting position and stimulus length. *Brain and Cognition*, *103*, 12–22. https://doi.org/10.1016/j.bandc.2015.12.001

Brooks, J. L., Sala, S. Della, & Darling, S. (2014). Representational pseudoneglect: A review. *Neuropsychology Review*, *24*(4), 148–165. https://doi.org/10.1007/s11065-013-9245-2

Brosnan, M. B., Demaria, G., Petersen, A., Dockree, P. M., Robertson, I. H., & Wiegand, I. (2018). Plasticity of the Right-Lateralized Cognitive Reserve Network in Ageing. *Cerebral Cortex*, *28*(5), 1749–1759. https://doi.org/10.1093/cercor/bhx085

Buysse, D. J., Monk, T. H., Carrier, J., & Begley, A. (2005). Circadian Patterns of Sleep, Sleepiness, and Performance in Older and Younger Adults. *Sleep*, *28*(11), 1365–1376. https://doi.org/10.1093/sleep/28.11.1365

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, *17*(1), 85–100. https://doi.org/10.1037/0882-7974.17.1.85

Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*, *17*(3), 1394–1402. https://doi.org/10.1006/nimg.2002.1280

Cabeza, R., Daselaar, S. M., Dolcos, F., Prince, S. E., Budde, M., & Nyberg, L. (2004). Task-independent and Task-specific Age Effects on Brain Activity during Working Memory, Visual Attention and Episodic Retrieval. *Cerebral Cortex*, *14*(4), 364–375. https://doi.org/10.1093/cercor/bhg133

Cabeza, R., Grady, C. L., McIntosh, A. R., Tulving, E., Kapur, S., Jennings, J. M., … Houle, S. (1997). Age-related differences in neural activity during memory encoding and retrieval: A positron emission tomography study. *Journal of Neuroscience*, *17*(1), 391–400. https://doi.org/10.1523/JNEUROSCI.17-01-00391.1997

Carriere, J. S. A., Cheyne, J. A., Solman, G. J. F., & Smilek, D. (2010). Age trends for failures of sustained attention. *Psychology and Aging*, *25*(3), 569–574. https://doi.org/10.1037/a0019363

Chandrakumar, D., Keage, H. A. D., Gutteridge, D., Dorrian, J., Banks, S., & Loetscher, T. (2019). Interactions between Spatial Attention and Alertness in Healthy Adults: A Meta-Analysis. *Cortex*. https://doi.org/10.1016/J.CORTEX.2019.03.016

Chen, J., & Niemeier, M. (2017). Altered perceptual pseudoneglect in ADHD: Evidence for a functional disconnection from early visual activation. *Neuropsychologia*, *99*(March), 12–23.

https://doi.org/10.1016/j.neuropsychologia.2017.02.022

Chen, P., Goedert, K. M., Murray, E., Kelly, K., Ahmeti, S., & Barrett, A. M. (2011). Spatial bias and right hemisphere function: Sex-specific changes with aging. *Journal of the International Neuropsychological Society*, *17*(3), 455–462. https://doi.org/10.1017/S135561771100004X

Chen, Y. C., & Spence, C. (2017). Hemispheric asymmetry: Looking for a novel signature of the modulation of spatial attention in multisensory processing. *Psychonomic Bulletin and Review*, *24*(3), 690–707. https://doi.org/10.3758/s13423-016-1154-y

Cicek, M., Deouell, L., & Knight, R. (2009). Brain activity during landmark and line bisection tasks. *Frontiers in Human Neuroscience*, *3*(May), 7. https://doi.org/10.3389/neuro.09.007.2009

Clark, V. P., & Hillyard, S. A. (1996). Spatial Selective Attention Affects Early Extrastriate But Not Striate Components of the Visual Evoked Potential. *Journal of Cognitive Neuroscience*, *8*(5), 387–402. https://doi.org/10.1162/jocn.1996.8.5.387

Colenbrander, A., & Fletcher, D. C. (2005). The MIXED CONTRAST Reading card, a new Screening Test for Contrast Sensitivity. *International Congress Series*. https://doi.org/10.1016/j.ics.2005.05.212

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The Reorienting System of the Human Brain: From Environment to Theory of Mind. *Neuron*, *58*(3), 306–324. https://doi.org/10.1016/J.NEURON.2008.04.017

Corbetta, M., & Shulman, G. L. (2011). *Spatial Neglect and Attention Networks*. *Annual Review of Neuroscience* (Vol. 34). Annual Reviews . https://doi.org/10.1146/annurev-neuro-061010-113731

Costa, T. L., Nogueira, R. M. T. B. L., Pereira, A. G. F., & Santos, N. A. (2013). Differential effects of aging on spatial contrast sensitivity to linear and polar sine-wave gratings. *Brazilian Journal of Medical and Biological Research*, *46*(10), 855–860. https://doi.org/10.1590/1414-431X20133117

Coull, J. ., Frackowiak, R. S. ., & Frith, C. . (1998). Monitoring for target objects: activation of right frontal and parietal cortices with increasing time on task. *Neuropsychologia*, *36*(12), 1325–1334. https://doi.org/10.1016/S0028-3932(98)00035-9

Cowie, R., & Hamill, G. (2011). Variation among Nonclinical Subjects on a Line-Bisection Task. *Perceptual and Motor Skills*, *86*(3), 834–834. https://doi.org/10.2466/pms.1998.86.3.834

Culham, J. C., Cavanagh, P., & Kanwisher, N. G. (2001). Attention response functions: characterizing brain areas using fMRI activation during parametric variations of attentional load. *Neuron*, *32*(4), 737–745. https://doi.org/10.1016/S0896-6273(01)00499-8

