Age-related changes in attentional modulation during dynamic attributes of visual attention

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Abstract

Age-related changes in vision (such as decline in visual acuity, contrast sensitivity, temporal resolution, spatial resolution and visual motion processing) and cognition (such as slowing of the information processing system) are a factor of normal, healthy ageing. This thesis investigated the application of attentional modulation during perceptual tasks involving temporal order judgement and motion discrimination. The main aim was to discover if there are any differences in the ways that young and older adults utilise attentional resources. When provided with training to use attentional cues, young and older adults showed enhanced performance during temporal order discrimination. Age differences were identified in the way that the two age groups utilised attentional resources, where older adults used the cues at lower levels of task difficulty compared to young adults. Age differences in attentional modulation were supported by fMRI results which indicated that older adults were utilising a different cortical network to that of young adults to modulate sensory processing in motion specific regions both when attention was focused on the prevailing task, and when attention was divided between two tasks concurrently.

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CHAPTER 1

General Introduction

1.1 Abstract

Age-related changes in vision (such as decline in visual acuity, contrast sensitivity, temporal resolution, spatial resolution and visual motion processing) and cognition (such as slowing of the information processing system) are present during normal, healthy ageing. Compared to young adults, older adults experience decreased performance on some perceptual tasks. It has been suggested that brain functionality changes throughout the ageing process in order to compensate for age-related changes in lower level sensory abilities (Cabeza, 2002; Grady et al., 2006; Spreng et al., 2010). Such changes may reflect the employment of different strategies in the ageing brain, which allows the maintenance of perceptual performance (Cabeza, 2002; Stern, 2009). Some of these age-related adaptations occur in the executive functioning regions of the brain, regions responsible for focused and divided attention (Cabeza, 2002; Madden, 2007; Reuter-Lorenz & Cappell, 2008).

Whilst there is evidence of age-related changes in cortical activity and perceptual and cognitive performance in the literature, the abilities are maintained usefully throughout the lifespan. This thesis attempts to address what strategies (behavioural and cortical) are employed to make this possible. The thesis was also concerned with whether the deployment of attention can enable older adults to improve their perceptual performance to a level comparable with young adults.

The following introductory chapter will review and discuss the literature surrounding age-related changes in visual processing and how attention serves to modulate such processes for both young and older adults.

1.2 Theories of visual processing

Traditional theories of visual processing have proposed that visual information passes through several hierarchical stages of visual cortex, from primary visual cortex to higher order areas (Rumelhart, 1970). Such feed forward models of visual processing state that visual features are initially extracted in lower-level areas (V1 and V2), where neurons first process local information, and are later passed to higher-level regions, where a visual representation of the input image is obtained (Van Essen and Maunsell, 1983).

More recent research has emphasized that the visual system also passes information back through the cortex, from higher to lower visual areas. Such integrated models of visual perception describe information being passed through the cortex in both a feed forward and feed-back manner (Bullier, 2001). For this purpose, visual information is first directed from primary visual cortex to the prefrontal and parietal cortices, where it is rapidly processed. The processed information is then back-projected to lower visual areas where it is sent on to be integrated into feed forward processing stages in the temporal cortex (Bullier, 2001; Bar, 2003).

Results from neuroimaging studies have demonstrated that attention can modulate neural activity from a very early point (as early as V1) of processing in the visual cortex, which suggests top-down influences via feedback projections (Bar et al., 2001, Bar, 2003). Results from the above experiments have led to the suggestion that the visual cortex makes

predictions based on partial information from incoming stimuli. Bar et al. (2001) suggested that the inferior frontal gyrus may have a role in the processing of visual stimuli that is briefly presented, as activity in this region was greater when input images were masked compared to non-masked items. Participants were significantly more successful at recognising non-masked objects compared to masked objects, and associated brain activity was found in inferior frontal regions during trials when masked objects were correctly recognised. This reflects cortical feed-back processes, in that the inferior frontal regions appeared to be modulating object recognition related regions. Furthermore, in conditions where recognition is difficult, top-down processes may enable successful recognition, and this process may activate before full recognition has occurred. Such facilitation implies that higher-level information is activated earlier than some relevant lower-level information (Bar, 2003).

1.3 The effects of normal ageing on low level visual processes

Distinct spatial frequency bandwidths (i.e. high and low spatial frequencies) contain differing information about the properties of a perceived image. Spatial frequency is the frequency at which alternating light and dark bands repeat in cycles across the visual stimulus. The spatial frequency content of the stimulus consists of the amplitude of light and dark information available, at differing frequencies, across the width of the stimulus (Campbell and Robson, 1968). Low spatial frequencies carry coarse information about the global structure of the input stimulus, whereas high spatial frequencies encode complex information about the perceived image, such as edges. High spatial frequencies allow a more detailed analysis by revealing characteristic features, and thus more accurate recognition of the incoming visual stimulus (Owsley et al., 1983).

At approximately 40 years of age, a person's contrast sensitivity begins to decline rapidly (Owsley et al., 1981). Contrast sensitivity at high spatial frequencies declines rapidly with advancing age; this is due to physiological changes in the eye (Owsley et al, 1983; Pardhan, 2004), for example, optical and structural changes (Gittings and Fozard, 1986). However, it has been documented that many healthy older adults also require greater contrast to detect gratings of low and intermediate spatial frequencies than young adults, and that this is likely to be due to neurological changes (Owsley et al, 1983), such as neural reorganisation within the retina and the cortex (Pardhan, 2004, Blake et al., 2008).

1.4 Attention during low level visual processing

During everyday visual events, the retina may be stimulated by several object images at any one time, which will include both task relevant and irrelevant objects. Selective attention provides a method of prioritizing what will be represented and what will be ignored (Desimone and Duncan, 1995).

Posner (1980) described the focus of spatial attention as a spotlight, which serves to enhance the processing of stimuli within a given region of space. Spatial attention can be overt, where the focus of attention is changed by the observer moving their eyes, or covert, where attention is deployed to a specific location without the use of eye-movements (Posner, 1980). Covert attention can be deployed to more than one location simultaneously and is thought to precede eye-movements (Kowler, 2011). There are two main systems of covert spatial attention: endogenous and exogenous. The endogenous system (drives attention top-down) is voluntarily activated and refers to the observer's ability to knowingly monitor information at a given location. The exogenous system (attention is driven bottom-up) is involuntary and refers to an automatic orienting response to abrupt changes in the visual

display (Posner 1980). Exogenous attention activates neurons in parietal areas, whereas, endogenous attention activates superior frontal regions (Corbetta et al, 1993).

Covert attention enables the observer to monitor the surrounding environment and to direct their gaze towards abrupt changes in the visual display (Posner, 1980), which improves perceptual performance in many laboratory based tasks such as discrimination and detection, and has important implications in daily human behaviours, such as driving, playing sports, searching for objects and crossing the road (Kowler, 2011).

The biased competition model (Desimone & Duncan, 1995) states that the strength of a representation is weaker when target item is presented alongside many other items than when it is presented in isolation, which leads to a competition for processing capacity between relevant and non-relevant stimuli (Beck & Kastner, 2009). Desimone and Duncan (1995) suggested that this bottom-up bias will influence what is selected from the visual array via sensory enhancement, where activation of attention improves processing of an early sensory representation by making relevant stimuli more salient.

When an observer attends to a particular location in the visual scene, neurons encoding information from that region become more active whilst neurons encoding different regions show a decline in activity (Desimone & Duncan, 1995). Features of a stimulus compete for control of neuronal resources; such competition can be influenced by directed attention. According to the biased competition model, there are two sources of incoming information that enable a stimulus to be processed at the expense of other competing stimuli: bottom-up information derived from the physical characteristics of the stimulus and top-down information based on the behavioural goals of the observer.

Bottom-up attentional processes are driven by the characteristics of the target stimulus, enabling the observer to detect objects on the basis of the sensory salience of target stimuli (Sarter et al., 2001). Early selection models of visual attention (e.g. Broadbent, 1958) argue that unattended items do not receive processing beyond their basic characteristics, that is, the selective filter ignores unattended items.

Other theories have argued that all incoming information is processed for meaning prior to selection (e.g. Deutsch and Deutsch, 1963), where information is selected on the basis of its relevance at a given time. Here, attention can be shifted from one source of information to another, depending on the relevance of the information to the task at hand.

Top-down attention is a knowledge driven mechanism that is used to enhance cortical processing of task relevant stimuli, which enables the observer to distinguish between target objects and non-relevant items (Sarter et al, 2001). Top-down attention mechanisms are widely thought to be a component of executive functions, mediated by frontal cortical regions (Posner and Petersen, 1990). Anterior cortical attention mechanisms are said to detect a target's characteristic features, while posterior attentional regions are thought to orient the observer to possible target sources (Posner, 1994).

Buschman and Miller (2007) demonstrated that bottom-up signals that are automatically generated by salient stimuli activate parietal regions, whereas top-down signals derived from task demands lead to initial activation in the frontal cortex, which then feeds back into sensory regions to assist processing. However, during the majority of perceptual tasks, bottom-up processes work together with top-down processes in order to enable optimal attentional performance.

It has been suggested that attentional control is critical for the maintenance of task-relevant goals (Braver and Barch, 2002), and is necessary during many demanding perceptual and cognitive tasks (e.g. maintaining two sources of information in working memory simultaneously (Verhaeghen and Cerella, 2002)). Attentional control is also required when

additional, task-irrelevant, information needs to be inhibited in order to successfully perform a task, for example, ignoring incongruent distracter information and focusing on task relevant elements of a display (Hasher and Zacks, 1988).

Research has demonstrated that the level of task demand can influence whether or not irrelevant information is attended to. Lavie (1995) described the Load Theory of Attention, which states that the ability to ignore irrelevant stimuli depends on the level of task load provided by the prevailing task. Tasks containing high levels of load lead to attentional resources being used up, leaving less resources available to process additional material. Tasks containing low levels of load require less attentional modulation and therefore free up cognitive resources, allowing for the processing of additional stimuli. This effect was demonstrated for stimuli that are spatially separate from the target, where during low load conditions, participants were found to involuntarily process task-irrelevant stimuli; but not during high load conditions (Lavie, 2005). However, more recent research (Taya, et al. 2009) has demonstrated that, when target and distracter are presented in the same location, the level of task load applied to the target does not affect processing of distracting elements. The authors argued that task-relevant information can be selectively attended to whilst suppressing task-irrelevant information.

fMRI research has demonstrated that top-down attentional regions in frontal cortex work to increase modulation in sensory areas during perceptual tasks (Kastner and Ungerleider, 2000). A network of frontoparietal cortical regions appears to mediate performance during detection tasks that require additional attention. Dorsal regions within this network are implicated in top-down attentional guidance, and ventral regions mediate bottom-up attention (Madden, 2007). Neuroimaging research has revealed that predictive visual processing proceeds from the frontal areas to lower level visual areas (Bar et al., 2006). In a combined fMRI and magnetoencephalography (MEG) study, they presented participants with

outline drawings or photographs of familiar objects or animals (comprising both low and high spatial frequency information). Participants responded by pressing a key when they recognised an object. fMRI was used to discover which areas are activated by high spatial frequencies and which by low spatial frequencies, by contrasting activity associated with high frequency components to that related to low frequency components. MEG was used to identify the temporal onset of activation. Results indicated that the right orbito-frontal cortex was activated 50ms before the right fusiform gyrus (the task specific sensory region). Furthermore, activity in the orbitofrontal cortex differed in its response to high compared to low spatial frequency stimuli. The authors concluded that specific regions within frontal cortex provide initial hypotheses of the most likely candidate objects to be considered by the temporal cortex. They suggested that low spatial frequency information reaches those frontal regions before it reaches lower visual areas, in order to back-project an initial guess of the objects identity.

1.5 Age-related changes in the use of attentional modulation

Older adults may use additional attentional mechanisms in order to carry out more complex sensory processing, for example, the inhibition of irrelevant information (Hasher & Zacks, 1988). Madden et al (2004) used fMRI to investigate age-related changes in cortical activity during visual detection. Participants responded as to whether an incoming stimulus was a target (circle), a standard (filled square) or a novel item (greyscale photograph of an everyday item). Responses to the standard and novel items were made using the same key-press (no response shift); however, in order to respond to the target, participants had to make a different key-press (response shift). In order to be successful, participants had to inhibit the standard response when a target was shown (and make the different response). Behavioural accuracy performance was equal for both age groups; however, older adults were slower to respond

throughout. Responding to targets elicited activation in frontal regions, including middle frontal gyrus, for both age groups. Responses to novel stimuli evoked activity in occipital regions, which was significantly greater in young compared to older adults. The task interaction of target > novels elicited activation in regions associated with executive control, including superior and middle frontal gyri, motor cortex and cingulate cortex, which was found to be similar for both young and older adults. Older adults also showed significantly greater activity in deep grey-matter regions, suggesting that they may have had to recruit additional resources to offset the reduced activity in visual regions.

Grady et al (1994) measured age-related changes in regional cerebral blood flow using PET. Older and young adults performed a face matching task, where they made judgements about which of two faces (a target and a distracter) was the same as the test face; and a location matching task, where they decided which of two dot locations (target and distracter) was the same as the test location. Older adults were slower than young adults during both tasks; however, there were no age differences in accuracy performance during either task. Young adults exhibited greater activity in visual areas, compared to older adults, whereas, older adults evoked greater activity in frontal and inferior parietal regions. Increased recruitment of frontal regions in older adults compared to young adults could be explained as a compensatory mechanism to counteract age-related changes in sensory processing.

Results from neuroimaging studies conducted on older adults have indicated an agerelated change within the frontoparietal network. Such research has highlighted that activity in the frontal lobes had a tendency to increase as a function of adult age (Cabeza et al., 2000). It is thought that this increased activity may be a result of age-related decline in the quality of bottom-up sensory input, which could promote an increased reliance on top-down attentional guidance in older adults (Whiting et al., 2005). Furthermore, Madden (2007) suggested that such degradation of the sensory input may actually lead to a top-down attentional compensatory mechanism in older adults during visual processing. Such facilitation could imply that higher-level information is being accessed earlier than some relevant lower-level information.

The compensation hypothesis (Cabeza, 2002) describes age-related additional neural recruitment from regions not typically recruited by young adults during a given task. Specifically, this new recruitment should be accompanied by more superior performance in older adults, or performance that is equated with that of young adults, in order to be described as compensatory. Evidence from neuroimaging studies has indicated that activity in frontal cortex typically shows less asymmetry than in young adults. This phenomenon has been termed Hemispheric Asymmetry Reduction in OLD Adults (HAROLD) (Cabeza, 2002). Increased bilateral activity in the older brain could improve performance in some cognitive tasks and even reduce age-related decline in some cognitive processes (Reuter-Lorenz and Cappell, 2008, Cabeza, 2002, Grady et al., 1994) by providing compensatory activity that may act to offset age-related changes in perceptual processing (Grady et al., 1994).

Increased activation in the older brain is said to be compensatory when older adults are performing the same task at the same level of performance as young adults but are recruiting different regions to that of young adults, and that this pattern of recruitment leads to maintained or improved performance in older adults (Cabeza et al., 2002, Grady et al., 2006, Grady, 2008). An alternative explanation is that as activity in the sensory region decreases, activity in frontal regions show an increase (Madden et al., 2004).

The cognitive reserve (CR) model promotes the idea that the ageing brain adjusts to declines in neural functioning by increasing recruitment of pre-existing cognitive processes used by young adults and that this increased recruitment of the similar network may lead to preservation of some cognitive abilities, although less efficiently (Stern, 2002). It has been

suggested that the ability of the older brain to cope with age-related changes may be influenced by social, intellectual and educational factors across the life span, for example, higher educational achievement, increased literacy and life-long learning, which can all lead to more cognitive reserve in older adults (Stern, 2009).

The Compensation-Related Utilisation of Neural Circuits Hypothesis (CRUNCH) postulated by Reuter-Lorenz and Cappell (2008) describes an increase in cortical activation as a result of increasing task load. It has been demonstrated that this pattern of activity is present in both young and older adults. As task load increases, young adults typically show an increase in activation of asymmetric prefrontal regions that 'spills over' into bilateral regions. Older adults show the same increase in activation at lower levels of task difficulty. When the task exceeds the difficulty threshold of older adults, task performance is reduced and associated cortical activity decreases (Reuter-Lorenz & Cappel, 2008; Schneider-Garces et al., 2009).

The scaffolding theory of ageing and cognition (Park and Reuter-Lorenz, 2009) proposes that, as cognitive ability declines, activation in pre-frontal regions increases in the older brain. The theory suggests that this increase in frontal recruitment reflects age-related adaptive cortical mechanisms which serve to maintain cognitive abilities in the face of structural and functional decline in other areas of the cortex. Cognitive scaffolding is not merely an effect of normal ageing, it is a process that is present at all ages and serves to aid cognition in challenging circumstances, such as when learning a new set of skills (e.g. learning a new hobby). Once the new set of skills has been thoroughly learned, and less effort is needed to exercise them, the learner becomes skilled at the task. The neural circuits involved in learning the new task now become a specialised network, optimally tuned to performing the task. This forms the basis for scaffolding. Park and Reuter-Lorenz (2009)

suggested that access to such scaffolding may explain the ability of older adults to have preserved cognitive function when faced with neuronal and structural decline.

1.6 Age-related changes in cortical function and structure

In interpreting results from fMRI studies, care must be exercised when drawing comparisons between different age groups as there is an age-related change in cerebral blood flow (D'Esposito et al., 2003). In order to account for this, experiments using distinct age groups avoid making direct comparisons of baseline activity by carrying out task interactions, which measure relative change from the baseline in both age groups.

fMRI uses the hemodynamic (blood flow) response of the body, and measures the blood oxygen level dependent (BOLD) signal. Therefore, instead of measuring a direct neurophysiological signal, MRI methods make an assumption that neural activity and blood flow are correlated. Although this method does not provide a direct measurement of neurophysiological signals, evidence from experiments combining fMRI with electrophysiological recordings indicate that the BOLD signal provides a close reflection of cortical neural activity (Logothetis et al., 2001, Logothetis and Pfeuffer, 2004).

During the ageing process the human brain experiences several detrimental structural changes; such as losses in synaptic connectivity, demyelination (Raz and Rodrigue, 2006), loss of white matter integrity (Madden et al., 2009) and shrinkage of grey matter density (Sowell et al., 2003). Sowell et al (2003) used MRI and cortical matching algorithms to map grey matter density across participants ranging in age from 7 – 87 years. They found age-related grey matter decline in the insula and superior parietal cortices, and in the most dorsal parts of the frontal and parietal regions. Madden et al. (2009) used Diffusion Tensor Imaging

to compare young and older adults' white matter integrity. Their results indicated that agerelated decline in white matter integrity was most prominent in frontal regions.

Such age-related changes in the structure and neuronal function of the cortex can lead to reduced ability in many aspects of cognition, such as a slowing of processing speed (Salthouse, 1996), deficits in attentional control and inhibitory processes (Hasher & Zacks, 1988), declines in the function of working memory (Grady et al., 1998) and declines in perceptual processing (Grady et al., 1994; Madden et al., 2004). The frontal lobe theory of ageing states that age-related changes to the structure and function of the frontal lobes are related to changes in cognition throughout the life-span (Buckner, 2004, Raz, 2000). As noted previously, regions in frontal cortex have been shown to exhibit different patterns of activity in young and older adults (e.g. Cabeza, 2002; Grady et al, 2006; Reuter-Lorenz & Cappell, 2008; Spreng et al, 2010). Whilst there is evidence of age-related changes in cortical activity and perceptual and cognitive performance in the literature, the abilities are maintained usefully throughout the lifespan. This thesis attempts to address what strategies (behavioural and cortical) are employed to make this possible.

1.7 Aims of the thesis

This thesis investigated the application of attentional modulation during perceptual tasks. The main aim was to discover if there are any differences in the ways that young and older adults utilise attentional resources. For example, whether attention is recruited on a larger scale by older compared to young adults. The experiments described within the first section of this thesis explored performance over varying levels of task difficulty to see if attention is engaged at lower levels of task difficulty by older compared to young adults. The thesis was

also concerned with whether the deployment of attention can enable older adults to improve their perceptual performance to a level comparable with young adults.

This chapter has provided an introductory overview of the themes explored within this thesis. Each of the following chapters contains its own more extensive review of specifically related research.

1.8 Overview of chapters

Chapter 2: This chapter examines age-related differences in temporal order processing and explores if cross-modally symbolic tones have an effect on attentional modulation during such processes. Young and older participants are tested with and without the presence of cross-modally symbolic auditory tones, to investigate whether or not there is a natural tendency to associate congruent information from different modalities.

Chapter 3: This chapter investigates the benefits of training participants to more effectively use symbolic auditory cues during temporal order discrimination. The employment of different strategies at different levels of task difficulty is also explored.

Chapter 4: This chapter extends the research conducted in chapter 3 by investigating age differences in training efficacy, and if such training evokes different strategies among young and older adults. The chapter also explores age-related differences in the use of attention at different levels of task difficulty.

Chapter 5: This chapter investigates age-related differences in the allocation of focused and divided attention during perceptual tasks. The underlying neuronal networks are also investigated via fMRI and connectivity analysis. Age-related differences in modulation of task specific sensory regions are also explored.

Chapter 6: The final chapter summarises the findings in this thesis, and brings together contributions from each of the chapters to give a greater understanding of the role of attentional modulation during dynamic vision throughout the ageing process.

CHAPTER 2

Age-related differences in temporal resolution and cross-modal integration effects

2.1 Abstract

This chapter is the first in a series of chapters investigating age differences in attentional modulation during temporal order judgement. This and the next four chapters investigate methods that may serve to improve temporal order performance for both young and older observers.

The first experiment in this chapter used temporal order judgement to test young and older adults' ability to judge which of two simple shape stimuli were presented first (one low spatial frequency filtered and the other high spatial frequency filtered). The two stimuli were separated at varying stimulus onset asynchronies and presented at three different levels of contrast. The findings indicated that young adults were more accurate at judging which of the shapes appeared first than were older adults. Performance in both age groups improved as a function of increasing SOA and of increasing contrast.

The second experiment in this chapter sought to identify if there was any naturally occurring bias to cross-modally congruent auditory tones. The findings indicated that young adults made more accurate decisions about which stimulus was shown first when the auditory tone was congruent compared to incongruent. This suggests that there is a naturally occurring association between the low pitch tone and low spatial frequency stimulus and the high pitch tone and high spatial frequency stimulus for young adults. Older adults showed no significant differences in use of congruent and incongruent tones.

2.2 Perception of temporal order

Temporal order judgement (TOJ) refers to the processing of sequentially successive events. A vast amount of research has been focussed on studying human temporal resolution, which is thought to underlie behavioural abilities in perception, language, memory and control of movement (for a review, see Pöppel 2004). During TOJ tasks, observers make judgements about the order in which two stimuli are presented (typically indicating which stimulus was presented first), separated by varying stimulus onset asynchronies (SOAs). Temporal order is not easily discriminated at SOAs less than 100ms (Jaskowski & Verleger, 2000). Timing at such short scales (sub-second) is automatic, whereas timing at longer scales (seconds, minutes) is due to cognitive processes (Pöppel, 1994).

The human visual system is unable to distinguish succession if two visual events are separated by onset asynchronies of less than 20ms (Hirsh & Sherrick, 1961, but also see Kanabus et al., 2002, who found the separation to be about 40ms). The same threshold has been reported for visual, auditory and tactile modalities (Hirsh & Sherrick, 1961), suggesting that there is a central timing mechanism controlling the perception of temporal order (Pöppel, 1994). The central timing mechanism is said to create high-frequency temporal processing units via neuronal oscillations of about 40Hz (Pöppel, 1994, 2004). Each time a stimulus is processed (visual, auditory or tactile), a neuronal oscillation occurs, which lasts approximately 30ms. If both stimuli are presented within one oscillation (SOAs of less than 30ms), they are perceived as occurring at the same time (Madler et al., 1991).

2.3 Age-related changes in the perception of temporal order

Recent research has provided evidence that older adults are less accurate than young adults at temporal order judgement and temporal gap detection (Humes et al., 2009, Busey et al., 2010). Humes et al (2009) tested young and older adults during a visual temporal gap detection paradigm. Participants were presented with LED light box sequences (display devices which emitted a red light at a predefined rate of separation) containing one standard and two test intervals. One of the intervals included a temporal gap, the size of which was varied adaptively to measure threshold gap size. Participants responded verbally as to which interval contained the temporal gap. Older adults were found to have significantly longer gap detection thresholds than young observers.

Busey et al. (2010) tested young (18-30 years), middle aged (40-55 years) and older (60-88 years) adults during a temporal order judgement experiment. Participants were presented with pairs of letter stimuli at six different SOAs. The task was to report what side (left or right) a letter was first detected. Critical durations (the shortest SOA at which participants could reliably perform the task) were measured for each age group and indicted that young adults could distinguish temporal order at 25.5ms, middle-aged adults at 39.6ms, and older adults at 75.8ms. Results for temporal order judgement accuracy indicated that young adults made significantly more accurate judgements than both middle-aged and older adults, and middle-aged adults were significantly more accurate than older adults.

The performance of older adults during temporal order judgement may be affected by decline in several different aspects of cognition, such as memory and response functions (Busey et al, 2010), general age-related temporal slowing (Salthouse, 1996), and decline in processing at the sensory level (Madden, 2007). It has been reported that age-related decline in cognitive factors such as alertness, intellectual abilities and vigilance contribute to age-

related decline in TOJ performance (Syzmaszek, Sereda, Pöppel & Szelag, 2009). However, other research has demonstrated that the human brain can adapt to decline and impairments in a way that it can compensate for losses in some abilities (Stern, 2003). This concept is termed cognitive reserve, which is an active process wherein a particular decline or impairment can be offset by recruiting other brain regions in a compensatory manner. Factors used to determine an individual's level of cognitive reserve are level of education, intellectual abilities, lifestyle, occupational status, and the participation in leisure, social, cognitive and educational pursuits (Stern, 2009). Therefore, the more physically and cognitively active an individual is, the more likely they are to maintain certain abilities through increased cognitive reserve.

2.4 Effects of attention on TOJ

Research has demonstrated that directing attention to a target stimulus can improve temporal order judgement (Stelmach and Herdman, 1991). Participants were presented with two stimuli in fast succession, over various SOAs. The task was to decide which stimulus was presented first whilst attending to one of the stimuli (cued target). The findings suggested that even when both stimuli appeared at the same time (equal onset times) the cued stimulus was detected first. However, it has been argued that this finding may have been due to bias, rather than directed attention (Jaskowski, 1993). That is, when participants are given the opportunity to make a response indicating that the stimuli were presented simultaneously, the directed attention effect disappears, suggesting that the two-response paradigm introduced bias by forcing observers to make a judgement when stimulus timing was indistinguishable (Jaskowski, 1993). It is possible that the improvement in performance when stimuli were

simultaneously presented was not due to directed attention but to participants just using the information provided by the cue.

2.5 Cross-modal integration and performance enhancement

Evans and Treisman (2010) reported that human beings have a naturally occurring, cross-modal mapping mechanism, which enables them to attach verbal labels to visual stimuli (for example, soft lighting or a loud shirt); and that such cross-modal correspondences are possibly due to the modulation of multisensory cortical regions on the specific modalities, which serves to amplify the relationship between the corresponding pairs of cross-modal inputs.

In order for successful integration of cross-modal information to occur, stimuli from both modalities need to be presented within a limited temporal interval, which has been termed the temporal binding window (Stein & Meredith, 1993; Hairston et al., 2005). This temporal window serves as a filter that determines whether or not information from different modalities occurs in close enough proximity to allow multisensory integration (Colonius & Diederich, 2004). Multisensory induced facilitation of performance have been shown for visual and auditory stimuli separated in time by 100ms – 250ms, with the beneficial effects most prominent at separations of 100ms – 150ms (Hairston et al., 2005).

Cross-modal mapping has been studied using stimulus position as a variable. Patching and Quinlan (2002) demonstrated that observers made more accurate responses regarding the position of a stimulus when it was accompanied by a corresponding high or low tone (stimuli positioned in the top section of the screen + a high tone; stimuli in the lower section + a low tone).

Interestingly, this phenomena has also been reported when making classifications about spatial frequency stimuli, where the verbal labels 'high' and 'low' do not naturally correspond to the visual stimuli. A series of novel experiments by Evans and Treisman (2010) reported the first experimental evidence of cross-modal mapping with spatial frequency stimuli. Using a speeded classification paradigm, they tested auditory pitch for cross-modal mappings across four visual variables: position, size, spatial frequency and contrast. Uncertainty was introduced by making some of the audio-visual pairings incongruent. The experiments included a direct task, which tested the observers' ability to successfully pair the congruent cue with the visual stimulus (e.g. a small stimulus with a high tone), and an indirect task, in which observers made judgements about auditory and visual features that differed from those expected (e.g. whether the auditory stimulus was a violin or a piano and whether the visual stimulus was to the left or right of the display). Their findings provided support for previous research on cross-modal mapping for position and size of stimulus, but found no evidence of cross-modal mapping between pitch and contrast. Results for spatial frequency and pitch correspondence indicated that for both the direct and indirect tasks, the same effect of congruence was found whether observers were making judgements about the spatial frequency of gratings (direct task) or their orientation (indirect task). The authors suggested that this was due to an automatic correspondence between congruent auditory and visual stimuli, which enabled simultaneous processing of both modality stimuli as a whole, prior to separate classification.

The cross-modal congruency effect described above was only tested using young adults (<30 years). The present chapter addresses this limitation, by testing for the presence of cross-modal congruency between spatial frequency stimuli and corresponding auditory tones in both young and older adults.

2.6 Age differences in cross-modal integration

Recent research has indicated that older adults integrate cross-modal information more readily than young adults (Laurienti et al., 2006; Peiffer et al., 2007; Campbell et al., 2010, Diaconescu et al., 2013). During a two-alternative forced choice experiment, Laurienti et al. (2006) presented young and older participants with a visual stimulus, an auditory stimulus, or both. The task was to discriminate between the colours red and blue (shown as coloured discs in the visual display and as verbal recordings of the words 'red' and 'blue' in the auditory presentations). The results indicated that both young and older adults had faster reaction times to the combined audio-visual stimuli compared to the unisensory stimuli. However, this speeded response effect was found to be greater in older compared to young adults, suggesting that older adults were more able to successfully integrate the cross modal information of the cue to provide preparatory information related to the target.

In a related study, Peiffer et al. (2007) tested young and older adults' ability to detect a stimulus when presented in the visual domain (two green light emitting diodes) and in the auditory domain (broadband white noise). Participants were also presented with multisensory trials, where both the visual and auditory information were provided concurrently. The task was to indicate when a stimulus had been detected (either auditory or visual). Young and older adults showed statistically equivalent performance during unisensory presentations. During multisensory trials, older adults outperformed young adults by providing faster responses. The authors suggested that this superior effect of multisensory integration in older adults could be due to an age-related inability to suppress concurrent cross-modal information, which may lead to enhanced multisensory interactions.

The inefficient inhibitory mechanisms explanation (Peiffer et al., 2007) suggests that as well as enhanced integration with congruent cross-modal information, older adults are

more prone to integrating incongruent information more readily than young adults (Campbell et al, 2010). This is likely to result from a combination of declining sensory input, leading to a greater reliance on assistance from other available information (e.g. Cerella (1985)) and also age-related changes in cortical function (Grady et al, 1994; Diaconescu et al, 2013), which preclude original strategies used by young adults.

This chapter sets out to explore firstly, if there is a naturally occurring bias to congruent cross-modal information compared to incongruent information. Secondly, to examine if there are any age differences in correspondence of cross-modally congruent information; as some research has shown that this is the case (Peiffer et al., 2007), but other research has shown that older adults integrate cross-modal information whether it is congruent or incongruent (Campbell et al., 2010).

2.7 The use of spatial scale during visual processing

The paradigm employed in this chapter (and the following two chapters) uses spatial scale as a stimulus. This was chosen as there appears to be a cross-modal correspondence between spatial frequency and auditory tone (Evans & Treisman, 2010) and also because research has demonstrated that it is possible to cue observers to different channels of spatial frequency (Sowden et al., 2003; Ozgen et al., 2005. This will be discussed further in chapter 3).

There are differences in the way that the visual system processes information from high spatial frequency and low spatial frequency stimuli (Bar, 2003; Peyrin et al., 2010). There are also age-differences in the processing of high spatial frequency and low spatial frequency information (e.g. Pardhan, 2004). Research has indicated that low spatial frequency information is processed first and fast by the visual system by way of a feedback process,

controlled by a fast-projection through the magnocellular pathway to dorsal and ventral regions in the frontal cortex, which is then back-projected to lower order regions in the striate cortex (Bullier, 2001, Bar, 2003, Peyrin et al., 2010). A theory proposed by Bar (2003) states that incoming visual information is quickly passed from visual cortex directly to prefrontal cortical regions for rudimentary processing. This fast-tracking provides the observer with an initial set of possibilities as to what the incoming stimulus may be. High spatial frequency information is extracted more slowly and analysed by a cascading series of regions, this feed-forward mechanism is propelled by the slower parvocellular pathway from V1 and beyond into extra striate regions (Bullier, 2001).

Peyrin et al. (2010) used fMRI and ERP to investigate cortical activation associated with the processing of low and high spatial frequency information. Participants were presented with three categories of natural scenes (city, beach or indoor) which comprised of either high spatial frequency or low spatial frequency information. Two images of scenes were presented in rapid succession, either low followed by high, or high followed by low spatial frequencies (coarse to fine / fine to coarse). Half of the image pairs were of two scenes from the same category and the other half contained scenes from differing categories. The task was to decide if the two scenes were from the same category or different categories. They found more frontal, parietal and temporal activation associated with low spatial frequency processing and more occipital activation for high spatial frequency processing. Furthermore, analysis of the event-related potential (ERP) data revealed that this frontal activation occurred very soon after stimulus presentation (140-160ms). The authors concluded that low spatial frequency information in a scene quickly engages top-down attention via higher order frontal regions, which then feedback diagnostic information to lower level visual areas to allow processing of the high spatial frequency components of the scene.

2.8 Age differences in spatial frequency processing

An observer's ability to detect contrast is expressed as a contrast sensitivity function (CSF), which is contrast sensitivity as a function of spatial frequency. Contrast sensitivity declines as a function of normal ageing (Owsley et al, 1983). Due to physiological changes in the eye, contrast sensitivity at high spatial frequencies begins to decline rapidly from approximately 40 years of age, which leads to a greater reliance on the use low spatial frequency information to form more global representations of the incoming stimulus (Owsley et al, 1983). However, research has indicated that low spatial frequency processing also declines with advanced ageing, reflecting age-related changes at the neural level within different levels of the visual system (Pardhan, 2004).

Pardhan (2004) measured the contrast sensitivity of young and older adults using an external noise paradigm, in order to demonstrate the contribution of optical and neural effects to age-related decline in contrast sensitivity. Here, participants underwent a two-alternative temporal forced choice procedure, where they had to discriminate a signal + noise image from a noise alone image. Participants were required to judge which of the two intervals contained the signal + noise image. Signals were sinusoidal gratings of spatial frequencies at three levels: low (1 cycle / degree), medium (4 cycles / degree) and high (10 cycles / degree). The external noise paradigm enabled the measurement of two parameters, sampling efficiency (indicates how the incoming information is processed by the visual system) and equivalent noise (provides an indication of the internal noise of the visual system). Sampling efficiency is used to determine the degradation of higher-level processing sites, whereas equivalent noise is used to determine changes at the optical level. Findings revealed that age-related changes at the neural level account for contrast sensitivity loss at low and medium spatial frequencies,

whereas reduced sensitivity to high spatial frequencies was mediated by changes in optical mechanisms (for example, a decrease in the amount of light transmitted by the retina).

