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THE UNIVERSITY OF QUEENSLAND  
AUSTRALIA

**The Emotional Ageing Brain: Cognitive Mechanisms and Neural Networks**

Maryam Ziaei

BA, MSc.

*A thesis submitted for the degree of Doctor of Philosophy at*

*The University of Queensland in 2016*

School of Psychology

## **Abstract**

Despite well-documented declines in most cognitive domains, some emotional processes appear to be preserved or even enhanced in late adulthood. A good example of this is the information processing bias older adults show towards positive relative to negative emotional stimuli, often referred to as the age-related positivity effect. The present thesis presents a series of experiments that were designed to better understand the mechanisms that contribute to age-related changes in emotional processing, focusing in particular on the role of cognitive mechanisms and neural networks.

In **Study 1** aimed to identify the underlying cognitive mechanisms of the positivity effect. The primary focus of this study was to explore the role of distractors during the early attention allocation stage, and to also measure how selective attentional processes during encoding influence later memory outcomes for emotional items. The results showed that consistent with prior literature, a memory positivity effect was found among older relative to younger adults. However, of particular interest was the finding that, participants' memory for negative targets was not influenced by the presence of positive distractors. This finding suggests that positive distractors did not automatically capture older adults' attention during encoding for negative items. Importantly, we found that participants' pupillary responses to negative items mediated the relationship between age and the memory positivity effect, indicating that older adults use their cognitive control resources when encoding negative information, perhaps to down regulate the impact of negative emotions on their memory. Collectively, these two findings provide converging support for the cognitive control account of the positivity effect.

**Study 2** used a similar paradigm to Study 1 to examine the underlying neural networks involved in processing emotional items during working memory encoding among older and younger adults. Results indicated that a cognitive control network that included fronto-parietal regions, was functionally connected to the left ventrolateral prefrontal cortex during the encoding of negative items among older adults. This network contributed to performance, both accuracy and response times, in older adults' group. A less distributed network was found for encoding of positive items among older and both items among younger adults. Although older adults recruited a same network that was functionally connected to the amygdala for encoding positive and negative items, younger adults recruited this particular network specifically for encoding negative items. This network facilitated older adults' higher accuracy and faster response times during retrieval.

Taken together, the results from these functional connectivity analyses suggest that there is differential engagement of brain networks connected to these two regions, which are modulated by the emotional valence. While two separate brain networks underlying the encoding of emotionally valence targets are connected to the vIPFC region, one distinct network is functionally connected to the amygdala and subserves the processing of both positive and negative targets.

In **Study 3** age-related differences in neural substrates involved when processing happy and angry expressions presented with direct versus averted gaze were investigated. This research was motivated by studies that show older adults not only have difficulties processing emotional cues such as facial expression and eye gaze cues, but also have problems integrating these cues. Study 3 provides the first empirical examination of the underlying neural correlates of age-related difficulties in integrating communicative cues. The results showed that for angry facial expressions, younger adults recruited distinct networks while processing direct versus averted eye-gaze cues, however, older adults showed a lack of neural sensitivity to these cues, recruiting a single network for both types of stimuli. In contrast, for happy facial expressions, only older adults showed neural sensitivity to eye gaze cues. Participants' performance on the scanner task was then correlated with a measure of theory of mind (TOM). Younger (but not older) adults' performance on a measure of TOM and recognition of angry expressions was differentially correlated with activation in two sets of brain regions as a function of eye gaze. Unlike younger adults, older adults' performance on TOM was also differentially correlated with the key node of mentalizing brain network during happy expressions as a function of eye gaze. The findings from Study 3 suggest that the age-related difficulties in integrating facial cues could be associated with the recruitment of the mentalizing network when the task imposes high demand on social-cognitive processing.

Taken together, the three Studies reported in this thesis provide novel insights into our understanding of age-related differences in the processing of emotionally valenced items, particularly with respect to initial encoding of this information, and how this relates to later memory outcomes. Moreover, for the first time the neural correlates of integrating two important types of facial cue has been identified, and potentially linked to broader social cognitive difficulties. Overall, the findings of this thesis have broad implications for understanding the underlying cognitive mechanisms and neural networks that contribute to age-related differences in the processing of emotional stimuli.

### **Declaration by author**

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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## **Publications during candidature**

### **Published papers**

Peira, N., Ziaei, M., Persson, J. (2015), Age differences in brain systems supporting transient and sustained processes involved in prospective memory and working memory. *NeuroImage*, 125, 745-755.

Ziaei, M., von Hippel, W., Henry, J.D., Becker, S.I. (2015), Are age effects in positivity influenced by the valence of distractors? *PLOS one*, 10(9): e0137604.

Burianová, H., Marstaller, L., Choupan, J., Seppehrband, F., Ziaei, M. & Reutens, D. (2015), The impact of ageing on the brain's structural integrity and task-related functional connectivity, *Neurobiology of aging*, 36(10), 2830–2837.

Ziaei, M., Peira, N. & Persson, J. (2014), Brain systems underlying attentional control and emotional distraction during working memory encoding, *NeuroImage*, 87, 276-286.

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Ziaei, M., von Hippel, W., Henry, J.D., Ebner, N.C., Burianová, H. A multivariate analysis of brain networks involved in facial gaze and emotion processing, **Australasian Social Neuroscience Society 2015**, Brisbane, Australia

Ziaei, M., Peira, N., Persson, J. Age-differences in brain correlates of attentional control of emotional items during working memory encoding, **12<sup>th</sup> International Cognitive Neuroscience Conference 2014**, Brisbane, Australia

Ziaei, M., Peira, N., Persson, J. Attentional modulation in response to emotional stimuli among older and younger adults, **Cognitive Neuroscience Society Annual Meeting 2014**, Boston, USA

Ziaei, M., Peira, N., Persson, J. The underlying neural mechanism in attentional control during encoding of emotional stimuli, **4th Australasian Cognitive Neuroscience Conference 2013**, Melbourne, Australia

Ziaei, M., Elands, R.J., Peira, N., Persson, J. Fusiform & Inferior Frontal Gyrus activation in attentional top-down modulation to emotional stimuli, **18th Annual Meeting of the Organization for Human Brain Mapping 2012**, Beijing, China

### **Publications included in this thesis**

This thesis contains three empirical chapters (Chapters 2, 3 and 4) that contain studies that have been published (Chapter 2). These studies are contextualized with a general introduction that has been published as a chapter book (Chapter 1), and a general discussion (Chapter 5). Below I list the contribution of authors to all of the published chapters.

### **Incorporated as Chapter 1**

**Ziaei, M.** & Fischer, H. (2016), Emotion and Aging: The impact of emotion on attention, memory, and face recognition in late adulthood. In J. R. Absher & J. Cloutier (Eds.), *Neuroimaging Personality, Social Cognition, and Character*.

Contributor	Statement of contribution
Maryam Ziaei (Candidate)	Wrote and edited the chapter (70%)
Håkan Fischer	Wrote and edited the chapter (30%)

## Incorporated as Chapter 2

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Contributor	Statement of contribution
Maryam Ziaei (Candidate)	Conceptualised & designed experiment (60%) Data collection (100%) Data analysis and interpretation (50%) Wrote and edited the paper (55%)
Bill von Hippel	Conceptualised & designed experiment (20%) Data analysis and interpretation (30%) Wrote and edited the paper (30%)
Julie D. Henry	Conceptualised & designed experiment (20%) Data analysis and interpretation (20%) Wrote and edited the paper (10%)
Stefanie I. Becker	Data preparation Wrote and edited the paper (5%)



### **Contributions by others to the thesis**

My supervisors, Julie D. Henry, Bill von Hippel, Jonas Persson, and Hana Burianová contributed to the conceptualisation, study design, interpretation of findings, and reviewed and commented on the thesis as a whole. Håkan Fischer, Alireza Salami, Natalie C. Ebner, and Louise H. Phillips also commented on the manuscripts included in this thesis. Caitlin B. Hawley helped in editing the book chapter incorporated as General Introduction of this thesis. Rebecca Laws and Reza Bonyadi also assisted in editing the General Discussion chapter. Aiman Al Najjar and Anne-Louise Bint assisted with the fMRI data collection of Study 3. Nathalie Peira helped in programming the task used in Study 2. Stefanie Becker assisted to set up the experiment in Study 1.

### **Statement of parts of the thesis submitted to qualify for the award of another degree**

None

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## **List of Abbreviations Used in Thesis**

ABC: Arousal-based competition

ABM: Ageing brain model

ACC: Anterior cingulate

ALE: Activation likelihood estimate

BOLD: Blood-oxygen-level dependent

CI: Confidence interval

CRUNCH: Compensation-related utilization of neural circuits hypothesis

DASS: Depression anxiety stress scales

DERG: Difficulties in emotion regulation questionnaire

dIPFC: Dorsolateral prefrontal cortex

DMN: Default-node network

EEG: Electroencephalography

EMG: Electromyography

EPI: Echo-planar image

ERP: Event-related potential

FA: False alarms

FACS: Facial action coding system

FADE: Fronto-amygdala differences in emotion

FG: Fusiform gyrus

fMRI: Functional magnetic resonance imaging

FOV: Field of view

GLM: General linear model

HAROLD: Hemispheric asymmetry reduction in older adults

IFG: Inferior frontal gyrus

IFG: Inferior occipital gyrus

LV: latent variable

MMSE: Mini mental state exam

MNI: Montreal neurological institute

mPFC: Medial prefrontal cortex

MSIT: Multi-source interference task

PASA: Posterior-anterior shift in ageing

PE: Positivity effect

PFC: Prefrontal cortex

PLS: Partial least squares

ROI: Region of interest

RT: Reaction times

SEM: Standard error of the mean

sMRI: Structural magnetic resonance imaging

SPL: Superior parietal lobule

SPM: Statistical parametric mapping software

SST: Socioemotional selectivity theory

STAC: Scaffolding theory of ageing and cognition

STS: Superior temporal sulcus

SVD: Singular value decomposition

TE: Echo time

TR: Repetition time

VBM: Voxel-based morphometry

vlPFC: Ventrolateral PFC

vmPFC: Ventromedial prefrontal cortex

WM: Working memory

# **Chapter 1**

## **General Introduction**

## **Introduction**

It has been estimated that by 2040, 1.5 billion people will be aged 65 or older, representing 16 per cent of the world's population (Suzman and Beard, 2011). Hence, gaining a more complete understanding of the psychological changes that occur with normal adult ageing could provide valuable insights into long-term planning for health, work policies, and opportunities for engaging and collaborating with older adults. Although ageing is associated with cognitive deficits, and these are associated with some functional costs, this does not provide a complete picture of the psychological changes that occur with ageing. In particular, increasing evidence from the emotional ageing literature offers a different perspective on how we age. Recent discoveries in functional neuroimaging also provide important insights into how the brain functions during various cognitive and emotional tasks as we age, granting a more comprehensive view of the ageing brain.

The primary focus of this chapter is to provide an overview of multidisciplinary evidence from both behavioural and neuroimaging studies in the emotional ageing literature. The chapter is organized based on the impact of age-related changes in emotional processing on three main categories of cognitive function: *attention*, *memory*, and *face recognition*. Before discussing the main findings from each of these three categories, I present some of the major discoveries and dominant models in the cognitive ageing domain briefly.

Throughout this chapter, I outline several questions in the field such as: Do older adults' positivity bias require cognitive control or it is automatic? How are attention and memory biases in processing emotional items linked? What are the underlying cognitive and neural mechanisms of the attentional biases toward positive items in ageing? What are the underlying mechanisms that contribute to the age-related difficulties in processing facial cues? How are the difficulties in decoding facial cues linked to social-cognitive performances in ageing? In the following chapters (Chapters 2-4), I present empirical investigations employing a range of behavioural, eye-tracking, and neurological approaches to address these questions.

## **Cognitive Ageing**

Emotional and cognitive functions are interrelated and overlooking either of these two critical aspects of ageing leaves us with an incomplete picture of ageing. Although the fine details of the cognitive ageing literature are beyond the scope of this chapter, I briefly acknowledge and discuss



the central existing theories of cognitive aspects of ageing, before discussing the emotion and ageing studies. Although most of these theories have not been applied to the emotional aging literature to date, it is important to gain a better understanding on the details of these theories so that they can potentially later be adapted to help explain emotional aging.

A substantial body of evidence now shows cognitive deficits among older adults in relation to speed of processing, memory, and attention (for a review see Grady (2008); Reuter-Lorenz and Park (2010)). Multiple cognitive ageing theories have been proposed and provide a foundation for understanding the underlying mechanisms associated with cognitive deficits as we age. Below I briefly present four particularly influential discoveries -- overactivation, dedifferentiation, frontal compensation, and Default Mode Network -- and then describe some of the dominant theories in this domain that have been proposed to explain such findings.

### **Major Discoveries about the Ageing Brain**

*Overactivation:* Older adults activate some areas of the brain to a greater extent than younger adults during performing cognitive tasks. These patterns of activity have been thought of as the neural correlates of cognitive decline (Reuter-Lorenz and Park, 2010). However, overactivation has been observed in high performing older individuals (Bergerbest et al., 2009; Cabeza et al., 2002). Therefore, overactivation could also reflect the compensatory mechanisms utilized by “successful” older adults who have greater cognitive ability and might recruit different neural networks relative to younger adults. However, it is still unclear whether older adults are using these additional brain regions to implement different strategies, or whether they are using the same cognitive strategies as young adults, but relying on different brain areas. In other words, overactivation might have a function, or it might be a by-product of ageing influencing the brain. The former view has been supported by the compensatory viewpoint, which suggests that the increased bilateral recruitment of both hemispheres among older adults is associated with enhanced cognitive performance and has a compensatory role (Grady, 2012).