De Agostini, M., Curt, F., Tzortzis, C., & Dellatolas, G. (1999). Comparing left and right hand in line bisection at different ages. *Developmental Neuropsychology*, *15*(3), 379–394. https://doi.org/10.1080/87565649909540756

de Schotten, M. T., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, *14*(10), 1245–1246. https://doi.org/10.1038/nn.2905

Dellatolas, G., Vanluchene, J., & Coutin, T. (1996). Visual and motor components in simple line bisection: an investigation in normal adults. *Cognitive Brain Research*, *4*(1), 49–56. https://doi.org/10.1016/0926-6410(96)00019-5

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/J.JNEUMETH.2003.10.009

Dobler, V. B., Anker, S., Gilmore, J., Robertson, I. H., Atkinson, J., & Manly, T. (2005). Asymmetric deterioration of spatial awareness with diminishing levels of alertness in normal children and children with ADHD. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *46*(11), 1230–1248. https://doi.org/10.1111/j.1469-7610.2005.00421.x

Dodds, C. M., van Belle, J., Peers, P. V., Dove, A., Cusack, R., Duncan, J., & Manly, T. (2008). The Effects of Time-on-Task and Concurrent Cognitive Load on Normal Visuospatial Bias. *Neuropsychology*, *22*(4), 545–552. https://doi.org/10.1037/0894-4105.22.4.545

Dolcos, F., Rice, H. J., & Cabeza, R. (2002). Hemispheric asymmetry and aging: Right hemisphere decline or asymmetry reduction. *Neuroscience and Biobehavioral Reviews*, *26*(7), 819–825. https://doi.org/10.1016/S0149-7634(02)00068-4

Donchin, E. (1981). Surprise!? Surprise? *Psychophysiology*, *18*(5), 493–513. https://doi.org/10.1111/j.1469-8986.1981.tb01815.x

Dufour, A., Touzalin, P., & Candas, V. (2007). Time-on-task effect in pseudoneglect. *Experimental Brain Research*, *176*(3), 532–537. https://doi.org/10.1007/s00221-006-0810-2

Eardley, A. F., Darling, S., Dumper, P., Browne, D., & Velzen, J. Van. (2017). Brain and Cognition Related but different : Examining pseudoneglect in audition , touch and vision. *Brain and Cognition*, *113*, 164–171. https://doi.org/10.1016/j.bandc.2017.01.011

Elliott, S., & Werner, J. (2010). Age-related changes in contrast gain related to the M and P pathways. *Journal of Vision*, *9*(8), 1071–1071. https://doi.org/10.1167/9.8.1071

Failla, C. V., Sheppard, D. M., & Bradshaw, J. L. (2003). Age and responding-hand related changes in performance of neurologically normal subjects on the line-bisection and chimeric-faces tasks. *Brain and Cognition*, *52*(3), 353–363. https://doi.org/10.1016/S0278-2626(03)00181-7

Falkenstein, M., Hoormann, J., & Hohnsbein, J. (2002). Inhibition-Related ERP Components: Variation with Modality, Age, and Time-on-Task. *Http://Dx.Doi.Org/10.1027//0269-8803.16.3.167*. https://doi.org/10.10270269-8803.16.3.167

Fimm, B., Willmes, K., & Spijkers, W. (2006). The effect of low arousal on visuo-spatial attention. *Neuropsychologia*, *44*(8), 1261–1268. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2006.01.027

Fjell, A. M., & Walhovd, K. B. (2004). Life-span changes in P3a. *Psychophysiology*, *41*(4), 575–583. https://doi.org/10.1111/j.1469-8986.2004.00177.x

Foxe, J. J., McCourt, M. E., & Javitt, D. C. (2003). Right hemisphere control of visuospatial attention: line-bisection judgments evaluated with high-density electrical mapping and source analysis☆. *NeuroImage*, *19*(3), 710–726. https://doi.org/10.1016/S1053-8119(03)00057-0

Friedman, D. (2003). Cognition and Aging: A Highly Selective Overview of Event-Related Potential (ERP) Data. *Journal of Clinical and Experimental Neuropsychology*, *25*(5), 702–720. https://doi.org/10.1076/jcen.25.5.702.14578

Friedrich, T. E., Hunter, P. V., & Elias, L. J. (2016). Developmental trajectory of pseudoneglect in adults using the greyscales task. *Developmental Psychology*, *52*(11), 1937–1943. https://doi.org/10.1037/dev0000202

Friedrich, T. E., Hunter, P. V., & Elias, L. J. (2018). The Trajectory of Pseudoneglect in Adults: A Systematic Review. *Neuropsychology Review*, *28*(4), 436–452. https://doi.org/10.1007/s11065-018-9392-6

Fujii, T., Fukatsu, R., Yamadori, a, & Kimura, I. (1995). Effect of age on the line bisection test. *Journal of Clinical and Experimental Neuropsychology*, *17*(6), 941–944. https://doi.org/10.1080/01688639508402443

Fukatsu, R., Fujii, T., Kimura, I., Saso, S.-I., & Kogure, K. (1990). Effects of hand and spatial conditions on visual line bisection. *The Tohoku Journal of Experimental Medicine*, *161*(4), 329–333. https://doi.org/10.1620/tjem.161.329

Giambra, L. M. (1989). Task-unrelated-thought frequency as a function of age: a laboratory study. *Psychology and Aging*, *4*(2), 136–143. https://doi.org/10.1037/0882-7974.4.2.136

Gilmore, R. (1995). Evoked potentials in the elderly. *Journal of Clinical Neurophysiology : Official Publication of the American Electroencephalographic Society*, *12*(2), 132–138. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7797627