The processing of global versus local elements can be viewed as being analogous to the processing of low spatial frequencies and high spatial frequencies (Flevaris et al, 2011). The global precedence hypothesis proposes that visual processing of global aspects of an input stimulus occurs before the processing of local elements (Navon, 1977). Studies on the effects of ageing on global versus local processing have yielded contrasting results. Some research has found that the global precedence effect is present in both young and older adults (Roux and Ceccaldi, 2001). Other studies have found an age-related reduction in the advantage typically observed for global processing (Lux et al., 2008, Staudinger et al., 2011).

Lux et al (2008) demonstrated age differences in reaction times during the processing of global and local form. Young and older participants were presented with global (made up of local elements) and local letter patterns (originally described by Navon, 1977). Young adults were found to have faster reaction times to global stimuli, whereas, older adults were found to be faster at processing local targets. The authors explained the results in terms of age-related cortical dysfunction, suggesting that the decline in global processing was as a result of more rapid age-related degradation of right hemisphere function, while the preserved performance during local processing was due to slower age-related loss of left hemisphere function.

In contrast, Roux & Ceccaldi (2001) found no evidence of age-differences in the global precedence effect. Using the global and local letter patterns described by Navon (1977), they presented participants with global H and global S letter stimuli, made up of local H's and S's. There were two conditions: consistent condition, where the same letter was used for both the global and local aspects; inconsistent condition, where the global and local letters

were different. Half of the participants directed their attention to global aspect (global letter was the target), while the other half directed attention to local elements (local letter was the target). The findings indicated a complete global precedence for both young and older adults, with both age groups responding significantly faster to global forms than to local elements. However, another finding was that older adults were more likely to be captured by global interference than young adults. That is, when attempting to make judgements about the local elements, older adults were significantly worse if the global and local elements were inconsistent, compared to when they were made up of the same letter. The authors suggested that this was due to inefficient inhibitory responses in the older brain.

2.9 Introduction to experiments 1 and 2.

This chapter sets out to explore age-related differences in temporal order judgement (TOJ) and sensitivity to cross-modal integration. The chapter serves to develop methods to be used in the following two chapters (3 and 4), which go on to test if training participants to form associations between visual stimuli and auditory tones has an effect on TOJ performance, and if there is an age-related difference in the effects manifested by training.

Experiment 1 tested young and older adults' performance on a temporal order judgement task. Experiment 2 used the same task, with the addition of symbolically linked auditory tones, to investigate if there is a natural tendency to favour congruent cross-modal information over incongruent information.

2.10 Aims and predictions of experiment 1.

The first experiment in this chapter aimed to explore possible age-related differences in discrimination accuracy of spatially filtered stimuli by comparing temporal order judgement performance between young and older adults using a task which required them to indicate which stimulus they saw first during sequential presentations. The experiment employed a two-alternative forced choice (2AFC) temporal order judgement paradigm. This experiment is the baseline experiment used throughout the following two chapters (3 and 4).

Participants made temporal order judgements on presentations of pairs of stimuli containing one high spatial frequency (HSF) and one low spatial frequency (LSF) shape. The task was to respond as to which side of the display the first shape appeared. It was expected that young adults would make more correct temporal order judgements than older adults (Humes et al., 2009; Busey et al., 2010). It was also expected that performance would improve as a function of increasing SOA (Hirsh & Sherrick, 1961; Humes et al. 2009) and increasing contrast (Owsley et al, 1983).

Stimuli were presented at two different positions: separate (either side of fixation) and overlapped (centrally overlapping, slightly to the left and right); the two different positions were applied 50% each over the course of the experiment. This was carried out to see if stimuli position had differing effects on the two age groups during TOJ. Some research has demonstrated that older adults experience a greater difficulty than young adults when localising peripheral stimuli during detection tasks (Ball et al., 1990). However, other research has reported that age-differences in discrimination performance arise when stimuli are presented in the same location, due to an age-related reduction in pattern-separation ability (Holden et al., 2012).

2.11 Methods

2.11.1 Participants

Twelve young (mean age 19.3, SD 1.4) and twelve older adults (mean age 71.8, SD 5.4) participated in this experiment. The young adult group included nine females, and all except two were right handed. The older adult group included five females, and all were right handed. All participants had normal or corrected to normal vision and normal hearing (all self reported), and provided informed written consent prior to taking part (see appendix A.1). Older adults were sampled from the psychology department's control participant pool and were paid for their involvement (young adults received course credits).

2.11.2 Stimuli and apparatus

Shape stimuli subtended a visual angle of 3.7°, and were displayed on a mean luminance grey background (26 cd/m²). Stimuli were generated using standard graphics software (Paint, part of Microsoft Windows). Simple outline drawings of nine shapes consisted of an arrow, bell, circle, crescent, heart, hexagon, square, star and triangle, presented in a random order. Prior to the experiment, the shapes were tested on a small group of participants to check that they were all equally identifiable. Identification accuracy was equal for all shapes at both spatial scales (see appendix A.2 for methods and results). Each shape was low-pass and high-pass filtered, thereby creating 18 stimuli images. The absolute cut off for the low-pass filter was 1.6 cycles / degree, and the absolute cut off for the high-pass filter was 6.5 cycles / degree (from centre of array). The selected frequencies were close to those used in various studies on spatial frequency discrimination (e.g. Özgen et al., 2005; Peyrin et al., 2010), in order to be certain the high and low spatial stimuli were activating different processing channels (Sowden

et al., 2003; Özgen et al., 2005). Image filtering was performed using a two-dimensional Fast Fourier Transform and a two-dimensional Ideal Low-Pass filter (which was also modified to perform high-pass filtering). Custom software for the experiment was written in Matlab (http://www.mathworks.com), using the Psychophysics Toolbox extensions (Brainard, 1997, Pelli, 1997).

Stimuli presentation was varied over four different stimulus onset asynchronies (~11, 33, 55 and 99 ms)¹. Stimuli were presented at three different contrast levels throughout the experiment (5%, 8% and 10%), order was counterbalanced across participants.

A mid-level, neutral tone was played to indicate that stimuli were about to be presented. The neutral tone was 524 Hz and was played back over standard desktop audio speakers at 8192 Hz sampling frequency. The tone was presented for 244ms, 150ms before the visual stimulus appeared.

Shape stimuli were presented on either side of fixation (separate items) in half of the trials, and centrally superimposed (overlapped items) in the remainder of trials. When stimuli were presented as separate items, the outer edges of each shape were offset by 3.8° visual angle from fixation. When presented as overlapped, stimuli were spatially superimposed in the centre of the screen, with outer edges slightly offset by 2° to the left and right of fixation so that left vs. right judgements could be made (figure 2.1). Stimuli were presented on a ViewSonic P225f monitor (resolution 1024 x 768 pixels) at 85 Hz. Participants used a standard QWERTY keyboard to make responses, left and right arrow keys were used to record responses throughout the experiment.

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¹ Monitor refresh rate 85Hz, giving rise to the minimal temporal difference that can be expressed between visual presentations. This dictated a minimum of ∼11ms, and multiples thereof, onset asynchrony. Identical monitor used throughout the study.

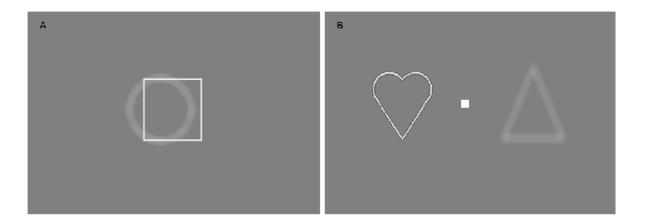


Figure 2.1: Stimuli. (A) Centrally presented stimuli (overlapped). (B) Spatially separate stimuli (HSF on left, LSF on right). Background luminance was 26 cd/m². Shapes were presented at full luminance.

2.11.3 Procedure

After receiving detailed written instructions (see appendix A.3), participants were seated 65cm from the screen (although their position was not constrained). Participants were requested to look toward a central fixation square throughout the experiment. A summary of the instructions were first displayed on the screen in order to clarify when and how to make responses.

Observers heard a mid-level, neutral tone for 244ms to indicate that stimuli was about to be presented (all participants were tested to make sure that they could clearly hear the tone prior to the experiment). Following a 150ms gap, they were briefly presented with pairs of simple shape stimuli which differed in onset over varying stimulus onset asynchronies (SOAs). The two shapes were presented for 100ms each. In each trial, one LSF shape and one HSF shape were presented (chosen randomly from the predefined set of shapes). Participants were then requested, by means of an onscreen prompt, to respond to which side they first detected a stimulus. This prompt remained on the screen until a response had been made and then the next trial began (see figure 2.2 for stimulus and tone timing and duration). No

feedback was given, as additional information may have affected the following trial, for example, slowing down the response following feedback indicating an error (Van Wert et al., 2009).

Observers had to judge which of two stimuli appearing on the screen was presented first; this was presented in a random order. Participants made left and right responses (left and right cursor keys) as to which side they first saw a shape appear. Responses were made with the right hand, using the left and right arrow keys. Each participant completed 8 runs of 108 trials (864 trials), which took approximately 30 minutes. Trials lasted (approximately, depending on individual response time) between 505 ms and 593 ms (depending on the SOA employed within the trial). Data were averaged for each condition.

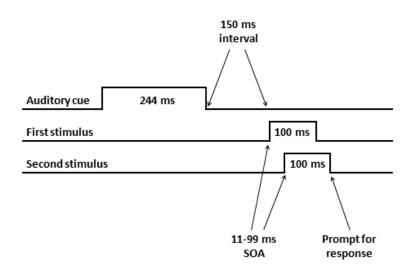


Figure 2.2: Timing and duration of stimuli. Auditory cue was played for 244ms. Following an interval of 150ms, the first stimulus was shown. Following a SOA of 11-99ms, the second stimulus was shown. Both stimuli were presented for 100ms. The participant was then requested to respond to which side they first saw a shape appear.

2.12 Results

Young and older participants made temporal order judgements about two different spatial frequency shape stimuli over varying SOAs and at three levels of contrast. It was expected that temporal order judgement performance would improve as SOA increased for both age groups (Humes et al., 2009). It was also expected that performance would be more impaired at lower contrasts, particularly in the older adult group (Owsley et al., 1983; Pardhan, 2004).

Data were first analysed to check for between group differences in bias towards either of the spatial frequency stimuli (HSF and LSF). A repeated measures ANOVA with a between-subjects factor of age (2 – older adults and young adults) and within-subjects factors of Position (2 – separate and overlapped), contrast (3 – 5%, 8% and 10%) and SOA (4 – 11, 33, 55 and 99 ms) was performed on percent of responses of LSF first (left or right response) See table 2.1 for ANOVA results, and table 2.2 for means and standard error.

Table 2.1: Repeated measures ANOVA results for LSF response bias.

Effects	Mean Square	DF	F	Р	Partial η ²
Age	399.48	1, 22	0.88	0.360	0.04
Position	9860.49	1, 22	15.57	0.001*	0.41
Contrast	8345.27	2, 34	8.05	0.003*	0.27
SOA	86.26	2, 36	0.12	0.850	0.01
SOA x Age	1287.03	3, 66	3.22	0.028*	0.13
Position x Age	118.37	1, 22	0.19	0.670	0.01
Contrast x Age	311.68	2, 44	0.38	0.683	0.02
Position x Contrast	716.69	2, 44	3.14	0.053	0.13
Position x SOA	52.89	3, 66	0.35	0.787	0.02
Contrast x SOA	142.21	6, 132	0.93	0.473	0.04
Position x Contrast x Age	1148.11	2, 44	5.03	0.011*	0.19
Position x SOA x Age	99.38	3, 66	0.66	0.578	0.03
Contrast x SOA x Age	126.62	6, 132	0.83	0.548	0.04
Position x Contrast x SOA	180.80	4, 92	0.92	0.458	0.04
Position x Contrast x SOA x Age	54.89	6, 132	0.40	0.878	0.02

Table 2.2: Means and standard error for LSF response bias

Factor	Level	Mean	Standard
l'actor	Level	ivicali	error
Age	Young	63.37	6.17
Age	Older	55.21	6.17
Position	Separate	63.43	4.74
Position	Overlapped	55.15	4.22
	5%	64.87	4.91
Contrast	8%	59.75	4.71
	10%	53.24	4.39
	11ms	59.84	5.07
SOA	33ms	59.38	4.80
JOA	55ms	59.45	4.72
	99ms	58.49	3.66

There was a main effect of contrast indicating that, as contrast increased, responses of LSF decreased. There was also a main effect of position, indicating that the bias to respond LSF was greater when stimuli were presented either side of fixation compared to when presented overlapped.

The interaction of age x SOA was significant. A two-way ANOVA of age (2 - young and older adults) x SOA (4 - 11, 33, 55, 99ms) indicated that young adults showed a trend towards more bias in responses of LSF compared to older adults, however, this was not significant at any SOA (See appendix A.4 for two-way ANOVA results).

The interaction of position x contrast x age was also significant. Further analyses (2 x 2 ANOVAs on position x contrast for young and older adults) showed that young adults made significantly more LSF responses at 10% contrast when stimuli were separated either side of fixation compared to when stimuli were overlapped (F(1, 22) – 12.42, p = 0.002, r = 0.60). There were no significant differences at 5% or 8% contrast between separate and overlapped presentations for young adults. Older adults showed no significant differences across all

contrast levels between separate and overlapped stimuli (see appendix A.5 for two-way ANOVA results).

Data were also analysed to identify if there was any left versus right response bias within the two age groups and conditions. Two repeated measures ANOVAs were performed, one for when HSF stimuli were presented first, and one for when LSF stimuli were presented first. Each ANOVA had a between-subjects factor of age (2 – older adults and young adults) and within-subjects factors of *Position* (2 – separate and overlapped), contrast (3 – 5%, 8% and 10%) and SOA (4 – 11, 33, 55 and 99 ms). Percent of left responses were analysed. See table 2.3 for HSF presented first ANOVA and table 2.4 for means and standard deviation. See table 2.5 for LSF presented first ANOVA and table 2.6 for means and standard deviation.

Table 2.3: Repeated measures ANOVA results for left responses when HSF was presented first.

Effects	Mean Square	DF	F	Р	Partial η ²
Age	209.84	1, 22	5.62	0.027*	0.20
Position	1337.85	1, 22	3.87	0.062	0.15
Contrast	1125.48	2, 44	3.37	0.044*	0.13
SOA	212.69	3, 66	1.03	0.387	0.05
SOA x Age	200.55	3, 66	0.97	0.414	0.04
Position x Age	403.58	1, 22	1.17	0.292	0.05
Contrast x Age	95.12	2, 44	0.28	0.754	0.01
Position x Contrast	371.34	2, 44	1.50	0.234	0.06
Position x SOA	241.23	3, 66	0.83	0.484	0.04
Contrast x SOA	815.95	6, 132	2.49	0.026*	0.10
Position x Contrast x Age	567.18	2, 44	2.29	0.113	0.09
Position x SOA x Age	244.99	3, 66	0.84	0.477	0.04
Contrast x SOA x Age	88.17	6, 132	0.27	0.950	0.01
Position x Contrast x SOA	341.10	6, 132	1.13	0.346	0.05
Position x Contrast x SOA x Age	191.55	6, 132	0.64	0.701	0.03

Table 2.4: Means and standard error of left responses when HSF was presented first

Factor	Level	Mean	Standard
ractor	Level	ivican	error
Age	Young	44.37	1.76
Age	Older	50.28	1.76
Position	Separate	48.85	1.53
Position	Overlapped	45.80	1.41
	5%	47.56	1.67
Contrast	8%	44.80	1.79
	10%	49.62	1.47
	11ms	47.53	1.79
SOA	33ms	48.80	1.67
JUA	55ms	45.86	1.67
	99ms	47.10	1.34

During trials where the HSF stimulus was presented first there was a significant main effect of age, indicating that young adults made fewer left responses then older adults. There was also a significant main effect of contrast indicating that left side responses decreased at 8% contrast compared to 5% and 10%.

There was a significant interaction of contrast x SOA. A two-way ANOVA of contrast x SOA revealed that at 99ms SOA, fewer left side responses were made at 10% contrast than at 5% or 8% (F(2, 33) = 8.50, p = 0.001, r = 0.58). There were no significant differences in response side across contrast levels for any other SOAs (see appendix A.6 for two-way ANOVA results).

Table 2.5: Repeated measures ANOVA results for left responses when LSF was presented first.

Effects	Mean Square	DF	F	Р	Partial η ²
Age	141.77	1, 22	11.71	0.002*	0.35
Position	4067.84	1, 22	15.24	0.001*	0.41
Contrast	171.62	2, 44	0.50	0.609	0.02
SOA	8.22	3, 66	0.03	0.992	0.00
SOA x Age	718.33	3, 66	2.77	0.048*	0.11
Position x Age	26.13	1, 22	0.10	0.757	0.00
Contrast x Age	117.40	2, 44	0.34	0.712	0.02
Position x Contrast	39.43	2, 44	0.14	0.872	0.01
Position x SOA	720.45	3, 66	2.69	0.054	0.11
Contrast x SOA	86.41	6, 132	0.35	0.907	0.02
Position x Contrast x Age	1680.37	2, 44	5.88	0.005*	0.21
Position x SOA x Age	325.73	3, 66	1.22	0.311	0.05
Contrast x SOA x Age	168.75	6, 132	0.69	0.658	0.03
Position x Contrast x SOA	980.55	6, 132	3.52	0.003*	0.14
Position x Contrast x SOA x Age	125.02	6, 132	0.45	0.845	0.02

Table 2.6: Means and standard error of left responses when LSF was presented first

Factor	Level	Mean	Standard
lactor	Level	IVICALI	error
Age	Young	46.62	1.01
Age	Older	51.48	1.01
Position	Separate	51.71	0.86
Position	Overlapped	46.39	1.10
	5%	48.00	1.13
Contrast	8%	49.32	1.48
	10%	49.83	1.27
	11ms	48.88	1.69
SOA	33ms	49.09	1.48
	55ms	48.86	1.00
	99ms	49.37	1.16

During trials where the LSF stimulus was presented first there was a significant main effect of age, indicating that young adults made fewer left side responses compared to older adults. There was also a significant main effect of position, indicating that more left responses were made to separate stimuli.

There was a significant interaction of age x SOA. A two-way ANOVA of age x SOA revealed that young adults made significantly fewer left responses compared to older adults at 11ms (F(1, 16) = 8.90, p = 0.009, r = 0.54) and 55ms (F(1, 22) = 9.03, p = 0.007, r - 0.54). There were no significant age differences at 33ms or 99ms (see appendix A.7 for two-way ANOVA results).

There was also a significant interaction of position x contrast x age. Further analysis (2 x 2 ANOVAs on position x contrast for young and older adults) showed that young adults made significantly more left responses to separate stimuli compared to overlapped stimuli when presented at 10% contrast (F(1, 22) = 8.94, p = 0.007, r = 0.54). No further significant differences were observed for young adults. Older adults made significantly more left responses to separate stimuli compared to overlapped stimuli when presented at 8% contrast (F(1, 22) = 8.04, p = 0.010, r = 0.52) and 5% (F(1, 22) = 4.37, p = 0.048, r = 0.41), but no significant difference in left responses between separate and overlapped at 10% contrast (see appendix A.8 for full ANOVA results).

The significant interaction of position x contrast x SOA indicated that, for stimuli separated either side of fixation and shown at 99ms SOA, significantly more left responses were made when stimuli were presented at 10% contrast, compared to 5% and 8% (F(2, 33) = 3.92, p = 0.030, r = 0.44). For overlapped stimuli, there were significantly more left responses made at 55ms SOA when stimuli were presented at 10% contrast, compared to 5% and 8% (F(2, 33) = 3.60, p = 0.039, r = 0.42). At SOA of 99ms, more left responses were made when stimuli were presented at 8% contrast, compared to 5% and 10% (F(2, 33) = 3.71, p = 0.035, r = 0.43). See appendix A.9 for table of ANOVA results.

Due to between groups differences in bias, data were analysed using d'. This a measure of sensitivity based on the separation between means of the hit rate and false-alarm

rate in units of standard deviation². This is particularly important when considering the LSF bias in young adults (table 2.1 and 2.2), as this bias may have reflected young adults making more false alarm responses to LSF stimuli.

The use of d' analysis is more appropriate than % correct for this type of data as it distinguishes between correct trials where stimuli are accurately detected (e.g. LSF presented first, LSF detected first), and correct trials where stimuli were perceived to be detected (e.g. LSF presented second, LSF detected first). Hit (H) and False Alarm (FA) were calculated as follows: H: Participant reported left (or right) when LSF was presented first on the left (or right). FA: Participant reported left (or right) when LSF was presented second on the left (or right). In order to explore temporal order discrimination, one stimulus had to be treated as the target stimulus throughout the analysis (e.g. when LSF is the target, HSF is the lure). The results described in this section relate to performance during trials where the LSF stimulus was the target. That is, when participants responded to LSF stimuli (correctly or incorrectly). LSF was chosen over HSF as a target due to research demonstrating that LSF information is processed first by the visual system (Bar, 2003; Peyrin et al., 2010). As age-related changes in HSF processing are due to optical factors, it was more relevant to the thesis to use LSF stimuli as the target, as age-related changes for LSF processing are due to changes at the neuronal level (Pardhan, 2004).

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² The experiments described in chapters 2-4 of this thesis measure the accuracy of participants' un-speeded performance to briefly presented stimuli. An advantage of using this method, as opposed to measurement of reaction times (RTs) for targets presented at longer durations, is that it provides a more sensitive measure of perceptual and cognitive processing (Prinzmetal, McCool & Park, 2005). This method is also more conducive to estimating and partialling out, guessing bias from participants' performance, therefore revealing the actual sensitivity to the stimuli. An effective method of analysis for such data collection is d', which has its origin in signal detection theory (e.g. Green & Swets, 1966). D' is a measure of sensitivity based on the separation between means of the hit rate (perceived and correct responses) and false-alarm rate (perceived but incorrect responses) in units of standard deviation, which results in one value that is indicative of the level of sensitivity a participant displays towards a stimulus.

An initial repeated measures ANOVA with a between-subjects factor of age (2 – older adults and young adults) and within-subjects factors of $side\ presented\ (2$ – left and right), $position\ (2$ – separate and overlapped), $contrast\ (3$ – 5%, 8% and 10%) and $SOA\ (4$ – 11, 33, 55 and 99 ms) revealed no significant effect of position (p = 0.213), and no significant interaction of position x age (p = 0.810). This indicated that both young and older adults were equally adept at discriminating temporal order when stimuli were presented separately and overlapped. Data were then collapsed across position for further analysis (See appendix A.10 for ANOVA and means tables for the full analysis including position).

A repeated measures ANOVA with a between-subjects factor of age (2 – older adults and young adults) and within-subjects factors of $side\ presented\ (2$ – left and right), $contrast\ (3$ – 5%, 8% and 10%) and $SOA\ (4$ – 11, 33, 55 and 99 ms) revealed significant main effects of age, side presented, contrast and SOA. There was also a significant interaction of age x SOA (figure 2.3). See table 2.7 for full ANOVA and table 2.8 for means.

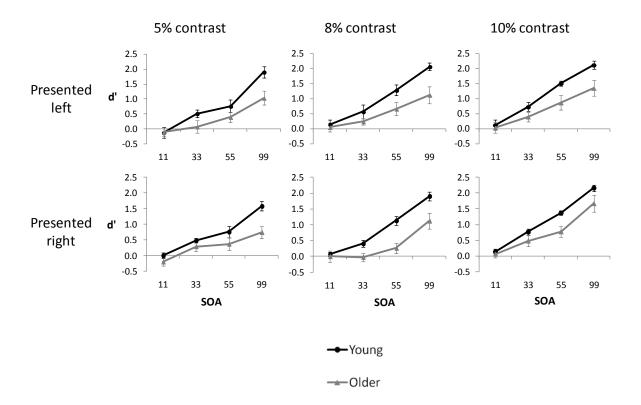


Figure 2.3: Age differences in temporal order discrimination

The x axis shows stimulus onset asynchrony. The y axis shows d'sensitivity index. A d' of 0 indicates chance performance, negative values indicate worse than chance and positive values show better than chance performance. The top row shows results from when LSF stimuli were presented first on the left. The bottom row shows results from when LSF stimuli were presented first on the right. Error bars depict standard error.

The significant interaction of age x SOA indicated that patterns of performance across SOAs differed between age group. Further analysis (two-way ANOVA of age x SOA) revealed that young adults' performance was significantly more accurate than older adults' performance at 33ms (F(1, 22) = 7.31, p = 0.013, r = 0.50), 55ms (F(1, 22) = 12.86, p = 0.002, r = 0.61) and 99ms (F(1, 22) = 11.48, p = 0.004, r = 0.59). Performance was statistically equivalent for both ages at 11ms, d' at this SOA reflected chance performance for both age groups (See appendix A.11 for two-way ANOVA results). This finding is in line with previous research (Humes et al., 2009; Busey et al., 2010) and supports the hypothesis that older adults would show less accurate performance during TOJ compared to young adults.

Table 2.7: Repeated measures ANOVA for temporal order discrimination

Effects	Mean Square	DF	F	р	Partial η ²
Age	1.19	1, 22	16.80	< 0.001*	0.43
Side presented (left / right)	0.55	1, 22	5.29	0.031*	0.19
Contrast	7.00	2, 44	13.97	< 0.001*	0.39
SOA	98.59	2, 42	93.84	< 0.001*	0.81
Side Presented x Age	0.02	1, 22	0.21	0.655	0.01
Contrast x Age	0.18	2, 44	0.37	0.696	0.02
SOA x Age	3.30	3, 66	4.89	0.004*	0.18
Side Presented x Contrast	0.45	2, 44	3.20	0.050	0.13
Side Presented x Contrast x Age	0.05	2, 44	0.39	0.681	0.02
Side Presented x SOA	0.12	3, 66	1.12	0.349	0.05
Side Presented x SOA x Age	0.11	3, 66	1.02	0.388	0.04
Contrast x SOA	0.89	4, 85	1.92	0.118	0.08
Contrast x SOA x Age	0.15	6, 132	0.52	0.796	0.02
Side Presented x Contrast x SOA	0.28	6, 132	1.79	0.106	0.08
Side Presented x Contrast x SOA x Age	0.07	6, 132	0.44	0.854	0.02

Table 2.8: Means and standard error for temporal order discrimination

Factor	Level	Mean	Std. Error
Λαο	Young	0.93	0.08
Age	Older	0.49	0.08
Side	Left	0.74	0.06
presented	Right	0.68	0.05
Contrast	5%	0.53	0.06
	8%	0.69	0.06
	10%	0.91	0.08
	11ms	0.02	0.05
SOA	33ms	0.41	0.06
	55ms	0.85	0.08
	99ms	1.57	0.12

Summary

Young adults correctly reported LSF as being presented first significantly more often than older adults. Performance improved significantly with increasing contrast and increasing SOA for both age groups. Age differences were significant at each SOA with the exception of 11ms, where no age differences were found and both groups were performing at chance. Significantly more correct judgements were made when LSF stimuli were presented first on the left compared to the right.

The significant main effect of SOA supports the hypothesis that participants would improve performance as a function of increasing SOA. The significant main effect of contrast supports the hypothesis that performance would increase as a function of increasing contrast. However, there was no interaction of age x contrast, suggesting that older and young adults improved performance at the same rate across contrast level. This is not what was expected, as older adults have been shown to be more impaired (compared to young adults) at visual tasks when stimuli are presented at low contrasts (Owsley et al., 1983). The significant main effect of side presented indicated that responses were more accurate for stimuli presented first on the left compared to the right. This may be due to a natural tendency to attend to visual information in a left to right manner (Ossandón et al., 2014).

2.13 Aims and predictions of experiment 2.

Experiment 2 uses the same temporal order judgement paradigm used in experiment 1, but with the addition of cross-modally symbolic auditory tones (high tone to be associated with the HSF stimuli, and low tone to be associated with the LSF stimuli). The aim was to investigate if there was a naturally occurring association between tone and stimulus. That is,

does the congruent tone produce greater accuracy than the incongruent tone, even when the tones are presented 50% each (therefore un-informative)?

Participants again had to judge which of two stimuli appearing on the screen was presented first; this was varied over four different stimulus onset asynchronies (~11, 33, 55 and 99 ms) presented in a random order. Stimuli were presented at three different contrast levels throughout the experiment (5%, 8% and 10%). Observers made left and right responses (left and right cursor keys) as to which side they first saw a shape appear.

It was expected that performance would be more accurate following presentations of the congruent tone compared to the incongruent tone (Evans & Treisman, 2010). It was also predicted that older adults would temporally bind the multisensory information more readily than young adults, leading to a greater effect in congruency and incongruency (Campbell et al., 2010). If older adults are more adept at integrating cross-modal information (Laurienti et al., 2006; Peiffer et al., 2007; Campbell et al., 2010, Diaconescu et al., 2013), there should be a greater effect of tone for the older adult group compared to the young adult group.

2.14 Methods

2.14.1 Participants

The same 12 young and 12 older adults from experiment 1 took part in experiment 2.

2.14.2 Stimuli and apparatus

Stimuli were as described in experiment 1, with the addition of cross-modally linked auditory tones. During each trial, an auditory tone preceded the visual stimulus. The high tone was

2358Hz and the low tone was 131Hz and both tones were played back over standard desktop audio speakers at 8192Hz sampling frequency. Each tone was presented for 244ms, 150ms before the visual stimulus appeared in order to be within an effective temporal binding window (Hairston et al., 2005).

2.14.3 Procedure

After receiving detailed written instructions (appendix A.12), participants were seated 65cm from the screen (un-constrained). Participants were requested to look towards a central fixation point throughout the experiment. A summary of the instructions were presented on the screen at the beginning of the experiment, to clarify when and how to make responses. During each trial, an auditory tone preceded the visual stimulus (high tone or low tone). All participants were screened to make sure that they could clearly hear each tone prior to the experiment. Following a 150ms interval, observers were presented with pairs of simple shape stimuli which differed in onset over four SOAs. The two shapes were presented for 100ms each. Participants had to judge which of the shapes were shown first. On 50% of these trials the auditory tone was congruent with the spatial frequency of the first presented shape stimulus (a high tone played before the HSF stimuli and low tone played before the LSF stimuli). In the remaining incongruent tone trials, tones were switched to precede the opposite spatial scale. Participants were asked to attend to the auditory tone during each trial. They were told that when they heard a high tone, it would be followed by a HSF stimulus, and when they heard a low tone, it would be followed by a LSF stimulus. They were also warned that on 50% of the trials, the tones would be misleading.

Each participant completed 8 runs of 108 trials (864 trials) of the experiment which took approximately 30 minutes. Trials lasted (approximately, depending on individual response time) between 505 ms and 593 ms (depending on the SOA employed within the trial). Data were averaged for each condition.

2.15 Results

Participants made temporal order judgements about spatially filtered shape stimuli, following presentation of a tone (50% congruent). It was expected that the congruent tone would give rise to greater accuracy compared to incongruent tones, due to a naturally occurring tendency to associate congruent cross-modal information (Evans and Treisman, 2010).

It was also expected that older adults would show indiscriminate integration of the tone + stimulus pairs, by more correct temporal order judgement with congruent pairs and less accurate with incongruent pairs (Campbell et al., 2010).

Data were analysed using d' to investigate differences in sensitivity for congruent versus incongruent tones between the two age groups. A repeated measures ANOVA with a between-subjects factor of *age* (2 – older adults and young adults) and within-subjects factors of *cue congruency* (2 – congruent and incongruent), *side presented* (2 – left and right), *contrast* (3 – 5%, 8% and 10%) and *SOA* (4 – 11, 33, 55 and 99 ms) revealed significant main effects of age, cue congruency and SOA. There were also significant interactions of age x cue congruency, age x SOA, cue congruency x contrast, cue congruency x SOA x age and cue congruency x contrast x SOA x age (figure 2.4). See table 2.6 for full ANOVA and table 2.7 for means. There was no main effect of side presented, nor were there any interactions containing side presented, therefore the graph shows data collapsed over side presented.

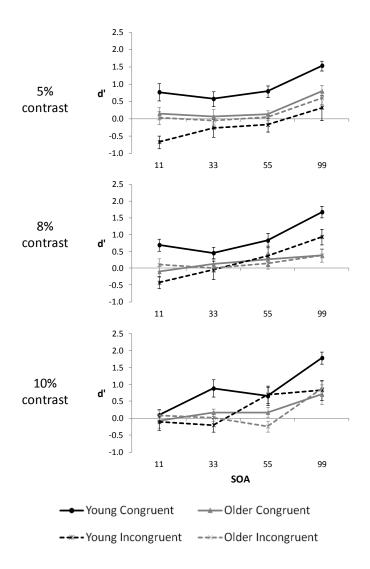


Figure 2.4: Age differences in performance with additional tones

The x axis shows stimulus onset asynchrony. The y axis shows d' sensitivity index. A d' of 0 indicates chance performance, negative values indicate worse than chance and positive values show better than chance performance. Error bars depict standard error.

Table 2.9: Repeated measures ANOVA results for congruent versus incongruent tones

Effects	Mean Square	DF	F	р	Partial η ²
Age	0.54	1, 22	10.75	0.003*	0.33
Cue (congruent / incongruent)	52.51	1, 22	8.30	0.009*	0.27
Side presented (left / right)	0.14	1, 22	0.20	0.663	0.01
Contrast	1.10	2, 44	1.73	0.189	0.07
SOA	42.52	3, 66	37.16	< 0.001*	0.63
Cue congruency x Age	38.00	1, 22	6.01	0.023*	0.22
Side presented x Age	0.08	1, 22	0.11	0.741	0.01
Contrast x Age	1.94	2, 44	3.06	0.057	0.12
SOA x Age	4.27	3, 66	3.73	0.015*	0.15
Cue congruency x Side presented	0.02	1, 22	0.03	0.872	0.00
Cue congruency x Side presented x Age	0.34	1, 22	0.37	0.550	0.02
Cue congruency x Contrast	2.76	2, 44	5.66	0.006*	0.21
Cue congruency x Contrast x Age	1.52	2, 44	3.12	0.054	0.12
Side presented x Contrast	0.21	2, 44	0.27	0.767	0.01
Side presented x Contrast x Age	1.01	2, 44	1.31	0.279	0.06
Cue congruency x Side presented x Contrast	0.20	2, 44	0.36	0.701	0.02
Cue congruency x Side presented x Contrast x Age	0.64	2, 44	1.15	0.327	0.05
Cue congruency x SOA	0.34	3, 66	0.51	0.680	0.02
Cue congruency x SOA x Age	2.11	3, 66	3.18	0.030*	0.13
Side presented x SOA	0.15	3, 66	0.20	0.897	0.01
Side presented x SOA x Age	1.16	3, 66	1.57	0.205	0.07
Cue congruency x Side presented x SOA	0.95	3, 66	2.02	0.119	0.08
Cue congruency x Side presented x SOA x Age	0.12	3, 66	0.25	0.863	0.01
Contrast x SOA	0.69	6, 132	0.88	0.509	0.04
Contrast x SOA x Age	0.94	6, 132	1.21	0.308	0.05
Cue congruency x Contrast x SOA	0.95	6, 132	1.96	0.077	0.08
Cue congruency x Contrast x SOA x Age	1.26	6, 132	2.59	0.021*	0.11
Side presented x Contrast x SOA	0.11	6, 132	0.16	0.986	0.01
Side presented x Contrast x SOA x Age	0.36	6, 132	0.55	0.768	0.02
Cue congruency x Side presented x Contrast x SOA	0.22	6, 132	0.41	0.873	0.02
Cue congruency x Side presented x Contrast x SOA x Age	0.76	6, 132	1.44	0.206	0.06

Table 2.10: Means and standard error for congruent versus incongruent tones

Factor	Level	Mean	Std. Error
Age	Young	0.50	0.07
Age	Older	0.20	0.07
Cue	Congruent	0.57	0.08
congruency	Incongruent	0.14	0.10
Side	Left	0.34	0.05
presented	Right	0.36	0.05
	5%	0.29	0.05
Contrast	8%	0.36	0.06
	10%	0.40	0.06
	11ms	0.05	0.06
SOA	33ms	0.15	0.05
	55ms	0.31	0.07
	99ms	0.90	0.10

A two-way ANOVA showed that the significant interaction of age x cue congruency indicated that young adults made significantly more accurate judgements than older adults about the temporal order of visual stimuli when congruent tones were applied (F(1, 22) = 19.32, p < 0.001, r = 0.68). No significant age differences were observed when incongruent tones were applied (see appendix A.13 for two-way ANOVA results). The significant interaction of age x SOA indicated that young adults made significantly more correct judgements about the order of stimuli than older adults at 55ms (F(1, 22) = 10.76, p = 0.003, r = 0.57) and 99ms (F(1, 22) = 7.51, p = 0.012, r = 0.50), whereas no age differences were observed at 11ms or 33ms (see appendix A.14 for two-way ANOVA results). This suggests that at longer SOAs the congruent tone appeared to facilitate performance in young adults compared to older adults.