The hemispheric asymmetry reduction in older adults (HAROLD)(Cabeza, 2002) model is consistent with the second interpretation of overactivation as a by-product of ageing. Evidence from episodic memory, semantic retrieval, working memory, perception, and inhibitory control provide converging evidence that older adults show increased activity in both hemispheres relative to younger adults, indicating that the overactivation can be considered a by-product of ageing.

*Dedifferentiation:* Dedifferentiation refers to reduced regional specialization or specificity in a particular area (Li et al., 2001). Over-activity of the prefrontal regions and dedifferentiation of the ventral visual system are typically construed as being consistent with a compensatory mechanism.

*Frontal compensation:* Over-recruitment of prefrontal regions in a wide range of tasks is often seen in studies of older adults. Importantly, this over-recruitment of alternative brain networks appears to be related to improvement in cognitive performances (Grady, 2012). Recruiting more anterior prefrontal cortex (PFC) regions is accompanied by deactivation of posterior regions such as the medial temporal lobe and ventral visual cortex. This pattern also relates to the posterior-anterior shift in ageing (PASA), which has been thought to reflect compensatory mechanisms with advancing age (Davis et al., 2008).

*Default mode network (DMN):* This network includes the medial PFC, posterior cingulate, and medial and lateral parietal regions, and seems to be involved “during mental explorations referenced to oneself including remembering, considering hypothetical social interactions, and thinking about one’s own future”(Buckner et al., 2008). In healthy young adults, the DMN is deactivated with increasing task demands. Several studies, however, reported that older adults failed to “deactivate” DMN during many cognitive tasks (Persson et al., 2007; Sambataro et al., 2010). One reason for such a pattern might be that older adults have a reduced ability to suspend DMN activity when other cognitive tasks require their attention (Persson et al., 2007). Results from longitudinal studies also indicate the task-induced deactivation in DMN remains stable over time among older adults (Persson et al., 2014).

## **Theories in Cognitive Ageing**

Three influential models, including the *inhibitory deficit hypothesis*, the *Compensation-Related Utilization of Neural Circuits Hypothesis* (CRUNCH), and the *Scaffolding Theory of Ageing and Cognition* (STAC model) have been proposed to explain the underlying mechanisms of the cognitive deficit that accompanies ageing. Although most of these theories have not been applied to the emotional aging literature to date, it is important to gain a better understanding on the details of these theories so that they can potentially later be adapted to help explain emotional aging.

One of the dominant hypotheses is the *inhibitory deficit hypothesis*, which could explain a wide range of age-related cognitive difficulties in working memory (Gazzaley et al., 2008; Gazzaley et al., 2005b), decision making, and social functioning (Henry et al., 2009b; Von Hippel and Dunlop, 2005b). Consistent with the notion that reduced inhibitory control underlies many age-related losses (Hasher and Zacks, 1988), this hypothesis focuses on the effect of inhibitory control on working memory by suppressing irrelevant information. A number of studies have also shown that specific deficits in inhibitory control can lead to working memory impairment in ageing. It has also been shown that age-related deficits in inhibitory control over distractors disrupt working memory performance (Gazzaley et al., 2005a; Gazzaley et al., 2005b). Recently, a top-down modulation model in ageing has been proposed (Gazzaley, 2012). According to this model, the “[t]op-down modulation defined as the modulation of neural activity in neurons of sensory or motor areas based on an individual’s goals, involves the enhancement of task-relevant representations and/or suppression for task-irrelevant representations” (Zanto and Gazzaley, 2014). Two forms of top-down modulations have been examined: external (e.g., environmental stimuli) and internal (e.g., goals). Several studies have suggested that changes in any form of top-down modulations can lead to the working memory deficit observed with ageing (Gazzaley, 2011; Gazzaley and Nobre, 2012).

The *Compensation-Related Utilization of Neural Circuits Hypothesis (CRUNCH)* accounts for age-related changes as a function of task difficulty. According to this hypothesis, older adults are likely to engage more neural circuits than younger adults to meet task demands. When task demands are low, older adults show more overactivation (frontal and bilateral) whereas younger adults show more focal activation. As task load increases, younger adults may show more bilateral recruitment or overactivation of the anterior regions. However, because of the restricted dynamic range of neural responses among older adults, they may reach their resources’ limit and may show underactivation and cognitive decline. Thus, neural compensation is more effective when task demands are low. However, by increasing task difficulty, cognitive resources’ limits are reached and decline in performance becomes more apparent (Reuter-Lorenz and Lustig, 2005; Reuter-Lorenz and Park, 2010).

Despite the changes in brain structure that come with age such as dopamine receptor depletion, white matter/gray matter deteriorations, and decline in capacity for neurogenesis, synaptogenesis, and angiogenesis, all systems remain functional and provide a means for building alternative neural circuitry. These structural challenges are accompanied by functional changes (i.e.,

overactivation, dedifferentiation, compensation, and DMN changes), and recruiting alternative neural circuitry (scaffolds) helps maintain a high level of cognitive functioning – though it might work less efficiently. The *Scaffolding Theory of Ageing and Cognition (STAC model)* describes how the scaffolding process starts during childhood when individuals face different challenges and their brains must adapt. Scaffolding is thus influenced by experiences such as learning new skills, engaging in new challenging activities, and cognitive training, all of which have the potential to enhance the brain’s ability to maintain high level function by creating new scaffolding (Goh and Park, 2009).

## **Emotion and Ageing**

Despite cognitive decline, there are small to moderate gains in some emotional domains, including emotion regulation and biases toward positive emotions in memory and attention – for a review see Reed et al. (2014). A considerable number of empirical studies support the relative preference of positive (over negative) materials in cognitive processing – known as the “positivity effect” (PE) (Carstensen, 2006; Mather and Carstensen, 2005). Despite the converging evidence supporting the positivity effect, the underlying mechanisms for such an effect remain unclear. Several theories such as the Socioemotional Selectivity Theory (SST) (Carstensen et al., 1999), the Ageing Brain Model (ABM) (Cacioppo et al., 2011), and the selective optimization with compensation model (Marsiske et al., 1995) have received considerable attention over the past decades in order to explain the positivity effect.

## **Theories in Emotional Ageing**

### **Socioemotional Selectivity Theory**

Socioemotional Selectivity Theory is the dominant theory in the field of emotional and social ageing (Carstensen et al., 1999). This theory posits that as people grow older and their time starts to be perceived as limited, their motivational orientation begins to change. A limited time perception results in chronic activation of the goals related to emotional meaning and influences motivational preferences, which changes goal hierarchies – that is, goals will be more person-focused (such as seeking emotion and meaning) rather than future oriented (such as gaining new knowledge or establishing new social contacts) (Charles and Carstensen, 2010). Goals, preferences, and cognitive processes change systematically as a subjective sense of remaining time becomes limited

(Carstensen, 2006). In one study testing this model, older and younger adults were asked to imagine that they were moving to the other side of the country. Findings showed that the effect of age disappeared and both groups preferred to spend more time with their familiar social partners. This study and similar studies showed how perceptions of time could influence the way people prioritize their social contacts – (see (Löckenhoff and Carstensen, 2004) for more details).

Well-being is also affected by such a goal shift. People are attuned to the relevance of incoming information to their goals. They experience negative or positive emotions if something obstructs their goals, or if their goals have been attained. Given the limitation of working memory and attention, for instance, it seems to be an adaptive strategy to prioritize features of events that facilitate or obstruct goals (Levine and Edelstein, 2009). As a result of this motivational shift, positive emotions will be prioritized and older adults reallocate their resources to attain positive emotions and reduce negative emotions. In line with this possibility, longitudinal studies have provided evidence of improvement in overall well-being with advancing age (Carstensen et al., 2011). The positivity preference in attention and memory will be discussed in more details in Emotion and Attention in Ageing and Emotional Memory and Ageing sections.

### **Ageing Brain Model**

An assumption underlying social neuroscience is that all humans' social behaviours are implemented biologically. The social neuroscience perspective focuses on fundamental changes in brain functions and how these changes in cognition and decision-making are associated with subjective well-being. The Ageing Brain Model (ABM), as a derivative from social neuroscience, attempts to explain a link between affective processing and age-related changes in brain functions (Cacioppo et al., 2011). For a long time, cognitive and emotional ageing were considered two separate constructs; ABM provides an important connection between these two fields of study.

In order to better understand the ABM, I provide one study as an example and interpret the results from both the SST and ABM perspectives. In a 2004 functional Magnetic Resonance Imaging (fMRI) study, Mather et al. (2004) presented negative, positive, and neutral pictures to older and younger participants, who were then asked to rate how excited or calm they felt when viewing each picture. Enhanced amygdala activation in response to positive (relative to negative) stimuli was found among older adults, whereas for younger participants, amygdala activation to positive and negative stimuli did not significantly differ. According to SST, this result would be

interpreted as the preference of focusing on positive emotional goals and recruiting regulatory strategies among older adults, which led to the reduced cognitive focus on negative stimuli. On the other hand, ABM would interpret the enhanced activity for positive over negative stimuli among older adults as a reduced arousal response to negative items due to attenuated amygdala function.

To further test the ABM, patients with a lesion in the amygdala/medial temporal regions were asked to rate their response toward emotional pictures (Berntson et al., 2007). The results indicated that patients with amygdala lesions rated negative pictures as lower in arousal, whereas the emotion categorization for these pictures remained intact. Thus, according to this model, age-related changes in memory for negative items among older adults could reflect changes in the function of the amygdala. Changes in amygdala function have an impact on how the arousal level of emotions is perceived (especially for negative emotions), and therefore reduce the impact of arousal on the memorability of emotional items. The reduction in arousal level to negative emotions can also be associated with enhanced well-being among older adults. Therefore, both the SST and ABM models predict that amygdala activation will be smaller for negative stimuli than positive stimuli among older adults; however, SST predicts that an increased focus on goals and emotional regulatory strategies may be the underlying mechanism leading to the reduced attention toward negative items among older adults (Carstensen et al., 2003). Alternatively, ABM suggests that “these amygdala changes are the cause of the reduced impact of negative stimuli and, consequently, diminished depressive symptomatology and improved subjective well-being”(Cacioppo et al., 2011). Such changes in amygdala responses could partially explain the age-related positivity effect.

### **Selective Optimization with Compensation Model**

Another proposal to reconcile the emotional and social aspects of ageing is the selective optimization with compensation model (Baltes and Baltes, 1990). According to this model, people become aware of their losses and gains across adulthood, and due to the naturally diminished resources that come with ageing, they select goals that are important or can be realistically obtained in their lifetimes. Therefore, less important goals will be sacrificed at the cost of obtaining other more important goals. If some of the goals cannot be achieved, people will engage in compensatory activities. According to this model, older adults engage in any task that is important for them despite their physical or biological constraints. In each case, there is individualization of selection, optimization, and compensation. To make it more tangible, consider a person who desires to run a marathon. If the runner wants to reach this level of running performance, he should give up other

activities (selection) and should increase or optimize his conditions, such as daily diet (optimization), in order to become an expert in the activity of marathon running. This will then reduce the impact of losses in other activities (compensation). Therefore, the combination of these three elements can contribute to successful ageing, which requires adaptation and concentration on domains that are high priority for older adults (Charles and Carstensen, 2010; Marsiske et al., 1995).

*Summary:* Taken together, various models and hypotheses have been developed in order to explain the underlying mechanisms of age-related changes in emotional processing, including the Socioemotional Selectivity Theory, The Ageing Brain Model, and selective optimization with compensation model. Emotions can influence various cognitive functions, such as attention, memory, and face recognition. Hence, in the following sections I will discuss the existing literature on the impact of emotion on three critical domains – attention, memory, and face recognition – in regard to the changes that occur in each of these domains with advancing age. In each section, relevant behavioural and neurological findings will be discussed.

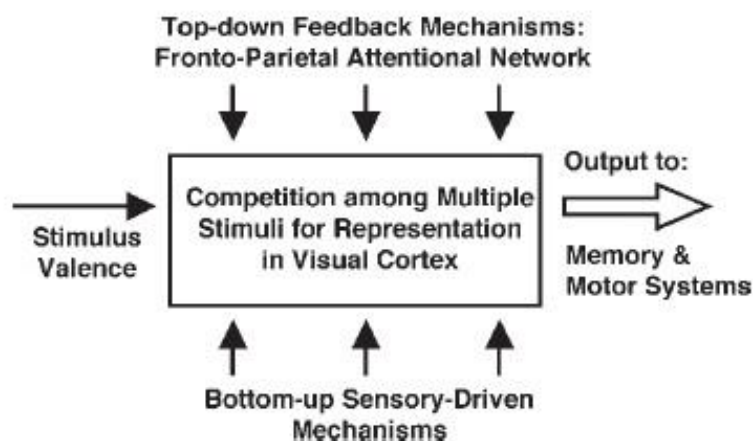
## **Emotion and Attention in Ageing**

In order to better understand how emotions have an impact on attentional processes in advancing age, it is crucial to first understand how emotion and attention interact. Interest in this area of research is rapidly growing empirically, but it is still in its infancy theoretically. Theories of selective attention have been borrowed and adapted to explain the processing of emotional materials by considering these stimuli as highly salient information. Therefore, these theories indicate that highly salient information, such as emotions, are often prioritized for attentional processing.