Goedert, K. M., Leblanc, A., Tsai, S. W., & Barrett, A. M. (2010). Asymmetrical effects of adaptation to left- and right-Shifting prisms depends on pPre-existing attentional biases. *Journal of the International Neuropsychological Society*, *16*(5), 795–804. https://doi.org/10.1017/S1355617710000597

Grady, C. L., Bernstein, L. J., Beig, S., & Siegenthaler, A. L. (2002). The effects of encoding task on age-related differences in the functional neuroanatomy of face memory. *Psychology and Aging*, *17*(1), 7–23. https://doi.org/10.1037/0882-7974.17.1.7

Green, J. J., Teder-Sälejärvi, W. A., & McDonald, J. J. (2005). Control mechanisms mediating shifts of attention in auditory and visual space: a spatio-temporal ERP analysis. *Experimental Brain Research*, *166*(3–4), 358–369. https://doi.org/10.1007/s00221-005-2377-8

Halligan, P. W., Manning, L., & Marshall, J. C. (1990). Individual variation in line bisection: A study of four patients with right hemisphere damage and normal controls. *Neuropsychologia*, *28*(10), 1043–1051. https://doi.org/10.1016/0028-3932(90)90139-F

Harvey, M., Milner, A. D., & Roberts, R. C. (1995). An Investigation of Hemispatial Neglect Using the Landmark Task. *Brain and Cognition*, *27*(1), 59–78. https://doi.org/10.1006/BRCG.1995.1004

Hatin, B., Sykes Tottenham, L., & Oriet, C. (2012). The relationship between collisions and pseudoneglect: is it right? *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *48*(8), 997–1008. https://doi.org/10.1016/j.cortex.2011.05.015

Heber, I. A., Siebertz, S., Wolter, M., Kuhlen, T., & Fimm, B. (2010). Horizontal and vertical pseudoneglect in peri- and extrapersonal space. *Brain and Cognition*, *73*(3), 160–166. https://doi.org/10.1016/j.bandc.2010.04.006

Heilman, K., Bowers, D., Valenstein, E., & Watson, R. T. (1987). Hemispace and hemispatial neglect. In *Advances in Psychology* (Vol. 45, pp. 115–150). North-Holland. https://doi.org/10.1016/S0166-4115(08)61711-2

Heilman, K. M., & Abell, T. V. D. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, *30*(3), 327–327. https://doi.org/10.1212/WNL.30.3.327

Heilman, K., & Valenstein, E. (1979). Mechanisms underlying hemispatial neglect. *Annals of Neurology*, *5*(2), 166–170. https://doi.org/10.1002/ana.410050210

Heilman, K., & Van Den Abell, T. (1979). Right hemispheric dominance for mediating cerebral activation. *Neuropsychologia*, *17*(3–4), 315–321. https://doi.org/10.1016/0028-3932(79)90077-0

Hertzog, C., & Rypma, B. (1991). Age differences in components of mental-rotation task performance. *Bulletin of the Psychonomic Society*, *29*(2), 209–212. https://doi.org/10.3758/BF03335237

Hess, T. M., Emery, L., & Neupert, S. D. (2012). Longitudinal relationships between resources, motivation, and functioning. *The Journals of Gerontology. Series B, Psychological Sciences and Social Sciences*, *67*(3), 299–308. https://doi.org/10.1093/geronb/gbr100

Hilgetag, C. C., Théoret, H., & Pascual-leone, A. (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced “virtual lesions” of human parietal cortex. *Nature Neuroscience*, *4*(9), 953–957. https://doi.org/10.1038/nn0901-953

Hoekstra, R., Morey, R. D., Rouder, J. N., & Wagenmakers, E. J. (2014). Robust misinterpretation of confidence intervals. *Psychonomic Bulletin and Review*, *21*(5), 1157–1164. https://doi.org/10.3758/s13423-013-0572-3

Huang, C. M., Polk, T. A., Goh, J. O., & Park, D. C. (2012). Both left and right posterior parietal activations contribute to compensatory processes in normal aging. *Neuropsychologia*, *50*(1), 55–66. https://doi.org/10.1016/j.neuropsychologia.2011.10.022

Ishihara, S. (1918). Tests for color blindness: By Dr. Shinobu Ishihara, Major, I. J. A. M. C., Tokyo, Japan. Sixteen colored plates with explanatory text. Tokyo, 1917. *American Journal of Ophthalmology*, *1*(5), 376. https://doi.org/10.5555/URI:PII:S000293941890663X

Jackson, J. D., & Balota, D. A. (2012). Mind-wandering in younger and older adults: converging evidence from the Sustained Attention to Response Task and reading for comprehension. *Psychology and Aging*, *27*(1), 106–119. https://doi.org/10.1037/a0023933

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*(1), 93–110. https://doi.org/10.1016/S0028-3932(99)00045-7

Jongen, E. M. M., Smulders, F. T. Y., & Van der Heiden, J. S. H. (2007). Lateralized ERP components related to spatial orienting: Discriminating the direction of attention from processing sensory aspects of the cue. *Psychophysiology*, *44*(6), 968–986. https://doi.org/10.1111/j.1469-8986.2007.00557.x

Kinsbourne, M. (1977). Hemi-neglect and hemisphere rivalry. *Advances in Neurology*, *18*, 41–49. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/920524

Krawietz, S. A., Tamplin, A. K., & Radvansky, G. A. (2012). Aging and mind wandering during text comprehension. *Psychology and Aging*, *27*(4), 951–958. https://doi.org/10.1037/a0028831