The significant interaction of age x cue congruency x SOA indicated that young adults were significantly more accurate when presented with the congruent tone versus the incongruent tone at 11ms (F(1, 22) = 14.58, p = 0.001, r = 0.63), 33ms (F(1, 22) = 9.76, p = 0.005, r = 0.55) and 99ms (F(1, 22) = 10.47, p = 0.004, r = 0.57). Older adults showed no

significant differences between congruent and incongruent tones at any SOA (see appendix A.15 for full ANOVA results).

The significant interaction of age x cue congruency x contrast x SOA indicated that young adults, when presented with the congruent tone, showed a significant decrease in correct temporal order judgements as a factor of increasing contrast level. This was only found at SOA of 11ms (F(2, 33) = 3.38, p = 0.046, r = 0.41), and is likely to be due to young adults just using the auditory tone to guide responses when temporal order of the visual stimuli couldn't be reliably distinguished. There were no further significant differences for the remaining SOAs during congruent trials, nor were there any significant differences during the incongruent trials at any SOA (see appendix A.16). Older adults showed no significant differences across any SOAs during both congruent and incongruent trials (see appendix A.17).

Summary

When stimuli were preceded by the congruent tone, young adults made significantly more correct temporal order judgements compared to older adults, whereas, no significant age differences were observed for incongruent tone trials. Performance was more accurate in the young group compared to the older group at longer SOAs (55ms and 99ms), whereas, at shorter SOAs (11ms and 33ms) performance did not differ significantly between age groups. Young adults made significantly more correct order judgements when the congruent tone was played compared to the incongruent tone at SOAs of 11ms, 33ms and 99ms. This supports the hypothesis that cross-modal mapping of congruent visual and auditory information is a naturally occurring phenomenon (Evans & Treisman, 2010). Older adults showed no significant performance differences between congruent and incongruent tones at any SOA.

This is not in line with the hypothesis that older adults would show enhanced integration (Peiffer et al., 2007; Campbell et al., 2010).

2.15 Discussion

This chapter set out to investigate age-related changes in temporal order judgement and to test the effects of congruent and incongruent tones on performance. Experiment 1 results indicated that young adults made more accurate temporal order judgements than older adults (Humes et al., 2009). This supported the hypothesis that young adults would make more correct order judgements than older adults overall. Performance improved as a function of SOA for both age groups. Temporal order judgement performance improved for both age groups as a function of increasing contrast. This was not expected, as older adults have previously been reported to show reduced performance at lower contrasts (Owsley et al., 1983).

Experiment 2 investigated if there was a natural tendency to respond to congruent cross-modal information more than incongruent. The cues were un-informative (50% congruent) so that the possibility of naturally occurring associations to the tones could be explored. It was predicted that the congruent auditory tone would give rise to more correct order judgements being made for each age group, but that this would be more prominent in the older group. The incongruent tone was expected to cause more disruption to the performance of older adults compared to young adults.

Findings indicated that young adults made significantly more correct temporal order judgements when congruent tones were presented (except at 55ms, where no difference was observed) compared to incongruent tones. Older adults showed no significant difference in

accuracy of order judgements between the tones. Young adults made significantly more correct judgements compared to older adults when congruent tones were applied, whereas, no age differences were observed for incongruent tones. This is not in line with the hypothesis that older adults would show enhanced integration of the cross-modal information compared to young adults.

Age differences in cross-modal integration

Evans & Treisman (2010) reported a cross-modal congruency effect in young adults using spatial frequency as a stimulus; where they found that symbolically linked tones improved spatial frequency classification. The aim of the present chapter was to address possible age differences in cross-modal integration with spatial frequency as a stimulus.

The effect of the congruent and incongruent tones on responses from young adults indicated that there may be a naturally occurring cross-modal correspondence for congruent information (Evans & Treisman, 2010). At shorter SOAs, this effect could be accounted for by young adults just using the information provided by the tone (Jaskowski, 1993; Landy et al., 2001). However, it could also reflect a linear weighting rule, where sources of information (from different modalities) are evaluated in order to discern the most reliable source (Ernst & Bülthoff, 2004).

Older adults did not show this effect of congruency. Furthermore, they showed no difference in performance between congruent and incongruent tones. This was not expected as previous research has highlighted enhanced cross-modal integration in older adults (Laurienti et al., 2006; Peiffer et al., 2007). Laurienti et al. (2006) used colour and verbalisations containing semantic information about colour. Their results may reflect enhanced integration of cross-modal information given the addition of semantic factors. Peiffer et al. (2007) used a

simple integration paradigm based on the detection of a simple visual stimulus, a simple auditory stimulus, and the integration of both stimuli. The present chapter used a complex visual stimulus (two spatial frequencies) and a difficult perceptual task (sub-second temporal order judgement). It is likely that the studies described by Laurienti et al. (2006) and Peiffer et al. (2007) offered an easier integration task than the present chapter and that this may explain the differences between their findings and those in this chapter.

In comparing the results from both experiments (1 and 2), it appears that older adults' TOJ performance is disrupted by the presence of the two tones (congruent and incongruent). In experiment 1, older adults showed an increase in TOJ as a function of increasing SOA. During experiment 2, their performance was shown to remain around the chance level across all SOAs. This could suggest that, as there was no information value contained in the tones, older adults were unable to adopt a useful strategy. That is, the tones may have effectively added additional noise to the perceptual process (Battaglia et al., 2003).

The next chapter explores if training participants to form associations between the tones and visual stimuli can enable more efficient cross-modal integration.

CHAPTER 3

Effects of sensitisation training on top-down cueing during temporal order discrimination

3.1 Abstract

This chapter investigates the effects of training participants to use top-down cueing via sensitisation techniques. Such techniques have been shown to provide an advantage when cueing observers to spatial scale (Sowden et al., 2003; Ozgen et al., 2005).

Participants were trained to associate two auditory cues (high tone and low tone) with spatial frequency stimuli containing symbolically linked characteristics (high spatial frequency and low spatial frequency respectively), in order to investigate if such cueing can improve participants' temporal judgement discrimination via cueing sensitivity to spatial scale.

Findings indicated that training can enable participants to form effective cue + stimulus associations, which may lead to improved detection of the cued spatial frequency, thereby reducing uncertainty during temporal order judgement.

3.1 Selectivity for spatial scale

The visual system has been shown to selectively attend to specific spatial scales depending on the information that is diagnostically required by the task at hand (Oliva & Schyns, 1997; Robertson & Ivry, 2000; Sowden et al., 2003; Ozgen et al., 2005).

The Double Filtering by Frequency (DFF) theory of spatial scale processing, proposes that there are two stages of spatial frequency filtering, which are carried out by opposing cortical hemispheres following initial visual processing in V1 (Robertson and Ivry, 2000). Here, attention is said to select a spatial frequency range from the incoming information that is most diagnostic for a given task. The relevant range is then forward-projected through both cortical hemispheres, where the left hemisphere processes high spatial frequency information from the selected range and the right hemisphere processes low spatial frequencies.

Support for the DFF model was provided by using Electroencephalography (EEG) while directing participants' attention to either global or local stimulus events (Flevaris et al., 2011). Participants made judgements as to whether the global or local letters in two sequential displays were the same or different. Behavioural results indicated a high degree of discrimination accuracy. EEG results indicated that there was a significantly greater decrease in alpha activity (which indicates active stimulus processing) in right hemisphere, compared to left hemisphere, following attentional selection of low spatial frequencies. This suggests that the right hemisphere mediates global processing. There were no significant differences in alpha reduction between the hemispheres following attentional selection of high spatial frequencies.

Rotshtein et al. (2007) identified regions within occipitotemporal cortex that extract distinct visual cues from face stimuli at different spatial frequency ranges. They used hybrid

face stimuli, in which both high and low spatial frequency components were superimposed and presented simultaneously. Different face identities were shown in each spatial frequency range. In order to manipulate top-down attention, observers were asked to attend to either the high or low range across different trials of the hybrid displays. Observers were required to detect infrequent target stimuli (e.g. a face containing inverted features), which was presented in a pre-cued spatial frequency range, while suppressing attention to the opposite range. Results demonstrated that the occipitotemporal cortex contains distinct areas of activation for processing the high and low spatial frequency components of face stimuli.

Studies such as those described above have led to the suggestion that people are able to modulate the use of spatial frequency channels by means of top-down attention, and that this happens early on in the visual processing stream. The studies described in this chapter highlighted experiments using faces, scenes and letter stimuli. If attentional modulation occurs early in visual cortex, then this effect should also extend to visual objects. The present chapter addresses this by using simple outline shape stimuli, spatially filtered to produce high and low spatial frequency counterparts.

3.2 Training and cue use during spatial frequency processing

During conditions where discrimination is difficult, (e.g. short stimulus onset asynchronies), top-down processes may be necessary to enable optimal performance. An effective method of manipulating the use of top-down attention is to employ a cueing paradigm, where attention is diagnostically directed towards the relevant information (Posner, 1994; Sowden et al., 2003; Özgen et al., 2005).

Hübner (1996) described two types of cueing. Iconic cues drive attention bottom-up and they are usually identical, or very similar, to the stimulus and presented in the same modality. Symbolic cues drive attention top-down, do not resemble the stimulus and can be cross-modal (Hübner, 1996). The use of symbolic auditory cueing has been shown to have a beneficial effect on performance during spatial frequency detection (Özgen et al., 2005).

The use of explicit top-down cueing has been shown to improve performance on spatial frequency detection (Snowden et al, 2003; Özgen et al, 2005). It has also been suggested that directed attention leads to an improvement in temporal order judgement (Stelmach & Herdman, 1991). Can cueing to spatial scale be generalised to improve performance on a secondary task (temporal order judgement)?

This chapter included a training component in which participants underwent a sensitisation session to enable a more robust association between cue and stimulus. Sensitisation (a form of perceptual training) has been shown to influence the processing of spatial scale by repeatedly exposing observers to spatial frequency filtered scenes and faces (Schyns and Oliva, 1999, Oliva and Schyns, 1997). Furthermore, sensitisation through explicit top-down cueing has been shown to direct attention to specific spatial frequency channels, in early stages of visual processing, which are required to perform a given perceptual task (Sowden et al., 2003, Özgen et al., 2005).

Oliva and Schyns (1997) successfully sensitised participants to two different spatial scales by repeatedly presenting them with scenes containing one type of spatial frequency content (high or low), combined with noise at the opposite scale. Participants categorised the displays as either city or highway during this sensitisation period. Following this, observers viewed hybrid scenes of the city and highway stimuli, where both the high and low spatial frequency components were displayed together. Results indicated that participants who had

been sensitised to low spatial frequency stimuli were more likely to report the low spatial frequency component of the hybrid scenes, and those sensitised to high spatial frequency scenes were more likely to report the high spatial frequency component. None of the participants reported seeing both components.

Özgen et al. (2005) investigated the flexible use of spatial frequency scale information by testing to see if attentional modulation at early stages of visual processing could be responsible. They demonstrated that auditory cues can drive attention (top-down) to the spatial scale of scene stimuli. During initial sensitisation, participants were required to make highway vs. city judgements regarding scene stimuli presented at threshold contrast; each scene was accompanied by noise at the opposite spatial frequency. Participants were then trained to attend to a verbally presented auditory cue, which signalled the spatial frequency of the scene (vocally presented word 'coarse' for low and 'fine' for high spatial frequencies). During the test phase, the auditory cue appeared to enhance detection by means of directing attention towards the diagnostically relevant scale (spatial frequency of the meaningful scene). Results suggested that sensitisation, as a result of explicit top-down cueing, directed attention to specific, diagnostically relevant spatial frequency channels in early visual cortex. It is possible that the verbal labels 'coarse' and 'fine' accompanying each spatial frequency (HSF and LSF) may have provided semantic information in addition to the cross-modal cues, rather than just an auditory cue.

3.4 Importance of matching contrast to individual sensitivity

The experiment described in chapter 2 used stimuli presented at three arbitrary, pre-defined contrast levels. However, individual differences in contrast sensitivity can dramatically affect

performance during a variety of visual tasks (Schefrin et al., 1999, Baker and Graf, 2009, Goodbourn et al., 2012). Therefore, it is useful to measure individual participants' contrast threshold in order to minimise the effects of differential sensory factors on task performance.

The experiments described in this chapter included a contrast matching component, where each participant was measured for their individual contrast threshold for high spatial frequency stimuli and low spatial frequency stimuli, prior to the main experimental conditions. Each participant's contrast threshold was then used to produce two individually tailored levels of contrast. The lower contrast level was calculated as three times each individual's threshold, whereas the higher contrast level was five times each original threshold. The levels were set as such to ensure that all participants could see the stimulus during each trial (if stimuli were presented at threshold, visibility might have interfered with performance on the discrimination task).

3.5 Introduction to experiment 3

This experiment employed the same two-alternative forced choice temporal order judgement paradigm as described in chapter 2, with the added control for individual contrast matching to the stimuli. The cross-modal component to the experiment also differed in that the ratio of congruent and incongruent information was adjusted to 75:25 (instead of 50:50), thereby allowing the tones to serve as more reliable cues.

This chapter employed experienced psychophysical observers to undertake the task. Such observers were employed so that results would reflect the 'best case scenario' of performance by removal of confounds such as lack instructional compliance, environmental unfamiliarity, poor motivation and inconsistent performance.

Participants first underwent the neutral cue experiment described in chapter 2 (experiment 1). This formed the baseline task against which comparisons could be made with the cross-modal experiment presented in this chapter. On a different day (within the same week) participants took part in a sensitisation session and the cross-modal condition. The sensitisation techniques tested in this chapter will be used in chapter 4, where both young and older adults will be tested.

It has been demonstrated that sensitisation techniques can successfully direct attention (top-down) to the relevant band of spatial frequency for a given task (Sowden et al., 2003; Özgen et al., 2005). It has also been reported that directed attention can lead to improved performance in TOJ performance (Stelmach & Herdman, 1991). This chapter explores whether sensitisation to spatial scale can be generalised to improve performance on a secondary task (TOJ).

During the cross-modal cue condition, congruently cued stimuli were accompanied by an auditory tone reflecting the first stimulus to be shown on each trial. During incongruent cueing, the first stimulus was accompanied by an incongruent cue (25% of trials).

It was expected that sensitisation would produce robust cue + stimulus associations, which would lead to improved performance on TOJ during trials where auditory cues were symbolically congruent with the visual stimulus. At shorter SOAs, it was expected that participants would be less accurate at making TOJ during incongruent trials.

3.6 Methods

3.6.1 Participants

Five experienced psychophysical observers (mean age 28.2, SD 1.6) from the vision group at the school of psychology took part in this experiment. Three were female and all but one was right handed. All had normal, or corrected to normal vision and normal hearing (self reported).

3.6.2 Design

Observers underwent two experimental sessions: Neutral cue (baseline) and cross-modal (congruent cue and incongruent cue). During each condition, participants had to judge which of two stimuli appearing on the screen was presented first (HSF or LSF); this was varied over five different stimulus onset asynchronies (11, 33, 55, 77 and 99 ms) presented in a random order. Prior to testing, each participant's contrast threshold was measured (stimuli and procedure described below). Stimuli were then presented at two personalised contrast levels throughout the experiment (3x and 5x the individual's contrast threshold for each spatially filtered stimulus (HSF and LSF)). Participants made left and right temporal order judgements about which appeared first. During the neutral cue condition, participants just made temporal order judgements. During the cross-modal condition, participants made temporal order judgements with the addition of cross-modally symbolic cues (high tone and low tone), intended to drive attention, top-down, to the relevant spatial scale.

3.6.3 Stimuli and apparatus

Stimuli for the neutral cue and cross-modal cue conditions were the same as in chapter 2.

To measure each observer's individual contrast threshold, sinusoidal grating stimuli were presented at each of the spatial frequency bandwidths (HSF absolute cut-off was 6.5 cycles / degree and LSF absolute cut-off was 1.6 cycles / degree). Participants were presented with the grating stimuli at diminishing contrast levels utilising a modified 4 up 1 down staircase method (Levitt, 1971). Contrast was reduced following each correct response; incorrect responses made the staircase go up again, increasing the contrast of the stimuli. The minimum contrast was .34 and the maximum was .80. Stimuli were presented for 60ms and subtended a visual angle of 3.8°. The last 15 reversals were averaged to give a single measure of contrast threshold for each of the two spatial frequency bands (for each individual participant). Two different contrast levels were then created by multiplying by a factor of 3 and a factor of 5 for each participant to produce two individually matched levels of contrast ('lower' and 'higher').

Stimuli for the sensitisation session were the same HSF and LSF shape stimuli as used in the main experiment (see chapter 2 for filtering methods). Shapes were presented either side of fixation, offset by 3.8°. Each shape stimulus was embedded (alpha blended) in a pattern of random noise generated in the opposite spatial scale. This was done to emulate the test phase (which would present both HSF and LSF stimuli in each trial) and to train participants to associate the cue with the target on each trial. Random noise was filtered in the same manner as the target stimuli, therefore creating two patterns (HSF and LSF noise). Stimuli were presented for 300ms. Each presentation was preceded 150ms by an auditory tone (high tone or low tone) that signified the spatial frequency of the shape presented (tone duration and interval duration were as described previously).

3.6.4 Procedure

Observers were first measured for individual contrast sensitivity. Here, they were presented with sinusoidal grating stimuli, first at the HSF and then at the LSF. Participants had to respond 'm' when they could detect a stimulus and 'x' when they could not detect anything (using the keyboard).

The neutral cue baseline condition then commenced (procedure was the same as described in chapter 2).

On a different day (within the same week), participants took part in the sensitisation session and the cross-modal condition.

During the sensitisation session participants were trained to associate two spatial frequencies: HSF and LSF with two cross-modally symbolic auditory cues (high tone and low tone). Stimuli were low and high spatial frequency shapes embedded in random noise of the opposite spatial scale. Shape + noise stimuli were presented at the higher (5x threshold) contrast level and were presented either side of fixation. The task was to indicate (via key press) what side of fixation the shape + noise stimulus had appeared. Each trial lasted approximately 694ms. Each participant completed 864 trials of the sensitisation phase, which took approximately 10 minutes.

The cross-modal cue experimental condition then began. The task was the same as described in chapter 2 (experiment 2), but with the adjustment of 75% congruency.

Both the neutral cue and cross-modal cue experimental conditions comprised of 16 runs of 135 trials (2160 trials in total) and lasted approximately 30 minutes. Trials lasted approximately between 505 ms and 593 ms depending on SOA between the two stimuli. The entire training + cue session lasted approximately 45 minutes.

3.7 Results

Participants made temporal order judgements during two experimental conditions. They first made order judgments with no cross-modal information presented (i.e. neutral condition). They then repeated the task with the presence of symbolically linked cross-modal cues. It was expected that the congruent cues would result in better performance than incongruent cues. It was also expected that congruent cues would improve performance from baseline, and that incongruent cues would lead to worse performance.

Data from the sensitisation phase were analysed to check that participants were sensitised equally to both spatial frequencies. A Paired t-test showed that both HSF and LSF stimuli + cue pairs received equal amounts of correct responses (t(4) = -0.513, p = 0.635, r = 0.25), suggesting that participants were equally sensitised to both spatial frequencies (figure 3.1).

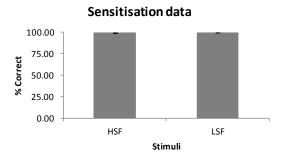


Figure 3.1: Sensitisation phase results. Data from the training (sensitisation) session showed that both LSF and HSF were sensitised in equal amounts. Participants had to respond left or right as to what side stimulus + noise occurred. Error bars depict standard error.

Data were analysed using d'. Hits and false alarms were calculated as described in chapter 2. Data from the neutral cue condition were first analysed (see appendix B.1). This

initial analysis revealed no effect of side presented, therefore data were collapsed across side presented for the cross-modal experiment.

A repeated measures ANOVA with factors of *cue-type* (3 - neutral, congruent) and incongruent), *contrast* (2 - lower) and higher) and SOA (5 - 11, 33, 55, 77, 99ms) revealed main effects of cue-type and SOA and an interaction of contrast x SOA (see table 3.1 for ANOVA results and table 3.2 for means and standard error).

The significant main effect of SOA indicated that performance increased as a function of increasing SOA for each cue type. The significant main effect of cue type indicated that performance was significantly different for each of the cue types (see figure 3.2). Contrasts revealed that performance was more accurate during trials preceded by the congruent cue compared to neutral baseline (F(1, 4) = 527.59, p < 0.001, Partial η^2 = 0.99) and performance was significantly less accurate during trials preceded by the incongruent cue (F(1, 4) = 61.31, p = 0.001, Partial η^2 = 0.94). The difference between congruent and incongruent cueing was significant F(1, 4) = 247.80, p < 0.001, Partial η^2 = 0.99).

The significant interaction of contrast x SOA indicated that at 33ms SOA, performance was significantly more accurate at the higher contrast compared to the lower contrast (F(1, 8) = 17.04, p = 0.003, r = 0.82). No significant differences were found between higher and lower contrast at any other SOAs (11ms: p = 0.747, 55ms: p = 0.387, 77ms: p = 0.176, 99ms: p = 0.065). See appendix B.2 for two-way ANOVA results.

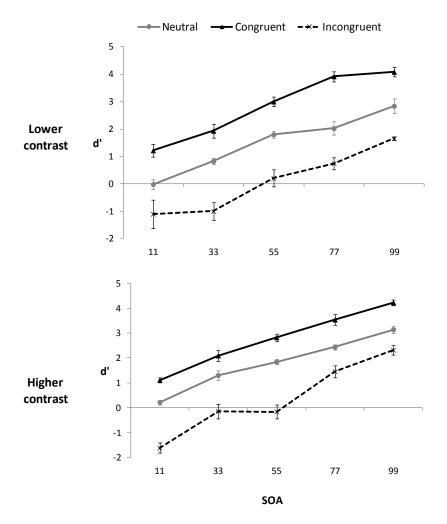


Figure 3.2: Neutral cue versus cross-modal cue results. The x axis shows SOA (ms). The y axis shows d' sensitivity index. A d' of zero indicates chance performance. Positive values indicate better than chance and negative values indicate worse than chance performance. Error bars depict standard error.

Table 3.1: ANOVA results for the three different cue contrasts

Effects	Mean Square	DF	F	р	Partial η ²
Cue Type	81.96	2, 8	167.89	< 0.001*	0.98
Contrast	0.93	1, 4	5.89	0.072	0.60
SOA	44.14	4, 16	227.60	< 0.001*	0.98
Cue type x Contrast	0.53	2, 8	3.63	0.075	0.48
Cue type x SOA	0.37	8, 32	1.59	0.166	0.29
Contrast x SOA	0.67	4, 16	5.14	0.007*	0.56
Cue type x Contrast x SOA	0.30	8, 32	0.98	0.467	0.20

Contrasts	Mean Square	DF	F	р	Partial η ²
Congruent vs. Neutral	6.60	1, 4	527.59	< 0.001*	0.99
Incongruent vs. Neutral	9.90	1, 4	61.31	0.001*	0.94
Congruent vs. Incongruent	32.67	1, 4	274.80	< 0.001*	0.99

Table 3.2: Means and standard deviation for the three different cue contrasts

Factor	Level	Mean	Std. Error
	Neutral	1.64	0.09
Cue type	Congruent	2.79	0.08
	Incongruent	0.24	0.10
Contrast	3x	1.48	0.05
Contrast	5x	1.64	0.05
	11ms	-0.03	0.10
	33ms	0.83	0.06
SOA	55ms	1.59	0.05
	77ms	2.35	0.08
	99ms	3.04	0.09

3.12 Discussion

This chapter aimed to explore if training could enable participants to form beneficial associations between cue and stimulus via sensitisation and top-down cueing. The experiment attempted to train participants to form cue + stimulus associations in order to enable top-down

attention to facilitate performance during the cued condition. Following successful cue + stimulus association, TOJ was significantly improved when cues were congruent compared to incongruent.

During congruent cueing, performance was significantly improved compared to when neutral cues were provided. This may indicate that sensitisation training led to successful integration of cross-modal information as the congruent cue provided facilitation of performance, whereas the incongruent cue produced a performance cost.

Strong conclusions should not be drawn from Experiment 1 as the sample size was limited. For other studies in the literature that involve either a simulation step or extraction of psychometric functions, this number of participants would be sufficient. However, this study necessitated the usage of d' to partial out guessing bias. Furthermore, results of the comparison between baseline (neutral condition) and cross-modal conditions may be confounded due to practice effects, as all participants took part in the neutral condition before the cross-modal condition (so that there would be no contamination of the neutral condition with the cross-modal cues). It is possible that any improvement in performance during the cross-modal condition may be due to participants getting better at the task through increased exposure to the task. However, incongruent cueing produced a cost of performance, which is incompatible with a practice effect (Özgen et al., 2006).

Effects of sensitisation to spatial scale on TOJ performance

Previous research has demonstrated robust effects of sensitisation to spatial scale (e.g. Özgen et al., 2005). The present chapter aimed to explore if sensitisation training techniques could improve performance on temporal order processing. Participants appeared to be successfully sensitised to spatial scale, indicated by significantly superior performance during congruent

trials compared to incongruent trials. Directed attention via top-down auditory cues was shown to have a beneficial effect on TOJ performance when cues were congruent with the stimuli compared to when neutral cues were provided. The fact that incongruent cueing produced a cost of performance relative to the neutral cue baseline suggests that this effect was as a results of the sensitisation session.

It is possible that at short SOAs, participants were using only the information provided by the auditory cue, as visual TOJ was indistinguishable (Jaśkowski, 1993) therefore using the modality with the highest prior estimate of reliability (Landy et al., 2001). It is also possible that participants were using a cue induced strategy at longer SOAs. In the presence of multimodal stimuli, several strategies can be employed to combine them into one unitary percept (Enrst & Bülthoff, 2004). One such strategy uses prior reliability of a given sensory modality, allowing the observer to weight that modality during the integration into a unitary percept (Stein & Stanford, 2008). This weight is inversely related to the noise of that modality and gives rise to the most 'reliable' multimodal percept (i.e. that with the lowest variance) (Battaglia et al., 2003). This integrated percept, whilst statistically optimal, may cause the binding of unrelated stimuli resulting in illusory hybrid percepts such as the "ventriloquist effect" (Alais & Burr, 2004). During incongruent cueing, participants may have continued to use weightings that combined the cue with the stimulus, which would result in the disruption of performance as the percept formed would not match either of the response choices available.

Summary

Findings from this chapter revealed highly a significant benefit of congruent cue and a cost of incongruent cue on TOJ performance. It is possible that this was due to attention being cued

to the relevant spatial scale, thereby reducing uncertainty in the resulting temporal order judgement. An alternative explanation is that sensitisation affects the internal weightings of modalities, leading to improved integration of congruent cross-modal stimuli.

CHAPTER 4

Age differences in top-down attentional modulation during temporal order processing following training intervention

4.1 Abstract

Older adults show a benefit from training on a number of perceptual and cognitive tasks. Older adults also show an enhanced ability to integrate cross-modal information compared to young adults. This chapter investigates whether training young and older participants to more effectively associate auditory cues with relevant visual target stimuli could improve performance during temporal order discrimination.

Results from chapter 2 indicated that older adults did not demonstrate a naturally occurring bias towards congruent cross-modal stimulus pairs. This may be due to a lack of reliable information offered by the cross-modal tones; therefore older adults may have been unable to develop an effective response strategy. Chapter 3 demonstrated that top-down cueing via sensitisation training may enable observers to form effective cue + stimulus associations, which may lead to enhanced performance at the cued spatial scale. It is therefore interesting to explore whether such associations could induce cross-modal integration in older adults, in order to directly affect task performance. This chapter used the same procedures set out in chapters 2 and 3 to test both young and older adults' temporal order judgement performance both with and without the presence of cross-modal cues.

The findings suggested that training enabled successful integration of the cross-modal auditory and visual information. Older adults were shown to use the cue at shorter SOAs than

young adults, suggesting that the cues provided an age-related compensatory benefit. It is suggested that this may be due to age differences in the strategy adopted to perform the task.

4.2 Effects of perceptual and cognitive training in older adults

Previous research has demonstrated that training produces improved performance in older adults during perceptual and cognitive tasks (Erickson et al., 2007, Bherer et al., 2005, Paxton et al., 2006, Berry et al., 2010, Ball et al., 2002). Beneficial effects of training have been recorded in short single session perceptual learning experiments (Fiorentini and Berardi, 1981) and short sessions over several days (Ball and Sekuler, 1987). Top-up or 'booster' sessions have been shown to further increase training gain specifically in older adults (Ball et al, 2002).

During a perceptual motion discrimination task, Berry et al (2010) tested young and older adults' performance pre and post training. Participants were presented with Gabor patterns which consisted of either expanding or contracting bands. Participants indicated whether they observed the bands expanding or contracting. Training significantly improved performance on this, and a secondary, untrained, perceptual task (compared to control groups who received no training). This secondary task involved motion discrimination of Random Dot Kinetograms (RDKs). The authors further tested participants on a third separate delayed recognition task utilising RDKs, to see if the effects of perceptual training could be generalised to carry over into working memory performance. There were three conditions: no interference, interrupting stimulus and passive viewing. In the passive viewing condition participants saw the cue and the disrupting presentation but made no response. The no interference condition (participants saw the cue, saw a delay and then responded to the probe)

showed a beneficial effect of training (where trained older adults were more successful than their untrained counterparts). The interrupted stimulus condition (participants saw the cue, encountered a disrupting presentation, and then responded to the probe) did not show an effect of training. Results of the no interference condition suggest that perceptual training can influence cognitive performance. However, results of the interrupted stimulus condition suggest that perceptual learning was unable to counteract the effects of age-related decline in inhibitory control (Hasher & Zacks, 1988), due to a decreased ability to reject non-informative information. The present chapter aimed to discover if sensitisation training can lead older adults to employ a strategy which allows the rejection of incongruent, disruptive information.

Previous research has demonstrated effective perceptual learning in older adults via demanding discrimination practice techniques (Fahle and Daum, 1997). Here participants are presented with increasingly difficult levels of a task and accuracy is measured. Typically, participants show little improvement during less taxing task manipulations (e.g. longer stimulus and inter-stimulus interval), whereas improvements have been shown at more demanding task load levels (e.g. short stimulus and inter-stimulus durations).

Using a go/no-go task, Paxton et al. (2006) provided evidence of training benefits in older adults' ability to utilise relevant task set information. Participants were presented with a target cue letter (i.e. A), followed by a target probe letter (i.e. X), and also with a non-target cue letter (i.e. B) and a non-target probe (i.e. Y). They had to make a target response to the task-relevant pairings (70% of trials) and a non-target response to the task-irrelevant cue / probe combinations (30% of trials). In order to make successful non-target responses to the irrelevant pairs, observers had to use information provided by the cue to inhibit the prepotent target response. The training involved participants self reinforcing by verbally categorising the cue stimulus (i.e. "A" or "not A"). The results indicated that training effectively enabled

older participants to change their pattern of performance to one reflecting that of young participants. This suggests that the older adults were able to adapt their strategy by forming appropriate cue + stimulus associations. This chapter explores if training young and older participants to form effective cue + stimulus associations leads to age-differences in strategic use of the cue information.

Using fMRI Erickson et al. (2007) performed a longitudinal dual-task training study to explore the relationship between training enhanced performance and the associated cortical activity in older versus young adults. Participants were presented with the letter 'X' in either yellow or green, and responded by button press to indicate the colour of the letter. In another task participants were presented with the letter 'B' or 'C' and had to respond to each letter. The prevailing task consisted of two conditions: 1) single mixed condition in which both previous tasks where presented at random, and 2) a dual-mix condition in which both tasks were presented simultaneously. Participants had to respond as quickly as possible. Following a three week break; five one hour training sessions on the previous tasks were provided to a participant group subset. The fMRI experiment was then repeated. They found beneficial training effects for both young and older adults, which were associated with a reduction in bilateral cortical recruitment, suggesting that training had the effect of reducing task difficulty (Nielson et al., 2002; Reuter-Lorenz & Park, 2010). They also observed similar patterns of task related activity for older and young adults in frontal attentional regions. The authors interpreted the results as the continued maintenance of cortical plasticity in older age. The present experiment investigates if such beneficial effects of training can be obtained using a different pattern of training.

It has been suggested that such time-consuming regimens (such as the 5 hours described above) are contraindicated in samples such as the very young, patients and older adults (Molloy et al., 2012). Therefore, the present chapter employs a short duration training

procedure. It has been reported that such minimal duration training may be more efficacious than time-consuming regimens (Aberg et al., 2009).

A longitudinal study (2 year duration) carried out by Ball et al. (2002) provided evidence that using cognitive interventions to train older adults resulted in specific improvements in targeted cognitive and perceptual abilities. They provided older adults with extensive training on a variety of visual tasks; including visual search skills, and speeded identification and location of visual targets during dual-tasks. Task load was manipulated by increasing the number of concurrent tasks to be carried out and adding either visual or auditory distracter stimuli to experimental conditions. Participants were first measured for pre-training abilities on a speed-of-processing experiment, where they had to identify and localise visual information under varying levels of task load. Post-training abilities were then assessed at three separate intervals: Immediate post-test (directly following training), after one year had elapsed, and after a second year. Results indicated that significantly beneficial effects of training were observed at each of the three assessment points (compared to control groups who received no training). This suggests that cognitive and perceptual training measures are robust and durable. Furthermore, 60% of the initially trained older adults received top-up training sessions (eleven months after initial training), which led to an even greater improvement in performance at the first year assessment. The present experiment uses a training method wherein each participant receives initial training and also receives top-up training at intervals during the experimental task. Although the present study was conducted over a much shorter time-scale than the study described above, it was considered that the underlying effect of using a top-up technique may still provide a benefit to performance. Due to the short duration of the sensitisation phase (described in chapter 3), this additional mechanism was deemed necessary.

4.3 Indiscriminate cross-modal integration in older adults

Research has demonstrated that older adults have an advantage compared to young adults at integrating cross-modal information (Laurienti et al, 2006; Peiffer et al, 2007, Diaconescu et al, 2013). However, this is an indiscriminate integration, whereby both congruent and incongruent information are integrated equally (Campbell et al., 2010). This unselective integration is in line with the inhibitory deficit hypothesis, which states that inhibiting task-irrelevant information is sensitive to ageing (e.g. Hasher & Zacks, 1988).