The feature integration theory of visual attention (Treisman and Gelade, 1980), for instance, describes how certain perceptual characteristics such as orientation or colour can be processed automatically prior to any attentional selection. “Attention is conceived as the process by which representations of more complex stimuli are formed through the combination of individual features (‘conjunctions of features’)”(Treisman and Gelade, 1980). In visual search paradigms, participants are presented with an array of stimuli and asked to identify or locate the different items as quickly as possible. Using this paradigm, the question of whether emotional information is a feature that acts as a “pop out” effect, or whether emotional information instead requires complex processing in order to evaluate its emotional significance and capture attention, has been investigated extensively.

Empirical studies support the former account that emotional information is a highly salient conjunction of features and pops out from the rest of the visual environment. For similar models pertinent to this theory, see Wolfe (1994).

Another influential theory in selective attention is the “biased competition model” (Desimone and Duncan, 1995). The central tenet of this model is that limited capacity in our information processing systems leads to competition for attention between represented information. Emotions can enhance perceptual processing due to their greater perceptual distinctiveness, leading to bottom-up prioritization of emotional stimuli. Moreover, top-down factors (such as past experience or environmental context) can similarly influence the competitive bias to enhance the prioritization of one stimulus over the rest. The main implication is that selective attention occurs when stimuli presentation allows for direct competition between stimuli (Figure 1).

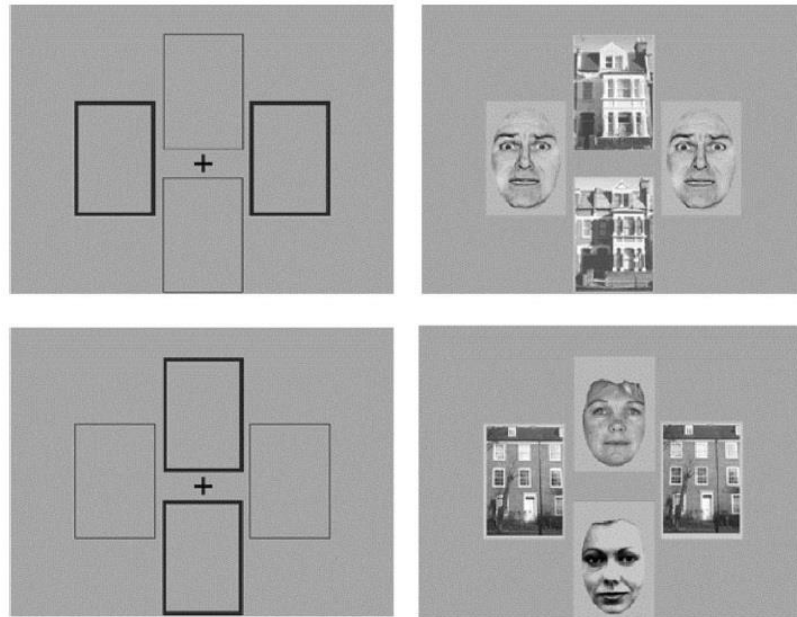


**Figure 1. Biased competition model.** The relation between visual attention and process of emotional information (Pessoa and Ungerleider, 2004)

In order to understand the interaction of emotion and attention at the neural level, researchers have looked at how particular brain regions such as the amygdala process emotional information when attentional resources are available and when they are limited. Previous brain imaging studies have reported mixed findings regarding the engagement of the amygdala under attention control conditions. While some studies found amygdala activation in response to threatening stimuli without engaging attentional resources, others have found that amygdala responses may be modulated by selective attention (Pessoa, 2008; Vuilleumier, 2005). In a study by Vuilleumier et al. (2001), emotion and attention were independently manipulated in a paradigm where participants were



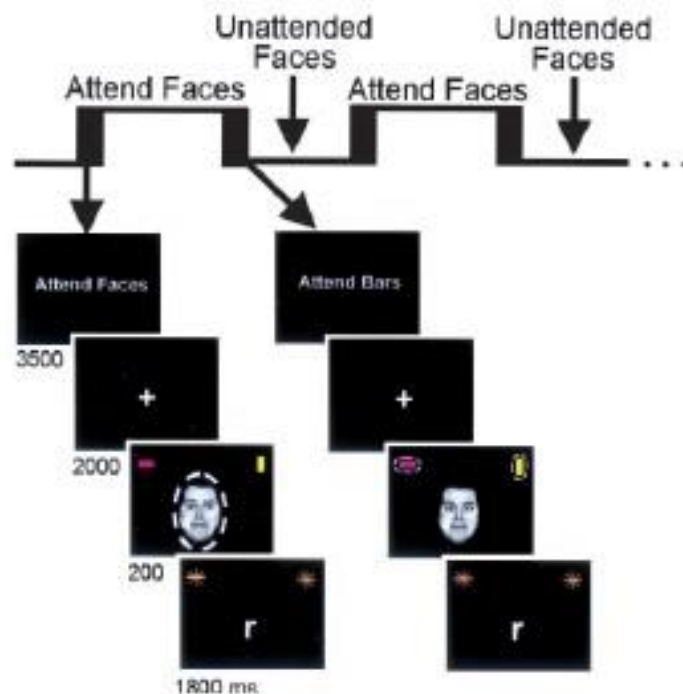
instructed to complete a matching task. Participants were presented with two faces and two houses arranged in horizontal or vertical pairs and asked to match two faces in either the horizontal pairs (upper picture) or on the vertical pairs (lower picture). The faces were sometimes emotional (fearful) and sometimes neutral in expressions (Figure 2). Findings showed that while activation of the fusiform face area (a primary region involved in face processing) was modulated by spatial attention manipulation, the amygdala showed consistent responses to the emotional expression of the faces, irrespective of the attentional manipulation.



**Figure 2. Example of experimental design presented by Vuilleumier et al. 2001**

Studies such as Vuilleumier et al. (2001) suggest that processing of facial expressions can occur automatically and support the possibility that the amygdala detects emotionally relevant stimuli quickly even without conscious awareness. Because the amygdala was unresponsive to the attentional manipulation in this study, it was suggested that emotional processing does not require attentional resources. In order to test this further, Pessoa et al. (2002) examined how emotional responses are modulated by attentional resources. Their design used the same images of faces but with two conditions: an attended face condition and an unattended face condition. In the attended face condition, subjects were required to indicate whether the face was male or female, while in the unattended face condition, subjects indicated whether the bars were of similar orientation (Figure 3). Contrary to previous findings such as Vuilleumier et al. (2001), it was found that when attentional resources were available, all brain regions responded to the emotional faces differently

than the neutral ones. However, when attentional resources were depleted by another task (judging the orientation of the bars), the differential activation in responses to emotional vs. neutral faces was diminished. Unlike the Vuilleumier study which showed no evidence for modulation of activity in the amygdala in response to attentional demand, Pessoa concluded that attention is necessary for the processing of emotional items. It is worth mentioning that Pessoa used a task manipulation that was more effective in depleting attentional resources than the Vuilleumier's study. Recent empirical studies provide evidence to reconcile the debates on the emotion and attention interaction by suggesting that individual differences, level of attentional demand( high vs. low load), as well as the emotional content of the distraction (least and most emotional conditions) are important factors contributing to such interaction (Shafer et al., 2012; Vytal et al., 2012).



**Figure 3. Example of experimental design presented by Pessoa et al. 2002**

In addition to the studies mentioned previously, there is now a considerable empirical literature (for a review see Yiend (2010)) focused on better understanding the relation between emotion and attention using various methods such as filtering (Stroop task, dichotic listening; e.g., Santangelo et al. (2008)), searching (visual search; e.g., Calvo and Nummenmaa (2008)), cueing (dot-probe, spatial cueing; e.g., Koster et al. (2004)), and multiple task paradigms (attentional blink; e.g., Smith et al. (2006)). Using these methods, behavioural studies shed light on some interesting

issues, such as whether attention to emotions during emotional bias occurs with/without awareness or if it requires attentional control, or what is the sufficient intensity level for threatening stimuli to influence our attentional biases. The basic conclusion that can be drawn from these studies is that emotional information, particularly negative information, can elicit prioritization of attentional resource allocation relative to non-emotional information. However, the main challenge facing researchers is to define how the classification of valence occurs and to what extent different types of classification of emotional information may bias attentional systems – for instance, perceptual (perceptual features of the faces such as eye region) vs. semantic (subjective rating) classification. Details of these studies are beyond the scope of this chapter, but for further information see Yiend (2010). Now that I have provided a brief background on how emotional information can influence attentional processes in general, I discuss studies that examined age-related changes in attentional biases toward emotional items.

### **Behavioural Findings on Emotion and Attention**

One of the early pieces of experimental evidence of attentional positivity preference in ageing comes from Mather and Carstensen (2003) using the dot probe task. In their dot probe paradigm, participants were shown a pair of faces: one emotional (either positive or negative) and one neutral. After the faces were removed, a dot appeared in the location of one of the faces. The participants were then required to respond by detecting the dot as quickly as possible. Older adults exhibited faster responses in detecting the dot when it was in the same location as neutral faces, compared to when the dot was presented in the location of negative faces. Based on these findings, it was argued that during the initial attentional phase, older adults were avoiding negative information, and therefore detecting the dots in the location of negative faces took longer than detecting the dots in the location of neutral faces.

Isaacowitz et al. (2006) investigated attentional biases among older adults using the dot probe task in conjunction with an eye-tracking device. Using an eye-tracker in this context has several advantages; first, it enables the researcher to track the gaze of participants, and second, it can provide an indirect measure of participants' attentional biases. The results from Isaacowitz et al.'s study showed that older adults spent more time looking at happy faces than sad and neutral faces, but younger adults spent equal amounts of time looking at both happy and sad faces. Moreover, among older adults, faster reaction times in detecting the dot were found when the dots were positioned with the happy faces. In addition to supporting the attentional bias toward positive items,

these studies suggest that the bias toward positive items occurs at a relatively early stage of attentional processing.

To clarify more precisely how early the positivity bias emerges during attentional processing, Isaacowitz et al. (2009a) examined the time course of the positivity effect and demonstrated that the positivity preference among older adults emerged 500ms following stimuli onset and increased over time. Thus, the question becomes whether we can conclude that positivity bias among older adults requires cognitive resources as it happens at a later stage of attention, or if it occurs without cognitive control resources. According to the cognitive control hypothesis, the positivity effect relies on the availability of cognitive resources (Sakaki et al., 2011), but some studies failed to support this account, suggesting that the positivity effect might not be fully dependent on cognitive control resources (Rosler et al., 2005; Thomas and Hasher, 2006). Thus, it remains unclear whether the positivity effect relies on cognitive control mechanisms or if it is automatic.

In order to investigate the underlying cognitive resource dependency of the positivity effect, some studies have used a dual task paradigm. In such paradigms, participants are asked to perform one task, while their attentional resources are divided and deployed in another secondary task. Knight et al. (2007) asked young and older adults to passively view emotional-emotional and emotional-neutral pairs of faces with angry, happy, and neutral valences while a secondary task was presented (auditory music). Both fixation and proportion of the fixations toward emotional items relative to the neutral items were measured using an eye-tracking device. The results suggested that when attentional resources are limited (divided attention condition or doing the dual task), attention is more likely to be drawn toward negative stimuli. When full cognitive resources were available (full attention condition), older adults exhibited a positivity preference, thus suggesting that the positivity effect requires cognitive resources. Following this study, Allard and Isaacowitz (2008) conducted a similar study using the dual task paradigm but with a within-subjects rather than between-subjects design. The results indicated that regardless of conditions (divided or full attention), older adults showed preference in their fixation for positive and neutral pictures relative to negative pictures. Hence, contrary to Knight's findings (Knight et al., 2007; Mather and Knight, 2005), this study suggests that the positivity effect might not be fully dependent on cognitive resources.

It has been argued that the gaze preference toward positive items in attention reflects the regulatory mechanism that older adults benefit from down-regulating their negative emotions and

moods. In the context of SST, the positivity effect in information processing can help older adults regulate their mood and optimize their affect. In order to test this possibility, several studies have examined gaze preference as a tool when older adults are in a negative mood. In line with hypotheses from SST, older adults demonstrated enhanced gaze preference to positive items when they were in a negative mood (Isaacowitz et al., 2008). This idea has prompted the question of whether the positive gaze preference functions to improve mood over time.

For instance, Isaacowitz et al. (2009b) investigated the link between fixation patterns and mood as a function of age. Older adults who started a task in a positive mood retained their positive mood throughout the experiment. Interestingly, those older adults who resisted decline in their mood over time were those with good executive control ability. They also displayed positive gaze preferences by looking at happy faces and away from angry faces. Therefore, it seems that older adults not only use their positive gaze preferences as a strategy for emotion regulation; they are also capable of using positive gaze preferences to regulate their mood in real time. In support of this finding, Larcom and Isaacowitz (2009) found that older adults were more likely to rapidly regulate their emotions than younger adults. Moreover, older individuals who rapidly regulated their negative mood had lower trait anxiety, neuroticism, and depressive symptoms, and a higher level of optimism, relative to those who did not regulate their negative mood. Thus, it seems that positive gaze preference can function as a regulatory mechanism among older adults, which they use over an extended period of time.