Kutas, M., Iragui, V., & Hillyard, S. A. (1994). Effects of aging on event-related brain potentials (ERPs) in a visual detection task. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *92*(2), 126–139. https://doi.org/10.1016/0168-5597(94)90053-1

Learmonth, G., Benwell, C. S. Y., Thut, G., & Harvey, M. (2017). Age-related reduction of hemispheric lateralisation for spatial attention: An EEG study. *NeuroImage*, *153*(April), 139–151. https://doi.org/10.1016/j.neuroimage.2017.03.050

Learmonth, G., Felisatti, F., Siriwardena, N., Checketts, M., Benwell, C. S. Y., Märker, G., … Harvey, M. (2017). No Interaction between tDCS Current Strength and Baseline Performance: A Conceptual Replication. *Frontiers in Neuroscience*, *11*, 664. https://doi.org/10.3389/fnins.2017.00664

Learmonth, G., Gallagher, A., Gibson, J., Thut, G., & Harvey, M. (2015). Intra-and inter-task reliability of spatial attention measures in pseudoneglect. *PLoS ONE*, *10*(9), e0138379. https://doi.org/10.1371/journal.pone.0138379

Learmonth, G., Gallagher, A., Gibson, J., Thut, G., & Harvey, M. (2018). Correction: Intra- and Inter-Task Reliability of Spatial Attention Measures in Pseudoneglect. *PLOS ONE*, *13*(10), e0205269. https://doi.org/10.1371/journal.pone.0205269

Learmonth, G., Märker, G., McBride, N., Pellinen, P., & Harvey, M. (2018). Right-lateralised lane keeping in young and older British drivers. *PLoS ONE*, *13*(9), 1–17. https://doi.org/10.1371/journal.pone.0203549

Learmonth, G., Thut, G., Benwell, C. S. Y., & Harvey, M. (2015). The implications of state-dependent tDCS effects in aging: Behavioural response is determined by baseline performance. *Neuropsychologia*, *74*, 108–119. https://doi.org/10.1016/j.neuropsychologia.2015.01.037

Lisi, M., Bonato, M., & Zorzi, M. (2015). Pupil dilation reveals top-down attentional load during spatial monitoring. *Biological Psychology*, *112*, 39–45. https://doi.org/10.1016/J.BIOPSYCHO.2015.10.002

Liu, H., Stufflebeam, S. M., Sepulcre, J., Hedden, T., & Buckner, R. L. (2009). Evidence from intrinsic activity that asymmetry of the human brain is controlled by multiple factors. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(48), 20499–20503. https://doi.org/10.1073/pnas.0908073106

Liu, K. P. Y., Hanly, J., Fahey, P., Fong, S. S. M., & Bye, R. (2019). A Systematic Review and Meta-Analysis of Rehabilitative Interventions for Unilateral Spatial Neglect and Hemianopia Poststroke From 2006 Through 2016. *Archives of Physical Medicine and Rehabilitation*, *100*(5), 956–979. https://doi.org/10.1016/j.apmr.2018.05.037

Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-Recruitment and Nonselective Recruitment: Dissociable Neural Mechanisms Associated with Aging. *Neuron*, *33*(5), 827–840. https://doi.org/10.1016/S0896-6273(02)00612-8

Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, *44*(6), 977–981. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2005.09.003

Longo, M. R., & Lourenco, S. F. (2007). Spatial attention and the mental number line: Evidence for characteristic biases and compression. *Neuropsychologia*, *45*(7), 1400–1407. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2006.11.002

Longo, M. R., & Lourenco, S. F. (2010). Bisecting the mental number line in near and far space. *Brain and Cognition*, *72*(3), 362–367. https://doi.org/10.1016/J.BANDC.2009.10.016

Longo, M. R., Trippier, S., Vagnoni, E., & Lourenco, S. F. (2015). Right hemisphere control of visuospatial attention in near space. *Neuropsychologia*, *70*, 350–357. https://doi.org/10.1016/j.neuropsychologia.2014.10.035

Loureiro-Silva, M., D'Almeida, O. ., Mateus, C., Oliveiros, B., & Castelo-Branco, M. (2010). The effect of normal development and aging on low-level visual field asymmetries. *Poster*, *2010*, 72029.

Lourenco, S. F., & Longo, M. R. (2009). The plasticity of near space: Evidence for contraction. *Cognition*, *112*(3), 451–456. https://doi.org/10.1016/J.COGNITION.2009.05.011

Lucci, G., Berchicci, M., Spinelli, D., Taddei, F., & Di Russo, F. (2013). The Effects of Aging on Conflict Detection. *PLoS ONE*, *8*(2), e56566. https://doi.org/10.1371/journal.pone.0056566

Luck, S. J. (1995). Multiple mechanisms of visual-spatial attention: recent evidence from human electrophysiology. *Behavioural Brain Research*, *71*(1–2), 113–123. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8747179

Luh, K. E. (1995). Line bisection and perceptual asymmetries in normal individuals: What you see is not what you get. *Neuropsychology*, *9*(4), 435–448. https://doi.org/10.1037/0894-4105.9.4.435

Madden, D. J., Spaniol, J., Whiting, W. L., Bucur, B., Provenzale, J. M., Cabeza, R., … Huettel, S. A. (2007). Adult age differences in the functional neuroanatomy of visual attention: A combined fMRI and DTI study. *Neurobiology of Aging*, *28*(3), 459–476. https://doi.org/10.1016/j.neurobiolaging.2006.01.005

Maillet, D., Beaty, R. E., Jordano, M. L., Touron, D. R., Adnan, A., Silvia, P. J., … Kane, M. J. (2018). Age-related differences in mind-wandering in daily life. *Psychology and Aging*, *33*(4), 643-653. https://doi.org/10.1037/pag0000260