Campbell et al. (2010) proposed a method for increasing top-down inhibition of taskirrelevant information. Young and older adults were presented with a visual target (letter 'o') either to the left or right of fixation. Distracter stimuli were presented either before or after the target. During unisensory trials, the visual display occurred alone; whereas during crossmodal trials, the target was accompanied by a tone indicating its spatial location (either to the left or right ear). Participants' saccadic movements were recorded with the use of an eye tracker. The task was to move the direction of gaze towards the target and away from the distracting elements. Results indicated that the presence of the auditory tone lead to greater inhibition of task-irrelevant information in both young and older adults. However, this was only the case when the distracter was presented before the target, suggesting that the effect could have been initiated by providing observers with prior knowledge of the distracter location (as seen in preview benefit paradigms e.g. Payne and Allen (2011)). The present experiment investigates the effects of providing both congruent and incongruent auditory information during a visual discrimination task. This was done in order to test if older adults are able to improve their discrimination performance in the presence of a congruent cue, and maintain their performance in the presence of the incongruent cue.

4.4 Introduction to experiment 4

Results from chapter 2 indicated that older adults did not have a naturally occurring bias towards congruency (as was found in young adults). It was speculated that this may have been due to an inability to employ an appropriate strategy (as tones were uninformative). Results reported in chapter 3 indicated that top-down cueing via sensitisation may enable observers to form effective cue + stimulus associations, thereby enhancing cross-modal integration. This was shown to have a beneficial effect on TOJ performance. The present experiment aimed to explore if such cueing could induce a cross-modal congruency effect in older adults, thereby allowing them to employ an effective strategy to improve TOJ performance.

This experiment used the same two-alternative forced choice temporal order judgement paradigm as detailed in the previous two chapters. SOAs were varied on a trial by trial basis (11, 22, 33, 44, 55, 66, 77, 88 and 99 ms). An increased number of SOAs were explored in this experiment, compared to the previous two chapters in order to obtain a greater range of performance in both age groups. Each participant's individual contrast threshold was measured using a grating detection paradigm (described in chapter 3); stimuli were then presented at two different contrast levels throughout the experiment (lower and higher).

Participants completed an initial experimental session with a neutral cue (baseline condition), as described in chapters 2 and 3. On a different day (within the same week) they underwent a sensitisation training session and took part in the cross-modal cueing experiment (described in chapter 3). Training sessions differed from those described in chapter 3. During the present experiment, participants were exposed to short 'top-up' training sessions, interleaved with the main experimental conditions. This was carried out as it was thought that the initial 10 minute training session may not have been sufficient for those that are not

trained psychophysical observers. Instead of extending the training session at the beginning of the main experiment, short top-up sessions were employed in order to retain participants' attention (by varying task) and also to maintain compliance.

It was predicted that training would enable participants to form robust cue + stimulus associations, which would lead to improved performance during temporal order discrimination. It was expected that older adults would use the additional information provided by the cues at shorter SOAs than young adults, due to enhanced integration (aided by informative cueing). It was also predicted that older adults would show enhanced integration of the cross-modal cues across all SOAs, compared to young adults.

4.5 Methods

4.5.1 Participants

Eight young (M = 19.63, SD = 1.41) and 8 older adults (M = 70.13, SD = 3.23) participated in this experiment. Of the young adults group, five were female and two were left handed. Of the older adults group, four were female and all were right handed. All gave informed written consent and had normal (or corrected to normal) vision and normal hearing (all self reported).

4.5.2 Stimuli and apparatus

Stimuli for each experimental session was as described in the methods sections of the two previous chapters.

4.5.3 Procedure

Observers were first measured for individual contrast sensitivity threshold (see chapter 3 for methods). Following two practice runs, participants took part in the neutral cue session (described in the previous two chapters), which comprised of 16 runs of 162 trials (2592 trials in total) and lasted approximately 40 minutes. Trials lasted (approximately, depending on individual response time) between 505 ms and 593 ms depending on SOA between the two stimuli.

On a different day (within the same week) observers underwent the sensitisation session (as described in chapter 3). Each participant completed 864 trials of the sensitisation session, which took approximately 10 minutes. Participants then took part in the cross-modal cueing condition (all participants were tested to make sure that they could clearly hear the tones prior to the experiment). Each cross-modal cue session comprised of 16 runs of 162 trials (2592 trials in total). Every 4 runs, cross-modal blocks were interleaved with short top-up blocks of the sensitisation phase (108 trials each). This resulted in one initial training session and a further 3 short training top-up sessions. The entire training and post-training session lasted approximately 80 minutes.

4.6 Results

This experiment aimed to investigate if training to use explicit top-down cues would have an effect on temporal order discrimination in young and older participants. Participants were required to decide which of two spatial frequency stimuli they detected first (responding left or right) at varying SOAs.

Data were analysed using d'. Hit (H) and False Alarm (FA) were calculated as described in chapter 2. Results from the neutral cue (baseline) condition can be found in appendix C.1. The neutral cue results revealed no significant effect or significant interactions containing side presented (left and right), therefore data were collapsed over side presented for future analyses.

A repeated measures ANOVA with a between-subjects factor of age (2 – young and older adults) and within-subject factors of cue-type (3 – neutral, congruent and incongruent), contrast (2 – lower and higher) and SOA (9 – 11, 22, 33, 44, 55, 66, 77, 88, 99ms) revealed significant main effects of age, cue-type, contrast and SOA. There were significant interactions of cue-type x age, SOA x age and contrast x SOA x age (figure 4.1). See table 4.1 for ANOVA results and table 4.2 for means and standard error.

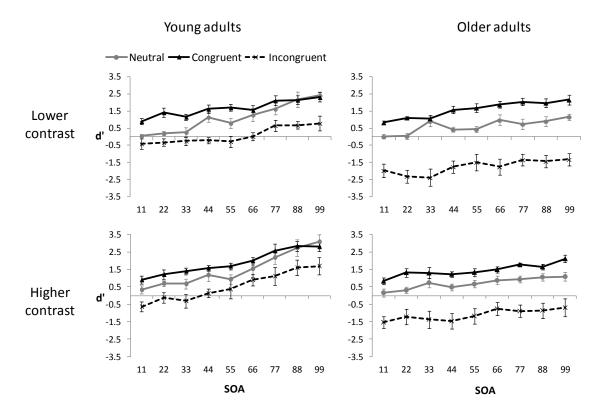


Figure 4.1: Age differences in TOJ with the presence of cross-modal cues. The x axis shows SOA (ms). The y axis shows d' sensitivity index. A d' of zero indicates chance performance. Positive values indicate better than chance, whereas negative values indicate worse than chance performance. The left column shows performance in the young group. The right column shows performance in the older group. Error bars depict standard error.

The significant main effect of age indicated that young adults made more correct temporal order judgements than older adults. The significant main effect of cue-type indicated different patterns of performance for each type of cue. Contrasts revealed that participants made significantly more correct order judgements during congruently cued trails compared to incongruent (F(1, 14) = 72.67, p < 0.001, partial $\eta^2 = 0.84$). Congruent cueing also produced better performance compared to the neutral condition (F(1, 14) = 10.91, p = 0.005, partial $\eta^2 = 0.44$). Incongruent cueing produced a performance cost relative to the neutral condition (F(1, 14) = 44.47, p < 0.001, partial $\eta^2 = 0.76$). The significant main effect of contrast indicated that performance was significantly better at the higher contrast compare to lower.

The significant main effect of SOA indicated that performance increased as a function of increasing SOA.

The significant interaction of age x cue-type indicated that young adults made more correct order judgements compared to older adults during the neutral cue condition (F(1, 14) = 4.71, p = 0.048, r = 0.50) and during incongruent trials (F(1, 14) = 19.39, p < 0.001, r = 0.76). There were no age differences in performance during congruent trials (F(1, 14) = 1.18, p = 0.295, r = 0.28). See appendix C.2 for 2x3 ANOVA results.

The significant interaction of age x SOA indicated that young adults made significantly more correct order judgements compared to older adults at each SOA except 33ms (see appendix C.3 for two-way ANOVA results).

There was also a significant three way interaction of age x contrast x SOA. Further analysis revealed that older adults made significantly more correct order judgements at the higher contrast compared to the lower contrast at SOA of 22ms (F(1, 14) = 10.10, p = 0.007, r = 0.65). There were no significant differences between contrast levels at any of the remaining SOAs. Young adults showed no significant difference between contrast levels at any SOAs (see appendix C.4 for two-way ANOVAs for young and older adults).

In summary, there was no age-related difference in modulation of the congruent cue, whereas, older adults showed greater modulation of the incongruent cue compared to young adults. This suggests that both young and older adults use congruent cross-modal information in a similar manner but age-related differences arise when cross-modal information is misleading, resulting in older adults being less able to inhibit incongruent information.

Table 4.1: ANOVA results for cross-modal experiment

Effects	Mean Square	DF	F	р	Partial η ²
Age	3.04	1, 14	29.05	< 0.001*	0.68
Cue type	369.27	2, 28	47.75	< 0.001*	0.77
Contrast	16.77	1, 14	20.49	< 0.001*	0.59
SOA	53.93	4, 55	58.58	< 0.001*	0.81
Cue type x Age	42.32	2, 28	5.47	0.010*	0.28
Contrast x Age	1.37	1, 14	1.67	0.217	0.11
SOA x Age	3.71	8, 112	8.23	< 0.001*	0.37
Cue type x Contrast	7.21	1, 19	3.32	0.074	0.19
Cue type x Contrast x Age	1.73	2, 28	1.19	0.320	0.08
Cue type x SOA	0.46	16, 224	1.14	0.320	0.08
Cue type x SOA x Age	0.56	16, 224	1.41	0.139	0.09
Contrast x SOA	0.46	8, 112	1.92	0.064	0.12
Contrast x SOA x Age	0.66	8, 112	2.78	0.008*	0.17
Cue type x Contrast x SOA	0.21	16, 224	0.83	0.646	0.06
Cue type x Contrast x SOA x Age	0.24	16, 224	0.97	0.492	0.07

Contrasts	Mean Square	DF	F	р	Partial η ²
Congruent vs. Neutral	7.09	1, 14	10.91	0.005*	0.44
Incongruent vs. Neutral	38.03	1, 14	44.47	< 0.001*	0.76
Congruent vs. Incongruent	77.97	1, 14	72.67	< 0.001*	0.84

Table 4.2: Means and standard deviation for cross-modal experiment

Factor	Level	Mean	Std. Error
Age	Young	1.12	0.11
Age	Older	0.25	0.11
	Neutral	0.98	0.15
Cue type	Congruent	1.64	0.12
	Incongruent	-0.56	0.20
Contrast	3x	0.55	0.07
Contrast	5x	0.83	0.10
	11ms	-0.05	0.05
	22ms	0.19	0.06
	33ms	0.26	0.10
	44ms	0.49	0.09
SOA	55ms	0.55	0.11
	66ms	0.83	0.11
	77ms	1.13	0.13
	88ms	1.29	0.12
	99ms	1.47	0.13

Additional analysis was performed to explore whether there were any age differences in modulation during cue use. In order to do this, the neutral cue condition data were subtracted from the congruent cue data and the incongruent cue data (congruent – neutral = congruent effect, incongruent – neutral = incongruent effect).

A repeated measures ANOVA with a between-subjects factor of age (2 – older adults and young adults) and within-subjects factors of cue-effect (2 – congruent effect and incongruent effect), contrast (2 – low and high) and SOA (9 – 11, 22, 33, 44, 55, 66, 77, 88 and 99 ms) revealed significant main effects of cue-effect and SOA, and significant interactions of cue-type x age and SOA x age (see table 4.3 for ANOVA results and table 4.4 for means and standard error). There was no effect of contrast or interactions containing contrast, so the graph shows data collapsed over contrast (see figure 4.2).

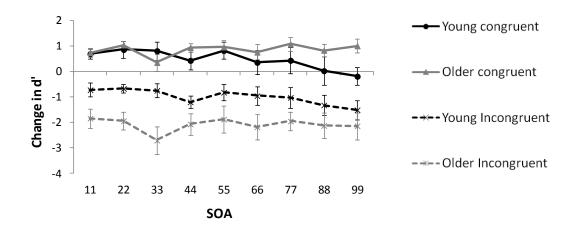


Figure 4.2: Age differences in attentional modulation. The graph shows age differences in change scores across all SOAs. Subtractions were performed for congruent cue – neutral cue and incongruent cue – neutral cue, resulting in two cue effects (congruent effect and incongruent effect). Older adults showed significantly more modulation for the incongruent effect compared to young adults when all SOAs were included in the analysis. When the analysis contained only SOAs of 44ms and above, this significant difference in modulation disappeared. No significant age differences were revealed for the congruent effect (across all SOAs and for SOAs of 44ms and above). Error bars represent standard error.

The significant interaction of age x cue indicated that there were no age differences in change scores for congruent – neutral (F(1, 14) = 0.90, p = 0.358, r = .25), whereas there were significant age differences in change scores for incongruent – neutral (F(1, 14) = 45.60, p = 0.033, r = .53). This suggests that older adults were weighting the incongruent cue more heavily than young adults (see appendix C.5 for two-way ANOVA results).

Further analysis of the age x SOA interaction (2-way ANOVA) revealed significant age differences in change scores at SOAs of 11ms (F(1, 14) = 4.70, p = 0.048, r = .50), 22ms (F(1, 14) = 5.59, p = 0.033, r = .53) and 33ms (F(1, 14) = 8.51, p = 0.011, r = .61), indicating that older adults' change in scores (from congruent – neutral and incongruent – neutral) was greater than young adults' (see appendix C.6 for two-way ANOVA results).

Together, the interaction results suggest that the age difference in modulation was only present at SOAs of 33ms and below. A further two-way ANOVA of age x cue-effect was performed on the data from SOAs of 44ms and above. This revealed no age differences in change scores for either congruent (F(1, 14) = 1.84, p = 0.197, r = .34) or incongruent (F(1, 14) = 3.36, p = 0.088, p = 0.0

 $Table\ 4.3:\ ANOVA\ results\ for\ change\ scores\ (cross-modal-baseline).$

Effects	Mean Square	DF	F	р	Partial η ²
Age	0.51	1, 14	1.05	0.324	0.07
Cue (congruent / incongruent)	701.76	1, 14	72.67	< 0.001*	0.84
Contrast	0.67	1, 14	0.37	0.553	0.03
SOA	2.25	8, 112	2.24	0.029*	0.14
Cue x Age	78.56	1, 14	8.14	0.013*	0.37
Contrast x Age	1.64	1, 14	0.90	0.358	0.06
SOA x Age	2.84	8, 112	2.83	0.007*	0.17
Cue x Contrast	9.42	1, 14	4.10	0.063	0.23
Cue x Contrast x Age	2.90	1, 14	1.26	0.280	0.08
Cue x SOA	0.16	8, 112	0.35	0.944	0.02
Cue x SOA x Age	0.18	8, 112	0.39	0.924	0.03
Contrast x SOA	0.54	8, 112	0.78	0.623	0.05
Contrast x SOA x Age	1.09	8, 112	1.58	0.140	0.10
Cue x Contrast x SOA	0.23	8, 112	0.88	0.534	0.06
Cue x Contrast x SOA x Age	0.12	8, 112	0.44	0.895	0.03

Table 4.4: Means and standard deviation for change scores

Factor	Level	Mean	Std. Error	
Λαο	Young	-0.26	0.25	
Age	Older	-0.62	0.25	
Cue	Congruent	0.67	0.20	
Cue	Incongruent	-1.54	0.23	
Contrast	3x	-0.47	0.17	
Contrast	5x	-0.40	0.19	
	11ms	-0.28	0.12	
	22ms	-0.18	0.12	
	33ms	-0.57	0.21	
	44ms	-0.47	0.17	
SOA	55ms	-0.23	0.20	
	66ms	-0.50	0.25	
	77ms	-0.37	0.25	
	88ms	-0.65	0.28	
	99ms	-0.71	0.24	

Summary

Congruent cueing led to better performance than incongruent cueing. Congruent cueing was also shown to improve performance compared to the neutral baseline. Incongruent cueing produced a performance cost relative to the neutral condition.

No age-related differences were found in performance when congruent cues were provided, suggesting that both young and older adults showed the same amount of facilitation from congruent cueing. Older adults showed greater modulation of the incongruent cue compared to young adults, where the cue appeared to disrupt performance. Change scores analysis revealed that this disruption was only present at short SOAs (33ms and less), suggesting that older adults were weighting the incongruent cue more than young adults when TOJ was indistinguishable (Kanabus et al., 2002). Further analysis of the change in scores revealed no age differences in change scores for either congruent or incongruent cueing for SOAs of 44ms and above, suggesting that young and older adults may have been using an identical underlying strategy to improve performance when TOJ was distinguishable.

4.7 Discussion

This chapter investigated the effects of training on effective cue use during temporal order judgment. Young and older adults made judgements about which stimulus appeared first (HSF or LSF), over two experimental sessions: neutral cue condition and training + cross-modal cue condition (congruent and incongruent).

Results indicated that training enabled participants to form effective cue + stimulus associations, which significantly improved their performance when congruent cues were

performance cost for both age groups (compared to neutral cue).

It is possible that at short SOAs, participants were just using the information provided by the auditory cue, due to this offering more reliable information than the visual stimulus (i.e. when TOJ was indistinguishable). Older adults appeared to weight the incongruent cue more than young adults at short SOAs. There were no age differences in weighting of the congruent cue. This suggests that older adults were unable to inhibit the incongruent information provided by the cue (Hasher & Zacks, 1988).

It is possible that the improvements in TOJ performance observed in the cross-modal conditions may have been as a result of practice effects, due to repeated exposure to the task. However, the observed significant effect of incongruent cueing is not in line with this notion.

Analysis was also performed on the change in scores from congruent – neutral and incongruent – neutral conditions. This method of analysis removed the influence of practice effects, as both age groups had received the same amount of practice on the task; therefore any change (or similarities) observed were considered a reflection of true effect.

Analysis of the change in performance (change scores) revealed that older adults displayed more modulation of the incongruent cue at short SOAs (33ms and less), whereas there were no age differences in modulation of the congruent cue. When SOAs of 33ms and below were removed from the analysis, the age-difference in incongruent modulation disappeared. Both young and older adults showed the same amount of improvement in TOJ performance with the presence of congruent cues, and the same amount of modulation of the congruent cue; this suggests that both age groups were employing similar strategies to complete the task.

It has been suggested that the human information processing system can reliably distinguish temporal order at SOAs of 40ms and above (Kanabus et al., 2002). Busey et al., (2010) found that older adults' critical duration for TOJ was significantly higher than that in young adults (approximately 76ms compared to 26ms). Results from this chapter suggest that the auditory cue enabled older adults to raise their performance to the level of young adults for SOAs of 44ms and above.

Effects of perceptual and cognitive training in older adults

The present experiment utilised a short training session (initial 10 minutes, with shorter repeated top-ups) to test if such short term training can form a useful association between cue and stimulus.

Previous research has reported that young adults tend to adopt a proactive strategy for cue usage in which they use this initial information to prime a set of responses. Older adults use a reactive strategy were they attend to the cue, but do not prime a set of responses until further information is provided by the probe (Paxton et al, 2006). Results from the present chapter suggest that this priming strategy may have resulted in young adults showing improved performance, even at short SOAs, as a primed response is a result of sensitisation training. Conversely, the suggested reactive strategy in older adults may have caused performance disruption at short SOAs.

Previous research has found that training on one perceptual task can aid performance in an untrained perceptual task (Berry et al, 2010). The present experiment demonstrated that training aided performance at the perceptual level, which aligns with the predictions made for this experiment. Training participants to form effective cue + stimulus associations reduced uncertainty during temporal order judgement.

Cross-modal integration in older adults

A variety of research demonstrates that older adults are better able to integrate cross modal cues (Campbell et al, 2010; Laurienti et al, 2006; Peiffer et al, 2006; Diaconescu et al, 2013). As well as showing increased integration for congruent cues (which can serve to aid performance), older adults show increased integration for incongruent cues (Campbell et al, 2010).

The present experiment revealed that both young and older adults demonstrated impaired performance with incongruent cueing compared to neutral and congruent cueing. This effect was greater in older adults at SOAs of 33ms and less, suggesting that older adults were more deficient at rejecting the incongruent information during response preparation. That is, when the target congruent cue was paired with a target stimulus, observers could achieve a singular representation that would allow for more efficient processing of the task. When the cue was followed by an incongruent stimulus, this simple representation could not be formed, causing more of a demand on working memory and hence disrupting performance. It is likely that older adults' greater integration of the incongruent cue at short SOAs was as a result of age-related inhibitory deficits that would amplify the disruptive effects of the task (Hasher & Zacks, 1988). At longer SOAs (44ms and above), older adults' performance was less disrupted by the incongruent cue, which may suggest that they were able to employ a strategy akin to that of young adults (proactive rather than reactive).

Controlling for the effects of ageing on contrast sensitivity

Without contrast thresholding it would be expected that older adults would have performed worse than young adults due to degradation of their perception of the input stimulus (Owsley et al., 1981, Cerella, 1985, Scialfa, 2002). However, the results show that contrast matching

was able to ameliorate this detrimental effect by individually tailoring the visual input to the individual level of acuity.

Summary

Top-down cueing via sensitisation to spatial scale appeared to have a beneficial effect on TOJ performance for both age groups. Results from chapter 2 indicated that young adults had a naturally occurring bias to congruent cross-modal information, whereas older adults showed no integration of the cross-modal information. Results from the present chapter indicated that sensitisation training enhanced the naturally occurring cross-modal bias in young adults, thereby enhancing performance on TOJ. Moreover, sensitisation training was shown to induce the cross-modal integration effect in older adults.

The fact that young and older adults experienced the same amount of improvement in TOJ performance when provided with congruent cues suggests that the underlying strategy is similar for both age groups. This was supported by change scores showing no age differences at longer SOAs. This suggests that both young and older adults use congruent cross-modal information in a similar manner, but that age-related differences arise when cross-modal information is misleading (incongruent cues at short SOAs), resulting in older adults being less able to inhibit incongruent information.

Interim summary

The previous three chapters focused on exploring age differences in attentional modulation during temporal processing. The key findings are summarised as follows:

- Young adults made more correct temporal order judgements than older adults when no additional information is provided.
- Young adults showed a naturally occurring bias towards congruent cross-modal information. Older adults showed no integration of cross-modal information.
- Sensitisation training enabled observers to form effective cue + stimulus associations,
 which had a beneficial effect on TOJ performance.
- Top-down cueing via sensitisation training enhanced the naturally occurring bias towards congruency found in young adults. This was displayed by improved performance during TOJ compared to baseline.
- Top-down cueing via sensitisation training was found to induce integration of cross-modally congruent information in older adults. This was shown by improved performance during TOJ compared to baseline.
- At short SOAs, older adults showed enhanced integration of incongruent information compared to young adults. This effect disappeared when SOAs exceeded 33ms.

Overall, the results of the last three chapters indicate that training is necessary for older adults to form appropriate cue + stimulus associations, and enhances the pre-existing bias in young adults. Furthermore, this training period does not need to be extensive, as participants showed cue association effects after short sensitisation sessions. Results also indicate that such perceptual learning techniques were carried over to a secondary element of the task, where cueing reduced temporal order uncertainty.

The following chapter continues with the theme of age differences in attentional modulation. The next two experiments utilise a motion discrimination paradigm in order to investigate age differences in focused and divided attention. The chapter includes a behavioural component and an fMRI component, allowing illumination of the underlying neural responses associated with the behaviour.

CHAPTER 5

Age-related changes in attentional modulation during selective attention

5.1 Abstract

This chapter sets out to explore age differences in attentional modulation when attention is focused on a prevailing task and when it is divided between two concurrent tasks. The main aims of the chapter are to investigate the following: 1. Do young and older adults utilise attentional resources in the same way? 2. Are there differences in the strategies adopted by young and older adults? 3. Do young and older adults recruit the same attentional regions during focused and divided attention, or are they using distinctly different networks?

The experiments in this chapter utilise a motion discrimination paradigm in order to examine how ignoring task-irrelevant stimuli (therefore, focusing attention) affects the process of discriminating visual patterns of global motion and also how the process is affected by performing a secondary, concurrent task (therefore, dividing attention). Cortical activity was also measured using fMRI, in order to investigate the networks of regions activated during selective attention, and any age-related differences in activation.

The findings suggested that older adults experienced more difficulty compared to young adults when they were required to divide attention between two concurrent tasks. The allocation of focused attention was preserved in older age, even when additional distracters were present.

The fMRI results indicated that young and older adults utilised distinctly different neuronal networks when dividing attention between two tasks. Functional connectivity

analyses revealed that young adults engaged bilateral prefrontal regions in synchrony with the primary sensory region (hMT+), whereas older adults showed synchronous activity between posterior cingulate and hMT+. Older adults also showed connectivity between regions activated during focused attention and hMT+ when ignoring irrelevant stimuli, which included regions known to be part of a network responsible for attention and arousal (Kinomura et al., 1996).

Together, the results indicated an age-related increase in the magnitude of synchronous activation during focused attention, whereby older adults were activating more of the areas thought to control the focus of attention than are young adults. Furthermore, the results revealed distinctly different patterns of activation for young and older adults during the division of attention. Here, young adults were recruiting regions typically activated during more challenging cognitive tasks. Older adults engaged a region that is said to specifically monitor and tune the focus of attention.

5.2 Introduction

From one moment to the next, the visual system is bombarded with a vast amount of information, from which it must obtain an understanding of the visual scene. It is impossible to process all incoming information due to the limited computation capacity of the brain (Kahneman, 1973) and it is therefore necessary to prioritise processing of the relevant information at any given time. Selective attention enables the observer to focus their attention on task-relevant information whilst ignoring task-irrelevant items (Corbetta et al, 1991). The process of selective attention is driven by a variety of factors such as knowledge about the surrounding environment, assumptions of the observer, the abrupt appearance of new stimuli

(whether relevant or irrelevant to the task at hand) and the behavioural state of the observer (Carrasco, 2011). It is often necessary to process more than one source of information at the same time. In this case, selective attention enables the observer to shift attention, or divide attention between multiple events (Kahneman, 1973). Aspects of focused and divided attention will be discussed next.

5.3 Focused attention

Several theories have been proposed to account for the mechanism by which focused attention improves perceptual performance (Morrone et al., 2002; Lu & Dosher, 1998; Dosher & Lu, 2000). One such theory is the signal enhancement hypothesis, which states that attention enhances the quality of the stimulus signal by increasing the gain on the relevant stimulus (Morrone et al., 2002).

Another explanation is provided by the external noise reduction hypothesis (Lu & Dosher, 1998), which comprises two distinct processes: noise exclusion and distracter suppression. The noise exclusion process is concerned with attention acting as a filter that allows certain specific information to be processed, whilst simultaneously suppressing unwanted or irrelevant information (Lu & Dosher, 1998). Here, attention serves to diminish the impact of external noise (which accompanies the relevant signals) by enhancing the signal component of the stimulus and attenuating the noise components, which are then dealt with by different filters (Dosher & Lu, 2000). The distracter suppression process uses attention as a spatial filter, which enables the observer to attend only to the stimuli in the focus of attention whilst ignoring stimuli outside of this (Lu & Dosher, 1998).

A useful tool to study the allocation of focused attention is the response inhibition paradigm. This method tests an observer's ability to remain focused on task relevant stimuli whilst ignoring task-irrelevant items in a display. Older adults have been shown to exhibit poorer performance than young adults when a task requires them to ignore irrelevant information (Jonides et al., 2000; Gazzaley et al, 2005, Nielson et al., 2002). Age differences in the ability to ignore task-irrelevant information will be discussed next.

5.4 Age-related changes in inhibitory control

Neuroimaging research has highlighted that older adults are unable to inhibit task irrelevant information due to a selective impairment in the early stages of visual processing (Gazzaley et al., 2005, Gazzaley et al., 2008, Jonides et al., 2000, Nielson et al., 2002). Using EEG, whilst participants performed a visual working memory task, Gazzaley et al. (2008) demonstrated that older adults show a selective deficit in inhibiting task-irrelevant information but that this deficit is only present in the early stages of visual processing. They argued that inhibition is not entirely absent in older adults, but that attentional suppressive mechanisms are delayed to a later stage of processing.

Age-related deficits in inhibitory processes had previously been linked to an agerelated decline in top-down attentional modulation (Gazzaley et al, 2005). Using fMRI during a working memory task, the authors found that enhancement of task-relevant stimuli was preserved for older adults, whereas, the inhibition of task-irrelevant information was impaired. Associated brain activity of the older adults matched that of young adults during focused attention (when they were asked to remember a stimulus), however, when participants were asked to ignore (or not remember) a stimulus, older adults showed less suppression in stimulus specific visual regions than young adults.

On the other hand, some research has demonstrated that when the task specifically requires participants to direct attention toward a particular stimulus or set of stimuli, older adults' performance has been shown to be preserved (Gottlob & Madden, 1999; Gazzaley et al, 2005). Gottlob and Madden (1999) demonstrated that older adults were just as proficient as young adults when allocating attention to relevant stimuli during multi-item displays. They compared the performance of older and young participants on visual search tasks while using a sequential cueing method in order to investigate age differences in the allocation of focused attention. They found age differences in the size of the cueing effect but no interactions with age in reaction times; suggesting that the allocation of focused attention was statistically equivalent across age.

Factors such as prior knowledge about the location of distracter stimuli, and position of distracters stimuli within the display can affect performance differentially in young and older adults. For example, processing speed and accuracy are compromised in older age when target stimuli are presented in the periphery. This is due to an age-related decrease in the field of view (Scialfa et al., 1987). However, this effect may also extend to distracter items, leading older adults to show less task interference from peripheral non-target items compared to young adults (Cerella, 1985). Uncertainty about the location of a stimulus, for example, looking for a target among distracters with no prior knowledge of where the target is, leads to more impaired performance in older adults compared to young adults (Cerella et al., 1987).

In summary, some research has highlighted that older adults fail to recruit appropriate cortical regions when attempting to ignore irrelevant material. Other research has reported increased activation in older adults during response inhibition.

In related research, Jonides et al. (2000) used fMRI to compare neural activity in older adults with that in young adults during a verbal working memory item recognition paradigm. In order to make successful responses, participants were required to inhibit their responses to distracter items that were similar to targets (to which they were to make a negative response). Older adults consistently made more positive responses to non-target stimuli (therefore more incorrect responses) than young adults, suggesting that they were unable to effectively inhibit their prepotent response. Young adults also showed an interference effect (to a lesser degree than in older adults), which was associated with left lateralised frontal activation. Such activation was not found to be significant in older adults, suggesting that older adults were unable to recruit critical regions involved in the inhibition process.

Findings from the study described above (Jonides et al., 2000) may reflect a decrease in activation due to an increase in cognitive load (as older adults showed more impaired performance during the behavioural task compared to young adults). One prominent theory of ageing proposes that increasing cognitive load has differential effects on brain activity between young and older adults. The compensation-related utilisation of neural circuits hypothesis (CRUNCH) (Reuter-Lorenz & Cappell, 2008) states that, as cognitive load increases (i.e. as the task gets more difficult), young adults typically show increased activity in regions specifically related to the goal of the task, which 'spills over' into bilateral regions as difficulty increases. However, older adults tend to show a decrease in activation, accompanied by a decline in performance, as task difficulty increases, which is said to be a consequence of older adults exhausting neural resources at lower cognitive loads (i.e. at easier levels of the task).

In contrast to Jonides et al. (2000), other research has demonstrated more frontal activity in older compared to young adults when only correct inhibition trials were analysed (Nielson et al., 2002). During event related fMRI, young and older adults were presented with sequences of letters and had to respond whenever the pre-defined target letters (X and Y) appeared on alternating presentations. If a target letter was shown without having been alternated with the other target, participants were to treat this as a distracter and ignore it. This process required participants to inhibit their prepotent response. Overall older adults were slower and less accurate during response inhibition. When only successful inhibition trials were analysed, more accurate inhibition was associated with activity in right frontal and parietal regions. Older adults showed additional activity in left frontal regions, suggesting that they required additional resources to be able to successfully inhibit unwanted information.

In a related study, Colcombe et al. (2005) investigated inhibitory control in young and older adults using event related fMRI during a flanker task where participants had to indicate the orientation of a central target arrow flanked by distracters that were either congruently or incongruently oriented. Young adults and good performing older adults consistently activated right lateralised frontal regions, whereas, poor performers additionally engaged left lateralised frontal regions. Although all older participants showed some bilateral activation, it was more significant in the poor performers. The results suggest that additional recruitment in older adults is not always compensatory and may instead cause interference.

This increase in older adults' brain activity also occurs when inhibitory control performance is equated between older and young adult. Using fMRI, Payne and Allen (2011) investigated age-related changes in attention and inhibition control during a visual preview search paradigm. Participants were first presented with a preview display (half of the distracters present), followed by the search display (all distracters plus the target). Participants were asked to judge the direction of tilt in the target item. Young adults and good performing

older adults were able to effectively ignore previously encountered distracter items during the search display. However, there were age differences in the pattern of activity associated with the behaviour. Older adults showed increased activity in frontal regions during the preview displays (to be ignored), whereas, during the full search displays, older adults showed increased activity in occipital and parietal regions compared to young adults. The results are consistent with the notion that while older adults displayed some frontal compensatory activity during the preview displays, they also needed to draw on more attentional resources during the search displays to gain any benefit of preview.

The distinction between 'good' and 'poor' performing older adults is an important factor to consider when reviewing the literature. Ageing research has highlighted the fact that older adults who lead an active lifestyle (physically and cognitively) are more likely to have access to a greater amount of cognitive reserve (additional cognitive resources that can be recruited when required), and that this has a positive effect on performance during many perceptual and cognitive tasks (Stern, 2007). It may be that studies reporting less activation in combination with reduced performance have recruited participants from a less active sample than those studies finding increased cortical activation combined with good performance (e.g. Jonides et al., 2000; Nielson et al., 2002).

The studies described above are concerned with the ability to ignore irrelevant incoming information in order to facilitate the focus of attention. Some research has highlighted age differences in the networks that underlie focused attention, with some reporting an age-related increase in activation, while others have reported an age-related decrease. One aim of the present chapter is to shed light on this discrepancy by comparing young and older adults' ability to perform a perceptual task whilst ignoring irrelevant distracters, and investigating the underlying brain activity associated with their performance.

Is there a specific network for focusing attention whilst ignoring task irrelevant information? If so, is this network comprised of the same or different regions in young and older adults?

5.5 Divided attention

Visual events seldom occur in isolation and it is often necessary to process several sources of incoming information at the same time (such as driving whilst referring to a satellite navigation instrument). In order to achieve this objective, the visual system must divide attention between the relevant sources of information. Kahneman (1973) proposed a model of divided attention, which states that successful performance on two or more simultaneous tasks depends largely on the level of difficulty of each task. Attentional resources towards a task may be increased or decreased depending on the level of task demand and the behavioural motivation of the observer. When task demand exceeds cognitive resources, performance declines on one or more of the tasks.

A robust test of divided attention can be performed by using the dual-task method, in which observers to divide or switch attention between two or more tasks. Dual-tasking requires cognitive flexibility and the ability of the attentional system to allocate resources to two or more tasks simultaneously (Hartley & Little, 1999; Hartley, 2001; Erickson et al, 2007).

Hartley and Little (1999) described two main theories of dual-task performance: the capacity sharing theory and the task sharing theory. The capacity sharing theory states that there is a fixed amount of cognitive resources available to share between the concurrent tasks. This capacity may be derived from a single common resource or from multiple resources (Wickens, 2002). The theory proposes that at the beginning of each trial, all cognitive

resources are tuned towards processing the first task. When the second stimulus is presented, the resources are shared between the two tasks, leading to impaired performance as less capacity is available for each singular task. Once a response has been made to the first task, the second task can receive increased cognitive resources, and therefore improved performance (Hartley & Little, 1999). In this case, the longer the temporal separation between tasks, the better the performance. Problems arise when tasks become very close together or overlapped, as this leads to more division of the available resources and therefore less capacity for each given task.