There is also the possibility that the positive gaze preference among older adults reflects their motivation or desire to change their bad mood, and consequently requires a substantial level of cognitive control. Therefore, a number of studies questioned whether full cognitive effort is required to display positive emotional preference among older adults. If positive gaze preference is a regulatory mechanism, then it might require cognitive resources to operate. Allard et al. (2010) conducted an experiment to test whether gaze is used among older adults as a regulatory strategy in the absence of explicit instruction. They investigated this effect by using mood induction (happy, negative, and neutral) in addition to recording pupillary responses while participants were viewing emotional pictures. Their results suggested that lower cognitive effort (as reflected in pupillary response) was expended when older adults were engaged in positive gaze preferences while experiencing a negative mood. Their findings suggest that gaze acts as an effortless regulatory tool used by older adults in order to display positivity preference while experiencing a negative mood.

*Summary:* There are still debates about how emotion influences attentional control and whether processing emotional information requires full attentional resources. In ageing, it seems that older adults' attentional bias toward positive emotions is perhaps an adaptive strategy to regulate their negative moods or emotions, which is consistent with the motivational account of the positivity effect (e.g., SST). The cognitive mechanisms underlying such an effect are still an open question, though. It is unclear whether the attentional bias toward positive items is effortless or requires cognitive control resources. Thus, in **Study 1** presented in Chapter 2, I present a behavioural study in which I employed an eye-tracker to investigate whether the positivity bias among older adults is automatic or requires cognitive control. Although there are discrepancies in what feature differentiate automatic or controlled processes, I refer to automaticity in this study in terms of the fast and rapid processes whereas controlled processes are operationalized as slow processes which require more cognitive effort.

### **Neurological Findings on Emotion and Attention**

Neuroimaging studies have also attempted to address similar questions. Although a number of studies have investigated the role of various brain regions such as the hypothalamus, amygdala, and prefrontal regions during emotional processes, it has been shown that these regions do not work in isolation, but instead form a highly connected network (Pessoa, 2008; Pessoa, 2010). The role of regions such as the hypothalamus, thalamus, basal ganglia, cingulate cortex, anterior insula, orbitofrontal cortex, and cerebellum in processing emotional items has been documented in a number of studies (Lindquist et al., 2012; Wager et al., 2015). However, it has recently been shown that each emotional category is uniquely associated with a pattern of activity across multiple brain regions and is not constrained within any one region or system (Wager et al., 2015).

The amygdala has been considered a particularly important region in emotional processes, and is a highly connected node integrating sensory and higher cognitive information (Figure 4). Also in the ageing literature, amygdala atrophy has been considered a major contributor to the positivity effect in attention and memory, for instance in the Ageing Brain Model. However, there are still unresolved arguments regarding the underlying mechanism of the positivity effect. In the following paragraphs, I briefly explain neuroimaging studies in this field and provide a summary of the current knowledge on the role of the amygdala in processing emotional items in the ageing brain.



relative to younger adults (for a review see Mather (2012)), which might reflect older adults' motivational tendency to regulate their negative affect. These neural patterns are generally consistent with the Posterior-Anterior Shift in Ageing (PASA) hypothesis (Davis et al., 2008). Recall from the earlier discussion of Cognitive Ageing Section that healthy ageing is associated with increased engagement of the anterior brain regions and decreased activity in the posterior regions during cognitive tasks. Enhanced activity of the frontal cortices and reduced activity of the amygdala and parieto-occipital regions has been reported during processing emotional items among older adults (Iidaka et al., 2002) as well, which resembles the PASA pattern. St Jacques and colleagues (2010) found support for the PASA pattern of activity during the processing of emotional stimuli in a study in which participants were asked to view three sets of emotional pictures and rate each picture. Their findings suggest that the right amygdala was functionally connected to the ventral anterior cingulate cortex among older adults, and was connected to the posterior regions – including the parahippocampus and visual cortices – among younger adults. Interestingly, this study also found functional activity preservation in the amygdala among older adults, which is consistent with a previous study by Wright et al. (2006) but fails to agree with several other empirical studies (Gunning-Dixon et al., 2003; Iidaka et al., 2002). These inconsistent patterns in amygdala activity might be related to the different paradigms used. For instance, in the study by Wright et al. (2006), novel fearful faces were compared to familiarized neutral faces, which revealed greater amygdala activity. In the studies by Gunning-Dixon et al. (2003), an emotion discrimination task was used, and participants were asked to rate the intensity of each emotional expression. Preserved amygdala activity among older adults in some of these studies suggests that the ageing positivity bias might not be due to impaired processing of negative emotions as has been suggested with the Ageing Brain Model.

Given the changes in amygdala and prefrontal activity observed during emotional processes in ageing, the pattern of Fronto-Amygdala Differences in Emotion (FADE) has been suggested by (St Jacques et al., 2009). According to the FADE hypothesis, amygdala function remains intact throughout ageing. According to these authors, this FADE pattern might reflect three potential mechanisms in age-related emotional processing. First, the increased activity in frontal regions could be related to the posterior-anterior shift in ageing, which has been observed in cognitive domains as well. This shift could reflect the compensatory mechanism, as increased frontal activity was found to be predictive of subsequent memory performance for negative stimuli. Second, the age-related increased activity in the medial PFC might reflect the recruitment of self-referential



processes, which have been shown to be associated with this region. In line with this interpretation, (Leclerc and Kensinger, 2008) argued that older adults recruit this region more for positive items and less for negative, suggesting that older adults might interpret positive stimuli in a self-relevant manner. Third, FADE could reflect enhanced emotion regulation strategies by older adults for processing negative stimuli. This is consistent with results from the emotion regulation literature indicating that emotion regulation imposes substantial demands on cognitive control operations (Ochsner and Gross, 2005; Wager et al., 2008), although some studies have failed to provide support for this model (see Fischer et al. (2005); Gutchess et al. (2007); Iidaka et al. (2002)).

*Summary:* It seems that neurological evidence supports the enhanced activity of prefrontal regions in response to emotionally valenced items. There are number of possible explanations for this change as proposed by St Jacques et al. (2009) such that enhanced PFC activity might be related to the emotion regulation strategies older adults are utilizing for down-regulating negative emotions, or it may be due to the general pattern observed in ageing (PASA pattern). However, it is still unclear whether older (relative to younger) adults recruit different networks for processing emotionally valenced items or whether the strength of connectivity between brain regions involved in processing emotional items might change as we age. In **Study 2** presented in Chapter 3, I present an fMRI study in which I employed a multivariate method to explore the functional brain networks involved in processing emotional items using a working memory paradigm.

## **Emotional Memory and Ageing**

There is a need to explore how attentional processes during encoding have an impact on subsequent outcome measures, such as memory for emotional items. The effect of emotion is not only limited to attentional functions. There is now a considerable literature on how emotion can influence memories, including working, autobiographical, and long-term memories. Some studies emphasize how emotion can enhance or disrupt memory in different circumstances (Levine and Edelstein, 2009), others have examined the distinctive role of valence and arousal features of emotional stimuli on memory functions (Kensinger and Corkin, 2004), and still others have investigated how some emotional information is likely to be forgotten. A number of studies have also investigated the role of different brain regions during different stages of memory such as encoding, storage, and retrieval.

Emotional information can constrain memory, a concept usually referred to as “memory narrowing”. This effect reflects the phenomenon whereby memory is better for central items, which in turn disrupts memory for unrelated or peripheral items. However, not all studies have reported memory narrowing for emotional items. Important emotional items are sometimes forgotten and peripheral information is preserved. According to Levine and Edelstein (2009), it seems that, “memory narrowing as a result of emotion, and a number of violations of the memory narrowing pattern, can be explained by the view that emotion enhances memory for information relevant to currently active goals”.

Recall that according to the biased competition model (Desimone and Duncan, 1995), information is prioritized for further processing based on the competition between stimuli to reach our attentional focus. Furthermore, according to the “Arousal-Based Competition” (ABC) model (Mather and Sutherland, 2011) and findings from Dolcos et al. (2004), arousal modulates the strength of mental representation and determines which item will be dominated for selective attention. This competitive process begins during perception and continues into long-term memory. Evidence indicates that arousal can lead to memory narrowing, enhance the memory for gist (rather than details), and enhance consolidation, although there are still somewhat mixed findings regarding these effects (for a review see Mather and Sutherland (2011)). Previous studies have also reported a distinction in recruitment of brain networks as a function of arousal and valence (Kensinger and Corkin, 2004). Therefore, both the valence and arousal dimension of the emotional items have the potential to modulate the strength of the memory for that item.

### **Behavioural Findings on Emotional Memory**

In a recent meta-analysis it has been shown that the ageing positivity effect in memory occurs in a wide range of paradigms including long term memory, working memory, and autobiographical memory, as well as decision making. A variety of stimuli such as faces, words, and pictures have also been used. Detailed descriptions of these studies are beyond the scope of this chapter, but in the following paragraphs I briefly review some of the key behavioural findings in this field before discussing the underpinning neurological mechanisms. For further details, see Reed and Carstensen (2012) and a recent meta-analysis by Reed et al. (2014).

One of the earliest studies to provide important insights into age-related changes in emotional memory was conducted by Charles and colleagues (2003), in which they assessed both recognition

and recall for emotional items. Overall, they found greater age differences for negative items compared to positive items as a function of age. In both recognition and recall memory, the memory advantage for negative items decreased with increasing age. These findings have been replicated over the last decade and number of studies examined this effect by using different materials, such as words and pictures (for a review see Reed et al. (2014)), and different memory indices, such as response bias.

For instance, in one study participants decided whether they truly remembered each of the items or if they knew them more vaguely. The response biases of both age groups were examined as well as memory accuracy. Findings showed that younger adults tended to say “old” or “remember” to negative items more frequently than positive and neutral items, whereas older adults responded “old” and “remember” to both positive and negative items equally frequently (Kapucu et al., 2008). These findings suggest that the positivity effect in late adulthood should be construed more broadly to include not only memory enhancement but also more receptiveness to positive stimuli indicated by response biases.

Although several studies show age-related positivity bias in memory, some studies failed to support such changes (Gallo et al., 2009; Kensinger et al., 2007b). The impact of instruction on the positivity effect has been suggested to be the main factor explaining some of these discrepancies in the literature. In the Charles et al. (2003) study, participants were instructed to passively view pictures as if they were watching TV. Across two experiments, participants were also instructed to emotionally evaluate the items (e.g., rating the picture based on how it makes them feel while viewing it) or perceptually evaluate them (e.g., rating the visual complexity of the picture). Perceptual evaluation decreased older adults’ ability to recall emotional items whereas the emotional evaluation did not have any impact on older adults’ memory. Hence, it seems that older adults’ memory for emotional items is at an optimum level when they are able to encode them using their own strategies like passive viewing, or when they can focus on the emotional ratings of the pictures, such as when they emotionally evaluated the pictures (Emery and Hess, 2008).

As mentioned, according to the Arousal Biased Competition (ABC) model (Mather and Sutherland, 2011), arousal dimension of emotions can influence memory storage. In line with this model, two separate neural networks processing arousal and valence have also been proposed (Leclerc and Kensinger, 2008). In the ageing literature, the question has become whether the positivity effect occurs equally for arousing and non-arousing words (Kensinger, 2008). The

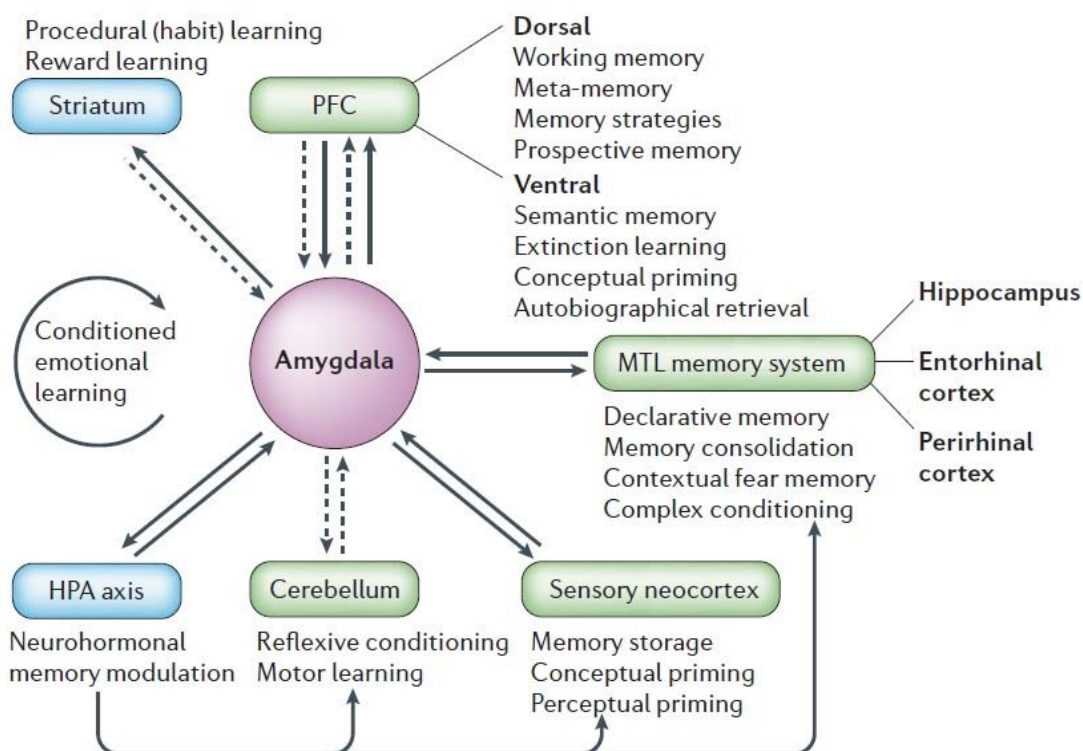
positivity effect has also been found for non-arousing words but not for arousing words. Given that non-arousing words are thought to be remembered as a result of engaging controlled processes, Kensinger (2008) concluded that the positivity effect relies on “controlled processing of emotional information”. In one recent study (Dolcos et al., 2014), the arousal levels of pictures were manipulated to examine how the arousal levels of stimuli have an impact on the emotional functioning in aging. Their findings suggest that emotional processing of high arousal pictures are preserved in aging; however, processing of low arousing stimuli is subject to alteration. Their neuroimaging findings corroborate Kensinger (2008) conclusion by pointing toward the engagement of controlled processes during low arousing negative stimuli by engaging ventral ACC/vmPFC and automatic processes while evaluating high arousing pictures by activating amygdala region.