Mangun, G., Hillyard, S., & Luck, S. (1993). Electrocortical substrates of visual selective attention. Retrieved from https://psycnet.apa.org/record/1993-97600-009

Manly, T., Dobler, V. B., Dodds, C. M., & George, M. A. (2005). Rightward shift in spatial awareness with declining alertness. *Neuropsychologia*, *43*(12), 1721–1728. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2005.02.009

Manning, L., Halligan, P. W., & Marshall, J. C. (1990). Individual variation in line bisection: A study of normal subjects with application to the interpretation of visual neglect. *Neuropsychologia*, *28*(7), 647–655. https://doi.org/10.1016/0028-3932(90)90119-9

Mattes, S. (2003). The Lane Change Task as a Tool For Driver Distraction Evaluation. *Quality of Work and Products in Enterprises of the Future*, 1–30. Retrieved from http://apps.usd.edu/coglab/schieber/ppt/MATTES2003-powerpoint.pdf

Matthias, E., Bublak, P., Costa, A., Müller, H. J., Schneider, W. X., & Finke, K. (2009). Attentional and sensory effects of lowered levels of intrinsic alertness. *Neuropsychologia*, *47*(14), 3255–3264. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2009.08.004

Mattingley, J. B., Berberovic, N., Corben, L., Slavin, M. J., Nicholls, M. E. R., & Bradshaw, J. L. (2004). The greyscales task: A perceptual measure of attentional bias following unilateral hemispheric damage. *Neuropsychologia*, *42*(3), 387–394. https://doi.org/10.1016/j.neuropsychologia.2003.07.007

McCourt, M. E., & Jewell, G. (1999). Visuospatial attention in line bisection: stimulus modulation of pseudoneglect. *Neuropsychologia*, *37*(7), 843–855. https://doi.org/10.1016/S0028-3932(98)00140-7

McGrath, C., & Morrison, J. D. (1981). THE EFFECTS OF AGE ON SPATIAL FREQUENCY PERCEPTION IN HUMAN SUBJECTS. *Quarterly Journal of Experimental Physiology*, *66*(3), 253–261. https://doi.org/10.1113/expphysiol.1981.sp002554

McVay, J. C., Meier, M. E., Touron, D. R., & Kane, M. J. (2013). Aging ebbs the flow of thought: Adult age differences in mind wandering, executive control, and self-evaluation. *Acta Psychologica*, *142*(1), 136–147. https://doi.org/10.1016/J.ACTPSY.2012.11.006

Mesulam, M. M. (1999). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *354*(1387), 1325–1346. https://doi.org/10.1098/rstb.1999.0482

Milner, a. D., Brechmann, M., & Pagliarini, L. (1992). To halve and to halve not: An analysis of line bisection judgements in normal subjects. *Neuropsychologia*, *30*(6), 515–526. https://doi.org/10.1016/0028-3932(92)90055-Q

Naert, L., Bonato, M., & Fias, W. (2018). Asymmetric Spatial Processing Under Cognitive Load. *Frontiers in Psychology*, *9*(April), 583. https://doi.org/10.3389/fpsyg.2018.00583

Nagamatsu, L. S., Carolan, P., Liu-Ambrose, T. Y. L. L., & Handy, T. C. (2011). Age-related changes in the attentional control of visual cortex: A selective problem in the left visual hemifield. *Neuropsychologia*, *49*(7), 1670–1678. https://doi.org/10.1016/j.neuropsychologia.2011.02.040

Nagamatsu, L. S., Liu-Ambrose, T. Y. L., Carolan, P., & Handy, T. C. (2009). Are impairments in visual-spatial attention a critical factor for increased falls risk in seniors? An event-related potential study. *Neuropsychologia*, *47*(13), 2749–2755. https://doi.org/10.1016/j.neuropsychologia.2009.05.022

Nagamatsu, L. S., Munkacsy, M., Liu-Ambrose, T., & Handy, T. C. (2013). Altered visual-spatial attention to task-irrelevant information is associated with falls risk in older adults. *Neuropsychologia*, *51*(14), 3025–3032. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2013.10.002

Nakajima, A., Ichikawa, H., Nakagawa, O., Majima, A., & Watanabe, M. (1960). Ishihara Test in Color-Vision Defects*. *American Journal of Ophthalmology*, *49*(5), 921–929. https://doi.org/10.1016/0002-9394(60)91811-0

Nasreddine, Z., Charbonneau, S., & Cummings, J. L. (2005). The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*(4), 695–699. https://doi.org/10.1111/j.1532-5415.2005.53221.x

Natale, E., Marzi, C. A., Girelli, M., Pavone, E. F., & Pollmann, S. (2006). ERP and fMRI correlates of endogenous and exogenous focusing of visual-spatial attention. *European Journal of Neuroscience*, *23*(9), 2511–2521. https://doi.org/10.1111/j.1460-9568.2006.04756.x

Nebes, R. D., Buysse, D. J., Halligan, E. M., Houck, P. R., & Monk, T. H. (2009). Self-Reported Sleep Quality Predicts Poor Cognitive Performance in Healthy Older Adults. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *64B*(2), 180–187. https://doi.org/10.1093/geronb/gbn037

Newman, D. P., O'Connell, R. G., & Bellgrove, M. A. (2013). Linking time-on-task, spatial bias and hemispheric activation asymmetry: A neural correlate of rightward attention drift. *Neuropsychologia*, *51*(7), 1215–1223. https://doi.org/10.1016/j.neuropsychologia.2013.03.027