The task sharing model proposes that there is a single response-selection mechanism underlying dual-task performance. That is, all cognitive resources are directed towards the first task until a response is made, and only then can resources begin to process the second task (Pashler, 1984).

5.6 The effects of ageing on divided attention

Older adults have consistently been shown to be more impaired than young adults during dual-task paradigms (Hartley and Little, 1999, Hartley, 2001, Bherer et al., 2005, Erickson et al., 2007). Furthermore, this has been found to be more evident when participants are required to make similar motor responses to the concurrent tasks, as opposed to manually responding to task 1 and verbally responding to task 2 (Hartley, 2001).

According to the capacity sharing model (Hartley & Little, 1999; Wickens, 2002), the fact that older adults experience decline in several sensory and cognitive domains makes it more likely that they will be more impaired at performing in dual-task paradigms. This is

particularly true when multiple items need to be processed, and already limited cognitive resources need to be divided (Hartley & Little, 1999).

The task sharing model (Hartley & Little, 1999; Pashler, 1984) predicts age-related impairment of performance as it requires the shifting of attention between two tasks in close succession, which as a result of age-related slowing of cognitive processes (Salthouse, 1996), could lead to interference between the processes adopted by the first and second tasks.

Verhaeghen et al. (2003) performed a meta-analysis of the research concerned with ageing and dual-task performance. They found dual-task performance costs on reaction time latency for both older and young adults, with older adults showing a larger effect than young adults. However, they found no evidence of age-related decline in accuracy for either the dual-task or single task performance. This suggests that age-related slowing of sensory processes may lead older adults to require a greater amount of time to make a response, and that this slowing becomes more apparent as task difficulty increases. The lack of decline in accuracy shows that, while the central sensory processes are compromised by age, the older brain is still able to engage such processes when required. The greater latency observed in older adults may reflect more dispersed cortical processing, where additional cortical regions are recruited in order to compensate for less modulation in specific sensory regions.

During a meta-analysis, Spreng et al. (2010) found that tasks requiring executive functions (e.g. working memory, task switching and dual-tasks) consistently showed that young and older adults reliably activate regions in parietal and frontal cortex. For young adults, activation was more predominantly right lateralised, whereas older adults showed more bilateral activation in frontal regions. Within the literature, age-related changes in functional activity have often been referred to as a result of age-related decline (Brown & Jaffe, 1975; Jonides et al., 2000; Zarahn et al., 2007). However, such changes could also be

viewed as a re-organisation of the information processing system, which serves to maintain optimal performance and function (Stern, 2007). Much of the research surrounding agerelated alterations in cortical function have highlighted increased activity in bilateral frontal regions in older adults (e.g. Cabeza, 2002). This chapter aims to explore if dividing attention between two concurrent tasks has a differential effect on performance between young and older adult. The second experiment in the chapter aims to discover if there are age differences the underlying neuronal networks responsible for behavioural performance.

5.7 Age-related reductions in asymmetry

The research reviewed above has highlighted that older adults may recruit different brain regions to apply similar cognitive strategies used by young adults. It has been suggested that this type of activity reflects compensatory mechanisms within the older brain. Cabeza et al (2002) used PET to investigate age-related bilaterality. They compared the behavioural performance of three groups (young adults, high-performing older adults and low-performing older adults) during a working memory recall task. They found comparable patterns of activity in right frontal cortex for young adults and older low-performing adults, suggesting the recruitment of a similar neural network. However, as task performance was worse in the low-performing older adults compared to the young adults, it was suggested that the older group were using this network inefficiently. In contrast, the high-performing older adults showed a pattern of activity that extended into bilateral frontal regions. Taking into account the superior performance of the high-performing group compared to the low-performing group, the authors suggested that a reduction in asymmetry was reflective of an age-related compensatory mechanism that served to reorganise brain functions. Another study using PET during a verbal working memory task found that those participants who engaged bilateral

regions of the cortex outperformed those who evoked unilateral patterns of activation (Reuter-Lorenz et al., 2000).

Age-related changes in cortical activity have been shown by increased activation in regions typically used by young adults during the same task. For example, Stern (2003) found that older adults evoked greater activation in the same network of regions used by young adults during a demanding non-verbal serial recognition task, where participants either had to respond to one item at a time or a list of several items. This pattern of activity was associated with better performance in young adults compared to older adults, suggesting that older adults were more inefficient in the recruitment of task specific regions. They also found that the more demanding condition of the task elicited different patterns of activation in older and young adults. This may suggest that older adults were engaging in different strategies to enable them to perform the task.

Townsend et al. (2006) demonstrated greater frontal activation for older compared to young adults during tasks requiring the top-down control of the shifting of attention between visual and auditory stimuli. However, as both age groups displayed increased activity in the same regions, the authors suggested that this was not an example of age-related reorganisation of attentional networks; instead it reflected a task-difficulty related increase in recruitment of regions typically employed by young adults.

Madden et al (2007) found increased frontal activity in older adults during a visual search paradigm where participants were required to select a target letter from an array. They observed that when top-down attention was needed to perform the task, older adults exhibited stronger activation in the frontal eye fields and superior parietal cortex than did young adults. Young adults showed greater activity in specific task-related sensory regions (such as the fusiform gyrus). Although there were age differences in response latency, accuracy on the

task was comparable across age, therefore, the increased frontal activation may reflect an agerelated compensatory mechanism, which enables older adults to maintain performance.

Research has demonstrated age-related differences in the magnitude of activation in relation
to task difficulty and the associated cognitive load. Reuter-Lorenz and Cappell (2008)
proposed the compensation-related utilisation of neural circuits hypothesis (CRUNCH) to
explain both increased recruitment and decreased recruitment of cortical regions in the older
brain. This theory states that functional and structural decline in the ageing brain leads to
increased neuronal activation in some cortical regions in comparison to young adults when
both age groups are performing the same cognitive task. This is indicated by older adults
exhibiting greater activation at lower cognitive loads than young adults. Young adults tend to
show activation in regions that are principally related to the goal of the task (e.g. fusiform
gyrus during a face matching task), which increases to include bilateral regions as the task
becomes more difficult. Older adults, on the other hand, begin to exhibit poorer performance
coupled with less activation as task demands increase. This is said to be due to older adults
using up their neural resources at lower cognitive loads (Reuter-Lorenz & Cappell, 2008).

In a further study Cappell et al. (2010) tested older and young participants on a working memory task and found an age-related increase in activation during low cognitive load and a decrease in activation during high cognitive load in older adults. Increased activation was present when behavioural performance was equated with the young group, which suggests age-related compensatory activity. However, when higher cognitive load led to poorer performance in the older group, it was accompanied by a decrease in activation. Their results indicated that older and young adults were recruiting the same network of regions but that older adults were recruiting them at an earlier stage when cognitive load was still low.

In line with this, Schneider-Garces et al. (2009) employed a working memory task in which participants had to memorise a set of upper-case letters and identify a lower-case probe within the sequence. Task difficulty was manipulated by varying the size of the memory set (2-6 items). At higher memory loads (over 4 items), older adults showed worse performance compared to young adults. fMRI results showed that older adults engaged more bilateral activation of regions in occipital and parietal cortex and in frontal regions. Young adults also showed this pattern of increased bilaterality during the most demanding task conditions (over 5 items). A decline in older adults' performance was associated with less cortical activity, suggesting cortical compensation had reached its limit, and at a lower task load than in young adults (4 items compared to 5).

Some research has suggested that compensatory mechanisms are not merely an effect of the ageing process, but are available throughout the life-span. One such theory is the scaffolding theory of ageing and cognition (STAC), which proposes that as cognitive ability declines, activation in frontal regions increases in the older brain (Park and Reuter-Lorenz, 2009). It has been suggested that this process affords older adults the ability to maintain acceptable cognitive processing, which is reflected by increased recruitment of frontal regions during increasingly demanding tasks (Reuter-Lorenz and Park, 2010).

Increased frontal activity in older brains may not always be compensatory. One theory defines such bilateral activity in the older brain as an age-related deficit in the ability to recruit specialised neuronal mechanisms. The dedifferentiation theory (Li & Lindenberger, 1999) posits that specific or specialised neuronal regions decline in processing with age due to increased levels of internal noise and decreased functional connectivity to complementary regions. Dedifferentiation is most likely when poor performing participants show activation in regions that good performers do not activate (Stern, 2009), which reflects a decline in the recruitment of specific neural mechanisms.

Zarahn et al. (2007) employed a delayed item recognition paradigm where participants were required to memorise letters stimuli. Observers were presented with sets of letters containing 1, 3 or 6 items and were requested to indicate whether or not a probe letter had been in the sequence. Older adults showed more impaired performance as a function of increasing memory set size but did not display evidence of age-related slowing. Load-related activation during the retention phase of the experiment reflected two different patterns of cortical recruitment. The first pattern included areas consistent with working memory performance (including frontal and parietal regions) and was engaged by both older and young adults. The second pattern (including only the parahippocampal gyrus at a significant level) was only used by older adults and was associated with less successful task performance. This pattern of activation could reflect inefficient recruitment by older adults. However, it could also be seen as compensatory to the degree that the older adults who engaged this region did so to maintain performance, even if there was no improvement.

When performance is poor, decreased cortical activation in older adults is likely to reflect an age-related reduction in the function of those underactive regions and possibly also in the neural circuitry surrounding them (Grady, 2008). However, when good performance is associated with reduced activation, it is possible that older adults are using the same neural regions as young adults to employ different strategies (Stern, 2009). Age-related increases in activation during poorer performance can be seen as compensatory, that is, to maintain rather than improve performance. Some of the studies described in this introduction demonstrated age-related changes in perceptual processing, and associated age-related differences in cortical activity in sensory regions. However, the studies discussed did not specifically explore the modulation of the sensory region and any age-related differences therein. This chapter aims to see if there will be increased cortical activity in older adults during the allocation of attentional resources. Do older adults use the same networks as young adults in a

different way (e.g. different strategy). Do they recruit additional resources form regions not typically employed by young adults? Are there differences in the magnitude of recruitment between tasks that require focused attention and tasks that require the division of attentional resources?

5.8 Motion processing and the effect of ageing

Some of the literature on age differences in motion discrimination argues that stimulus contrast determines motion coherence performance (Allen et al., 2010). If performance is due to such lower level attributes alone, then it is interesting to investigate the effects of selective attention on this process in order to obtain understanding of how attention affects modulation of the sensory mechanism. On the other hand, some research has suggested that speed of the stimulus is the defining characteristic (Snowden & Kavanagh, 2006), which implies higher level processing. If this is the case, it is important to consider the effects of enhancing and disrupting attention on cognitive processes in order to uncover potential changes in strategy.

Motion processing is carried out through a progressive hierarchy within the dorsal stream of the cortex, which is fed by the magnocellular pathway. This begins early on in V1 where non-directionally selective filters containing small receptive fields analyse spatial differences in luminance. These non-directional filters are then combined to form directionally-selective filters (some of which are monocular and some binocular), which are then projected to V2 (Hawken et al., 1988). Cells in V1 and in V2 pass the combined local motion signals to human middle temporal motion area (hMT+), where they are combined to form one global percept of the incoming information (Livingstone et al., 2001). This information is then passed to medial superior temporal (MST), where large receptive fields

allow the analysis of global motion patterns, such as translational motion and radial flow (Morrone et al., 2000, Perrone and Thiele, 2001, Royden and Vaina, 2004).

Translational global motion occurs when local, spatially separate, moving elements of a scene are consolidated to form one percept (Gilmore et al., 1992). This occurs in such instances as seeing birds flying in a flock and is closely related to the Gestalt theory of common fate (Anstis and Kim, 2011). Perceiving optic flow of the nearest element of a target, for limited visual angles, can be used to estimate time-to-collision i.e. ratio of visual angle over the rate of change of the visual angle (Lee, 1976). The perception of global optic flow (Gibson, 1977) is important for instances where the observer may be moving, giving rise to differences in expansion fields for background and target, hence differing rates of change of visual angle. Older adults have been shown to be more impaired in such instances due to conflating the background and target rates of change of visual angle (Andersen and Enriquez, 2006).

The processing of global motion has been widely investigated using the 'coherent motion detection task' first described by Newsome and Paré (1988). Throughout the task, observers are presented with random dot kinematograms (RDK) patterns, which consist of visual displays containing many individual local dots moving along different trajectories (figure 5.1). Some of the dots are 'signal' dots (moving in a pre-assigned direction, manipulated by the experimenter) and some are 'noise' dots (moving in random directions). The task is to judge the direction of the signal dots (up or down; expanding or contracting; clockwise or anti-clockwise). Manipulating the proportion of signal dots in the display from trial to trial gives a measure of each participant's motion coherence threshold (the minimum proportion of signal dots within a display needed to distinguish the direction of motion). At 5-10 % signal dots per display, human observers can accurately judge motion direction (Newsome & Paré, 1988). It has been suggested that this is not due to tracking individual

dots, but to combining sets of local information, as with such a small proportion of signal dots within the display, it is likely that an observer would end up tracking a noise dot (Edwards and Badcock, 1994).

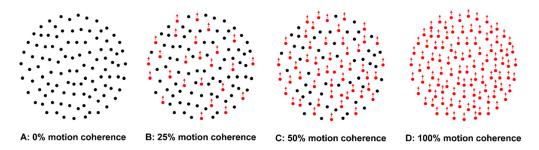


Figure 5.1: An example of RDK stimuli during translational motion. Signal dots are shown in red and noise dots in black. A = all noise dots moving in random directions, which produces 0% motion coherence. B = 25% signal dots move in a common direction, the rest are randomly moving noise dots. This produces 25% motion coherence. C = equal amount of signal and noise dots, which produces a motion coherence level of 50%. D = the entire pattern is made up of signal dots, therefore producing 100% motion coherence (Hutchinson et al., 2012).

Clear evidence of age-related decline in sensitivity to translational motion has been found by testing observers with RDK patterns (Ball and Sekuler, 1986, Gilmore et al., 1992, Snowden and Kavanagh, 2006, Bennett et al., 2007, Billino et al., 2008).

Ball and Sekuler (1986) found age-related impairment in performance on a same / different task. Young and older adults were presented with a two-interval display where the location of the stimuli was different between the two intervals. Participants judged whether the direction of motion was similar or different across the two intervals. Older adults' performance on discriminating similar directions of motion was more impaired than that of young adults. The authors concluded that observed age differences were not a result of age-related changes in sensory acuity, but that they reflected age-related changes at the perceptual level.

Varying the speed of the dots within a motion display has been shown to evoke differential results with regards to age-related decline. At faster dot speeds (over 6°/s), older adults show a clear decline in performance (Atchley and Andersen, 1998, Ball and Sekuler, 1987, Billino et al., 2008). However, at slower dot speeds (less than 6°/s), older and young participants show similar patterns of performance (Snowden & Kavanagh, 2006; Allen et al., 2010; Atchley & Anderson, 1998).

Contrast has also been shown to affect performance during global motion tasks. Using dot speeds of 5.6°/s, Allen et al. (2010) found no age differences in performance when dot contrast was high. However, when making judgements about low contrast stimuli, older adults were more impaired at distinguishing the direction of global motion patterns (translational, radial and rotational) compared to young observers. They argued that incoming stimuli that is of low contrast, and therefore low visibility, provides less information in the visual scene for older adults. This suggests that it is not an age-related problem with motion processing but that the visual stimulus is too poor to afford appropriate cues to the observer, which leads to impaired performance in motion processing.

Some research has explored the effects of attentional modulation on motion discrimination. Huk and Heeger (2000) argued that performance on motion tasks can be improved by selectively attending to the motion of an incoming stimulus, which enhances neuronal responses in hMT+ and produces an increase in the signal to noise ratio. Using fMRI, they found more activation in hMT+ when participants discriminated between two different speeds of motion compared to when the same stimuli were passively observed. This suggests that the enhancement of cortical activation in hMT+ is modulated by focusing attention on the task. This notion is further explored in the present chapter, where participants are required to make motion discrimination judgements during trials in which they focus attention (distracters are to be ignored) and trials where they divide attention (distracters are

to be counted). If focusing on motion discrimination enhances processing, what happens to performance when additional distracting elements are included in the display?

5.9 Introduction to experiments 5 and 6.

The experiments in this chapter explored if focusing attention on a perceptual task produces different modulation of the sensory region (hMT+) compared to when dividing attention between two tasks. This was tested on both young and older adults using a behavioural component and a neuroimaging component. The main questions are: 1. Do age differences exist in the strategies employed when focusing and divided attention? 2. Are there differences in cortical networks recruited during focused and divided attention? 3. Does this additional cortical recruitment reflect age differences in modulation of the sensory region?

The following experiments tested young and older adults' ability to discriminate motion direction whilst ignoring task-irrelevant information (focusing attention), and also their ability to simultaneously perform an additional attention task whilst making judgements regarding the direction of motion stimuli (dividing attention). The associated brain activity was recorded using fMRI in order to explore brain regions involved in sensory modulation during focused and divided attention.

The first experiment compared the ability of young and older adults to judge the direction of translational motion patterns while focusing attention (ignoring irrelevant distracters) and while dividing attention (counting distracters). The additional distracter items were squares that appeared in the periphery of the display during one condition (peripheral distracters) and in the centre of the display during another condition (central distracters).

The second experiment used fMRI to investigate the underlying neuronal activation associated with the behavioural tasks. Connectivity analyses (psychophysiological interaction (PPI)) were also performed to investigate regions that were functionally connected to the primary sensory region (hMT+). Participants were presented with patterns of global motion and were required to judge the direction. Additional distracters were included during some trials and participants were instructed to ignore them and focus on the motion task (focused attention trials), or to count them and respond to how many they saw whilst still discriminating the direction of motion (divided attention trials). The distracters appeared in the centre of the display and comprised of full luminance squares that were presented between 0-4 times during each trial.

5.10 Experiment 5: Age differences in performance during focused and divided attention

The first experiment investigated the effects of focused and divided attention during a motion discrimination task. The experiment tested if there are any age-related differences in performance when focusing attention and when dividing attention. Stimuli were translational global motion patterns. There were three experimental conditions: motion only (participants made judgements about the direction of global motion patterns); focused attention (participants were requested to ignore distracter items whilst making judgements about the direction of global motion patterns); divided attention (participants were instructed to count distracter items and respond to how many were present in each trial, whilst making judgements about the direction of global motion patterns). Distracter stimuli were peripheral during one condition and centrally presented in another condition. Peripheral distracters could

occur at any location around the edge of the motion patterns, whereas central distracters were presented at the same location in the centre of the display (fixation).

It was expected that older adults would experience less difficulty when attempting to ignore distracter items in the periphery, compared to in the centre of the display, during the focused attention condition. It has been demonstrated that processing speed and accuracy are compromised in older age when target stimuli are in the periphery due to an age-related decrease in the field of view (Scialfa et al., 1987). Furthermore, it has been demonstrated that older adults show a decline in extra-foveal acuity that negatively affects their performance compared to young adults during visual search tasks when target items are in the periphery. However, this effect may also extend to distracter items, leading older adults to show less task interference from peripheral non-target items (Cerella, 1985). Centrally occurring distracters should interfere more readily with the participants' field of view and should therefore induce more difficulty when attempting to suppress attention to this.

The divided attention task was expected to produce a cost of motion coherence performance for both young and older adults, compared to the focused attention condition. This cost was predicted to be greater in older adults compared to young adults. That is, older adults were expected to be less adept at switching attention between the two tasks (Wickens, 2002; Hartley & Little, 1999).

During the divided attention condition, it was predicted that an age-related reduction in participants' field of view would lead to items in the periphery receiving less, or more delayed attention (Carella, 1985), which would be supported if older adults were more successful at accurately counting central distracters compared to those presented in the periphery.

A further factor to consider is prior knowledge about the position of the stimuli. Uncertainty about the position of a stimulus, such as in the peripheral distracter conditions (could occur anywhere in the periphery of the display), leads to more impaired performance in older adults compared to young adults (Cerella et al., 1987). When additional attention stimuli are presented in the centre of the display, participants have prior knowledge of where each stimulus will appear and so may be able to adjust their attentional set to include this information. It was predicted that motion discrimination performance would suffer less in the divided attention condition if distracter items were presented centrally, as they would be less of a drain on attentional resources This benefit of prior knowledge of stimulus location should facilitate older adults' performance to a greater magnitude than that of young adults.

5.11 Methods

5.11.1 Participants

Eight young (mean age = 19.25, SD = 1.49) and 8 older adults (mean age = 73.38, SD = 4.37) took part in the experiment. Of the young adults, all were right handed and six were female. Of the older adults, all were right handed and four were female. Each had normal, or corrected to normal vision (self reported). Each participant gave informed, written consent and was paid for their participation.

5.11.2 Design

A single interval, two-alternative forced choice paradigm was used to measure global translational motion thresholds during direction discrimination tasks. Both young and older

participants were tested during three task conditions: motion only (judge the direction of global motion patterns), focused attention (judge the direction of global motion patterns whilst ignoring distracter stimuli) and divided attention (judge the direction of global motion patterns whilst counting distracter stimuli). Distracter stimuli were full luminance squares presented in the periphery (peripheral distracters) and in the centre (central distracters) of the display. Between 0-4 distracter squares were presented on each trial during focused and divided conditions. During the focused attention condition, participants were instructed to ignore the distracter stimuli and just report the direction of motion. During the divided attention condition, participants first had to indicate (using the keyboard) how many squares had appeared and then report the direction of motion. When distracters were peripheral, the squares could occur at any location in the periphery of the display. When distracters were central, the squares appeared in the same location in the centre of the display (fixation). Data were not conditionalised on correct counting over a predefined set of trials. Counting performance was monitored by the examiner at the end of each experimental run to check that a reasonable level of performance was being attained. For young adults this was deemed to be 50%, for older adults, this level was reduced to 40%, to account for age-related differences in dividing attention. If the level was not attained, participants were asked to provide another run.

Stimuli were presented at two different contrast levels: low (the lowest contrast at which each participant could reliably perform the task) and medium (the contrast at which their performance reached ceiling). These contrast levels were measured prior to the main experiment.

5.11.3 Stimuli and apparatus

Stimuli were translational random-dot-kinematograms (RDKs) depicting translational global motion patterns, which were presented in a circular window (12° diameter) at the centre of the display. Viewing distance was 92 cm, which was measured but not restricted. Dot stimuli were presented on a mean luminance grey background (68cd/m2). The visibility of the dots (expressed as Michelson contrast) could be varied in the range of 0.004–0.33 by increasing the luminance of the dots, in relation to the background. The following equation describes the relationship:

Dot contrast =
$$(L_{dots} - L_{background}) / (L_{dots} + L_{background})$$

There were three experimental conditions: motion only, focused attention (ignore distracters) and divided attention (count distracters). The last two conditions included distracter stimuli, which were 1.4° white squares (always presented at full contrast). During distracter trials, between 0-4 distracter squares were sequentially presented in the periphery of the display (13.1° from fixation), or in the centre of the display (fixation). See figure 5.2 for illustration of the stimuli.

Each RDK was composed of a sequence of 16 images (each 53.3 ms), which produced continuous motion lasting 852.8ms. Each image contained 50 non-overlapping dots (dot diameter 0.47°; density 0.44 dots / 2°). At the start of each motion sequence, the position of each dot was randomly placed within the pattern. Following this, each dot was shifted by 0.3° (on separate frames), resulting in a speed of 5.6°/s. Once a dot moved off the edge of the motion pattern, it was re-plotted at a random spatial position within the RDK.

Manipulation of the global coherence level of the stimulus was achieved by maintaining a set proportion of signal dots on each image update to move toward the same direction. Noise dots could move in any random direction (including the same direction as signal dots).

The proportion of signal dots present was varied throughout each run using a 3-down, 1-up adaptive staircase method (Levitt, 1971). This adjusted coherence of the stimuli according to the participants' recent pattern of response. The step size of the staircase began at 8 signal dots and was halved after each reversal (staircase ended after 8 reversals). Thresholds of 79% correct performance were recorded as the mean of the last six reversals (step size was one signal dot).

The screen refresh rate was 75Hz. Stimuli were presented on a P255f Professional Series monitor, for which gamma-correction was carried out using a psychophysical motion-nulling task (Ledgeway and Smith, 1994). This minimum motion-nulling procedure finds the 50% correction point (the point at which no direction of motion is perceived) during viewing of a bi-directional drifting grating (contrast is varied using a staircase procedure).

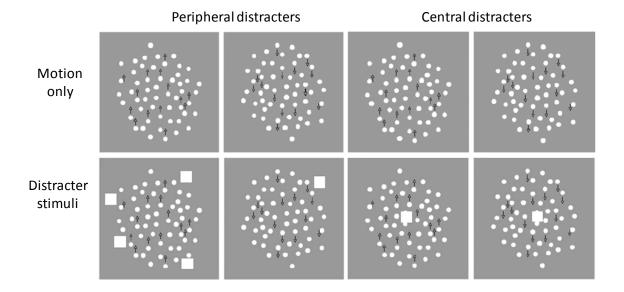


Figure 5.2: Illustrations of stimuli used in the experiment. Dots are illustrated at maximum contrast and their motion indicated by arrows on a subset of dots (arrows not shown in experiment). On each trial, participants indicated whether they saw the pattern indicated on the left or right (up or down). The top row depicts motion only trials and the bottom row depicts distracter stimuli (left 2 panels = peripheral distracters, right 2 panels = central distracters). Distracter stimuli: Between 0-4 full luminance, squares were serially presented on separate frames during each trial. During the peripheral distracters condition, distracters were presented around the edge of the RDK, where they could occur at any location. During central distracter condition, distracters were presented centrally, at fixation. Participants either had to ignore or report the number of squares. Participants continued to make judgements on the direction of motion throughout.

5.11.4 Procedure

Testing took place in a dimly lit room where the monitor was the only light source. Observation was monocular (with the aid of an eye-patch); participants used their preferred eye (typically right eye) and used the same eye throughout the entire experiment. Monocular viewing was used as binocular viewing gives rise to lower coherence thresholds as a function of contrast sensitivity (Hess et al., 2007). As contrast sensitivity is known to decline as a

function of age (Owsley et al., 1983; Pardhan, 2004), it was necessary to address this confounding factor.

Participants received verbal instructions at the beginning of each session, which consisted of the following information:

For the motion only condition: "You are going to be presented with circular patterns of moving dots. Your task is to respond to which direction the dots are moving, either up or down (experimenter demonstrated the keys to be used throughout the experiment). This will sometimes be difficult to determine. Please keep your gaze directed toward the fixation cross during each trial. Please respond as quickly and accurately as possible".

For the focused attention condition, the above information was repeated but with the following additions: "White squares will appear in the display. The number of squares will vary between 0 and 4. The squares can appear at any location around the edge of the circular dot pattern (or in the centre during the central distracter condition). Your task is to ignore these squares and continue to respond to the direction of the moving dots".

For the divided attention condition, instructions were as above, except for the following adjustment: "Your task is to count the squares and make a response as to how many you counted. You must make the responses in the following order: first respond to how many squares were counted using the number pad on the keyboard, then respond to the direction of the moving dots, either up or down".

Prior to taking part in the tasks, each participant underwent a practice session, which enabled them to familiarise themselves with the motion patterns (practice included just the motion only task). Participants were then measured for contrast thresholds to be used in the main experiment. This required obtaining measurements over varying levels of contrast (described in stimuli section) in order to find the contrast at which participants could reliably

perform the task, and at which performance reached ceiling. Participants viewed the stimuli over decreasing levels of contrast (starting at a high contrast and decreasing at each progressive run) and made judgements about the direction of dots within the translational RDK (upward or downward). Coherence thresholds were averaged for each separate run and each participant completed 8 runs at each decreasing contrast level. Two levels of contrast were then chosen to be used throughout the main experiment. The low contrast level was chosen as the lowest contrast at which participants could consistently perform the task, and the medium contrast level was chosen as the level at which performance reached a plateau. See figure 5.3 for an illustration of one participant's contrast threshold plot.

Following this, each participant took part in the main experiment. There were three conditions: motion only (where they judged the direction of global motion patterns); focused attention (where they judged the direction of global motion patterns whilst ignoring peripheral distracter stimuli); divided attention (where they judged the direction of global motion patterns whilst counting peripheral distracter stimuli). During each condition, participants observed the global configuration of dots moving either upwards or downwards (both directions equally likely), presented in a random order. During focused attention trials, participants made motion discrimination judgements whilst simultaneously attempting to ignore distracters (between 0-4 full luminance squares presented serially). During divided attention trials, participants first made a response to indicate how many distracters they had counted and then responded to the direction of global motion. Distracters were presented over two conditions (peripheral distracters and central distracters).

Observers completed eight runs of each task with peripheral distracters and eight runs of each task with central distracters, at both levels of contrast. This led to each participant completing 96 runs in total, which took approximately 7 hours (longer for older adults), completed during individual sessions over the course of several days.

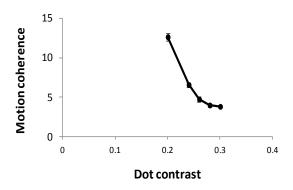


Figure 5.3: Individual contrast matching. Each individual participant was measured for contrast sensitivity during translational motion processing. The figure above shows data across the contrast matching session for one participant. The low contrast level was chosen as the point at which the task becomes difficult but can still be reliably executed, which for this participant was 0.24. The medium contrast level was chosen as the point at which performance reaches ceiling, which for this participant was 0.28. Error bars depict standard error.

5.12 Results

Participants were presented with RDK patterns containing translational global motion during three experimental conditions: motion only, focused attention and divided attention. The experiment was conducted at two individually matched (for each participant) levels of contrast (low and medium). During focused attention, participants had to ignore distracter stimuli that were presented both centrally and peripherally (separate conditions). During divided attention, participants had to attend to and count the number of distracters while concurrently attending to and judging the direction of motion stimuli.

Analyses were performed to investigate age differences within and between focused and divided attention. The motion only baseline task results were subtracted from those of the focused attention condition and also from the divided attention condition to give a measure of change in performance from baseline. This technique is particularly useful when comparing results from different age groups, as it does not rely on absolute baseline measures (where there are likely to be age-differences fundamental to the task), but instead compares task-

interactions by age in order to measure within-group changes. This method of analysis addresses and attempts to control for individual differences in baseline conditions, which may be subject to age-related sensory decline. Treating the data in this manner makes it more likely that attentional and strategy changes are being reported rather than changes at the perceptual level. Measurements were change in motion coherence threshold, where positive values indicated impaired performance and negative values indicated improved performance.

A repeated measures ANOVA with a between-subjects factor of *age* (2 – young and older adults), and within-subjects factors of *distracter location* (2 – peripheral and central), *attention task* (2 – focused and divided) and *contrast* (2 – low and medium) revealed significant main effects of distracter location and attention task. There was also a significant interaction of distracter location x attention task. There was no significant main effect or any interactions containing contrast, therefore the graph depicts data collapsed over contrast levels (figure 5.4).

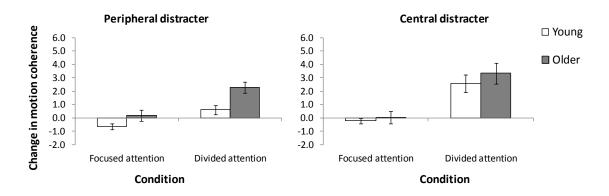


Figure 5.4: Age differences within and between focused and divided attention. The x axis shows the two attention conditions (focused and divided). The y axis shows change in motion coherence after subtraction of the baseline (motion only). Positive values reflect impaired performance, negative values reflect improved performance. Error bars depict standard error.

The significant main effect of distracter location indicated that motion coherence thresholds were significantly higher when distracters were central compared to peripheral. The

significant main effect of attention task indicated that coherence thresholds were significantly higher during the divided attention condition compared to the focused attention condition (see table 5.1 for ANOVA results and table 5.2 for means and standard error). The interaction of distracter location x attention task indicated that the focused attention condition gave rise to a similar pattern of performance for both central and peripheral distracters (F(1, 14) = 0.22, p = 0.643, r = 0.13), whereas during the divided attention condition, significantly higher coherence thresholds were produced for central distracters compared to peripheral distracters (F(1, 14) = 7.98, p = 0.013, r = 0.60). See appendix E.1 for 2 x 2 ANOVA results.

Table 5.1: ANOVA results for age differences within and between focused and divided attention (central versus peripheral distracters)

Effects	Mean Square	DF	F	р	Partial η²
Age	3.13	1, 14	3.63	0.078	0.21
Distracter location	22.09	1, 14	7.43	0.016*	0.35
Attention task	179.24	1, 14	81.53	< 0.001*	0.85
Contrast	0.34	1, 14	0.15	0.700	0.01
Distracter location x age	4.37	1, 14	1.47	0.245	0.10
Attention task x age	3.69	1, 14	1.68	0.216	0.11
Contrast x age	5.55	1, 14	2.54	0.133	0.15
Distracter location x attention task	14.75	1, 14	6.08	0.027*	0.30
Distracter location x attention task x age	0.28	1, 14	0.12	0.740	0.01
Distracter location x contrast	0.38	1, 14	0.20	0.666	0.01
Distracter location x contrast x age	4.41	1, 14	2.24	0.157	0.14
Attention task x contrast	2.89	1, 14	1.46	0.247	0.10
Attention task x contrast x age	2.25	1, 14	1.14	0.304	0.08
Distracter location x attention task x contrast	0.27	1, 14	0.11	0.750	0.01
Distracter location x attention task x contrast x age	0.33	1, 14	0.13	0.723	0.01

Table 5.2: Means and standard error for age differences within and between focused and divided attention (central versus peripheral distracters)

Factor	Level	Level Mean	
Age	Young	0.57	0.33
Age	Older	1.46	0.33
Distracter	Peripheral	0.60	0.21
location	Central	1.43	0.33
Attention	Focused	-0.17	0.20
task	Divided	2.20	0.32
Contrast	Low	1.07	0.27
	Medium	0.96	0.26

Data from the counting task (count distracters) were also analysed to test for age differences in performance accuracy when distracters were central and when they were peripheral (figure 5.5). A 2 x 2 ANOVA of age x distracter location revealed significant age differences in performance when distracters were peripheral (F(1, 14) = 8.21, p = 0.019, r = 0.61), with young adults showing a greater degree of accuracy for counting distracters; but not central, where no significant age differences were observed (F(1, 14) = 1.40, p = 0.256, r = 0.30). See table 5.3a for 2 x 2 ANOVA results. To explore differences in distracter location for young adults, a one-way ANOVA was performed. This revealed a significant benefit on performance of peripheral items versus central items (table 5.3b).

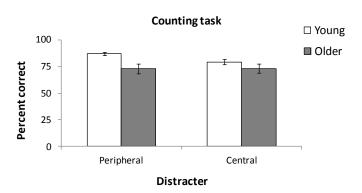


Figure 5.5: Age differences in the additional attention task. The x axis shows the two different locations of the distracters. The y axis shows percent correct from the counting task. Error bars depict standard error.

Table 5.3a: 2 x 2 ANOVA for the counting task showing age differences in distracter location

Distracter location	Age	Mean	Std. Error	DF	Mean Square	F	р	r
Peripheral	Young	86.90	1.71	1, 9	787.64	8.21	0.019	0.61
	Older	72.86	4.59					
Central	Young	79.33	2.50	1. 14	150.06	1.40	0.256	0.30
	Older	73.21	4.53	1, 17	150.00	1.40	0.230	0.30

Table 5.3b: 2 x 2 ANOVA for the counting task showing performance differences between central and peripheral distracters in young adults

Distracter location	Mean	Std. Error	DF	Mean Square	F	р	r
Central	79.33	2.50	1 1/1	228.77	6.24	0.026	0.56
Peripheral	86.90	1.71	1, 14	228.77	0.24	0.026	0.50

In order to investigate age differences in use of strategy, motion coherence performance was compared with accuracy on the counting task for each participant during the divided attention task (figure 5.6). There was a significant negative correlation between motion coherence and count accuracy for young adults (r = -0.77, p = 0.025) when counting central distracters. As they became more accurate at the counting task, their motion coherence performance also improved. This could indicate that the counting task led to more focused attention and therefore an increase in signal to noise ratio.