*Summary:* Emotional items can constrain memory processing, referring to memory narrowing phenomenon. Arousal features of emotional information have been shown to influence memory narrowing as well as enhance memory for gist. Evidence suggests that positivity effect in ageing might occur in different stages of informational processes, such as attention, memory, or decision making. In Chapter 2, I address the relation between different stages of the memory in the positivity effect and explore whether the cognitive efforts exerted during encoding of emotional items is associated with the memory positivity effect. However, it should be noted that several studies failed to find the positivity effect (for examples see Gallo et al. (2009); Grühn et al. (2005); Kensinger et al. (2002)). One of the potential reasons that has been suggested is that the fact that these experiments imposed explicit instructions on how to process information, which are thought to constrain the positivity effect and consequently not allowing for positive chronic goals to emerge naturally.

### **Neurological Findings on Emotional Memory**

The amygdala is a major node in processing emotional items, but the role of this region is not limited to the attentional stage. The amygdala can modulate both the encoding and storage of information by interacting with the hippocampal region (Phelps, 2004). Buchanan and Adolphs (2002) described the role of the amygdala in emotional memory by providing converging evidence from lesion, pharmacological, and neuroimaging studies. One pathway by which the amygdala is argued to influence memory is via neurotransmitter and hormonal output. Specifically, the connection between the amygdala and hypothalamus mediates the release of both epinephrine and

cortisol when encountering emotionally arousing information, which consequently can influence the central nervous system and amygdala. The other pathway by which the amygdala may influence memory is via noradrenergic neurotransmission in the lateral/basolateral nuclei of amygdala. Animal studies have provided important insights into how the manipulation of activity within these sub nuclei of the amygdala could influence hippocampal and cortical function. Additionally, in a review paper, LaBar and Cabeza formulated how the amygdala mediates the role of arousal of emotional stimuli on memory, depicted in Figure 5 (for more details, see LaBar and Cabeza (2006)).



**Figure 5. Mechanism by which the amygdala mediates the influence of emotion on memory** proposed by LaBar and Cabeza, 2006

Neuroimaging studies have shown that so-called “emotional regions” (e.g. amygdala) and medial temporal regions (e.g., the hippocampus) can influence higher cognitive areas (e.g., the prefrontal regions) to encode and store emotional information. The influence of emotional regions during each memory stage serves to modulate mnemonic function and increase the likelihood of retaining the details of attended information (see Kensinger and Schacter (2007) for more details). This conclusion has been supported by a review paper using the Activation Likelihood Estimate

(ALE) method (Murty et al., 2011) to examine a wide range of brain regions involved during the encoding of emotional items, including the bilateral amygdalae, anterior hippocampus, anterior and posterior parahippocampal gyri, and the ventral visual stream (including the middle temporal, middle occipital, fusiform gyri, left lateral PFC, and the right ventral parietal cortex). It has been concluded that the amygdala interacts with the prefrontal and parietal cortices to enhance perceptual processing, semantic elaboration, and attention – which in turn influence subsequent emotional memory performance.

Interactions between emotional and cognitive processes occur at multiple levels of processing and across many different types of memory, e.g. working memory, and cognitive tasks. Recently the relation between emotion and working memory has been investigated. It has been found that emotional distraction during a WM task reduces performance (Dolcos and McCarthy, 2006). This behavioural effect has been shown to be related to enhanced activation in brain regions involved in emotional processing, along with decreased activity in brain regions associated with active maintenance of relevant information in WM. Furthermore, it has been shown that top-down attentional regions were involved while attending to the relevant and ignoring the irrelevant items during the encoding stage of the working memory task. The important consequence of goal-directed attention during encoding is to enhance the impact of behaviourally relevant stimuli at the expense of irrelevant stimuli. Thus, emotional stimuli may affect goal-directed behaviour by either enhancing or disrupting task-relevant processes during both the encoding and retrieval stages of WM. Such results led to proposing a distinct role of two systems known as “cold/ dorsal system” and “hot/ ventral system” during performing an on-going memory task while irrelevant emotional distractors were presented (Dolcos et al., 2011). The decreased activity of cold system and increased engagement of ventral system has been observed in clinical and non-clinical populations while processing irrelevant emotional distractors. In other words, coping with emotional distraction involves top-down control brain areas, such as ACC and dlPFC, in order to counteract the bottom-up influence of emotional distraction, which involved regions such as amygdala (Jordan et al., 2013).

Underlying neural mechanisms that might explain behavioural asymmetry in memory with ageing have been examined in a number of studies. In one study, Kensinger and Schacter (2008) examined the emotional memory network by using a subsequent memory paradigm. In this paradigm, participants viewed a series of pictures during encoding and were then asked to judge

whether each picture would fit inside a cabinet drawer. Outside the scanner, participants had to indicate whether each picture was the same, similar, or new. This paradigm previously showed enhanced memory for negative items in younger adults, and an emotional memory bias relative to neutral items in older adults (Kensinger et al., 2007a, 2007b). Kensinger and Schacter (2008) found an age-related effect emerged during the encoding of positive items, in which older adults showed stronger activity than younger adults in the medial PFC. As this region has been shown to be activated during self-referential tasks (Gutchess et al., 2007), it was argued that older adults might process positive information in a more self-referential manner, which in turn will result in better memory for positive items (Leclerc and Kensinger, 2008). The activity of frontal region replicated in another study during processing of positive (relative to negative) words but not pictures (Leclerc and Kensinger, 2011).

Effective connectivity has been used to examine age-related changes in connectivity between regions involved in emotional memories (Addis et al., 2010). Age-related changes were observed only for successful encoding of positive items, and not negative. The results showed that older adults' hippocampal activity was modulated by the amygdala and ventromedial regions, and no age differences were observed during encoding of negative items. These results indicate that there might be age-related changes in how positive items are being processed, rather than changes in the processing of negative items (Addis et al., 2010).

The functional relationship between subcortical regions (such as the amygdala and hippocampus) and cortical regions during both memory encoding and retrieval has been examined by Murty et al. (2009). They investigated age-related changes in declarative memory using neutral and aversive stimuli in both younger and older adults. During encoding, older adults showed significantly greater dorsolateral prefrontal cortex (dlPFC) activity for aversive stimuli relative to younger adults. During retrieval, older adults showed greater coupling between the dlPFC and amygdala, whereas younger adults showed increased valence related activity (aversive > neutral) in the amygdala and hippocampus. These findings are in line with the compensatory hypothesis (see Major Discoveries about the Ageing Brain Section), as older adults recruited more prefrontal regions during both recognition and encoding. Moreover, these results also suggest that older adults recruit PFC regions to a greater extent than younger adults to down-regulate their negative emotional reactions, a finding that has also been identified in a number of other studies (St Jacques et al., 2009; St Jacques et al., 2010).

There is mounting evidence regarding age-related changes in the way that older adults process and remember emotional expressions on faces (see Emotion Recognition and Ageing Section for more details). To extend previous studies on emotion recognition, Fischer et al. (2010) investigated the memory of facial expressions of fearful and neutral faces among younger and older adults. No memory recognition advantage for emotional items (relative to neutral items) was found in either age group, but older adults recruited more PFC and insular regions while processing negative faces. This finding is consistent with the general pattern of age-related shift in cortical-subcortical recruitment, as discussed in Cognitive Ageing Section and Emotion and Attention in Ageing Section. It is also important to consider the link between different stages of cognitive processes, such as attention, recognition, and memory, in order to form a more comprehensive picture of emotional processes in ageing.

*Summary:* Although growing body of evidence suggests the age-related changes on the process of emotionally-valenced items as a function of age, there are still needs for further investigation in this area of research to provide direct evidence on the brain networks involved during encoding of emotional items. It seems that different brain networks might be engaged in processing emotionally-valenced items as a function of age, but the evidence is disparate. In **Study 2** presented in Chapter 3, I present an fMRI study that aimed to explore the brain networks that are involved during encoding of positive and negative items across two age groups, with a particular focus on the networks connected to amygdala and prefrontal regions.

## **Emotion Recognition and Ageing**

Recognising emotions on the face is one of the most fundamental aspects of our social communication. There is now a considerable literature focused on how different facial emotions are processed in late adulthood. In this section I introduce behavioural evidence in relation to the most studied emotions, happy and angry emotions, and then describe some of the neuroimaging findings on the topic. There is an increasing interest in understanding the link between the way older adults process emotional items and their ability to detect and respond to social cues in everyday life. However, the social cognitive aspect of ageing is beyond the scope of this chapter. For more information on this topic, refer to Phillips et al. (2014) and von Hippel and Henry (2012).

Empirical evidence suggests that relative to younger adults, older adults have difficulty recognising negative emotions such as fear, anger, and sadness – findings which have been



reviewed in a meta-analysis (Ruffman et al., 2008). However, critical issues have been raised regarding the studies examining emotion recognition in ageing. First, the people who model various emotional facial expressions in the photos used in these studies are typically either young or middle-aged. Second, the use of static images lowers the ecological validity of these studies. Such methodological issues make the conditions for facial emotion recognition dissimilar from everyday life experiences, and might affect our understanding of emotion recognition with advancing age. Therefore, it is important to address some of these methodological issues in more detail before discussing the relevant findings.

One of the methodological caveats that have been addressed in several studies is the age of the models used for facial expression photos. Some of the earliest evidence regarding the potential importance of model age was presented in a study using the Multi-Source Interference Task (MSIT) by Ebner and Johnson (2010). It was shown that both younger and older adults were more distracted by faces similar in age to themselves. They extended this initial study by investigating the visual scan patterns of different ages displayed with different facial expressions (Ebner et al., 2011). The results suggested that age of model influences visual inspection of the face (measured by total gaze times). That is, both age groups spent more time looking at faces similar to their own age relative to other-age faces. Moreover, they found that spending a longer time looking at the own-age faces predicted better own-age emotion identifications. According to a review paper by Folster et al. (2014), “[l]ower expressivity, age-related changes in the face, less elaborated emotion schemas for older faces, negative attitudes toward older adults, and different visual scan patterns may lower decoding accuracy for older faces”. Therefore, it seems that using older models might add insight into our understanding of emotion recognition, a view that previously had not been considered widely.

Also in order to enhance the ecological validity of stimuli used in emotion recognition studies, more dynamic stimuli sets have recently been used to examine age differences in emotion expression identification. Sze et al. (2012), for instance, found that older adults had difficulty judging emotional expressions from static images (e.g., angry and disgusted), while they outperformed younger adults involving continuous emotion judgments of dyadic interactions - an audio-visual interaction between couples discussing important marital topics. Using dynamic emotional expressions will not only increase ecological validity but also enhance activity in neural areas involved in emotion and processing socially relevant information (Krumhuber et al., 2013).

For instance, Schultz and Pilz (2009) reported more activation in response to dynamic faces in face-sensitive areas, including the bilateral fusiform gyrus, the left inferior occipital gyrus (IOG), and the right superior temporal sulcus (STS).

It is worth noting that there are mixed findings regarding dynamic stimuli such as video clips (Krendl and Ambady, 2010). For instance, using video stimuli for recognition of basic emotions in the face and body, as well as incorporating body, facial, and situational cues, some studies have shown that older adults still perform worse than younger adults in recognising some emotions (Sullivan and Ruffman, 2004). Indeed, Ruffman (2011) has argued that using static images for emotion recognition has reasonable ecological validity - and more importantly, explains age differences in various tasks such as social understanding, using a faux pas task (Halberstadt et al., 2011), verbosity (Ruffman et al., 2010), deception (Ruffman et al., 2012). Therefore, it seems that although using dynamic stimuli is an important methodological consideration and a number of studies provide support for the use of dynamic stimuli, static emotional stimuli are also informative.

Given that the most commonly assessed of the six basic emotions are the emotions of anger and happiness, in the following section, empirical evidence regarding these two specific emotions will be discussed.