Nicholls, M. E. ., Bradshaw, J. L., & Mattingley, J. B. (1999). Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size. *Neuropsychologia*, *37*(3), 307–314. https://doi.org/10.1016/S0028-3932(98)00074-8

Nicholls, M. E. R., Hadgraft, N. T., Chapman, H. L., Loftus, A. M., Robertson, J., & Bradshaw, J. L. (2010). A hit-and-miss investigation of asymmetries in wheelchair navigation. *Attention, Perception, and Psychophysics*, *72*(6), 1576–1590. https://doi.org/10.3758/APP.72.6.1576

Nicholls, M. E. R., Loftus, A., Mayer, K., & Mattingley, J. B. (2007). Things that go bump in the right: The effect of unimanual activity on rightward collisions. *Neuropsychologia*, *45*(5), 1122–1126. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2006.07.015

Niemeier, M., Stojanoski, B., & Greco, A. L. (2007). Influences of time and spatial frequency on the perceptual bias: Evidence for competition between hemispheres. *Neuropsychologia*, *45*(5), 1029–1040. https://doi.org/10.1016/j.neuropsychologia.2006.09.006

Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus--norepinephrine system. *Psychological Bulletin*, *131*(4), 510–532. https://doi.org/10.1037/0033-2909.131.4.510

Nijboer, T. C. W., Kollen, B. J., & Kwakkel, G. (2013). Time course of visuospatial neglect early after stroke: A longitudinal cohort study. *Cortex*, *49*(8), 2021–2027. https://doi.org/10.1016/j.cortex.2012.11.006

O’Connell, R. G., Balsters, J. H., Kilcullen, S. M., Campbell, W., Bokde, A. W., Lai, R., … Robertson, I. H. (2012). A simultaneous ERP/fMRI investigation of the P300 aging effect. *Neurobiology of Aging*, *33*(10), 2448–2461. https://doi.org/10.1016/J.NEUROBIOLAGING.2011.12.021

O’Connell, R. G., Schneider, D., Hester, R., Mattingley, J. B., & Bellgrove, M. A. (2011). Attentional Load Asymmetrically Affects Early Electrophysiological Indices of Visual Orienting. *Cerebral Cortex*, *21*(5), 1056–1065. https://doi.org/10.1093/cercor/bhq178

Olk, B., & Harvey, M. (2002). Effects of visible and invisible cueing on line bisection and Landmark performance in hemispatial neglect. *Neuropsychologia*, *40*(3), 282–290. https://doi.org/10.1016/S0028-3932(01)00095-1

Paladini, R. E., Diana, L., Nyffeler, T., Mosimann, U. P., Nef, T., & Müri, R. M. (2016). The asymmetrical influence of increasing time-on-task on attentional disengagement. *Neuropsychologia*, *92*, 107–114. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2016.02.026

Partala, T., & Surakka, V. (2003). Pupil size variation as an indication of affective processing. *International Journal of Human-Computer Studies*, *59*(1–2), 185–198. https://doi.org/10.1016/S1071-5819(03)00017-X

Paus, T., Zatorre, R. J., Hofle, N., Caramanos, Z., Gotman, J., Petrides, M., & Evans, A. C. (1997). Time-related changes in neural systems underlying attention and arousal during the performance of an auditory vigilance task. *Journal of Cognitive Neuroscience*, *9*(3), 392–408. https://doi.org/10.1162/jocn.1997.9.3.392

Peers, P. V., Cusack, R., & Duncan, J. (2006). Modulation of spatial bias in the dual task paradigm: Evidence from patients with unilateral parietal lesions and controls. *Neuropsychologia*, *44*(8), 1325–1335. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2006.01.033

Pérez, A., Peers, P. V., Valdés-Sosa, M., Galán, L., García, L., & Martínez-Montes, E. (2009). Hemispheric modulations of alpha-band power reflect the rightward shift in attention induced by enhanced attentional load. *Neuropsychologia*, *47*(1), 41–49. https://doi.org/10.1016/j.neuropsychologia.2008.08.017

Petit, L., Zago, L., Mellet, E., Jobard, G., Crivello, F., Joliot, M., … Tzourio-Mazoyer, N. (2015). Strong rightward lateralization of the dorsal attentional network in left-handers with right sighting-eye: An evolutionary advantage. *Human Brain Mapping*, *36*(3), 1151–1164. https://doi.org/10.1002/hbm.22693

Piazza, E. A., & Silver, M. A. (2017). Relative spatial frequency processing drives hemispheric asymmetry in conscious awareness. *Frontiers in Psychology*, *8*(APR), 1–7. https://doi.org/10.3389/fpsyg.2017.00559

Picton, T. W., Stuss, D. T., Champagne, S. C., & Nelson, R. F. (1984). The Effects of Age on Human Event-Related Potentials. *Psychophysiology*, *21*(3), 312–326. https://doi.org/10.1111/j.1469-8986.1984.tb02941.x

Polich, J. (1996). Meta-analysis of P300 normative aging studies. *Psychophysiology*, *33*(4), 334–353. https://doi.org/10.1111/j.1469-8986.1996.tb01058.x

Polich, J. (1997). On the relationship between EEG and P300: individual differences, aging, and ultradian rhythms. *International Journal of Psychophysiology*, *26*(1–3), 299–317. https://doi.org/10.1016/S0167-8760(97)00772-1

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019

Polich, J., & Criado, J. R. (2006). Neuropsychology and neuropharmacology of P3a and P3b. *International Journal of Psychophysiology*, *60*(2), 172–185. https://doi.org/10.1016/j.ijpsycho.2005.12.012