Older adults showed a trend (not significant) towards increasing motion coherence thresholds as they became more accurate at the counting task (r = 0.64, p = 0.085) when distracters were central. This suggests that there was a trade-off in performance between the two tasks, which could indicate that the older adults were unable to move their attention efficiently from one task to the other.

There were no significant correlations between counting peripheral distracters and motion coherence (young: r = -0.03, p = 0.935; older: r = 0.20, p = 0.627). See table 5.4 for correlation table.

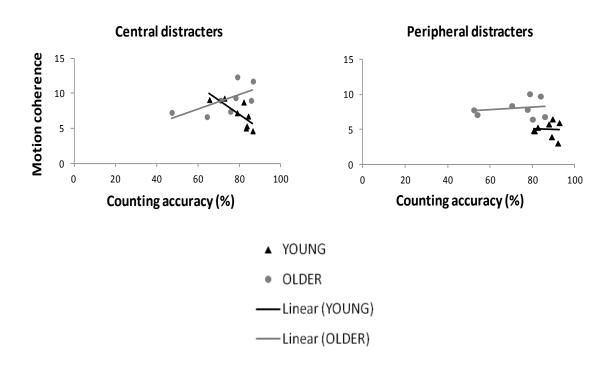


Figure 5.6: Relationship between counting performance and motion coherence. The x axis shows percent correct from the counting task. The y axis shows motion coherence performance during the divided attention condition.

Table 5.4: Correlation results for motion discrimination versus counting accuracy

Age	Distracter location	Task	Mean	Standard deviation	N	r	р	R²
	Central	Discrimination	7.03	1.89	8	-0.77	0.025*	0.59
Young		Counting	79.33	7.06	0			0.55
Tourig	Peripheral	Discrimination	5.06	1.12	8	-0.03	0.935	0.41
	renphierai	Counting	86.90	4.85	0	-0.03	0.333	0.41
	Central	Discrimination	9.11	2.05	8	0.64	0.085	0.00
Older		Counting	73.21	12.83	0	0.04	0.063	0.00
	Peripheral	Discrimination	8.06	1.31	8	0.20	0.627	0.04
	renphierai	Counting	72.86	12.97	o	0.20	0.027	0.04

Summary

Overall, participants demonstrated more impaired motion coherence with the presence of central distracters than with peripheral distracters. No age differences were present when distracters were presented centrally. The focused attention task (ignore distracters) had no significant age differences in performance whether distracters were central or peripheral.

Correlations between motion coherence performance and dual-task accuracy indicated that the additional task requirement (count distracters) may have had a beneficial effect on young adults' performance, perhaps as a result of more attentional allocation. However, older adults showed a tendency to decrease motion coherence performance as a function of dual-task accuracy (not significant), suggesting that they were not able to efficiently switch between the two tasks, leading to less attentional modulation for both tasks.

Furthermore, the spatial location of the attention stimuli had some bearing on performance during divided attention, with centrally occurring stimuli leading to worse performance than peripherally presented items for young adults. This could be due to the central distracters being presented at the same location, therefore creating uncertainty as to how many distracters were presented. During the peripheral distracter condition, the fact that each distracter appeared at a spatially different location may have made it easier to count how many appeared (spatial cue). When distracters were central, more attentional resources may have been required to distinguish between distracter stimuli, thereby leaving fewer resources to process the motion discrimination task.

The next experiment uses fMRI and functional connectivity analysis to explore the neuronal activity associated with the behaviour described in experiment 5.

5.13 Experiment 6: Underlying neuronal activity during focused and divided attention using fMRI

Studies on age-related cortical changes during visual processing have found that older adults show increased activity in frontal, attention related regions in response to declines in bottom-up sensory input (Grady et al, 1994; Madden et al, 2004; Madden et al, 2007). Research investigating motion processing has demonstrated that hMT+ is selectively activated by the perception of motion patterns (Morrone et al., 2008). This experiment explored possible age differences in modulation in motion specific regions when attentional load is manipulated. Specifically, patterns of activation during focused attention (directed towards global motion) and divided attention (shared between motion discrimination and a concurrent distracter task) were examined.

Region of interest analyses were performed for each participant, where hMT+ (which is associated with the processing of visual motion patterns) was defined for each individual participant (both left and right hemisphere). This was carried out explore age-related changes in modulation of the sensory region involved; something that has not been investigated prior to this study.

The use of functional localiser scans has been criticised for not accounting for anatomical specificity, and being contextually biased (Friston et al., 2006). However, it can be a useful tool when used in conjunction with pre-existing evidence of anatomical landmarks. Localising ROIs is also more advantageous for subsequent data analysis, as the analysis is restricted to responses within the specified area (averaged over voxels within the ROI), providing a focused and concise indication of responses. Moreover, analysing individual ROIs for each participant minimises anatomical variability and individual differences across observers.

In line with the compensation hypothesis, it was also predicted that older adults would show more bilateral activity during the most demanding task (i.e. divided attention). The compensation hypothesis (Cabeza, 2002) states that if performance is equivalent for older and young adults or if older adults out-perform young adults, then more a bilateral pattern of activation should be present in the older group; and this may reflect a compensatory mechanism. Furthermore, this bilateral activity should be more apparent in the most demanding of the tasks. The dedifferentiation hypothesis predicts that poorer performance in the older group would be accompanied by increased activation in older brains, and that this activity would reflect an age-related inefficiency in the recruitment of specific neural populations.

For the focused attention tasks, it was predicted that older adults would show greater frontal bilateral activity during successful inhibition of task-irrelevant information (Nielson et al., 2002). During poor performance, they would show reduced activity in frontal, attentional regions (Jonides et al., 2000).

5.14 Methods

5.14.1 Participants

Eight young (M = 20.5, SD = 2.5 years old) and 8 healthy older (M = 69.5, SD = 6.0 years old) adults participated in this experiment. Of the young adults, all were right handed and six were female. Of the older adults, six were right handed and four were female. Testing was monocular (one eye was covered with an eye patch), where participants used their preferred eye to view stimuli (all young participants and six older participants used their right eye to view). All participants had normal, or corrected to normal vision (as measured by their

optician). All experimental methods were approved by the University of Birmingham Central Ethics Committee. All participants provided informed written consent and were paid for their participation. Older adults underwent a mini mental state (MMS) test prior to the experiment (six participants scored 100% and two produced just 1 error).

5.14.2 Data acquisition

Scanning took place at the Birmingham University Imaging Centre (BUIC) and at the Sir Peter Mansfield Magnetic Resonance Imaging Centre (SPMMRC) at The University of Nottingham.

Scans were conducted on a Philips Achieva MRI scanner, Sense (SENSitivity Encoding) = P2. Functional T2 weighted echo-planar image volumes with blood oxygen level dependent (BOLD) contrast were collected with the pulse sequence: TE (echo time) = 35ms, TR = 2000ms, flip angle = 79.1° , field of view (FOV) = $240 \times 240 \times 80$ mm, voxel size = $2.5 \times 2.5 \times 2.$

During the scan session, a separate localiser scan was performed to define the borders of hMT+. During this scan, participants viewed coherently moving dots in one condition, and randomly placed static dots in another condition (Huk et al., 2002). A T2 weighted motion localiser scan was performed with the following pulse sequence: TE = 34ms, TR = 2000ms, flip angle = 79.1° , $FOV = 192 \times 192 \times 56$ mm, voxel size = $1.5 \times 1.5 \times 1.5$ mm³. 168 volumes were obtained from each participant during a scan that lasted 322s. Each volume consisted of 28 slices. Each participant underwent 10 blocks, each consisting of 32 trials.

5.14.3 Region of interest analyses

In order to explore the hypothesis about age-related changes in neural activity in area hMT+, region of interest (ROI) analyses were performed in this area (for both left and right hemisphere). The blood oxygen level dependent (BOLD) signal was extracted from voxels in those regions that were active during the observation of moving stimuli compared to static stimuli. An 8mm spherical ROI was created for each individual participant's left and right hMT (figure 5.7) based on the centre of peak activity within the region (see table 5.5 for young and table 5.6 for older adults' ROI co-ordinates). The co-ordinates were in similar locations to those described in a variety of neuroimaging literature relating to apparent motion (Watson et al., 1993, De Jong et al., 1994, Dumoulin et al., 2000, Dukelow et al., 2001, Kolster et al., 2010). The % signal change in activation during each of the experimental conditions was then extracted from each ROI using the FSL Featquery tool (Smith et al., 2004, Woolrich et al., 2009). Further analysis was then performed using SPSS.

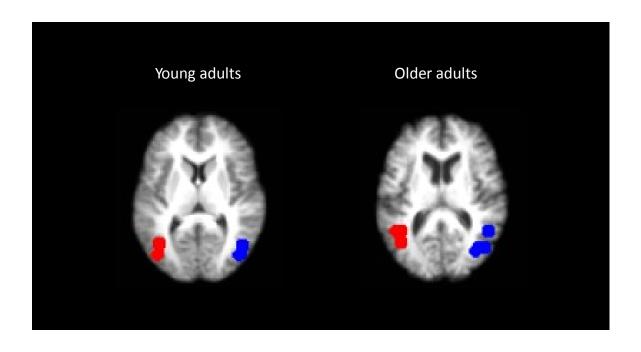


Figure 5.7: Young adults' and older adults' individual ROI locations for left (red) and right (blue) hMT+.

Table 5.5: Young adults ROI locations for motion related activity greater than activation to static patterns

	Left hemisphere				Right hemisphere			
Young adult	z-score	x	у	z	z-score	x	у	z
YA_1	10.03	-42	-76	0	12.72	48	-72	0
YA_2	7.10	-44	-78	6	6.70	44	-78	6
YA_3	8.39	-44	-76	0	6.36	46	-66	0
YA_4	8.81	-42	-74	0	11.30	48	-76	0
YA_5	5.20	-42	-66	8	7.09	48	-68	8
YA_6	3.53	-44	-70	2	3.23	48	-78	4
YA_7	12.68	-48	-76	2	10.36	44	-78	0
YA_8	3.53	-44	-70	2	3.23	48	-78	4

Table 5.6: Older adults ROI locations for motion related activity greater than activation to static patterns

	Left hemisphere				Right hemisphere			
Older adult	z-score	x	у	z	z-score	x	у	z
OA_1	3.00	-48	-74	0	2.85	42	-72	14
OA_2	1.76	-50	-54	8	1.23	46	-66	0
OA_3	2.82	-44	-54	14	2.37	52	-54	14
OA_4	2.62	-48	-60	4	1.47	38	-76	8
OA_5	3.48	-44	-70	4	1.00	44	-76	2
OA_6	4.56	-44	-66	10	2.69	48	-72	10
OA_7	3.78	-40	-54	4	3.61	40	-74	6
OA_8	2.82	-44	-54	14	2.37	52	-54	14

5.14.4 Stimuli

Stimuli were generated using a Macintosh computer and were written in C using OpenGL and the Xcode development environment available from Apple. The screen had an update rate of 75Hz and gamma correction was carried out using the minimum motion nulling method described in experiment 5. Stimuli were back-projected on a translucent screen mounted in the bore of the scanner through a JVC SX21 projector (refresh rate 75Hz).

Stimuli were the same images of global motion RDKs as described in experiment 5, however, this time the set of stimuli included translational, radial and rotational motion patterns (figure 5.8). This meant that the radial and rotational patterns had a flat speed gradient (i.e. stimuli speed was not proportional to the distance from the centre of expansion or rotation) (Burr & Santoro, 2001). This was done so that direct comparisons could be made between the three motion patterns (Allen et al., 2010). This experiment is not concerned with differences in individual motion types. They were again presented in a circular window at the centre of the display. Dot contrast was held constant at 0.30 (Michelson contrast). Each image again contained 50 non-overlapping dots. At the beginning of each motion sequence, the

position of each dot was randomly assigned. There were three experimental conditions: motion only, focused attention and divided attention. All distracter stimuli were presented centrally at fixation throughout the experiment. Distracters were full luminance squares presented serially between 0 and 4 times during each trial.

The images were presented in a block design consisting of 9 experimental blocks and 3 rest periods. Each block lasted 48.85s and consisted of 16 randomly generated images of each motion (translational, radial and rotational) x task (motion only, focused and divided) condition; each rest period lasted 39.25s. Participants received a new set of on screen instructions each time there was a change in the task required of them.

Stimuli were presented to each participant at their individual coherence threshold (measured prior to entering the scanner) in order to equate visibility and therefore match difficulty. To do this, each participant was tested outside of the scanner on the motion only condition. Six blocks of the experiment were run for each type of motion and results were averaged to give an individual measure of each participant's coherence to each motion type. This value was multiplied by 2 in order to ensure that the stimuli would be visible to all participants. This resulted in three coherence values, one for each motion type; which were then entered into the fMRI experimental program for each participant at the start of their scanning session.

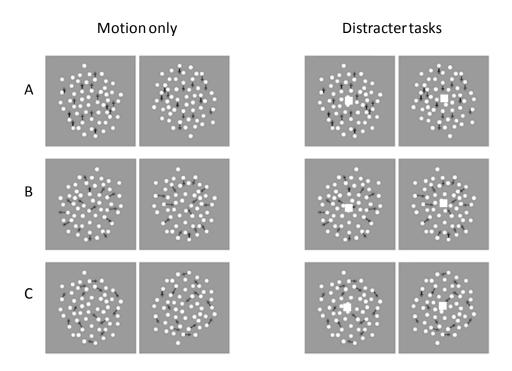


Figure 5.8: Stimuli used in the fMRI experiment. Row A = translational motion (up or down), row B = radial motion (expanding or contracting), row C = rotational motion (clockwise or anticlockwise). During motion only (left panel), judgements were made about the direction of the moving dots. During the distracter conditions (right panel), between 0 and 4 white distracter squares were serially presented in the centre of the display (at full contrast). For the focused attention condition, motion judgements were made whilst ignoring the squares. For the divided attention condition motion judgements were made whilst counting how many squares were presented. The participants first made a response as to how many squares they counted and then as to the direction of motion.

5.14.5 Behavioural task

The participants first took part in two practice sessions of the fMRI behavioural experiment. This was done outside of the scanner and within the same week as the scan was due to take place.

Prior to beginning each task block, participants' viewed an on-screen set of instructions that clearly explained the task about to begin. The behavioural task was similar to that described in experiment 5. During motion only, participants had to judge the direction of

motion (up / down, expanding / contracting, clockwise / anticlockwise) for each motion type. During the focused attention task, participants were requested to respond to the direction of the motion stimuli whilst ignoring the distracter stimuli. During the divided attention task, participants were requested to count the number of distracter squares appearing on the screen at the same time as attending to the direction of motion. They first made a response to indicate how many squares they had counted and then responded to the direction of motion. Responses were made via fiber optic response boxes, with the right hand making the motion discrimination responses and the left hand making the count distracter responses. No response was made when there were 0 squares counted. For 1-4 squares, participants made a response with their left hand with 1 corresponding to a little finger press and 4 corresponding to an index finger press (to map how the number keys are set out on a standard QWERTY keyboard, as used in the behavioural experiment (5)). Data were not conditionalised on correct counting.

5.14.6 Data processing and statistical analysis

Data analysis was carried out using FEAT (fMRI Expert Analysis Tool) Version 5.91, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Prior to the statistical analysis, raw data were examined for motion artifacts, using MCFLIRT motion correction (Jenkinson et al., 2002). Estimated mean motion displacement was 0.37 mm. Checking for artefacts was performed using MELODIC (Smith et al., 2004, Beckmann and Smith, 2004), where all slices were examined and those with any artefacts (e.g. blurring, large clusters) were removed from further analyses.

The following pre-statistics processing was also applied: slice-timing correction using Fourier-space time-series phase-shifting, non-brain removal using BET (Smith, 2002), spatial smoothing using a Gaussian kernel of FWHM 5mm (double the voxel size), grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma=64.0s).

The data were then analysed using a general linear model (GLM) correlation test. Time-series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich et al., 2001). Registration to individual participants' high resolution structural and MNI space images was carried out using FLIRT (Jenkinson and Smith, 2001, Jenkinson et al., 2002).

As this chapter is not exploring differences in motion processing, the three motion types were averaged over creating 3 overall task conditions (motion only, focused attention and divided attention). This is a multi-use experiment designed as part of a larger body of research and is intended to be used for a variety of purposes. The three conditions were then used to make comparisons between tasks and to look at age differences in activation between tasks.

A higher level analysis was then carried out to average across the data from the three scans for each participant; time series and registration were as stated above (fixed effects, variance was forced to zero). The data were then analyzed as a group (mixed effects). Thresholds were corrected for multiple comparisons using cluster thresholding (Z = 2.1, p = 0.05). Cluster thresholding was favoured over voxel thresholding as results showed less peaks but more widespread activity over many voxels. There is a trade-off between using a conservative method of analysis, which highlights peak activity within regions, and a more liberal method, which takes into account the distribution of activity across regions. Due to

activation being more widespread over many voxels, cluster thresholding was chosen as it is a more liberal method than voxel thresholding. The older brain has been reported as having more diffuse patterns of activation compared to young brains (Cabeza et al., 2002; Stern, 2009; Reuter-Lorenz & Cappell, 2010). To capture these patterns, cluster thresholding was necessary.

5.15 Results

5.15.1 Behavioural results (during scanning)

Data from the behavioural experiment performed in the scanner were analysed. To explore task interactions between each condition, subtractions of each attention task were performed. The change in percent correct was measured for focused attention minus motion only (focused attention) and divided attention minus motion only (divided attention). This method of analysis addresses and attempts to control for individual differences in baseline conditions, which may be subject to age-related sensory decline.

A 2 x 2 ANOVA of *age* (2 – young and older) by *attention task* (2 – focused attention and divided attention) revealed no significant age differences during focused attention (F(1, 14) = 0.47, p = 0.506, r = 0.18) or divided attention (F(1, 14) = 0.01, p = 0.912, r = 0.03). See figure 5.9 and table 5.7

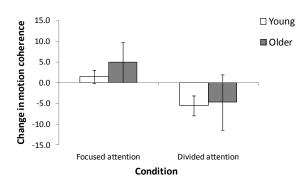


Figure 5.9: Young and older adults' performance during focused and divided attention (in scanner). The x axis shows the two attention conditions (focused and divided attention). The y axis shows change in motion coherence after subtracting the baseline (motion only). Positive values indicate improvement in performance; negative values indicate impairment in performance. Error bars depict standard error.

Table 5.7: 2 x 2 ANOVA for age x attention task

Attention task	Age	Mean	Std. Error	DF	Mean Square	F	р	r
Focused	Young	1.45	1.61	1, 14	48.44	0.47	0.506	0.18
1 ocuseu	Older	4.93	4.84	1, 14	40.44			0.10
Divided	Young	-5.49	2.39	1 1/1	2.55	0.01	0.912	0.03
Divided	Older	-4.69	6.69	1, 14	2.33			0.03

Performance during the additional counting task was also analysed. During this task participants counted distracter stimuli and responded as to how many they observed (between 0-4). A one-way ANOVA of age x accuracy revealed a significant difference in performance between the two age groups, with older adults out-performing the young adults (F(1, 14) = 30.31, p < 0.001, r = 0.83). See figure 6.13.

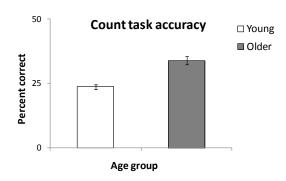


Figure 5.10: Young and older adults' performance during the additional counting task. The x axis shows age group. The y axis shows percent correct. Error bars depict standard error.

Table 5.8: One-way ANOVA results for age differences in counting accuracy

Age	Mean	Std. Error	DF	Mean Square	F	р	r
Young	23.70	0.90	1. 14	412.60	30.30	< 0.001*	0.83
Older	33.85	1.61	1, 14	412.00	30.30	< 0.001	0.65

5.15.2 ROI results

To investigate activation in hMT during each contrast, ROIs were created for each individual participant (left and right hemisphere).

Comparisons between young and older adults were made by looking at the group by task interactions. This was to ensure that results were not merely reflecting baseline differences in cerebral blood flow (CBF) between the two age groups. This analysis technique highlights differences in the relative performance between two behavioural tasks and therefore does not directly compare the two age groups on a single task (D'Esposito, et al, 2003). The difference in % signal change was measured for focused attention minus motion

only (focused attention condition) and divided attention minus motion only (divided attention condition).

A repeated measures ANOVA with a between-subjects factor of *age* (2 – older adults and young adults), and within-subjects factors of *hemisphere* (2 – left and right) and *attention task* (2 – focused attention and divided attention) revealed significant main effects of age and attention task. There were no significant interactions (see table 5.9 for ANOVA results and table 5.10 for means). There was no significant effect of hemisphere, therefore the graph shows data collapsed over hemisphere (figure 5.11). The significant main effect of age reflected greater modulation in hMT+ for young adults compared to older adults. The significant main effect of attention task reflected more modulation in hMT+ during divided attention compared to focused attention.

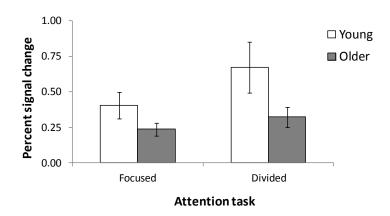


Figure 5.11: Young and older adults' activation in hMT+ during the two attention tasks. The x axis shows attention task. The y axis shows % signal change in BOLD activity. The graph shows results collapsed across hemisphere as there were no significant effects involving hemisphere. Error bars depict standard error.

Table 5.9: Repeated measures ANOVA for % signal change analysis

Effects	Mean Square	DF	F	р	Partial η²
Age	0.26	1, 14	5.66	0.032*	0.29
Hemisphere	0.07	1, 14	0.63	0.441	0.04
Attention task	0.49	1, 14	6.19	0.026*	0.31
Hemisphere x age	0.01	1, 14	0.07	0.790	0.01
Attention task x age	0.13	1, 14	1.66	0.218	0.11
Hemisphere x attention task	0.00	1, 14	0.01	0.947	0.00
Hemisphere x attention task x age	0.02	1, 14	1.15	0.302	0.08

Table 5.10: Means and standard error for % signal change analysis

Factor	Level	Mean	Std. Error	
Age	Young	0.54	0.08	
Age	Older	0.28	0.08	
Hemisphere	Left	0.38	0.08	
пеннарнете	Right	0.44	0.06	
Attention task	Focused	0.32	0.03	
Attention task	Divided	0.50	0.09	

5.15.3 Whole head analysis

Differences in cortical activity between age groups were measured for task interactions and age x task interactions. Subtractions were performed to remove the motion only baseline results from contrasts of interest. Recall that the motion only condition was where participants just made responses to the direction of motion. The focused attention condition was where participants made responses to the direction of motion whilst concurrently ignoring distracter stimuli. The divided attention condition was where participants counted, and responded to, targets whilst concurrently responding to the direction of motion. Therefore, focused attention activity maps resulted from the following subtraction:

Data from focused attention condition – data from motion only condition = focused attention contrast

Divided attention activity maps resulted from the following subtraction:

Data from divided attention condition – data from motion only condition = divided attention contrast

In order to identify regions that were specifically active during each condition, further subtractions were performed to remove 1. the divided attention contrast from the focused attention contrast, and 2. the focused attention contrast from the divided attention contrast, in the following manner:

- Focused attention contrast divided attention contrast = focused attention related activity.
- 2. Divided attention contrast focused attention contrast = divided attention related activity.

The task interactions were performed to ensure that results were not merely reflecting baseline differences in cerebral blood flow (CBF) between the two age groups. Co-ordinates of the sites of significant activation can be found in table 5.11 for young and table 5.12 for older adults. Details for age x task interactions are in table 5.13.

During focused attention (focused – divided contrast) young adults evoked activity in left lateralised regions including superior frontal gyrus and superior parietal cortex (precuneus and superior lateral occipital) (see figure 5.12). Older adults showed no significant whole brain activity during this contrast.

Superior frontal regions have been identified as part of a network responsible for the voluntary control of attention (Hopfinger et al., 2000). Therefore, this could reflect participants voluntarily orienting their attention towards the motion stimuli and moving attention away from the distracter stimuli.

The precuneus cortex has been implicated in successful ignoring of irrelevant stimuli (Payne & Allen, 2011).

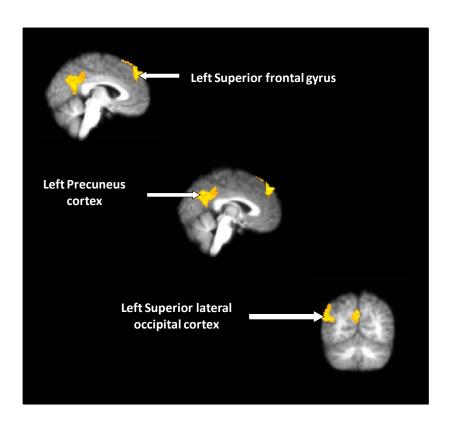


Figure 5.12: Activation during focused attention in young adults (focused – divided attention). Activity was evoked in left lateralised frontal and superior parietal regions.

During divided attention (divided – focused) young adults engaged bilateral prefrontal regions (precentral and postcentral gyri), left superior parietal regions (supramarginal gyrus), right superior frontal gyrus, right supplementary motor area and right paracingulate (see figure 5.13).

Right frontal and parietal regions are known to be part of a network responsible for the focus of attention (Corbetta et al., 1991; Coull et al., 1996). The fact that young adults engaged bilateral prefrontal regions may reflect task difficulty (i.e. the shifting of attention between two concurrent sources of information). This can be explained by the CRUNCH theory of brain circuitry, which states that during more difficult task conditions, young adults tend to activate bilateral regions that are complementary to the task specific region (Reuter-Lorenz & Cappell, 2008).

Right paracingulate has been reported as being active during spatial tasks requiring attentional control, particularly in spatial working memory tasks (Baker et al., 1996; Owen & Evans, 1996). This could be due to participants having to hold information regarding the amount of distracters presented in working memory in order to make a response.

Right supplementary motor area was also activated. This region has been implicated in preparatory activity when selecting appropriate motor responses based on characteristic features of incoming information (Hopfinger et al., 2000). It is likely that this activity reflects the planning required to make two separate responses to two different types of stimuli (motion pattern and distracter squares).

Right superior frontal gyrus has previously been associated with the shifting of attention from one spatial location to the next (Corbetta et al., 1993). The superior frontal activity demonstrated here in young adults may reflect that they had to move their focus of attention from one task to the next (and one response to the next).

Upon comparing activity patterns between the focused and divided attention conditions, it can be seen that young adults are significantly activating left hemisphere regions during the focusing of attention, whereas during divided attention, they are recruiting from largely right hemisphere regions.

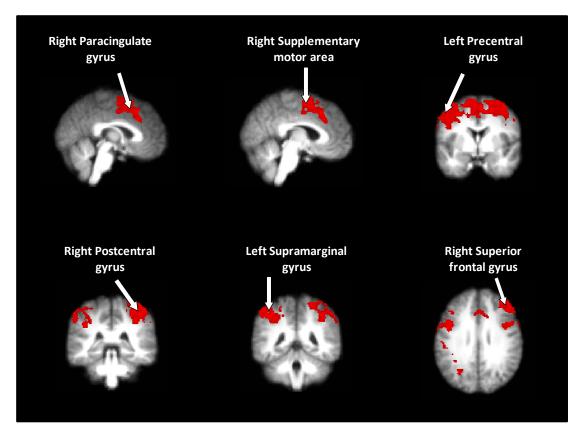


Figure 5.13: Activation during divided attention in young adults (divided – focused). Activity was evoked in bilateral prefrontal regions, right superior frontal gyrus, left superior parietal, right SMA and right paracingulate.

During divided attention (divided – focused contrast) older adults recruited left prefrontal regions (precentral and postcentral gyri), bilateral middle frontal and inferior frontal gyri and right superior frontal and parietal regions (figure 5.14).

Prefrontal regions are implicated in the focus of attention, however, during spatial tasks these are typically shown to be right lateralised (e.g. Corbetta et al, 1993). The left hemisphere activity seen here in older adults may reflect compensatory activity. If older adults are recruiting right prefrontal regions but not significantly, then activity may 'spill over' into complimentary left lateralised regions in order to maintain task performance (Stern,

2003; Reuter-Lorenz & Cappell, 2008). This view is further supported by the bilateral recruitment of further frontal regions (middle frontal and inferior frontal gyri).

Right superior frontal and parietal regions were active (as seen in young adults during the same task). These regions are implicated in the shifting of attention (Corbetta et al., 1993) and may reflect the movement of the focus of attention from one task to another.

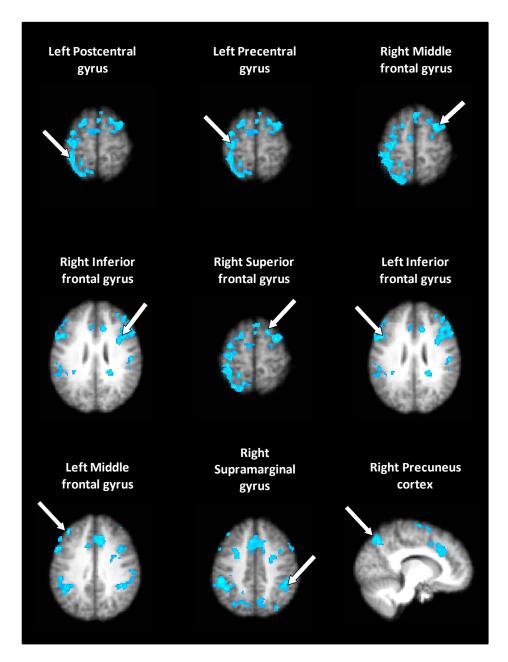


Figure 5.14: Activation during divided attention in older adults (divided – focused). Older adults activated left precentral and postcentral gyri, bilateral middle frontal gyrus, bilateral inferior frontal gyrus, right superior frontal gyrus and right superior parietal regions.

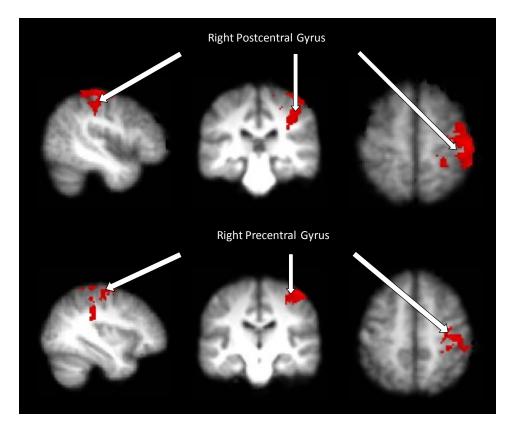


Figure 5.15: Activation during divided attention for young > older adults. Young adults showed significantly greater activity compared to older adults in right lateralised frontoparietal regions.

Age x task contrasts (young > older adults) on the divided attention condition (divided > focused attention) revealed that young adults significantly activated right lateralised precentral and postcentral regions more than older adults during divided attention (figure 5.15). These are known to be key regions in the frontoparietal attention network and are consistently activated during tasks of selective attention (Corbetta et al., 1991; Corbetta et al., 1993; Coull et al., 1996). Older adults did not show any greater significant activity than young adults during this age x task contrast. It may be that young adults are recruiting tasks specific regions (shown by more significant activity than in older adults) and older adults are recruiting a wider network of more dispersed regions (as shown by the bilateral recruitment of frontal regions (figure 5.14). This activation could be described as compensatory as older adults were shown to perform this task to the same level as young adults (see laboratory based

behavioural experiment (5)). Therefore, this could be evidence of age-related neuronal reorganisation in order to compensate for decline in task specific regions (Madden, 2007).

Figure 5.16 shows overlays of young and older cortical activity during divided > focused attention. Activity for young > older adults is also included. Young adults displayed more activation in right lateralised frontal regions (precentral and postcentral gyrus) which were not activated by older adults. Older adults show predominantly left lateralised activity, branching into right frontal regions, whereas young adults show a more bilateral pattern of activity, which is more significant in right frontal regions.

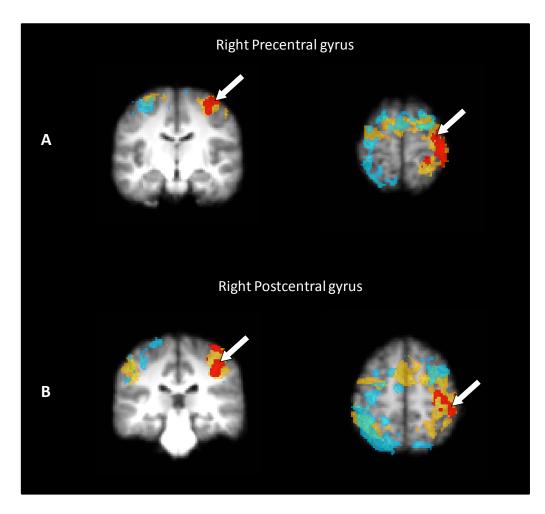


Figure 5.16: Overlay of activation for young and older adults during divided attention. Yellow / orange = young adults' activity; Light blue = older adults' activity; Red = Young > Older adults' activity. Young adults activated right prefrontal regions more significantly than older adults. Young adults show more modulation in right hemisphere. Older adult's activity was more left lateralised.

Table 5.11: Regions activated during each attention condition for young adults.

Region	Voxels	z-score	х	у	z	Attention condition
L Precuneus cortex	1059	3.62	-2	-68	32	Focused
L Superior frontal gyrus	828	3.64	-4	48	44	Focused
L Superior lateral occipital cortex	805	3.88	-56	-64	26	Focused
R Paracingulate gyrus	10543	5.17	2	14	44	Divided
R Suplementary motor area	10543	4.88	4	0	62	Divided
L Precentral gyrus	10543	4.36	-44	0	58	Divided
R Postcentral gyrus	10543	4.29	48	-36	64	Divided
L Supramarginal gyrus	2479	4.18	-52	-44	54	Divided
R Superior frontal gyrus	729	4.37	40	50	28	Divided

Table 5.12: Regions activated during each attention condition for older adults.

Region	Voxels	z-score	x	у	z	Attention condition
L Postcentral gyrus	5736	4.19	-38	-38	64	Divided
L Precentral gyrus	5736	3.83	-38	-18	64	Divided
R Middle frontal gyrus	2634	3.45	30	10	60	Divided
R Inferior frontal gyrus	2634	3.41	40	12	28	Divided
R Superior frontal gyrus	2634	3.32	20	18	62	Divided
L Inferior frontal gyrus	723	3.25	-50	14	28	Divided
L Middle frontal gyrus	723	3.21	-40	38	36	Divided
R Supramarginal gyrus	645	3.48	42	-44	44	Divided
R Precuneus cortex	474	2.44	12	-70	48	Divided

Table 5.13: Regions activated during each attention condition for young > older adults.

Region	Voxels	z-score	х	у	Z	Attention condition
R Precentral gyrus	1241	4.18	34	-14	66	Divided
R Postcentral gyrus	1241	3.44	48	-28	56	Divided

Summary of whole head analysis

Young adults recruited distinctly different cortical networks when focusing attention compared to when dividing attention. During focused attention, the recruited regions showing significant activity were left lateralised frontal and parietal regions. During divided attention, recruited regions were largely right lateralised. This supports previous findings that have reported left cortical involvement when attention needs to be focused and irrelevant items need to be suppressed (Payne & Allen, 2011). The results are also in line with research demonstrating a right frontoparietal network that is responsible for the control, orienting and shifting of attention (Corbetta et al., 1991; Corbetta et al., 1993).