## **Behavioural Findings on Emotion Recognition**

### **Anger**

There are evolutionary reasons why threat-related stimuli should be detected more rapidly than other types of stimuli, as any failure to detect threat has clear and immediate implications for survival. There is also empirical support for this perspective, with younger adults able to detect angry faces more quickly than non-threatening faces (Öhman et al., 2001). Mather and Knight (Mather and Knight, 2006) demonstrated a similar effect in older adults, by using a visual search task in which nine schematic faces were presented in a search array. Both age groups tended to identify angry faces more quickly than sad and happy faces, known as the pop-out effect. In another study, real faces were used in addition to schematic faces (Ruffman et al., 2009). In the first experiment, participants were asked to identify whether all faces were identical or if one of the faces was different in the array of faces. In the second experiment, they were asked to label the emotion of the face that was different from the rest of the faces in the search array. The results

indicated that although older adults were less accurate in explicitly labelling the angry schematic and real faces compared to younger adults, they responded as quickly as younger adults to the angry faces when they had to identify the different face from the array. On the basis of such findings, it has been argued that at some level (probably more an implicit level) older adults are able to differentiate angry faces equally as fast as younger adults.

Older adults' responses to angry facial expressions have also been studied using electromyography (EMG) (Bailey et al., 2009). EMG measures changes in activity of the facial muscles, and so can be used to index implicit mimicry responses toward facial stimuli. No age differences in *corrugator supercilii* (which pulls the eyebrow muscles into frowning) responses to angry expressions were found in the early stage (200-500ms post-stimulus onset). However, older adults' *corrugator supercilii* responses to anger in the later stage (500-800ms post-stimulus onset) were associated with difficulties in labelling the emotions. Although older adults demonstrate intact implicit mimicry to angry facial expressions, mimicry in the later stage of post stimulus-onset might have been confounded by their difficulties in labelling the expressions. Future studies examining dynamic stimuli and unfolding emotional responses over time by assessing mimicry responses are necessary to better understand when age-related differences in identifying angry emotions emerge, and whether such differences have consequences in everyday life interactions.

## **Happiness**

While converging evidence supports the idea that younger adults outperform older adults in recognising negative emotions, the evidence for age-related changes in identifying positive emotions is less clear. In a review paper by Isaacowitz et al. (2007), 11 out of 13 studies reviewed showed no age effect for recognition of happiness, possibly due to ceiling effects. However, Ruffman et al. (2008) reported moderate sized age deficits recognising happiness, both from voices (mean effect size,  $M = .37$ ) and from matching voices to faces ( $M = .42$ ). Because dynamic stimuli provide additional temporal cues and resemble more naturalistic occurrences of daily social interaction, they may allow for more accurate emotion discrimination. Using dynamic stimuli rather than static images may allow older adults to use their lifetime experience in distinguishing different emotional expressions, such as happiness (Murphy et al., 2010).

Given older adults' exhibit a preference toward positive stimuli, it has also been assessed whether this preference is seen in relation to different types of smiles, and specifically posed versus

spontaneous smile. Different forms of smiles can be distinguished based on the activity of certain facial muscles. While spontaneous smiles are associated with experience of positive affect, posed smiles are generally associated with social norms or social markers. In order to investigate older adults' ability in discriminating different types of smiles, Murphy et al. (2010) utilized dynamic stimuli in which actors were videotaped while they made expressions in response to three situations: receiving news that they won a prize, being invited on a cruise with friends, or being excluded from a group. The actors' posed and spontaneous smiles were identified by coders using the Facial Action Coding System (FACS) (Ekman and Friesen, 1978). Results from two experiments using these video clips suggested that older adults were better than their younger counterparts at distinguishing posed relative to spontaneous smiles. Given that dynamic stimuli contain temporal information about emotional expressions and are an approximation of real word experiences, older adults may have used this information to judge and discriminate between smile types.

The question of age-related changes in emotion recognition of faces has been brought forward to investigate whether sensitivity in discriminating different types of smiles relates to the social meaning underlying these smiles. The ability to distinguish smiles has been shown to play a crucial role in interpersonal functioning (Ekman, 2009). For example, increased difficulty distinguishing between smiles is associated with greater social functioning impairments among autistic individuals (Boraston et al., 2008). The question is how these changes in emotion recognition are linked to older adults' social functioning. In one study (Slessor et al., 2010a), older adults were asked to indicate whether they would ask a favour from targets displaying either a spontaneous enjoyable smile, a posed enjoyable smile, or a deliberately-posed non-enjoyment smile. Although there were no age differences in discriminating between spontaneous and posed smiles, contrary to the Murphy et al. (2010) study, older adults were more likely than younger adults to ask for a favour from a person displaying a non-enjoyment smile relative to enjoyment/spontaneous smiles. Hence, it seems that older adults are less likely to base their judgment on these social cues (enjoyment smiles/genuine), which can offer cooperation, approachability, or reciprocation in social interaction. Whether this age difference in approaching the non-enjoyment smile could influence older adults' social functioning, and in turn, could make them more prone to fraud as a result of approaching deceptive smiles, is a topic for further investigation in the field of emotion recognition and ageing.

Additionally, dynamic stimuli were used in another study to investigate age-related changes in identifying emotional experiences accompanying three different smile expressions (Riediger et al., 2014). In this study, smile expressions were shown in different emotional contexts, including when people feel happy or amused. Thus, rather than using two types of smiles (posed/non-enjoyment vs. spontaneous/enjoyment), actors were filmed in three different conditions in which they were asked to display a smile: first, as if they were being accused of something unfairly; second, as if they were watching an amusing film or cartoon; and third, in an affectively neutral situation. Older and younger adults were asked to identify the emotional experience of each of these models. Overall, they found that younger adults were more accurate than older adults in identifying the emotional experiences accompanying each smile. Older adults were better at correctly ascribing positive affective experiences to the older models than the younger ones. Although these results are in contrast with some previous findings (Murphy et al., 2010; Slessor et al., 2010a), it seems that the context of displayed emotions associated with different types of smiles is an important factor in understanding age-related changes in recognition of happy facial expressions.

Slessor et al. (2014) have looked at the time course of mimicry responses to enjoyment and non-enjoyment smiles. The activity of the *Zygomaticus major* muscle region (which pulls the corner of the lips into a smile) and the *Orbicularis oculi* muscle region (which forms wrinkles around the outer corners of the eyes) were recorded. No age differences were found in the pattern and timing of *Zygomaticus major* activity in response to either type of smile. However, older adults showed extended *Orbicularis oculi* contraction in response to the non-enjoyment smiles. Moreover, older adults rated both types of smile as happy, independent of the *Orbicularis oculi* responses. These results suggest that emotion recognition and mimicry responses might rely on different processes. Further investigation is warranted to replicate these findings and examine the timing of these two processes by using high temporal resolution techniques such as Electroencephalography (EEG) to investigate the time-course of this effect more closely.

## **Neurological Findings on Emotion Recognition**

In addition to the role of the amygdala in attention and memory functions, the amygdala plays a crucial role in processing emotional expressions from faces and decoding other socially relevant cues such as eye gaze (for reviews see Itier and Batty (2009); Shepherd (2010)). One of the earliest insights into the key role of the amygdala in processing facial expressions was provided by a review on brain lesion and neuroimaging studies by Adolphs (1999). Most of the neuroimaging studies of

emotion at the time confounded the encoding, retrieval, experience, and reaction to emotions, which made it difficult to attribute activation of the amygdala to any one of these psychological functions. However, our understanding of the neural mechanisms involved in processing facial expression has advanced from brain lesions and neuroimaging studies.

Two visual streams have been identified in primates: one for object recognition leading to the temporal lobe called the ventral stream, and one for localizing objects in space leading to the parietal lobe called the dorsal stream (Ungerleider and Mishkin, 1982). Although a number of studies have addressed the dissociation between the two streams in processing concrete information, this dissociation has not been addressed in relation to emotion. Adolphs et al. (2003) investigated the naming and recognition of emotion in a patient known as Patient B., who had complete damage of both amygdalae, hippocampi, as well as adjacent perirhinal, entorhinal, parahippocampal cortices (greater on the right than on the left), as well as bilateral damage of temporal neocortical areas (Brodmann area of 38, 20/21, and most of area 37) on the right. They hypothesized that this patient might be able to recognise emotion from dynamic stimuli, but not from static ones. The results suggested that patient B. was able to recognise emotions at the basic level of categorization if the stimuli contained temporal information. The fact that this patient was impaired in recognising and verbally labelling emotions from static pictures suggests that recognising emotions and labelling emotions rely on distinct neural systems. Although the case studies are informative and provide valuable knowledge about the causal role of these brain regions in emotion recognition, neuroimaging techniques can provide alternative perspectives in order to understand the underlying neural networks and the relation between brain regions during emotion recognition.

One of the early studies in emotion recognition in ageing using fMRI was carried out by Iidaka et al. (2002), in which participants were shown pictures of the six basic facial emotions (happy, angry, disgusted, fearful, sad, and surprised). Participants were asked to label the gender of the actor modelling the emotional expressions, as well as the intensity of each emotion. Relative to younger participants, older adults showed reduced activity in the medial temporal lobe in response to both negative (e.g., left amygdala) and positive emotions (e.g., right parahippocampal gyrus). None of these regions showed increased activity among older adults. This dissociation in decreased activity of the medial temporal lobe may suggest that ageing affects the neural networks involved in processing emotionally valenced facial expressions differently.

In another study, Gunning-Dixon et al. (2003) investigated facial emotion processing using a task in which they asked participants to discriminate the age of the models during an emotion discrimination task. Older adults recruited more frontal regions relative to the temporo-limbic regions, which were more activated among younger adults. The authors argued that the decreased activity of the amygdala in the emotion discrimination task relative to younger adults was consistent with post-mortem studies of age-related loss of neurons in the limbic regions. However, these data need to be interpreted cautiously, as the sample size of this study was very small (8 participants), and consequently low statistical power could affect the generalizability of the findings.

It has been argued that emotion recognition difficulties observed with ageing might be associated with cognitive declines associated with advanced age. In order to minimize the role of cognitive mechanisms involved in processing emotional items, a passive viewing paradigm was administered by Fischer et al. (2005). They examined age-related changes in emotional face processing by using a relatively larger sample size than previous studies (24 younger and 22 older adults). Pictures of angry and neutral faces were presented to participants. The results showed reduced amygdala activity for negative faces among older adults relative to younger adults. Moreover, increased activity in the anterior-ventral insula cortex was found among older adults in response to negative faces. Again, the age-related increases in engagement of cortical regions for processing emotional faces could reflect “compensatory mechanisms” older adults use for processing emotional faces (Fischer et al., 2005). The inconsistencies of the results of amygdala activity in Fischer’s study and previous studies mentioned above (Gunning-Dixon et al., 2003; Iidaka et al., 2002) could simply be related to methodological differences. Specifically Fischer’s (2005) study used a passive viewing paradigm, whereas the other two studies included labelling and emotion discrimination tasks, which could potentially involve more top-down modulation of sensory information contributing to the discrepancy between the results.

In a neuroimaging study, Ebner et al. (2012a) addressed the role of identified regions of interests (ROIs), such as the ventromedial prefrontal cortex (vmPFC), dorsomedial prefrontal cortex (dmPFC), and amygdala, in identifying emotional expressions. First, the results showed that greater vmPFC activity emerged for identifying happy (relative to angry) faces. Second, both age groups showed enhanced activity of the amygdala in identifying happy relative to negative emotions, suggesting the saliency of positive affective processing. Greater activity of dmPFC, a region mainly involved for executive control, was found in response to angry faces more than happy that was

more pronounced among older than younger adults. The finding of angry expression reflects increased cognitive control resources that might be required for processing angry expressions. Moreover, this finding is in line with the SST and suggests the age-related increase in controlled regulatory processing of negative than positive emotions.

As discussed, the ecological validity of stimuli, such as using own-age faces, is a critical methodological factor in emotion recognition studies in ageing. Ebner et al.'s (2013) study further addressed this issue and demonstrated the importance of the age of faces used as stimuli in ageing studies. In this study, the ability to identify emotion was examined in younger and older adults as a function of own-age vs. other-age biases and emotional expressions of the faces. In both age groups, the results indicated greater activity in the ventromedial PFC and insula for own-age faces, particularly for happy and neutral faces, but not for angry faces. These findings provide additional support for the differential neural mechanisms involved in processing own-age faces relative to other-age faces, which need to be considered in facial emotion recognition studies when comparing different age groups.

*Summary:* Although several studies shed light on processing facial expressions, there are still contradictory findings and several questions remained to be addressed in the future at both behavioural and neurological levels. In **Study 3** presented in Chapter 4, I present an fMRI study that aimed to extend prior literature by exploring the underlying neural correlates involved in processing and integrating facial cues among older adults, with a particular focus on the relation between decoding facial cues and social-cognitive performance.

## **General Summary**

The main focus of this chapter was to introduce recent findings in the field of emotional ageing. To gain a better understanding of age-related changes, the underlying mechanisms of how emotion impacts various cognitive functions needs to be fully understood. There are several questions in the emotional ageing literature that inform the empirical studies included in each of the chapter of my thesis. For instance, does the positivity effect rely on cognitive control processes? What is the relation between encoding and recognition memory stages for emotional items? (**Study 1 in Chapter 2**). Are there any age-related alterations in the networks recruited during encoding of different emotionally valenced items? (**Study 2 in Chapter 3**). Can the changes in emotional



processing, specifically in facial processing, have consequences/implications for social-cognitive aspects of ageing? (**Study 3 in Chapter 4**).