Polich, J., & Kok, A. (1995). Cognitive and biological determinants of P300: an integrative review. *Biological Psychology*, *41*(2), 103–146. https://doi.org/10.1016/0301-0511(95)05130-9

Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. https://doi.org/10.1080/00335558008248231

Ptak, R. (2012). The frontoparietal attention network of the human brain: Action, saliency, and a priority map of the environment. *Neuroscientist*, *18*(5), 502–515. https://doi.org/10.1177/1073858411409051

Reuter-Lorenz, P. A., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, *17*(3), 177–182. https://doi.org/10.1111/j.1467-8721.2008.00570.x

Reuter-Lorenz, P. A., Jonides, J., Smith, E. E., Hartley, A., Miller, A., Marshuetz, C., & Koeppe, R. A. (2000). Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *Journal of Cognitive Neuroscience*, *12*(1), 174–187. https://doi.org/10.1162/089892900561814

Reuter-Lorenz, P. A., & Park, D. C. (2010). Human neuroscience and the aging mind: A new look at old problems. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, *65 B*(4), 405–415. https://doi.org/10.1093/geronb/gbq035

Roberts, R., & Turnbull, O. H. (2010). Putts that get missed on the right: Investigating lateralized attentional biases and the nature of putting errors in golf. *Journal of Sports Sciences*, *28*(4), 369–374. https://doi.org/10.1080/02640410903536467

Robertson, I. H. (2013). A noradrenergic theory of cognitive reserve: implications for Alzheimer's disease. *Neurobiology of Aging*, *34*(1), 298–308. https://doi.org/10.1016/J.NEUROBIOLAGING.2012.05.019

Robertson, I. H. (2014). A right hemisphere role in cognitive reserve. *Neurobiology of Aging*, *35*(6), 1375–1385. https://doi.org/10.1016/J.NEUROBIOLAGING.2013.11.028

Robertson, I. H., Mattingley, J. B., Rorden, C., & Driver, J. (1998). Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature*, *395*(6698), 169–172. https://doi.org/10.1038/25993

Robinson, D. L., & Kertzman, C. (1990). Visuospatial attention: Effects of age, gender, and spatial reference. *Neuropsychologia*, *28*(3), 291–301. https://doi.org/10.1016/0028-3932(90)90022-G

Rode, G., Pagliari, C., Huchon, L., Rossetti, Y., & Pisella, L. (2017). Semiology of neglect: An update. *Annals of Physical and Rehabilitation Medicine*, *60*(3), 177–185. https://doi.org/10.1016/j.rehab.2016.03.003

Rossini, P. M., Rossi, S., Babiloni, C., & Polich, J. (2007). Clinical neurophysiology of aging brain: From normal aging to neurodegeneration. *Progress in Neurobiology*, *83*(6), 375–400. https://doi.org/10.1016/J.PNEUROBIO.2007.07.010

Santos, N. A., Simas, M. L. B., & Nogueira, R. M. T. B. L. (2004). *Comparison of angular frequency contrast sensitivity in young and older adults*. *Brazilian Journal of Medical and Biological Research* (Vol. 37). Retrieved from http://www.scielo.br/pdf/bjmbr/v37n3/5128.pdf

Schmitz, R., Dehon, H., & Peigneux, P. (2013). Lateralized processing of false memories and pseudoneglect in aging. *Cortex*, *49*(5), 1314–1324. https://doi.org/10.1016/j.cortex.2012.06.005

Schmitz, R., Deliens, G., Mary, A., Urbain, C., & Peigneux, P. (2011). Selective modulations of attentional asymmetries after sleep deprivation. *Neuropsychologia*, *49*(12), 3351–3360.

https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2011.08.009

Schmitz, R., & Peigneux, P. (2011). Age-related changes in visual pseudoneglect. *Brain and Cognition*, *76*(3), 382–389. https://doi.org/10.1016/j.bandc.2011.04.002

Schwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R. J., & Driver, J. (2005). Attentional Load and Sensory Competition in Human Vision: Modulation of fMRI Responses by Load at Fixation during Task-irrelevant Stimulation in the Peripheral Visual Field. *Cerebral Cortex*, *15*(6), 770–786. https://doi.org/10.1093/cercor/bhh178

Seiss, E., Gherri, E., Eardley, A. F., & Eimer, M. (2007). Do ERP components triggered during attentional orienting represent supramodal attentional control? *Psychophysiology*, *44*(6), 987–990. https://doi.org/10.1111/j.1469-8986.2007.00591.x

Smith, G. A., & Brewer, N. (1985). Age and individual differences in correct and error reaction times. *British Journal of Psychology*, *76*(2), 199–203. https://doi.org/10.1111/j.2044-8295.1985.tb01943.x

Stam, C. J., & Bakker, M. (1990). The prevalence of neglect: superiority of neuropsychological over clinical methods of estimation. *Clinical Neurology and Neurosurgery*, *92*(3), 229–235. https://doi.org/10.1016/0303-8467(90)90025-Z

Starns, J. J., & Ratcliff, R. (2010). The effects of aging on the speed-accuracy compromise: Boundary optimality in the diffusion model. *Psychology and Aging*, *25*(2), 377–390. https://doi.org/10.1037/a0018022

Starns, J. J., & Ratcliff, R. (2012). Age-related differences in diffusion model boundary optimality with both trial-limited and time-limited tasks. *Psychonomic Bulletin & Review*, *19*(1), 139–145. https://doi.org/10.3758/s13423-011-0189-3

Staub, B., Doignon-Camus, N., Bacon, É., & Bonnefond, A. (2014). The effects of aging on sustained attention ability: An ERP study. *Psychology and Aging*, *29*(3), 684–695. https://doi.org/10.1037/a0037067