Older adults showed no significant activity in the whole head analysis during focused attention. This may suggest less efficient recruitment of task specific regions (Jonides et al., 2000). However, it could also reflect a more dispersed pattern of activity including several regions that did not show up in the analysis as significantly active. This account is more likely, as older adults showed comparable task performance to that of young adults during the behavioural task (see experiment 5 results). If this is the case, it could be described as compensatory related activity, as performance was equated across age but older adults were using a different strategy compare dot young adults (Cabeza et al., 2002). This possibility will

be investigated in the next section, which explores functional connectivity between the sensory region and other cortical regions.

During the divided attention task, older adults cortical activity was largely left lateralised, this is in contrast to the young adults (who showed more right hemisphere activity). While young adults recruited task specific regions in the frontoparietal network (i.e. right precentral and postcentral gyri), older adults engaged left lateralised prefrontal regions (left precentral and postcentral gyri). Furthermore, older adults activated bilateral middle and inferior frontal regions, which suggests that they were recruiting additional resources in complimentary regions for the task at hand (Reuter-Lorenz & Park, 2010). Both young and older adults showed common activation of right superior frontal gyrus, which is responsible for the shifting of attention (Corbetta et al., 1993) and appears to be necessary for both age groups to perform the divided attention condition.

5.15.4 Psychophysiological interaction analyses

Further investigations were carried out on the whole head results in order to ascertain if any activity was synchronised with activity in hMT+. Psychophysiological interaction (PPI) analysis was used to discover if any of the active regions were functionally linked to the region of interest in hMT+. Mean activity time courses were extracted from each individual participants' ROI scan (from left and right hemisphere). The first level of a PPI analysis was carried out on each separate scan (from each participant) and included three regressors. Each regressor represented the interaction between the time course of hMT+ activity from ROI scans and the three experimental conditions (motion only, focused attention and divided attention). Contrasts of interest were focused attention – motion only, and divided attention –

motion only. Age x task contrasts were created, resulting in young – older adults activity for the three conditions; and older – young adults activity for the three conditions. Fixed effects analysis was performed to average data within each participant. A group level mixed effect analysis was performed to average across age groups (Z > 2.1, p < 0.05). See data processing and statistical analysis section (5.14.6) for more details of parameters used. See table 5.14 for co-ordinates and z-scores of significant sites of activation.

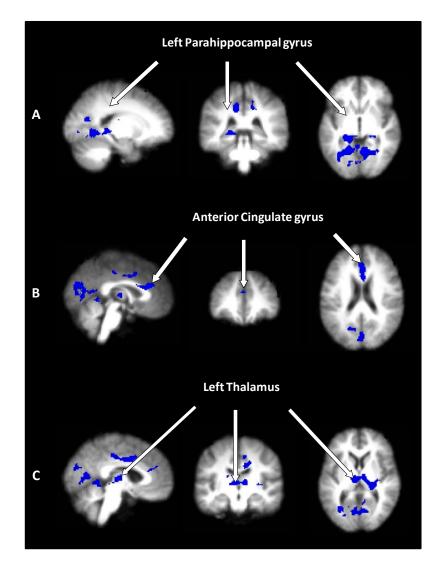


Figure 5.17: Functional connectivity during focused attention in older adults > *young adults*. Blue depicts synchrony with left hMT+. Row A shows synchronous activity between left hMT+ and left parahippocampal gyrus (-20, -36, -2). Row B shows synchronous activity between left hMT+ and anterior cingulate gyrus (0, 40, 22). Row C shows synchronous activity between left hMT+ and left thalamus (-4, -16, 6). Young adults showed no significant functional connectivity between hMT+ and other cortical regions.

Figure 5.17 shows activation in older adults > young adults during focused attention (focused attention – motion only). Fuctional connectivity was exhibited between left hMT+ and a variety of regions previously identified as elements of a network responsible for the focus and contol of attention (Posner & Peterson, 1990).

The left parahippocampal gyrus is implicated in the knowledge driven analysis of incoming information (Davachi et al., 2001). This region has strong connections to hippocampal regions thought to be involved in arousal and attentional control (Pribram & McGuinness, 1975). Parahippocampal activity was observed only when older participants were focusing attention while ignoring task-irrelevant stimuli. This could reflect observers prior knowledge about the shape and / or location of the distracter stimuli (e.g. dimension to attend, location to attend).

The anterior cingulate gyrus has been reported as responsible for disengaging attention away from sudden onsets of behaviourally irrelevant stimuli (Corbetta et al, 1991).

Posner and Petersen (1990) described a sustained visual attention system that acts to focus attentional processes on behaviourally relevant stimuli, while attenuating distracting or competing stimuli. This system includes parts of the frontoparietal attention network (inferior and superior parietal regions, and prefrontal regions) and anterior cingulate cortex. These regions work together to create a control system for the focus of attention.

Medial parts of the thalamus have been associated with attention and planning for action. This region has been indicated as being involved in an arousal-activation system (Kinomura et al., 1996). Within this system there is increased connectivity between right frontal and parietal regions and the thalamus (Coull et al, 1996).

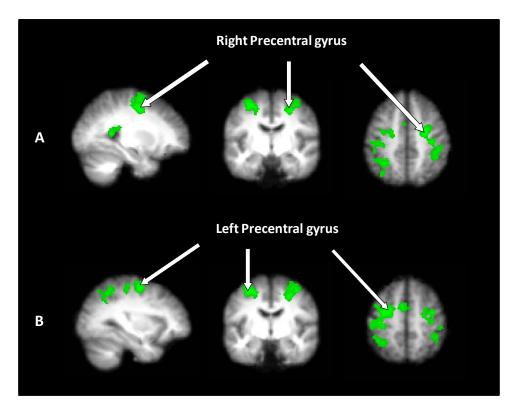


Figure 5.18: Functional connectivity during divided attention in young adults > older adults. Green depicts synchrony with left hMT+. Row A shows synchronous activity between left hMT+ and right precentral gyrus (28, -10, 50). Row B shows synchronous activity between left hMT+ and left precentral gyrus (-32, -8, 56).

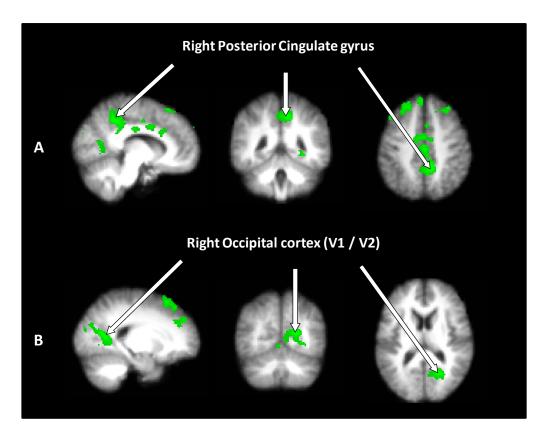


Figure 5.19: Functional connectivity during divided attention in older adults > young adults.

Green depicts synchrony with right hMT+. Row A shows synchronous activity between right hMT+ and right posterior cingulate gyrus (10, -46, 46). Row B shows synchronous activity between right hMT+ and right occipital cortex (22, -64, 14).

During the divided attention condition, young adults showed functional connectivity between left hMT+ and bilateral prefrontal regions (precentral gyrus). This activity was not elicited in older adults. Prefrontal regions have consistently been implicated in tasks that require cognitive control (Corbetta et al., 1991; Corbetta et al., 1993; Coull et al., 1996). Activity in this region is typically right lateralised during tasks requiring the allocation of focused attention and the shifting of attention (Corbetta et al, 1991; Corbetta et al, 1993), however, during the present experiment, functionally connected prefrontal activity was bilateral. This may reflect task difficulty, in that more cognitive resources were required during the more challenging task (Reuter-Lorenz & Cappell, 2008).

During the divided attention condition older adults showed functional connectivity between right hMT+ and right posterior cingulate cortex and also with right hemisphere visual regions (activation not seen in the young adults). Posterior cingulate cortex has been reported to play an important role in regulating the focus of attention (Hampson et al, 2006; Hahn et al, 2007). More recently, it has been revealed that the posterior cingulate cortex is involved in monitoring and tuning the focus of attention in order to respond to behaviourally relevant perceptual stimuli that occur outside of the cognitive tasks (Leech & Sharp, 2014). This may reflect older adults recruiting additional resources in order to maintain focused attention on motion discrimination (perceptual aspect) whilst concurrently processing the additional attention stimuli (cognitive aspect).

Table 5.14: Regions significantly activated in synchrony with hMT+

Young adults > older adults

Region	Voxels	z-score	x	у	z	hMT+ location	Task interaction
L Precentral gyrus	1805	3.93	-32	-8	56	Left	DA
R Precentral gyrus	2177	3.97	-24	-70	58	Left	DA

Older adults > young adults

Region	Voxels	z-score	х	у	z	hMT+ location	Task interaction
L Parahippocamplal gyrus	2391	3.78	-20	-36	-2	Left	FA
Anterior cingulate gyrus	1139	3.51	0	40	22	Left	FA
L Thalamus (medial dorsal nucleus)	813	3.25	-4	-16	6	Left	FA
R posterior cingulate gyrus	6192	4.07	10	-46	46	Right	DA
R Occipital cortex (V1 / V2)	1497	4.05	22	-64	14	Right	DA

Key for task contrasts:

FA	Focused attention - motion only
DA	Divided attention - motion only

5.16 General discussion

This chapter investigated the effects of focused and divided attention on a perceptual motion discrimination task. This was carried out in order to explore possible age differences in behavioural performance when observers are focusing attention on the prevailing task (ignoring task-irrelevant information) and when they are dividing attention between the prevailing task and another concurrent attention task (counting additional items in the display). The chapter also investigated the underlying cortical activity associated with the behavioural performance to see if young and older adults were engaging different neuronal networks and / or different strategies to perform the task. Region of interest analyses were undertaken to localise activity within the sensory region (hMT+) for both age groups. This was carried out in order to identify age-related changes in modulation of the sensory region. Functional connectivity between hMT+ and other cortical regions was also explored to see if there were any age related differences in regions displaying synchronous activity with the sensory region.

Previous neuroimaging studies have provided evidence of age-related sensory decline in task relevant regions during detection and discrimination tasks (Madden et al., 2004). Associated with this sensory decline was an increased activation of frontal regions in older adults (Grady et al, 1994; Madden et al, 2004). The present experiment found an age-related reduction of modulation in motion specific sensory regions, which was accompanied by a more dispersed pattern of frontal activation in older adults compared to young adults. This included left lateralised prefrontal and parietal regions and bilateral frontal regions. Young adults also showed a bilateral pattern of activity, which included left and right prefrontal and parietal regions.

Behavioural performance during focused and divided attention

Behavioural results from experiment 5 indicated that both young and older adults showed significantly higher coherence thresholds during the divided attention task compared to the focused attention task. During the focused attention task, the location of the distracter stimuli had no significant effect on performance for either age group. During divided attention, coherence thresholds were lower when distracters were presented in the periphery compared to centrally for both age groups.

Previous research indicated that older adults are more prone to interference from task-irrelevant stimuli than young adults (Gazzaley, 2008), possibly due to a failure of top-down attentional processes (Gazzaley, 2005). This was not supported by the findings of the present set of experiments. No age differences were found during performance on the focused attention task, indicating that both young and older adults were equally adept at ignoring task-irrelevant distracters. This is not line with the hypothesis, which anticipated that older adults would experience more difficulty when attempting to suppress central distracters compared to peripheral distracters (Cerella, 1985; Scialfa et al., 1987). There were also no age differences in performance on the divided attention task. Again, this does not support the original hypothesis that older adults would experience more difficulty when dividing attention between two tasks compared to young adults (Wickens, 2002; Hartley & Little, 1999).

During the divided attention condition, young adults showed a significant advantage in performance when additional attention stimuli were presented in the periphery compared to centrally presented. That is, when dividing attention between the prevailing motion discrimination task and the additional attention task (counting the attention stimuli), both motion coherence performance and counting performance were improved when additional items were in the periphery compared to centrally. Performance suffered for motion

coherence and counting when additional items were presented centrally. This could reflect the peripheral items affording young participants with a task specific cue (i.e. spatial location), thereby making it easier to distinguish how many items appeared. This, in turn, could lead to less attentional resources being required for the counting task, therefore freeing up more resources for processing the direction of motion.

Older adults displayed lower coherence thresholds when distracters were presented in the periphery, however, performance during the counting task was not significantly different for peripheral items versus centrally presented items. This suggests that motion discrimination performance is disrupted when additional attention items (to be counted) appear in the centre of the display.

Correlation analysis from the peripheral distracter condition indicated that counting accuracy increased as a function of decreasing motion coherence performance for young adults. Old adults showed a trade-off in performance between counting and coherence, indicated by a proportional rise in motion coherence versus counting accuracy. This suggests an age-related difference in the strategy adopted to perform the task. It could be that young adults are accessing additional information provided by the distinctly different locations of peripheral distracter stimuli (i.e. spatial cue), whereas, older adults are possibly not benefiting from this due to reduced peripheral acuity (Scialfa et al., 1987).

In-scanner behavioural data were also collected. Results indicated no age differences in performance across any of the tasks. The addition of task-irrelevant stimuli (focused attention) to the display had no effect on performance for either age group. This suggests that older and young adults were equally successful in inhibiting the irrelevant information, and that performance matching was successful (see methods for description). The divided attention condition also showed no age-differences in performance, suggesting that both

young and older adults could effectively switch between tasks (task matching was successful). However, the accuracy results from the additional counting task showed low levels of accuracy for both age groups. This suggests that they were focusing the majority of their attention on the motion discrimination task and not dividing attention effectively.

The accuracy data (rate of correct counting of distracters) from within the scanner indicated that both young and older adults performed worse than in the laboratory based behavioural task (described in experiment 5). Furthermore, the in-scanner accuracy data showed that older adults out-performed young adults on counting distracters. This was not the case in the behavioural experiment, where both age groups showed equal performance when counting central distracters. This result is intriguing and not in line with what was expected from results within experiment 5. Exploring this result is a possible avenue for future work. Despite these performance differences, the underlying task was still replicated in the scanner, as shown by greater activation during divided attention for both young and older adults.

Age differences in modulation of the sensory region (hMT+)

Sensory modulation in hMT+ during the three tasks was explored using ROI analyses. Results indicated significantly greater modulation in left hemisphere for young adults compared to older adults. No age differences were observed for modulation in right hMT+. This was the case for both types of attention task (focused and divided).

This supports previous findings of less sensory activation in older adults during perceptual tasks (Grady et al, 1994; Madden et al, 2004). However, previous studies did not specifically explore modulation of the sensory region. The results of the present experiment suggest that while older adults maintained performance to the level of young adults during the experimental tasks, the sensory region typically associated was not modulated to the same

degree as in young adults. Furthermore, this age difference in modulation was associated with recruitment of regions not engaged by young adults in this study. This addressed more fully in the next section.

Age-related differences in cortical activation during inhibitory control

Previous research has shown that successful inhibitory control in young adults evokes activity in right frontal and parietal regions in young adults (Nielson et al., 2002). It has been reported that, when inhibitory control fails in older adults, there is a decrease in activation in the frontal cortex, suggesting older adults are unable to recruit regions specific to inhibitory control (Jonides et al., 2000). The present experiment found that inhibitory control performance was similarly successful for older as well as young adults. Associated brain activity showed that young adults activated left hemisphere superior frontal and parietal regions. Functional connectivity analysis revealed that these regions were not activated in synchrony with the sensory region, suggesting that left superior frontal and parietal regions were not directly associated with the prevailing task, but served to mediate the effects of distracter stimuli; a finding previously reported during active ignoring of task irrelevant items (Payne & Allen, 2011).

Older adults showed no significant cortical activity during focused attention from the whole brain analysis. However, functional connectivity analyses revealed that older adults were recruiting a left hemispheric network of regions (parahippocampal gyrus, anterior cingulate gyrus and medial dorsal parts of the thalamus), previously reported to be implicated in the maintenance of attention and arousal (Posner & Peterson, 1990; Corbetta et al., 1991; Kinomura et al., 1996). This suggests that these regions were operating in synchrony with modulation in the sensory region, therefore, contributed to task performance.

Age differences in cortical activation during divided attention

During the divided attention task, age x task interactions revealed that young adults significantly activated right prefrontal and parietal regions (precentral and postcentral gyri), whereas older adults showed no significant activation of this region. These regions have previously been implicated in tasks requiring the shifting of attention (Corbetta et al., 1991; Corbetta et al., 1993; Coull et al., 1996).

Within-age task interactions revealed that young adults showed a bilateral pattern of recruitment in prefrontal and parietal regions, which was predominantly right hemisphere. Older adults recruited bilateral frontal (middle and inferior frontal gyri) regions, and left hemisphere prefrontal and parietal regions. It was expected that older adults would display a more bilateral pattern of activation (Cabeza, 2002). However, the results demonstrated asymmetric recruitment in the left hemisphere in older adults of regions typically activated in right hemisphere in young adults during shifting attention.

Functional connectivity analysis revealed that the pattern of prefrontal activation seen in young adults from the whole brain analysis was synchronous with modulation in the sensory region. This suggests that prefrontal regions were enabling the shifting of attention between the two tasks, in order to maintain performance on both. On the other hand, older adults were shown to have functional connectivity between the sensory region and right posterior cingulate gyrus, which has been reported to be involved in the maintenance and tuning of focused attention (Leech & Sharp, 2014). This suggests that while older adults did not show activity in regions typically thought to control divided attention (right prefrontal and parietal regions), they were still recruiting additional resources from attention specific regions to maintain task performance.

Possible confounds of the study

It has been reported that there is a gender disparity in BOLD responses during cognitive tasks (Thomsen et al., 2000; Bell et al., 2006). Some research has found a significantly greater mean activation and greater number of active voxels in males compared to females during cognitive tasks, when performance is matched between groups (Bell et al., 2006). In the present study, the older group was matched for sex, therefore it was presumed that this gender disparity was ameliorated by averaging within the group. However, the young group had a greater number of females to males (6:2). The averaging process here would give rise to an effective diminished BOLD response compared to if the group were matched for sex. This is not deemed to have adversely affected the illumination of age differences in the recruitment of typical attention related regions (right hemisphere prefrontal and parietal), as age differences were still present even with this purported diminished response.

It has been reported that leftward asymmetry is markedly less pronounced in left handed subjects (Hervé et al., 2006). The present study included a young group made up of entirely right handed individuals, whereas the older group contained two left handed people. This is a potentially confounding factor as the older group was found to elicit greater activity in the left hemisphere compared to the young group. It could be that this difference in activation patterns was influenced by the two left handed older adults. In order to account for this discrepancy, it would be required to repeat the experiment with only right handed groups. To achieve this, it would be necessary to have a much larger pool of participants available, where some could be rejected; this was not the case in the present study.

Summary

This chapter investigated age related changes in attentional modulation during perceptual motion processing. fMRI methods were utilised to illuminate cortical activation during focused attention and divided attention whilst measuring performance on a motion discrimination task. Focusing attention involved inhibiting task-irrelevant information, whilst dividing attention involved performing a secondary attention task. ROI analyses were undertaken to explore age-related differences in modulation of motion sensory regions and also to enable functional connectivity analyses to be carried out.

Behavioural results revealed a different pattern of performance for focused and divided attention. Focused attention performance was equivalent for both young and older adults, whereas, divided attention produced a significant performance cost for both age groups. The secondary attention task elicited equal accuracy between young and older adults.

ROI analysis revealed that older adults showed less modulation of the motion sensory region compared to young adults in left hemisphere. Whole head analyses revealed that, during focused attention, young adults activated left lateralised superior frontal and parietal regions. This is in line with previous research highlighting activity in these regions during the suppression of task irrelevant items (Payne & Allen, 2011) and top-sown attentional control (Hopfinger et al., 2000). Older adults showed no significant activity during the focused attention condition from whole head analysis. However, functional connectivity analyses revealed that older adults were recruiting a left laterlised network of regions thought to mediate an attention-arousal system (Posner & Peterson, 1990; Kinomura et al., 1996).

During divided attention, young adults showed a more right lateralised pattern of activity from whole head analyses, which is in line with previous literature (e.g. Corbetta et al., 1993). Functional connectivity analyses revealed that prefrontal regions activated by

young adults in the whole head analysis were functionally connected to modulation in the sensory region.

On the other hand, older adults showed greater recruitment from left hemisphere regions (including those regions activated by young adults in right hemisphere), which is not anticipated from the literature. It was expected that older adults would show a bilateral pattern of activation during the more cognitively demanding task (Cabeza, 2002; Reuter-Lorenz & Cappell, 2008). Functional connectivity analyses revealed a distinctly different pattern of activity to the whole head analysis, which consisted of right posterior cingulate; thought to be important in regulating the focus of attention (e.g. Hahn et al., 2007).

This chapter provides evidence that older adults were recruiting a functionally connected, task-specific network of regions, which was correlated with less modulation of the sensory region (compared to young adults). This activity was not found in young adults. It is therefore suggested that this age-specific activation may be an age-related compensatory mechanism, employed to maintain performance throughout the lifespan.

CHAPTER 6

General Discussion

6.1 Literature and motivation

Age-related changes in structure and function of the brain have been addressed previously (e.g. Cabeza, 2002; Grady, 1998; Grady, 2008; Reuter-Lorenz and Cappell, 2008). Research investigating cortical functioning has found that activation in frontal regions increases as task demand rises in young and older adults (e.g. Cabeza, 2002; Park and Reuter-Lorenz, 2009). However this pattern of increased activity differs between young and older adults (e.g. Cabeza et al, 2002). Studies on perceptual changes in older age have found that there is a visual sensory decline as a function of age (Grady et al, 1994; Madden et al 2004). Such declines affect performance during many lower level visual tasks, such as spatial frequency processing (Pardhan' 2004; Owsley et al., 1983), temporal order processing (Humes et al., 2009) and perceptual motion discrimination (Ball and Sekuler, 1986).

It has been demonstrated that additional recruitment of executive function areas, which mediate attention, can lend support to sensory processing in older adults thereby reducing age-related decline in sensory performance (Grady et al, 1994; Madden et al, 2004, Madden, 2007). Research on age-related changes during visual processing have identified an age-related change in bottom-up processing, and a corresponding increase in recruitment of attentional resources in the frontal cortex (Madden et al, 2007). Although research has highlighted age-related changes in patterns of activity in sensory regions, it

has not yet fully addressed age differences in modulation of the sensory regions.

Studies utilising perceptual training methods for older and young adults have found beneficial effects in post-training performance on perceptual and cognitive tasks (e.g. Berry et al., 2010; Ball et al., 2002; Paxton et al., 2006). In some studies older adults were shown to benefit to a greater extent (e.g. Paxton et al., 2006). Although robust effects have been found for perceptual training, the majority of studies examining this effect used lengthy, time consuming training programmes. There has been less focus on the effects of short session perceptual training, which would be indicated in the very young, patient populations and older adults (Molloy et al., 2012).

This thesis investigated the application of attentional modulation during lower level perceptual tasks. The main aim was to discover if there were any differences in the way that young and older adults utilise attentional resources.

Chapter 2 introduced a task with cross-modal symbolic information to explore congruency effects on performance in temporal order judgement (TOJ). Chapters 3 & 4 explored the benefit that short session sensitisation training might offer young and older adults during the TOJ task. Chapter 5 addressed age-related differences in the allocation of focused and divided attention during perceptual motion tasks. The underlying neuronal networks were also investigated via fMRI and functional connectivity analysis. Age-related differences in modulation of task specific sensory regions were also explored.

It was expected that older adults would use attentional resources at lower levels of task demand (e.g. when TOJ is less difficult to distinguish, long SOAs) (Lavie, 2005). Young adults were expected to utilise attentional cues at short SOAs, when TOJ is difficult to distinguish.

Older adults were expected to show reduced performance compared to young adults when tasks required the dividing of attention (Verhaeghen et al., 2003). It was predicted that fMRI results would show enhanced recruitment of bilateral frontal regions in older adults during divided attention (e.g. Cabeza, 2002).

6.2 Discussion of chapters 2-4

Training procedures have been found to induce a beneficial effect on performance in young and older adults during various perceptual and cognitive tasks (Erickson et al, 2007; Paxton et al, 2006; Berry et al, 2010; Ball et al, 2002). Chapters 2 & 4 indicated age-related differences in temporal order discrimination when no additional information was provided. Chapter 2 investigated age-related changes in temporal order judgement and the effects of congruent and incongruent tones on performance. It was found that older adults did not experience a beneficial effect of congruent tone, shown by no difference in performance between the two tones. Young adults made significantly more correct order judgements when congruent tones were present (compared to incongruent), supporting the literature, which suggests that young adults have a naturally occurring bias toward cross-modal congruency (Evans & Treisman, 2010).

At shorter SOAs, this effect could be accounted for by young adults using the sensory dominance strategy, i.e. the information of the first presented modality, which in this case was the auditory tone (Jaskowski, 1993; Landy et al., 2001). However, it could also reflect a weighed integration, using weights which encode the inverse of the differing modalities' noise (Ernst & Bülthoff, 2004). It could also support the effect of naturally occurring bias to integrate congruent information (Evans & Treisman,

The notion of a naturally occurring bias suggests the enhancement of a proactive effect, whereby young adults have an expectation of ensuing stimuli (i.e. the expectation would be for successive stimuli to be those that have this bias toward integration), priming the integration of congruent tone (Paxton et al., 2006). This could form a single congruent percept, enabling improved performance in the congruent TOJ task. Paxton et al., (2006) suggested that a reactive strategy is employed by older adults, which in this case would result in the apprehension of the tone, without the observer being primed to form a percept with the ensuing congruent visual stimuli.

Given the chance performance when both cross-modally incongruent and congruent tones were played it suggested formation of a percept combining the HSF and the LSF resulting in no match to the response choices offered, preventing effective performance on the TOJ task. Similarly, a reactive strategy in the absence of a natural bias to integrate congruent tones, would account for the performance decline in older adults relative to younger adults. In the weighting of modality explanation, the effect of the tones is essentially to add noise to the perceptual process (Battaglia et al., 2003), due to them offering no meaningful information.

It was expected that older adults would integrate the cross-modal information more than young adults, as previous research has highlighted enhanced cross-modal integration in older adults (Laurienti et al., 2006; Peiffer et al., 2007). It is likely that the Laurenti et al. (2006) task offered additional semantic information, which accounts for the greater performance in older adults during their reported tasks. Similarly for Pfeiffer et al. (2007), the cross modal integration task was easier in that it was the integration of the mere presence of cross modal information (on/off) as

opposed to the two frequency bands utilised in this study.

Chapter 3 explored training experienced psychophysical observers to form effective cue + stimulus associations, in order to enable top-down attention to facilitate performance during a cued condition. The use of observers was motivated by the desire to test the effects of beneficial associations between cue and stimulus, via sensitisation and top down cueing, in a 'best case scenario'. It was predicted that experienced observers would offer maximal compliance, familiarity with the testing environment and consistent performance.

Performance was shown to benefit from sensitisation, indicated by significantly superior performance during congruent trials compared to incongruent trials. Given incongruent cueing was detrimental to performance, relative to the neutral cue baseline, is considered evidence that effects were as a result of the sensitisation session.

Chapter 4 demonstrated that top-down cueing via sensitisation can induce improved cue + stimulus associations in young and older adults. Furthermore, it demonstrated that this effect can be elicited by providing short sensitisation sessions. Results suggested that older adults may have adopted a strategy akin to young adults, as a result of the sensitisation training.

Chapter 2 showed no cross-modal integration in older adults. Results from chapter 4 indicted that sensitisation enabled cross-modal integration in older adults, as had been noted in (Laurienti et al., 2006; Peiffer et al., 2007). This suggests that beneficial sensitisation to the attention cues provided a performance benefit of the same order as the semantic information provided in the Laurenti et al. (2006) study.

Previous research has emphasised relatively long training sessions (over many hours, often interspersed over a lengthy time period) (Erikson et al., 2007). This type of

training is contraindicated for older adults as it has a negative effect on motivation, compliance and retention of participants (Molloy et al., 2012).

The short term training method used in chapter 4 of this thesis was shown to offer a measurable effect in young and older adults. This has important ramifications for studies which aim to recruit, and maintain attendance, and enhance compliance (Aberg et al., 2009).

Results from chapter 4 indicated that young and older adults were modulating the cue information to the same degree. Change scores analysis at 44ms and greater revealed no age-difference in cue use during congruent or incongruent conditions. Young and older adults also showed similar improvements in TOJ performance when presented with congruent cues. Taken together, the results suggested that both age groups were employing similar strategies to improve task performance.

At short SOAs (less than 44ms) both young and older adults appeared to use the 75% reliable auditory cue. Older adults indiscriminately integrated the incongruent cue more than young adults, suggesting that they were unable to suppress task irrelevant information (Hasher & Zacks, 1988).

In summary, results from chapters 2-4 suggest that short duration sensitisation methods, which enable effective top-down cueing, can serve to induce a cross-modal integration effect in older; which serves to benefit performance on a secondary task. The results also suggest that the naturally occurring cross-modal congruency effect found in young adults can be enhanced via short duration training, leading to a beneficial effect on performance of a secondary task. The efficacy of the short duration training method explored within this thesis may be of use to variety of other perceptual tasks.

6.3 Discussion of chapter 5

This chapter investigated age related changes in attentional modulation during perceptual motion processing. Research has demonstrated age-related under-activation of sensory regions and a corresponding increase in attention regions within the cortex (Grady et al, 1994, Madden et al, 2004). However, such research has not specifically addressed attentional modulation of sensory regions. During this chapter, fMRI methods were utilised to illuminate cortical activation during focused attention and divided attention whilst measuring performance on a motion discrimination task. Focusing attention involved inhibiting task-irrelevant information, whilst dividing attention involved performing a secondary attention task. ROI analyses were undertaken to explore age-related differences in modulation of motion sensory regions and also to enable functional connectivity analyses to be carried out.

Behavioural results revealed no age differences in performance during focused attention, indicating that both young and older adults were equally able to ignore task irrelevant distracters. During divided attention, young and older adults showed the same level of cost of performance compared to focused attention, reflecting the differences in task difficulty (e.g. dividing attention placed more of a drain on working memory).

ROI and functional connectivity analyses revealed an age difference in modulation of the sensory region. This corresponded to an increase in activation in functionally connected regions in older adults (but not young), during focused attention. This functionally connected network of regions included left laterlised regions thought to mediate an attention-arousal system (Posner & Peterson, 1990; Kinomura et al., 1996). Young adults showed complimentary activation from the whole head analysis, which included left lateralised

superior frontal and parietal regions thought to aid the suppression of task irrelevant items (Payne & Allen, 2011).

During divided attention, young adults activated regions in right frontal and parietal cortex typically thought to control the shifting of attention between two tasks (Corbetta et al., 1993). This activity was shown to spill over into bilateral regions, reflecting task difficulty (Reuter-Lorenz & Cappell, 2008). Functional connectivity analyses revealed that these regions showed correlative activation with the sensory region.

Older adults showed greater recruitment from left hemisphere regions (including those regions activated by young adults in right hemisphere) during the divided attention task (from the whole head analysis). This was not expected as previous research has highlighted increased bilateral activation during difficult tasks (e.g. Cabeza, 2002). Functional connectivity analyses revealed a distinctly different pattern of activity to the whole head analysis, which consisted of right posterior cingulate; thought to be important in regulating the focus of attention (e.g. Hahn et al., 2007).

This chapter provided evidence that older adults were recruiting a functionally connected, task-specific network of regions, which was correlated with less modulation of the sensory region (compared to young adults). This activity was not found in young adults. It is therefore suggested that this age-specific activation may be an age-related compensatory mechanism, employed to maintain performance throughout the lifespan.

Limitations

For chapter 5, there were some limitations to the way in which the participant pool was composed. In that the two samples were not equally matched for gender or handedness.

These are possible confounds when conducting neuroimaging research (e.g. Bell et al., 2006). It would be interesting to repeat the study with a matched cohort and a larger cohort, as this would more effectively tease those effects that are solely due to ageing.

Summary

The aim of this thesis was to examine age-related changes in attention modulation in perceptual and cognitive processing. Results suggested that short duration training can induce an effect of cue modulation in older adults, perhaps by enabling an appropriate strategy to be formed.

Age differences in attentional modulation were supported by the fMRI results which indicated that older adults showed less modulation in hMT+ during motion discrimination tasks. Patterns of activity indicated that older adults were utilising a different cortical network to that of young adults to modulate performance.

These findings support much of the previous literature reviewed in this thesis, but lend new insights into research on ageing and attention. Firstly, that short session training methods can assist both young and older adults during perceptual tasks. Furthermore, that older adults show less modulation in motion sensory regions compared to young adults, and appear to utilise a different cortical network in order to counter the effects of reduced sensory activation. This thesis has also highlighted a variety further research avenues and possible training applications.

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Appendix A

A.1: Copy of consent form for experiments 1 and 2.

Temporal Order Judgement Experiment

Thank you for taking part in this study. The experiment takes approximately 30 minutes in total. You will receive instructions prior to beginning. This is a computer based experiment where you will first hear a tone and then see a pattern on the screen and make a response via key press. This response will record your accuracy, so please be a quick and accurate as possible.

To take part you need to have normal, or corrected to normal, vision; and normal hearing.

If you have any questions regarding the experiment, please ask the experimenter. If you have any further questions following the experiment, please email nxk331@bham.ac.uk.

If you are willing to take part in this study, please complete the form below.

Participant signature:
Participant name:
Experimenter signature:
Experimenter name:

A.2: Methods and results for identification accuracy for the 9 shape stimuli

Methods:

Six female members of the vision department (within the school of psychology) aged 24-36 (mean = 28.83, SD = 4.62) participated in the experiment, all were right handed.

Participants were presented with 9 simple shape stimuli, filtered to produce both a HSF and a LSF counterpart (stimuli were filtered as described in chapter 2 methods section). Shapes were presented at full luminance contrast and at two spatial frequencies (1.6 and 6.5 cycles / degree). Each participant saw each shape 88 times (44 HSF filtered and 44 LSF filtered).

Participants were presented with onscreen instructions. Following a 200ms fixation period, shapes were presented 100ms each, during single item displays (in a random order). Participants responded to which shape they had detected, using the keyboard (sticky labels depicting each shape were attached to the number keys to ensure the correct key was pressed). Participants had to judge which shape had appeared, as quickly and accurately as possible.

Results:

A repeated measures ANOVA was performed with factors of spatial frequency (SF) (2 – HSF and LSF) and shape (9 – Arrow, bell, circle, crescent, heart, hexagon, square, star and triangle). This revealed no significant main effects or interactions, indicating that all shapes were equally identifiable (for both HSF and LSF). This suggests that no one shape was more salient than the next. See table A.2a for ANOVA results and table A.2b for means and standard error.

Table A.2a: ANOVA table for shape identification

Effects	Mean Square	DF	F	р	Partial η²
SF	6.56	1, 5	0.11	0.758	0.02
Shape	15.09	8, 40	0.53	0.829	0.10
SF x Shape	16.43	8, 40	0.46	0.877	0.08

Table A.2b: Means table for shape identification

Factor	Level	Mean	Std. Error
SF	HSF	79.20	0.46
ЭГ	LSF	78.71	1.30
	Arrow	77.80	2.32
	Bell	79.98	1.57
	Circle	80.70	1.14
	Crescent	78.91	1.82
Shape	Heart	77.61	1.31
	Hexagon	78.60	0.50
	Square	79.37	0.76
	Star	79.92	2.05
	Triangle	77.70	1.78

A.3: Copy of instructions to participants for experiment 1.

Temporal Order Judgement Experiment 1

Thank you for taking part in this experiment.