Staub, B., Doignon-Camus, N., Després, O., & Bonnefond, A. (2013). Sustained attention in the elderly: What do we know and what does it tell us about cognitive aging? *Ageing Research Reviews*, *12*(2), 459–468. https://doi.org/10.1016/j.arr.2012.12.001

Stern, Y., Alexander, G. E., Prohovnik, I., & Mayew, R. (1992). *Inverse Rehtionshp Between Education and Parietotemporal Perfusion Deficit in Alzheimer's Disease*. Retrieved from https://onlinelibrary.wiley.com/doi/pdf/10.1002/ana.410320311

Sturm, W., & Willmes, K. (2001). On the Functional Neuroanatomy of Intrinsic and Phasic Alertness. *NeuroImage*, *14*(1), S76–S84. https://doi.org/10.1006/NIMG.2001.0839

Sutton, S., Braren, M., Zubin, J., & John, E. R. (1965). Evoked-Potential Correlates of Stimulus Uncertainty. *Science*, *150*(3700), 1187–1188. https://doi.org/10.1126/science.150.3700.1187

Swan, E. F., Hutchinson, C. V., Everard, M., & Shimozaki, S. S. (2015). Aging effects in cueing tasks as assessed by the ideal observer: Peripheral cues. *Journal of Vision*, *15*(2), 5–5. https://doi.org/10.1167/15.2.5

Takio, F., Koivisto, M., & Hämäläinen, H. (2014). The influence of executive functions on spatial biases varies during the lifespan. *Developmental Cognitive Neuroscience*, *10C*, 170–180. https://doi.org/10.1016/j.dcn.2014.09.004

Taylor, M. J. (2002). Non-spatial attentional effects on P1. *Clinical Neurophysiology*, *113*(12), 1903–1908. https://doi.org/10.1016/S1388-2457(02)00309-7

Thomas, N. A., Churches, O., White, I., Mohr, C., Schrag, Y., Obucina, S., & Nicholls, M. E. R. (2017). An investigation of left/right driving rules on deviations while walking. *PLOS ONE*, *12*(10), e0186171. https://doi.org/10.1371/journal.pone.0186171

Thomas, N. A., Loetscher, T., & Nicholls, M. E. R. (2014). Asymmetries in attention as revealed by fixations and saccades. *Experimental Brain Research*, *232*(10), 3253–3267. https://doi.org/10.1007/s00221-014-4015-9

Tomporowski, P. D., & Tinsley, V. F. (1996). Effects of Memory Demand and Motivation on Sustained Attention in Young and Older Adults. *The American Journal of Psychology*, *109*(2), 187. https://doi.org/10.2307/1423272

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*(1), 97–136. https://doi.org/10.1016/0010-0285(80)90005-5

Turnbull, O. H., Carey, D. P., & McCarthy, Rosaleen, A. (1997). The neuropsychology of object constancy. *Journal of the International Neuropsychological Society*, *3*, 288–298. Retrieved from https://www.cambridge.org/core/product/18FD9D95D299E32B536C2DDE6EDA75B8

Varnava, A., McCarthy, M., & Beaumont, J. G. (2002). Line bisection in normal adults: direction of attentional bias for near and far space. *Neuropsychologia*, *40*(8), 1372–1378. https://doi.org/10.1016/S0028-3932(01)00204-4

Varnava, Alice, & Halligan, P. W. (2007). Influence of Age and Sex on Line Bisection: A Study of

Normal Performance with Implications for Visuospatial Neglect. *Aging, Neuropsychology, and Cognition*, *14*(6), 571–585. https://doi.org/10.1080/13825580600826454

Verdon, V., Schwartz, S., Lovblad, K.-O., Hauert, C.-A., & Vuilleumier, P. (2010). Neuroanatomy of hemispatial neglect and its functional components: a study using voxel-based lesion-symptom mapping. *Brain*, *133*(3), 880–894. https://doi.org/10.1093/brain/awp305

Verleger, R. (2008). P3b: Towards some decision about memory. *Clinical Neurophysiology*, *119*(4), 968–970. https://doi.org/10.1016/J.CLINPH.2007.11.175

Veronelli, L., Vallar, G., Marinelli, C. V., Primativo, S., & Arduino, L. S. (2014). Line and word bisection in right-brain-damaged patients with left spatial neglect. *Experimental Brain Research*, *232*(1), 133–146. https://doi.org/10.1007/s00221-013-3726-7

Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, *37*(2), 190–203. https://doi.org/10.1111/1469-8986.3720190

Weintraub, S., & Mesulam, M.-M. (1987). Right Cerebral Dominance in Spatial Attention. *Archives of Neurology*, *44*(6), 621. https://doi.org/10.1001/archneur.1987.00520180043014

West, R., Schwarb, H., & Johnson, B. N. (2010). The influence of age and individual differences in executive function on stimulus processing in the oddball task. *Cortex*, *46*(4), 550–563. https://doi.org/10.1016/J.CORTEX.2009.08.001

Wiegand, I., Töllner, T., Dyrholm, M., Müller, H. J., Bundesen, C., & Finke, K. (2014). Neural correlates of age-related decline and compensation in visual attention capacity. *Neurobiology of Aging*, *35*(9), 2161–2173. https://doi.org/10.1016/J.NEUROBIOLAGING.2014.02.023

Wilcox, R. R., & Keselman, H. J. (2003). Modern Robust Data Analysis Methods: Measures of Central Tendency. *Psychological Methods*, *8*(3), 254–274. https://doi.org/10.1037/1082-989X.8.3.254