When you begin the experiment, you will see a set of instructions on the screen. Read the instructions carefully and make sure you understand the task before starting the experiment.

Look at the fixation point at the start of each trial.

Two shapes will be presented together, one on the left and one on the right. One of the shapes will be on the screen before the other. Each presentation will be preceded by a 'beep' sound to indicate that a stimulus is about to be presented.

Your task is to indicate which side you saw the shape, using the left and right arrow keys.

It will often be difficult to tell exactly which shape was shown first, and the stimuli will sometimes be difficult to detect. However, please make a response on each trial.

Please respond as quickly and accurately as possible.

If you have any questions about the experiment, feel free to ask the experimenter. Your results will remain anonymous at all times and you can withdraw from the experiment at any time if you wish.

A.4: Further analysis for LSF response bias. Interaction of Age x SOA.

Two-way ANOVA Age x SOA

SOA	Age	Mean	Standard Error	DF	Mean Square	F	р	r
11ms	Young	66.51	4.98	1, 22	1069.07	1.73	0.202	0.27
111113	Older	53.16	8.83	1, 22		1.75	0.202	0.27
33ms	Young	65.28	3.84	1, 22	836.38	1.51	0.232	0.25
331113	Older	53.47	8.81					0.23
55ms	Young	63.20	3.14	1, 14	336.15	0.63	0.441	0.17
331113	Older	55.71	8.90	1, 14	330.13	0.03		
99ms	Young	58.49	1.34	1, 12	0.00	0.00	1.000	0.00
331115	Older	58.49	7.19	1, 12	0.00			

A.5: Further analysis for LSF response bias. Interaction of Position x contrast x age.

Two-way ANOVA position x contrast: Young adults

Contrast	Position	Mean	Standard Error	DF	Mean Square	F	р	r
5%	Separate	72.45	4.57	1, 22	116.03	0.60	0.448	0.16
3%	Overlapped	68.06	3.39	1, 22	110.05	0.00	0.440	0.10
Q 0/	Separate	64.35	5.86	1, 22	8.06	0.03	0.866	0.04
8%	Overlapped	63.19	3.38	1, 22	8.00	0.05	0.800	0.04
100/	Separate	64.35	3.16	1, 22	1643.58	12.42	0.002*	0.60
10%	Overlapped	47.80	3.47	1, 22	1043.58	12.42	0.002	0.60

Two-way ANOVA position x contrast: Older adults

Contrast	Position	Mean	Standard Error	DF	Mean Square	F	р	r
5%	Separate	62.50	9.39	1, 22	217.32	0.21	0.649	0.10
5%	Overlapped	56.48	9.06	1, 22	217.52	0.21	0.045	0.10
8%	Separate	62.15	9.18	1, 22	990.48	1.05	0.317	0.21
0/0	Overlapped	49.30	8.54	1, 22	330.46	1.05		0.21
10%	Separate	54.75	8.19	1, 22	451.97	0.53	0.474	0.15
	Overlapped	46.07	8.65	1, 22				0.15

A.6: Further analysis for left response bias when HSF was presented first. Interaction of Contrast x SOA.

Two-way ANOVA of contrast x SOA

SOA	Age	Mean	Standard Error	DF	Mean Square	F	р	r
	5%	49.62	1.93					
11ms	8%	47.98	2.25	2, 33	66.20	1.16	0.326	0.26
	10%	44.99	2.33					
	5%	51.55	3.23		·			·
33ms	8%	45.01	3.50	2, 33	137.89	1.11	0.343	0.25
	10%	49.85	2.92					
	5%	44.19	2.23					
55ms	8%	44.93	2.52	2, 33	62.55	0.94	0.403	0.23
	10%	48.46	2.32					
	5%	44.86	2.76					
99ms	8%	41.27	2.59	2, 33	626.62	8.50	0.001	0.58
	10%	55.19	2.03					

A.7: Further analysis of left response bias when LSF was presented first. Interaction of Age x SOA.

Two-way ANOVA of age x SOA

SOA	Age	Mean	Standard Error	DF	Mean Square	F	р	r
11ms	Young	43.82	3.07	1, 16	613.07	8.90	0.009	0.54
111113	Older	53.93	1.44		013.07	0.50	0.005	0.54
33ms	Young	47.11	2.32	1 22	94.25	1.79	0.195	0.27
331113	Older	51.07	1.85	1, 22				0.27
55ms	Young	45.86	1.55	1, 22	216.72	9.03	0.007	0.54
331118	Older	51.87	1.26	1, 22	210.72	3.03	0.007	0.34
99ms	Young	49.69	1.85	1, 22	2.41	0.08	0.787	0.06
331115	Older	49.05	1.40	1, 22	2.41	0.08	0.787	0.06

A.8: Further analysis of left response bias when LSF was presented first. Interaction of Position x contrast x age.

Two-way ANOVA of position x contrast: Young adults

Contrast	Position	Mean	Standard Error	DF	Mean Square	F	р	r
5%	Separate	47.17	2.31	1, 22	36.19	0.59	0.452	0.16
3%	Overlapped	44.72	2.23	1, 22	30.13	0.55	0.752	0.10
8%	Separate	47.07	2.21	1 22	28.10	0.28	0.605	0.11
6/6	Overlapped	44.91	3.48	1, 22	20.10	0.20		0.11
10%	Separate	54.22	2.69	1, 22	953.06	8.94	0.007	0.54
10/6	Overlapped	41.62	3.24	1, 22	955.00			0.54

Two-way ANOVA of position x contrast: Older adults

Contrast	Position	Mean	Standard Error	DF	Mean Square	F	р	r
5%	Separate	53.17	2.00	1, 22	233.63	4.37	0.048	0.41
3%	Overlapped	46.93	2.22	1, 22	255.05	4.57	0.040	0.41
8%	Separate	57.71	2.68	1, 22	614.99	8.04	0.010	0.52
6/6	Overlapped	47.59	2.36	1, 22	014.55			0.32
10%	Separate	50.89	1.80	1, 22	17.31	0.33	0.574	0.12
10/6	Overlapped	52.59	2.37	1, 22	17.51			0.12

A.9: Further analysis of left response bias when LSF was presented first. Interaction of Position x contrast x SOA.

Two-way ANOVA of contrast x SOA: Separate stimuli

SOA	Age	Mean	Standard Error	DF	Mean Square	F	р	r
	5%	49.81	2.16					
11ms	8%	55.83	2.93	2, 33	119.08	1.09	0.348	0.25
	10%	51.22	3.75					
	5%	55.83	3.41					
33ms	8%	54.34	2.84	2, 33	20.40	0.15	0.864	0.09
	10%	53.23	3.86					
	5%	47.58	2.31					
55ms	8%	54.17	3.20	2, 21	135.43	1.35	0.281	0.32
	10%	49.74	1.63					
	5%	47.47	3.04					
99ms	8%	45.23	3.24	2, 33	390.32	3.92	0.030	0.44
	10%	56.04	2.26					

Two-way ANOVA of contrast x SOA: Overlapped stimuli

SOA	Age	Mean	Standard Error	DF	Mean Square	F	р	r
	5%	48.48	4.51					
11ms	8%	42.51	3.36	2, 33	106.94	0.40	0.671	0.15
	10%	45.39	5.88					
	5%	41.04	2.94					
33ms	8%	42.98	3.92	2, 33	116.50	0.91	0.413	0.23
	10%	47.14	2.83					
	5%	45.18	2.92					
55ms	8%	43.54	2.73	2, 33	304.05	3.60	0.039	0.42
	10%	52.96	2.25					
	5%	48.60	2.96					·
99ms	8%	55.97	4.21	2, 33	512.87	3.71	0.035	0.43
	10%	42.93	2.83					

A.10: Repeated measures ANOVA including position.

ANOVA table for experiment 1 (including position)

Effects	Mean Square	DF	F	р	Partial η²
Age	1.19	1, 22	16.80	< 0.001*	0.43
Side presented (left / right)	1.11	1, 22	5.29	0.031*	0.19
Position	3.20	1, 22	1.64	0.213	0.07
Contrast	13.99	2, 44	13.96	< 0.001*	0.39
SOA	197.18	2, 42	93.85	< 0.001*	0.81
Side Presented x Age	0.04	1, 22	0.21	0.655	0.01
Position x Age	0.12	1, 22	0.06	0.810	0.00
Contrast x Age	0.37	2, 44	0.37	0.697	0.02
SOA x Age	6.60	3, 66	4.90	0.004*	0.18
Side Presented x Position	0.04	1, 22	0.11	0.747	0.01
Side Presented x Position x Age	0.26	1, 22	0.71	0.408	0.03
Side Presented x Contrast	0.90	2, 44	3.21	0.050	0.13
Side Presented x Contrast x Age	0.11	2, 44	0.39	0.680	0.02
Position x Contrast	0.01	2, 44	0.01	0.987	0.00
Position x Contrast x Age	0.18	2, 44	0.22	0.803	0.01
Side Presented x Position x Contrast	0.69	2, 44	2.74	0.076	0.11
Side Presented x Position x Contrast x Age	0.24	2, 44	0.95	0.394	0.04
Side Presented x SOA	0.24	3, 66	1.12	0.349	0.05
Side Presented x SOA x Age	0.22	3, 66	1.02	0.389	0.04
Position x SOA	1.73	3, 66	2.88	0.042*	0.12
Position x SOA x Age	0.71	3, 66	1.19	0.321	0.05
Side Presented x Position x SOA	0.04	3, 66	0.11	0.953	0.01
Side Presented x Position x SOA x Age	0.61	3, 66	1.90	0.139	0.08
Contrast x SOA	1.79	4, 85	1.91	0.118	0.08
Contrast x SOA x Age	0.31	6, 132	0.52	0.796	0.02
Side Presented x Contrast x SOA	0.55	6, 132	1.79	0.106	0.08
Side Presented x Contrast x SOA x Age	0.14	6, 132	0.44	0.854	0.02
Position x Contrast x SOA	0.69	6, 132	1.33	0.249	0.06
Position x Contrast x SOA x Age	0.08	6, 132	0.16	0.987	0.01
Side Presented x Position x Contrast x SOA	0.15	6, 132	0.52	0.795	0.02
Side Presented x Position x Contrast x SOA x Age	0.36	6, 132	1.27	0.274	0.06

Means table for experiment 1 (including position)

Factor	Level	Mean	Std. Error
Age	Young	0.93	0.08
Age	Older	0.49	0.08
Side	Left	0.74	0.06
presented	Right	0.68	0.05
Position	Separate	0.66	0.07
Position	Overlapped	0.76	0.07
	5%	0.53	0.06
Contrast	8%	0.69	0.06
	10%	0.91	0.08
	11ms	0.02	0.05
SOA	33ms	0.41	0.06
	55ms	0.85	0.08
	99ms	1.57	0.12

A.11: Further analysis from experiment 1. Interaction of age x SOA.

Two-way ANOVA results for Age x SOA

SOA	Age	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	Young	0.06	0.07	1, 22	0.04	0.81	0.377	0.19
11113	Older	-0.02	0.06	1, 22	0.01	0.01	0.577	0.15
33ms Young	0.58	0.10	1, 22	0.67	7.31	0.013	0.50	
331113	Older	0.25	0.08	1, 22	0.07	7.51	0.015	0.50
55ms	Young	1.14	0.08	1, 22	2.03	12.86	0.002	0.61
331113	Older	0.56	0.14	1, 22	2.03	12.00	0.002	0.01
99ms	Young	1.96	0.10	1, 16	3.67	11.48	0.004	0.59
221113	Older	1.18	0.21	1, 10	5.07	11.46	0.004	0.59

A.12: Copy of instructions given to participants for experiment 2.

Temporal Order Judgement Experiment 2

Thank you for taking part in this experiment.

When you begin the experiment, you will see a set of instructions on the screen. Read the instructions carefully and make sure you understand the task before starting the experiment.

Look at the fixation point at the start of each trial.

Two shapes will be presented together, one on the left and one on the right. One of the shapes will be on the screen before the other.

Each presentation will be preceded by a high or low pitched auditory tone. Low spatial filtered shapes (fuzzy) will be preceded by a low 'buzz' sound, and high spatial filtered shapes (fine edged) will be preceded by a high 'beep' sound. This will be true on 50% of trials. For the remaining 50% of trials, the tones will be switched around (high beep before low spatial frequency shapes, low buzz before high spatial frequency shapes).

Your task is to indicate which side you first saw a shape appear (left and right arrows).

It will often be difficult to tell exactly which shape was shown first, and the stimuli will sometimes be difficult to detect. However, please make a response on each trial.

Please respond as quickly and accurately as possible.

If you have any questions about the experiment, feel free to ask the experimenter. Your results will remain anonymous at all times and you can withdraw from the experiment at any time if you wish.

A.13: Further analysis from experiment 2. Interaction of age x cue-congruency

Two-way ANOVA results for Age x cue-congruency

Cue	Age	Mean	Std. Error	DF	Mean Square	F	р	r
Congruent	Young Older	0.90 0.23	0.14 0.06	1, 22	2.65	19.32	< 0.001	0.68
Incongruent	Young Older	0.11 0.17	0.18 0.06	1, 14	0.02	0.10	0.755	0.07

A.14: Further analysis from experiment 2. Interaction of age x SOA.

Two-way ANOVA results for Age x SOA

SOA	Age	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	Young	0.06	0.06	1, 22	0.00	0.05	0.824	0.05
111112	Older	0.03	0.10	1, 22	0.00	0.03	0.024	0.05
33ms	Young	0.23	0.06	1, 22	0.19	3.57	0.072	0.37
331115	Older	0.06	0.07	1, 22	0.19	5.57	0.072	0.57
55ms	Young	0.53	0.11	1, 22	1.17	10.76	0.003	0.57
331115	Older	0.09	0.08	1, 22	1.17	10.70	0.003	0.57
99ms	Young	1.18	0.15	1, 22	1.88	7.51	0.012	0.50
991115	Older	0.62	0.14	1, 22	1.00	7.51	0.012	0.50

A.15: Further analysis from experiment 2. Interaction of age x cue-congruency x SOA.

Two-way ANOVA for cue-congruency x SOA: Young adults

SOA	Cue	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	Congruent	0.52	0.16	1, 22	5.09	14.58	0.001	0.63
111113	Incongruent	-0.40	0.18	1, 22	5.05	14.50	0.001	0.03
33ms	Congruent	0.64	0.18	1, 22	3.94	9.76	0.005	0.55
331113	Incongruent	-0.17	0.19	1, 22	J.J-	3.70	0.005	0.55
55ms	Congruent	0.76	0.20	1, 22	1.29	2.83	0.106	0.34
331113	Incongruent	0.30	0.19	1, 22	1.29	2.65	0.100	0.34
99ms	Congruent	1.67	0.15	1, 22	5.61	10.47	0.004	0.57
331118	Incongruent	0.70	0.26	1, 22	5.01	10.47	0.004	0.57

One-way ANOVA for cue-congruency x SOA: Older adults

SOA	Cue	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	Congruent	-0.01	0.12	1, 22	0.04	0.25	0.621	0.11
111112	Incongruent	0.08	0.10	1, 22	0.04	0.25	0.021	0.11
33ms	Congruent	0.12	0.12	1, 16	0.10	0.94	0.347	0.20
331113	Incongruent	-0.01	0.06	1, 10	0.10	0.51	0.547	0.20
55ms	Congruent	0.19	0.09	1, 22	0.25	2.37	0.138	0.31
331113	Incongruent	-0.01	0.09	1, 22	0.23	2.37	0.136	0.31
99ms	Congruent	0.63	0.14	1, 22	0.00	0.00	0.984	0.00
331113	Incongruent	0.62	0.15	1, 22	0.00	0.00	0.984	0.00

A.16: Further analysis from experiment 2. Interaction of age x cue-congruency x contrast x SOA: Young adults.

Two-way ANOVA for contrast x SOA: Congruent tone

SOA	Contrast	Mean	Std. Error	DF	Mean Square	F	р	r
	5%	0.77	0.25					
11ms	8%	0.70	0.18	2, 33	1.66	3.38	0.046	0.41
	10%	0.09	0.17					
	5%	0.58	0.22					
33ms	8%	0.46	0.17	2, 33	0.58	1.03	0.368	0.24
	10%	0.88	0.26					
	5%	0.80	0.17					
55ms	8%	0.83	0.21	2, 33	0.10	0.17	0.841	0.10
	10%	0.66	0.28					
	5%	1.54	0.15					
99ms	8%	1.68	0.18	2, 33	0.19	0.55	0.581	0.18
	10%	1.79	0.18					

Two-way ANOVA for contrast x SOA: Incongruent tone

SOA	Contrast	Mean	Std. Error	DF	Mean Square	F	р	r
	5%	-0.67	0.18					
11ms	8%	-0.43	0.18	2, 33	0.95	1.94	0.159	0.32
	10%	-0.11	0.24					
	5%	-0.26	0.26					
33ms	8%	-0.05	0.28	2, 33	0.14	0.19	0.830	0.11
	10%	-0.20	0.21					
	5%	-0.17	0.20					
55ms	8%	0.37	0.30	2, 33	2.35	3.06	0.060	0.40
	10%	0.70	0.25					
	5%	0.32	0.37					
99ms	8%	0.94	0.23	2, 33	1.31	1.17	0.323	0.26
	10%	0.84	0.30					

A.17: Further analysis from experiment 2. Interaction of age x cue-congruency x contrast x SOA: Older adults.

Two-way ANOVA for contrast x SOA: Congruent tone

SOA	Contrast	Mean	Std. Error	DF	Mean Square	F	р	r
	5%	0.15	0.18					
11ms	8%	-0.10	0.16	2, 33	0.24	0.58	0.566	0.18
	10%	-0.07	0.20					
	5%	0.07	0.21					
33ms	8%	0.12	0.16	2, 33	0.03	0.11	0.901	0.08
	10%	0.17	0.11					
	5%	0.13	0.12					
55ms	8%	0.27	0.19	2, 33	0.06	0.22	0.808	0.11
	10%	0.17	0.15					
	5%	0.79	0.18					
99ms	8%	0.38	0.18	2, 33	0.58	0.98	0.384	0.24
	10%	0.71	0.29					

Two-way ANOVA for contrast x SOA: Incongruent tone

SOA	Contrast	Mean	Std. Error	DF	Mean Square	F	р	r
	5%	0.03	0.19					
11ms	8%	0.10	0.19	2, 33	0.02	0.04	0.960	0.05
	10%	0.09	0.16					
	5%	-0.05	0.15					
33ms	8%	0.00	0.11	2, 33	0.02	0.09	0.914	0.07
	10%	0.02	0.10					
	5%	0.06	0.10					
55ms	8%	0.15	0.16	2, 33	0.49	1.97	0.156	0.33
	10%	-0.24	0.16					
	5%	0.60	0.17					
99ms	8%	0.39	0.20	2, 33	0.71	1.53	0.231	0.29
	10%	0.87	0.21					

Appendix B

B.1: Repeated measures ANOVA for baseline condition in experiment 3.

There were 16 runs of 135 trials (2160 trials in total).

A repeated measures ANOVA with within-subjects factors of *side presented* (2 - left and right), *contrast* (2 - lower and higher) and SOA (5 - 11, 33, 55, 77 and 99 ms) revealed no significant effect of side presented (p = 0.267). There were also no significant interactions containing side presented (see table B.1a for ANOVA and B.1b for means), therefore data were collapsed over side presented.

Table B.1a: Repeated measures ANOVA for baseline condition in experiment 3

Effects	Mean Square	DF	F	р	Partial η ²
Side presented (left / right)	0.49	1, 4	1.66	0.267	0.29
Contrast	2.10	1, 4	7.79	0.049	0.66
SOA	24.53	4, 16	185.60	< 0.001*	0.98
Side Presented x Contrast	0.16	1, 4	0.46	0.535	0.10
Side Presented x SOA	0.23	4, 16	1.24	0.333	0.24
Contrast x SOA	0.14	4, 16	0.53	0.715	0.12
Side Presented x Contrast x SOA	0.31	4, 16	2.00	0.144	0.33

Table B.1b: Means and standard deviation for baseline condition in experiment 3

Factor	Level	Mean	Std. Error
Sido procontod	Left	1.57	0.07
Side presented	Right	1.71	0.13
Contrast	3x	1.50	0.13
Contrast	5x	1.79	0.07
	11ms	0.10	0.10
	33ms	1.06	0.10
SOA	55ms	1.82	0.10
	77ms	2.23	0.13
	99ms	2.99	0.15

B.2: Further analysis for cross-modal condition in experiment 3. Interaction of contrast x SOA.

Two-way ANOVA for interaction of contrast x SOA

SOA	Contrast	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	3x	0.03	0.11	1, 8	0.01	0.11	0.747	0.11
11113	5x	-0.02	0.08		0.01	0.11	0.747	0.11
33ms	3x	0.65	0.07	1, 8	0.59	17.04	0.003	0.82
331113	5x	1.14	0.10	1, 0	0.55	27.101	0.005	0.02
55ms	3x	1.70	0.12	1, 8	0.04	0.84	0.387	0.31
331113	5x	1.59	0.05	1, 0	0.04	0.04	0.307	0.51
77ms	3x	2.18	0.15	1, 8	0.20	2.21	0.176	0.46
771113	5x	2.46	0.11	1, 0	0.20	2.21	0.170	0.40
99ms	3x	2.86	0.14	1, 8	0.30	4.56	0.065	0.60
331113	5x	3.20	0.09	1, 0	0.30	4.56	0.065	0.60

Appendix C

C.1: Repeated measures ANOVA for the neutral baseline condition from experiment 4.

A repeated measures ANOVA with a between subjects factor of *age* (2 - young and older) and within subjects factors of *side presented* (2 - left and right), *contrast* (2 - lower and higher) and *SOA* (9 - 11, 22, 33, 44, 55, 66, 77, 88 and 99 ms) revealed significant main effects for age, contrast and SOA, and a significant interaction of age x SOA (see table C.1a for ANOVA results and table C.1b for means and standard error). There was no significant effect of side presented (p = 0.655) and no significant interactions containing side presented.

Therefore data were collapsed over side presented for further analysis.

The significant main effect of contrast indicated that performance was better at the higher contrast compared to the lower contrast. The significant main effect of SOA indicated that performance improved as a function of increasing SOA. The significant main effect of age indicated that young adults made more correct TOJ than older adults.

The interaction of age x SOA indicated that there were no significant age differences in performance at SOAs of 11ms (p = 0.561), 22ms (p = 0.139), 33ms (p = 0.324), 44ms (p = 0.058), 55ms (p = 0.357), 66ms (p = 0.326). Significant age differences were observed at SOAs of 77ms (F(1, 14) = 7.63, p = 0.015, r = 0.59), 88ms (F(1, 14) = 8.53, p = 0.015, r = 0.62) and 99ms (F(1, 14) = 28.14, p < 0.001, r = 0.82). See table C.1c for two-way ANOVA results.

Table C.1a: ANOVA results for the neutral baseline condition from experiment 4

Effects	Mean Square	DF	F	р	Partial η ²
Age	1.61	1, 14	4.71	0.048	0.25
Side presented (left / right)	0.14	1, 14	0.21	0.655	0.02
Contrast	7.82	1, 14	7.72	0.015*	0.36
SOA	24.16	8, 112	32.62	< 0.001*	0.70
Side Presented x Age	0.42	1, 14	0.65	0.434	0.04
Contrast x Age	3.27	1, 14	3.23	0.094	0.19
SOA x Age	6.77	8, 112	9.13	< 0.001*	0.40
Side Presented x Contrast	0.04	1, 14	0.11	0.741	0.01
Side Presented x Contrast x Age	0.01	1, 14	0.03	0.865	0.00
Side Presented x SOA	0.23	8, 112	0.62	0.757	0.04
Side Presented x SOA x Age	0.31	8, 112	0.84	0.573	0.06
Contrast x SOA	0.50	4, 62	0.63	0.660	0.04
Contrast x SOA x Age	0.30	8, 112	0.68	0.708	0.05
Side Presented x Contrast x SOA	0.17	8, 112	0.40	0.920	0.03
Side Presented x Contrast x SOA x Age	0.37	8, 112	0.87	0.542	0.06

Table C.1b: Means and standard deviation for the baseline condition from experiment 4

Factor	Level	Mean	Std. Error
Age	Young	1.30	0.21
Age	Older	0.66	0.21
Side	Left	0.96	0.15
presented	Right	0.99	0.15
Contrast	3x	0.86	0.14
Contrast	5x	1.09	0.17
	11ms	0.14	0.09
	22ms	0.31	0.09
	33ms	0.64	0.17
	44ms	0.81	0.17
SOA	55ms	0.71	0.17
	66ms	1.17	0.24
	77ms	1.37	0.19
	88ms	1.72	0.25
	99ms	1.94	0.15

Table C.1c: Two-way ANOVA for interaction of age x SOA.

SOA	Age	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	Young	0.20	0.09	1, 14	0.05	0.36	0.561	0.16
11113	Older	0.09	0.16	1, 17	0.05	0.50	0.501	0.10
22ms	Young	0.45	0.12	1, 14	0.31	2.46	0.139	0.39
221113	Older	0.17	0.13	1, 14	0.51	2.40	0.139	0.39
33ms	Young	0.47	0.26	1, 14	0.51	1.05	0.324	0.26
331113	Older	0.82	0.23	1, 14	0.31	1.05	0.324	0.20
44ms	Young	1.16	0.29	1, 11	1.99	4.47	0.058	0.49
441115	Older	0.46	0.17	1, 11	1.99	7.7/	0.030	0.43
55ms	Young	0.86	0.28	1, 14	0.40	0.91	0.357	0.25
331115	Older	0.55	0.18	1, 14	0.40	0.51	0.557	0.23
66ms	Young	1.41	0.42	1, 14	0.96	1.03	0.326	0.26
Ooms	Older	0.92	0.24	1, 14	0.30	1.03	0.320	0.20
77ms	Young	1.90	0.32	1, 14	4.58	7.63	0.015*	0.59
771113	Older	0.83	0.22	1, 14	4.50	7.05	0.015	0.53
88ms	Young	2.46	0.45	1, 11	8.70	8.53	0.015*	0.62
001113	Older	0.98	0.23		0.70	0.33	0.013	0.02
99ms	Young	2.75	0.25	1, 14	10.52	28.14	< 0.001*	0.82
221113	Older	1.13	0.18	1, 14	10.52	20.14	\ 0.001	0.02

C.2: Two-way ANOVA from cross-modal condition in experiment 4. Interaction of age x cue-type.

Two-way ANOVA for interaction of age x cue type

Cue	Age	Mean	Std. Error	DF	Mean Square	F	р	r
Neutral	Young	1.30	0.24	1, 14	1.61	4.71	0.048*	0.50
Neutrai	Older	0.66	0.17	1, 14	1.01	, ±	0.040	0.50
Congruent	Young	1.77	0.19	1, 14	0.25	1.18	0.295	0.28
Congruent	Older	1.52	0.13	1, 14		1.10		0.20
Incongruent	Young	0.30	0.25	1, 14	11.96	19.39	0.001*	0.76
incongruent	Older	-1.43	0.30	1, 14	11.50	15.55	0.001	0.70

C.3: Two-way ANOVA from cross-modal condition in experiment 4. Interaction of age x SOA.

Two-way ANOVA for interaction of Age x SOA

SOA	Age	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	Young	0.19	0.06	1, 14	0.58	14.46	0.002*	0.71
111113	Older	-0.19	0.08	1, 14	0.56	14.40	0.002	0.71
22ms	Young	0.50	0.07	1, 14	1.21	24.00	< 0.001*	0.79
221115	Older	-0.05	0.09	1, 14	1.21	24.00	< 0.001	0.79
33ms	Young	0.48	0.16	1 11	0.24	1.35	0.264	0.30
331118	Older	0.24	0.13	1, 14	0.24	1.55	0.204	0.50
44ms	Young	0.97	0.18	1, 14	2.53	15.30	0.002*	0.72
441115	Older	0.18	0.10	1, 14	2.55	15.50	0.002	0.72
55ms	Young	0.87	0.21	1, 8	1.20	5.92	0.039*	0.55
331115	Older	0.32	0.07	1, 0	1.20	3.32	0.033	0.55
66ms	Young	1.26	0.25	1, 14	1.94	6.38	0.024*	0.56
OOMS	Older	0.57	0.12	1, 14	1.54	0.36	0.024	0.30
77ms	Young	1.76	0.24	1, 10	5.22	18.96	0.002*	0.76
771115	Older	0.61	0.11	1, 10	3.22	10.50	0.002	0.70
88ms	Young	2.13	0.26	1, 9	8.71	27.88	0.001*	0.82
001115	Older	0.66	0.10	1, J	0.71	27.00	0.001	0.02
99ms	Young	2.32	0.22	1, 9	8.76	37.04	< 0.001*	0.85
331113	Older	0.84	0.09	1, 3	0.70	37.04	V 0.001	0.65

C.4: Further analysis from cross-modal condition in experiment 4. Interaction of age x contrast x SOA.

Two-way ANOVA for interaction of contrast x SOA: Young adults

SOA	Contrast	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	3x	0.15	0.06	1, 14	0.03	0.35	0.564	0.16
111113	5x	0.23	0.13	1, 14	0.05	0.55	0.504	0.10
22ms	3x	0.37	0.09	1, 14	0.26	4.49	0.052	0.49
221115	5x	0.62	0.08	1, 14	0.20	4.43	0.032	0.43
33ms	3x	0.35	0.18	1, 14	0.27	0.97	0.340	0.25
331115	5x	0.61	0.19	1, 14	0.27	0.57	0.340	0.23
44ms	3x	0.92	0.19	1, 14	0.03	0.11	0.742	0.09
441115	5x	1.02	0.20	1, 14	0.03	0.11	0.742	0.03
55ms	3x	0.75	0.22	1, 14	0.21	0.55	0.470	0.19
331118	5x	0.98	0.22	1, 14	0.21	0.55	0.470	0.19
66ms	3x	1.03	0.21	1, 14	0.87	1.60	0.226	0.32
Ooms	5x	1.50	0.30	1, 14	0.87	1.00	0.220	0.32
77ms	3x	1.50	0.18	1, 14	1.06	1.97	0.182	0.35
771115	5x	2.02	0.32	1, 14	1.00	1.57	0.102	0.55
88ms	3x	1.79	0.22	1, 14	1.89	3.07	0.102	0.42
001115	5x	2.48	0.32	1, 14	1.05	3.07	0.102	0.42
99ms	3x	1.98	0.19	1 1/1	1.91	3.37	0.088	0.44
331118	5x	2.67	0.32	1, 14	1.91	3.37	0.000	0.44

Two-way ANOVA for interaction of contrast x SOA: Older adults

SOA	Contrast	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	3x	-0.29	0.10	1, 14	0.15	1.20	0.292	0.28
111113	5x	-0.09	0.14	1, 14	0.15	1.20	0.232	0.28
22ms	3x	-0.29	0.13	1, 14	0.86	10.10	0.007*	0.65
221115	5x	0.18	0.07	1, 14	0.80	10.10	0.007	0.03
33ms	3x	0.12	0.17	1, 14	0.22	1.06	0.320	0.27
331113	5x	0.35	0.15	1, 14	0.22	1.00	0.320	0.27
44ms	3x	0.17	0.10	1, 14	0.00	0.01	0.915	0.03
441115	5x	0.18	0.11	1, 14	0.00	0.01	0.913	0.03
55ms	3x	0.26	0.09	1, 14	0.05	0.77	0.394	0.23
551115	5x	0.37	0.09	1, 14	0.03	0.77	0.354	0.23
66ms	3x	0.51	0.15	1, 14	0.05	0.31	0.585	0.15
Ooms	5x	0.62	0.13	1, 14	0.03	0.51	0.363	0.13
77ms	3x	0.54	0.16	1, 14	0.08	0.59	0.454	0.20
771115	5x	0.69	0.11	1, 14	0.08	0.39	0.434	0.20
88ms	3x	0.59	0.17	1, 9	0.08	0.61	0.455	0.20
001115	5x	0.73	0.07	1, 3	0.06	0.01	0.433	0.20
99ms	3x	0.79	0.12	1 1/	0.05	0.51	0.487	0.19
331115	5x	0.90	0.11	1, 14	0.05	0.51	0.487	0.19

C.5: Further analysis from the change scores ANOVA in experiment 4. Interaction of age x cue-type.

Two-way ANOVA for the interaction of age x cue-type from the change scores analysis

Cue	Age	Mean	Std. Error	DF	Mean Square	F	р	r
Congruent	Young	0.47	0.35	1, 14	0.59	0.90	0.358	0.25
	Older	0.86	0.21	1, 14	0.55	0.50	0.556	0.23
Incongruent	Young	-0.99	0.20	1, 14	4.79	5.60	0.033	0.53
	Older	-2.09	0.42	1, 14	4.73	3.00	0.033	0.33

C.6: Further analysis from the change scores ANOVA in experiment 4. Interaction of age x SOA.

Two-way ANOVA for the interaction of age x SOA from the change scores analysis

SOA	Age	Mean	Std. Error	DF	Mean Square	F	р	r
11ms	Young	-0.01	0.09	1, 14	1.16	4.70	0.048	0.50
	Older	-0.55	0.23	_,			0.0.0	
22ms	Young	0.10	0.14	1, 14	1.18	5.59	0.033	0.53
ZZIII3	Older	-0.45	0.18	1, 17	1.10	3.	0.055	0.55
33ms	Young	0.03	0.27	1, 14	5.82	8.51	0.011	0.61
331113	Older	-1.17	0.32	1, 14	3.02	6.51	0.011	0.01
44ms	Young	-0.38	0.27	1, 14	0.13	0.27	0.610	0.14
441113	Older	-0.56	0.21	1, 14	0.13	0.27	0.010	0.14
55ms	Young	0.01	0.25	1, 14	0.86	1.39	0.258	0.30
331113	Older	-0.46	0.30	1, 14	0.00	1.55	0.230	0.50
66ms	Young	-0.30	0.38	1, 14	0.68	0.67	0.428	0.21
Ooms	Older	-0.71	0.33	1, 14	0.00	0.07	0.420	0.21
77ms	Young	-0.29	0.41	1, 14	0.08	0.09	0.774	0.08
771113	Older	-0.44	0.28	1, 14	0.08	0.03	0.774	0.08
88ms	Young	-0.65	0.45	1, 14	0.00	0.00	0.999	0.00
OOIIIS	Older	-0.65	0.33	1, 14	0.00	0.00	0.333	0.00
99ms	Young	-0.85	0.31	1, 14	0.33	0.37	0.554	0.16
331115	Older	-0.56	0.36	1, 14	0.33	0.37	0.554	0.10

C.7: Further analysis from the change scores ANOVA in experiment 4. Interaction of age x cue-type: 44ms and above.

Two-way ANOVA for the interaction of age x cue-type from the change scores analysis: 44ms and above.

Cue	Age	Mean	Std. Error	DF	Mean Square	F	р	r
Congruent	Young	0.32	0.40	1, 14	1.51	1.84	0.197	0.34
	Older	0.93	0.22	1, 17	1.51	1.0	0.137	0.54
Incongruent	Young	-1.14	0.25	1, 14	3.37	3.36	0.088	0.44
incongruent	Older	-2.05	0.44	1, 14	3.37	5.50	0.000	0.44

Appendix D

D.1: Further analysis for experiment 5. Interaction of distracter location x attention task.

Two-way ANOVA for attention task x distracter location (central versus peripheral distracters)

Attention task	Distracter location	Mean	Std. Error	DF	Mean Square	F	р	r
Focused	Peripheral	-0.25	0.24	1, 14	0.09	0.22	0.643	0.13
	Central	-0.09	0.21					
Divided	Peripheral	1.44	0.24	1, 14	9.14	7.98	0.013	0.60
	Central	2.95	0.48					