As has been discussed, widespread networks linking emotional and cognitive domains suggest that these areas are working in concert, and this perspective needs to be considered in life-span developmental research as well. Hence, rather than looking at changes with age in isolated areas (such as the amygdala as a major node in emotional processes), change in the network and interregional connections needs to be a primary focus. In **Study 2 (Chapter 3)** and **Study 3 (Chapter 4)** I have employed multivariate approach to investigate the underlying neural networks involved in encoding of emotional items and recognition of facial expression. Furthermore, to reach a more comprehensive understanding of emotional changes in ageing, there is a need for research that addresses the relation between different stages of the cognitive processes and the implications of emotional processes on other psychological functions. In **Study 2 (Chapter 2)**, I addressed this issue by investigating the link between the effort exerted during encoding and the memory positive effect. In **Study 3 (Chapter 4)**, I investigate the relation between emotional facial recognition and social-cognitive processes.

There are several questions in the emotional ageing literature that inform the empirical studies included in each of the chapter of my thesis. For instance, does the positivity effect rely on cognitive control processes? What is the relation between encoding and recognition memory stages for emotional items? (**Study 1 in Chapter 2**). Are there any age-related alterations in the networks recruited during encoding of different emotionally valenced items? (**Study 2 in Chapter 3**). Can the changes in emotional processing, specifically in facial processing, have consequences/implications for social-cognitive aspects of ageing? (**Study 3 in Chapter 4**).

## References

- Addis, D. R., Leclerc, C. M., Muscatell, K. A., & Kensinger, E. A. (2010). There are age-related changes in neural connectivity during the encoding of positive, but not negative, information. *Cortex; a journal devoted to the study of the nervous system and behavior*, *46*(4), 425-433. doi:10.1016/j.cortex.2009.04.011
- Adolphs, R. (1999). The human amygdala and emotion. *Neuroscientist*, *5*, 125-137. doi:10.1177/107385849900500216
- Adolphs, R., Tranel, D., & Damasio, A. R. (2003). Dissociable neural systems for recognizing emotions. *Brain Cogn*, *52*(1), 61-69.
- Allard, E. S., & Isaacowitz, D. M. (2008). Are preferences in emotional processing affected by distraction? Examining the age-related positivity effect in visual fixation within a dual-task paradigm. *Neuropsychol Dev Cogn B Aging Neuropsychol Cogn*, *15*, 725-743. doi:10.1080/13825580802348562
- Allard, E. S., Wadlinger, H. A., & Isaacowitz, D. M. (2010). Positive gaze preferences in older adults: assessing the role of cognitive effort with pupil dilation. *Neuropsychol Dev Cogn B Aging Neuropsychol Cogn*, *17*, 296-311. doi:10.1080/13825580903265681
- Bailey, P. E., Henry, J. D., & Nangle, M. R. (2009). Electromyographic evidence for age-related differences in the mimicry of anger. *Psychology and Aging*, *24*(1), 224-229. doi:10.1037/a0014112
- Baltes, P. B., & Baltes, M. M. (1990). Psychological perspectives on successful aging: The model of selective optimization with compensation. *Successful aging: Perspectives from the behavioral sciences*, *1*(1), 1-34.
- Bergerbest, D., Gabrieli, J. D. E., Whitfield-Gabrieli, S., Kim, H., Stebbins, G. T., Bennett, D. A., & Fleischman, D. A. (2009). Age-associated reduction of asymmetry in prefrontal function and preservation of conceptual repetition priming. *Neuroimage*, *45*(1), 237-246. doi:<http://dx.doi.org/10.1016/j.neuroimage.2008.10.019>
- Berntson, G. G., Bechara, A., Damasio, H., Tranel, D., & Cacioppo, J. T. (2007). Amygdala contribution to selective dimensions of emotion. *Soc Cogn Affect Neurosci*, *2*(2), 123-129. doi:10.1093/scan/nsm008
- Boraston, Z. L., Corden, B., Miles, L. K., Skuse, D. H., & Blakemore, S.-J. (2008). Brief report: Perception of genuine and posed smiles by individuals with autism. *Journal of autism and developmental disorders*, *38*(3), 574-580.
- Buchanan, T. W., & Adolphs, R. (2002). The role of the human amygdala in emotional modulation of long-term declarative memory. In S. Moore & M. Oaksford (Eds.), *Emotional cognition: From brain to behavior* (pp. 9-34). London, UK.: Benjamins.

- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.*, *1124*, 1-38. doi:10.1196/annals.1440.011
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychology and Aging*, *17*(1), 85-100.
- Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging Gracefully: Compensatory Brain Activity in High-Performing Older Adults. *Neuroimage*, *17*(3), 1394-1402. doi:<http://dx.doi.org/10.1006/nimg.2002.1280>
- Cacioppo, J. T., Berntson, G. G., Bechara, A., Tranel, D., & Hawkley, L. C. (2011). Could an aging brain contribute to subjective well-being? The value added by a social neuroscience perspective. In A. Todorov, S. Fiske, & D. Prentice (Eds.), *Soc Neurosci* (pp. 249-262). Oxford; New York: Oxford University Press.
- Calvo, M. G., & Nummenmaa, L. (2008). Detection of emotional faces: salient physical features guide effective visual search. *Journal of Experimental Psychology: General*, *137*(3), 471.
- Carstensen, L. L. (2006). The influence of a sense of time on human development. *Science*, *312*, 1913-1915. doi:10.1126/science.1127488
- Carstensen, L. L., Fung, H. H., & Charles, S. T. (2003). Socioemotional Selectivity Theory and the regulation of emotion in the second half of the life *Motivation and Emotion*, *27*, 103-123.
- Carstensen, L. L., Isaacowitz, D. M., & Charles, S. T. (1999). Taking time seriously: A theory of socioemotional selectivity. *American Psychologist*, *54*(3), 165.
- Carstensen, L. L., Turan, B., Scheibe, S., Ram, N., Ersner-Hershfield, H., Samanez-Larkin, G. R., . . . Nesselroade, J. R. (2011). Emotional experience improves with age: evidence based on over 10 years of experience sampling. *Psychol Aging*, *26*(1), 21-33. doi:10.1037/a0021285
- Charles, S. T., & Carstensen, L. L. (2010). Social and emotional aging. *Annu Rev Psychol*, *61*, 383-409. doi:10.1146/annurev.psych.093008.100448
- Charles, S. T., Mather, M., & Carstensen, L. L. (2003). Aging and emotional memory: the forgettable nature of negative images for older adults. *Journal of Experimental Psychology. General*, *132*(2), 310-324. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12825643>
- Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The posterior-anterior shift in aging. *Cerebral Cortex*, *18*(5), 1201-1209. doi:10.1093/cercor/bhm155
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, *18*(1), 193-222.
- Dolcos, F., Jordan, A. D., & Dolcos, S. (2011). Neural correlates of emotion-cognition interactions: A review of evidence from brain imaging investigations. *J Cogn Psychol (Hove)*, *23*(6), 669-694. doi:10.1080/20445911.2011.594433

- Dolcos, F., LaBar, K. S., & Cabeza, R. (2004). Dissociable effects of arousal and valence on prefrontal activity indexing emotional evaluation and subsequent memory: an event-related fMRI study. *Neuroimage*, 23(1), 64-74.
- Dolcos, F., & McCarthy, G. (2006). Brain systems mediating cognitive interference by emotional distraction. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 26(7), 2072-2079. doi:10.1523/JNEUROSCI.5042-05.2006
- Dolcos, S., Katsumi, Y., & Dixon, R. A. (2014). The role of arousal in the spontaneous regulation of emotions in healthy aging: a fMRI investigation. *Front Psychol*, 5, 681. doi:10.3389/fpsyg.2014.00681
- Ebner, N. C., He, Y., & Johnson, M. K. (2011). Age and emotion affect how we look at a face: Visual scan patterns differ for own-age versus other-age emotional faces. *Cognition & Emotion*, 25(6), 983-997.
- Ebner, N. C., & Johnson, M. K. (2010). Age-Group Differences in Interference from Young and Older Emotional Faces. *Cogn Emot*, 24(7), 1095-1116. doi:10.1080/02699930903128395
- Ebner, N. C., Johnson, M. K., & Fischer, H. (2012). Neural mechanisms of reading facial emotions in young and older adults. *Emotion Science*, 3, 223.
- Ebner, N. C., Johnson, M. R., Rieckmann, A., Durbin, K. A., Johnson, M. K., & Fischer, H. (2013). Processing own-age vs. other-age faces: neuro-behavioral correlates and effects of emotion. *Neuroimage*, 78, 363-371.
- Ekman, P. (2009). *Telling Lies: Clues to Deceit in the Marketplace, Politics, and Marriage (Revised Edition)*: WW Norton & Company.
- Ekman, P., & Friesen, W. V. (1978). *The Facial Action Coding System*.
- Emery, L., & Hess, T. M. (2008). Viewing instructions impact emotional memory differently in older and young adults. *Psychology and Aging*, 23(1), 2-12. doi:10.1037/0882-7974.23.1.2
- Fischer, H., Nyberg, L., & Backman, L. (2010). Age-related differences in brain regions supporting successful encoding of emotional faces. *Cortex*, 46(4), 490-497. doi:10.1016/j.cortex.2009.05.011
- Fischer, H., Sandblom, J., Gavazzeni, J., Fransson, P., Wright, C. I., & Backman, L. (2005). Age-differential patterns of brain activation during perception of angry faces. *Neuroscience letters*, 386(2), 99-104. doi:10.1016/j.neulet.2005.06.002
- Folster, M., Hess, U., & Werheid, K. (2014). Facial age affects emotional expression decoding. *Front Psychol*, 5, 30. doi:10.3389/fpsyg.2014.00030
- Gallo, D. A., Foster, K. T., & Johnson, E. L. (2009). Elevated false recollection of emotional pictures in young and older adults. *Psychol Aging*, 24, 981-988. doi:10.1037/a0017545

- Gazzaley, A. (2011). Influence of early attentional modulation on working memory. *Neuropsychologia*, *49*(6), 1410-1424. doi:10.1016/j.neuropsychologia.2010.12.022
- Gazzaley, A. (2012). Top-down modulation deficit in the aging brain: an emerging theory of cognitive aging. In D. T. Stuss & R. T. Knight (Eds.), *Principles of Frontal Lobe Function* (second ed.). Oxford; New York: Oxford University Press.
- Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R. T., & D'Esposito, M. (2008). Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proc. Natl. Acad. Sci. U. S. A.*, *105*(35), 13122-13126. doi:10.1073/pnas.0806074105
- Gazzaley, A., Cooney, G. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down Enhancement and Suppression of the Magnitude and Speed of Neural Activity. *Journal of Cognitive Neuroscience*, *17*, 507–517. doi:10.1162/0898929053279522
- Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature neuroscience*, *8*, 1298-1300. doi:10.1038/nn1543
- Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: bridging selective attention and working memory. *Trends in Cognitive Science*, *16*(2), 129-135. doi:10.1016/j.tics.2011.11.014
- Goh, J. O., & Park, D. C. (2009). Neuroplasticity and cognitive aging: the scaffolding theory of aging and cognition. *Restorative neurology and neuroscience*, *27*(5), 391-403.
- Grady, C. (2012). The cognitive neuroscience of ageing. *Nature Reviews Neuroscience*, *13*(7), 491-505.
- Grady, C. L. (2008). Cognitive neuroscience of aging. *Ann N Y Acad Sci*, *1124*, 127-144. doi:10.1196/annals.1440.009
- Grühn, D., Smith, J., & Baltes, P. B. (2005). No aging bias favoring memory for positive material: Evidence from a heterogeneity-homogeneity list paradigm using emotionally toned words. *Psychol Aging*, *20*(4), 579-588. doi:10.1037/0882-7974.20.4.579
- Gunning-Dixon, F. M., Gur, R. C., Perkins, A. C., Schroeder, L., Turner, T., Turetsky, B. I., . . . Gur, R. E. (2003). Age-related differences in brain activation during emotional face processing. *Neurobiol Aging*, *24*(2), 285-295. doi:[http://dx.doi.org/10.1016/S0197-4580\(02\)00099-4](http://dx.doi.org/10.1016/S0197-4580(02)00099-4)
- Gutchess, A. H., Kensinger, E. A., & Schacter, D. L. (2007). Aging, self-referencing, and medial prefrontal cortex. *Soc Neurosci*, *2*(2), 117-133.
- Halberstadt, J., Ruffman, T., Murray, J., Taumoepeau, M., & Ryan, M. (2011). Emotion perception explains age-related differences in the perception of social gaffes. *Psychology and Aging*, *26*(1), 133-136. doi:10.1037/a0021366

- Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In G. H. Bower (Ed.), *The Psychology of Learning and Motivation* (Vol. 22, pp. 193-225): New York: Academic Press.
- Henry, J. D., Von Hippel, W., & Baynes, K. (2009). Social inappropriateness, executive control, and aging. *Psychol Aging, 24*, 239. doi:10.1037/a0013423
- Iidaka, T., Okada, T., Murata, T., Omori, M., Kosaka, H., Sadato, N., & Yonekura, Y. (2002). Age-related differences in the medial temporal lobe responses to emotional faces as revealed by fMRI. *Hippocampus, 12*(3), 352-362. doi:10.1002/hipo.1113
- Iordan, A. D., Dolcos, S., & Dolcos, F. (2013). Neural signatures of the response to emotional distraction: a review of evidence from brain imaging investigations. *Front Hum Neurosci, 7*, 200. doi:10.3389/fnhum.2013.00200
- Isaacowitz, D. M., Allard, E. S., Murphy, N. A., & Schlangel, M. (2009). The time course of age-related preferences toward positive and negative stimuli. *J. Gerontol. B Psychol Sci Soc Sci, 64B*(2), 188-192. doi:10.1093/geronb/gbn036
- Isaacowitz, D. M., Löckenhoff, C. E., Lane, R. D., Wright, R., Sechrest, L., Riedel, R., & Costa, P. T. (2007). Age differences in recognition of emotion in lexical stimuli and facial expressions. *Psychol Aging, 22*(1), 147.
- Isaacowitz, D. M., Toner, K., Goren, D., & Wilson, H. R. (2008). Looking while unhappy: mood-congruent gaze in young adults, positive gaze in older adults. *Psychological Science, 19*(9), 848-853. doi:10.1111/j.1467-9280.2008.02167.x
- Isaacowitz, D. M., Toner, K., & Neupert, S. D. (2009). Use of gaze for real-time mood regulation: Effects of age and attentional functioning. *Psychol Aging, 24*, 989-994. doi:10.1037/a0017706
- Isaacowitz, D. M., Wadlinger, H. A., Goren, D., & Wilson, H. R. (2006). Selective preference in visual fixation away from negative images in old age? An eye-tracking study. *Psychol Aging, 21*, 40-48. doi:10.1037/0882-7974.21.1.40
- Itier, R. J., & Batty, M. (2009). Neural bases of eye and gaze processing: the core of social cognition. *Neurosci Biobehav Rev, 33*(6), 843-863. doi:10.1016/j.neubiorev.2009.02.004
- Kapucu, A., Rotello, C. M., Ready, R. E., & Seidl, K. N. (2008). Response bias in "remembering" emotional stimuli: a new perspective on age differences. *J Exp Psychol Learn Mem Cogn, 34*(3), 703-711. doi:10.1037/0278-7393.34.3.703
- Kensinger, E. A. (2008). Age differences in memory for arousing and nonarousing emotional words. *J. Gerontol. B Psychol Sci Soc Sci, 63B*, 13-18.
- Kensinger, E. A., Brierley, B., Medford, N., Growdon, J. H., & Corkin, S. (2002). Effects of normal aging and Alzheimer's disease on emotional memory. *Emotion, 2*, 118-134. doi:10.1037/1528-3542.2.2.118

- Kensinger, E. A., & Corkin, S. (2004). Two routes to emotional memory: distinct neural processes for valence and arousal. *Proc. Natl. Acad. Sci. U. S. A.*, *101*(9), 3310-3315. doi:10.1073/pnas.0306408101
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007a). Effects of emotion on memory specificity in young and older adults. *J. Gerontol. B Psychol Sci Soc Sci*, *62*(4), P208-P215.
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007b). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of memory and language*, *56*(4), 575-591.
- Kensinger, E. A., & Schacter, D. L. (2007). Memory and emotion. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.), *The handbook of emotions* (3rd ed., pp. 601-617). New York: Guilford.
- Kensinger, E. A., & Schacter, D. L. (2008). Neural processes supporting young and older adults' emotional memories. *Journal of Cognitive Neuroscience*, *20*(7), 1161-1173.
- Knight, M., Seymour, T. L., Gaunt, J. T., Baker, C., Nesmith, K., & Mather, M. (2007). Aging and goal-directed emotional attention: distraction reverses emotional biases. *Emotion*, *7*, 705-714. doi:10.1037/1528-3542.7.4.705
- Koster, E. H., Crombez, G., Verschuere, B., & De Houwer, J. (2004). Selective attention to threat in the dot probe paradigm: Differentiating vigilance and difficulty to disengage. *Behaviour research and therapy*, *42*(10), 1183-1192.
- Krendl, A. C., & Ambady, N. (2010). Older adults' decoding of emotions: role of dynamic versus static cues and age-related cognitive decline. *Psychology and Aging*, *25*(4), 788-793. doi:10.1037/a0020607
- Krumhuber, E. G., Kappas, A., & Manstead, A. S. R. (2013). Effects of Dynamic Aspects of Facial Expressions: A Review. *Emotion Review*, *5*(1), 41-46. doi:10.1177/1754073912451349
- LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*(1), 54-64. doi:10.1038/nrn1825
- Larcom, M. J., & Isaacowitz, D. M. (2009). Rapid emotion regulation after mood induction: age and individual differences. *J. Gerontol. B Psychol Sci Soc Sci*, *64*(6), 733-741. doi:10.1093/geronb/gbp077
- Leclerc, C. M., & Kensinger, E. A. (2008). Age-related differences in medial prefrontal activation in response to emotional images. *Cognitive, Affective, & Behavioral Neuroscience*, *8*(2), 153-164. doi:10.3758/cabn.8.2.153
- Leclerc, C. M., & Kensinger, E. A. (2011). Neural processing of emotional pictures and words: A comparison of young and older adults. *Developmental neuropsychology*, *36*(4), 519-538.

- Levine, L. J., & Edelstein, R. S. (2009). Emotion and memory narrowing: A review and goal-relevance approach. *Cognition & Emotion*, 23(5), 833-875. doi:10.1080/02699930902738863
- Li, S.-C., Lindenberger, U., & Sikström, S. (2001). Aging cognition: from neuromodulation to representation. *Trends Cognit. Sci.*, 5(11), 479-486.
- Lindquist, K. A., Wager, T. D., Kober, H., Bliss-Moreau, E., & Barrett, L. F. (2012). The brain basis of emotion: a meta-analytic review. *Behavioral and Brain Sciences*, 35(3), 121-143. doi:10.1017/S0140525X11000446
- Löckenhoff, C. E., & Carstensen, L. L. (2004). Socioemotional selectivity theory, aging, and health: The increasingly delicate balance between regulating emotions and making tough choices. *Journal of Personality*, 72(6), 1395-1424.
- Marsiske, M., Lang, F. B., Baltes, P. B., & Baltes, M. M. (1995). Selective optimization with compensation: life-span perspectives on successful human development.
- Mather, M. (2012). The emotion paradox in the aging brain. *Ann. N. Y. Acad. Sci.* doi:10.1111/j.1749-6632.2012.06471.x
- Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K. N., . . . Carstensen, L. L. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, 15(4), 259-263.
- Mather, M., & Carstensen, L. L. (2003). Aging and Attentional Biases for Emotional Faces. *Psychological Science*, 14(5), 409-415. doi:10.1111/1467-9280.01455
- Mather, M., & Carstensen, L. L. (2005). Aging and motivated cognition: the positivity effect in attention and memory. *Trends in Cognitive Science*, 9, 496-502. doi:10.1016/j.tics.2005.08.005
- Mather, M., & Knight, M. (2005). Goal-directed memory: the role of cognitive control in older adults' emotional memory. *Psychol Aging*, 20(4), 554-570. doi:10.1037/0882-7974.20.4.554
- Mather, M., & Knight, M. R. (2006). Angry faces get noticed quickly: Threat detection is not impaired among older adults. *J. Gerontol. B Psychol Sci Soc Sci*, 61(1), P54-P57.
- Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspect Psychol Sci*, 6(2), 114-133. doi:10.1177/1745691611400234
- Murphy, N. A., Lehrfeld, J. M., & Isaacowitz, D. M. (2010). Recognition of posed and spontaneous dynamic smiles in young and older adults. *Psychology and Aging*, 25(4), 811-821.
- Murty, V. P., Ritchey, M., Adcock, R. A., & LaBar, K. S. (2011). Reprint of: fMRI studies of successful emotional memory encoding: A quantitative meta-analysis. *Neuropsychologia*, 49(4), 695-705. doi:<http://dx.doi.org/10.1016/j.neuropsychologia.2011.02.031>



- Murty, V. P., Sambataro, F., Das, S., Tan, H.-Y., Callicott, J. H., Goldberg, T. E., . . . Mattay, V. S. (2009). Age-related alterations in simple declarative memory and the effect of negative stimulus valence. *Journal of Cognitive Neuroscience*, *21*(10), 1920-1933.
- Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Science*, *9*(5), 242-249. doi:10.1016/j.tics.2005.03.010
- Öhman, A., Lundqvist, D., & Esteves, F. (2001). The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of personality and social psychology*, *80*(3), 381-396.
- Persson, J., Lustig, C., Nelson, J. K., & Reuter-Lorenz, P. A. (2007). Age differences in deactivation: a link to cognitive control? *Journal of Cognitive Neuroscience*, *19*(6), 1021-1032.
- Persson, J., Pudas, S., Nilsson, L.-G., & Nyberg, L. (2014). Longitudinal assessment of default-mode brain function in aging. *Neurobiol Aging*, *35*(9), 2107-2117. doi:<http://dx.doi.org/10.1016/j.neurobiolaging.2014.03.012>
- Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews Neuroscience*, *9*(2), 148-158. Retrieved from <http://dx.doi.org/10.1038/nrn2317>
- Pessoa, L. (2010). Emergent processes in cognitive-emotional interactions. *Dialogues in Clinical Neuroscience*, *12*(4), 433-448.
- Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proc. Natl. Acad. Sci. U. S. A.*, *99*(17), 11458-11463. doi:10.1073/pnas.172403899
- Phelps, E. A. (2004). Human emotion and memory: interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology*, *14*(2), 198-202. doi:10.1016/j.conb.2004.03.015
- Phillips, L. H., Slessor, G., Bailey, P. E., & Henry, J. D. (2014). Older Adults' Perception of Social and Emotional Cues. *The Oxford Handbook of Emotion, Social Cognition, and Problem Solving in Adulthood*, *9*.
- Reed, A. E., & Carstensen, L. L. (2012). The theory behind the age-related positivity effect. *Front Psychol*, *3*, 339. doi:10.3389/fpsyg.2012.00339
- Reed, A. E., Chan, L., & Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: Age differences in preferences for positive over negative information. *Psychol Aging*, *29*, 1-15. doi:10.1037/a0035194
- Reuter-Lorenz, P. A., & Lustig, C. (2005). Brain aging: reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology*, *15*(2), 245-251. doi:10.1016/j.conb.2005.03.016

- Reuter-Lorenz, P. A., & Park, D. C. (2010). Human neuroscience and the aging mind: A new look at old problems. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *65B*, 405-415. doi:10.1093/geronb/gbq035
- Riediger, M., Studtmann, M., Westphal, A., Rauters, A., & Weber, H. (2014). No smile like another: adult age differences in identifying emotions that accompany smiles. *Front Psychol*, *5*(480).
- Rosler, A., Ulrich, C., Billino, J., Sterzer, P., Weidauer, S., Bernhardt, T., . . . Kleinschmidt, A. (2005). Effects of arousing emotional scenes on the distribution of visuospatial attention: changes with aging and early subcortical vascular dementia. *Journal of Neurological Sciences*, *229-230*, 109-116. doi:10.1016/j.jns.2004.11.007
- Ruffman, T. (2011). Ecological Validity and Age-Related Change in Emotion Recognition. *Journal of Nonverbal Behavior*, *35*(4), 297-304. doi:10.1007/s10919-011-0116-3
- Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: implications for neuropsychological models of aging. *Neurosci Biobehav Rev*, *32*(4), 863-881. doi:10.1016/j.neubiorev.2008.01.001
- Ruffman, T., Murray, J., Halberstadt, J., & Taumoepeau, M. (2010). Verbosity and emotion recognition in older adults. *Psychology and Aging*, *25*(2), 492-497. doi:10.1037/a0018247
- Ruffman, T., Murray, J., Halberstadt, J., & Vater, T. (2012). Age-related differences in deception. *Psychol Aging*, *27*(3), 543.
- Ruffman, T., Ng, M., & Jenkin, T. (2009). Older adults respond quickly to angry faces despite labeling difficulty. *J. Gerontol. B Psychol Sci Soc Sci*, *64*(2), 171-179. doi:10.1093/geronb/gbn035
- Sakaki, M., Gorlick, M. A., & Mather, M. (2011). Differential interference effects of negative emotional states on subsequent semantic and perceptual processing. *Emotion*, *11*(6), 1263-1278. doi:10.1037/a0026329
- Sambataro, F., Murty, V. P., Callicott, J. H., Tan, H.-Y., Das, S., Weinberger, D. R., & Mattay, V. S. (2010). Age-related alterations in default mode network: impact on working memory performance. *Neurobiol Aging*, *31*(5), 839-852.
- Santangelo, V., Ho, C., & Spence, C. (2008). Capturing spatial attention with multisensory cues. *Psychonomic Bulletin & Review*, *15*(2), 398-403.
- Schultz, J., & Pilz, K. S. (2009). Natural facial motion enhances cortical responses to faces. *Experimental Brain Research*, *194*(3), 465-475.
- Shafer, A. T., Matveychuk, D., Penney, T., O'Hare, A. J., Stokes, J., & Dolcos, F. (2012). Processing of emotional distraction is both automatic and modulated by attention: Evidence from an Event-related fMRI investigation. *Journal of Cognitive Neuroscience*, *24*(5), 1233-1252.

- Shepherd, S. V. (2010). Following gaze: gaze-following behavior as a window into social cognition. *Front Integr Neurosci*, 4, 5. doi:10.3389/fnint.2010.00005
- Slessor, G., Bailey, P. E., Rendell, P. G., Ruffman, T., Henry, J. D., & Miles, L. K. (2014). Examining the time course of young and older adults' mimicry of enjoyment and nonenjoyment smiles. *Emotion*, 14(3), 532-544. doi:10.1037/a0035825
- Slessor, G., Miles, L. K., Bull, R., & Phillips, L. H. (2010). Age-related changes in detecting happiness: discriminating between enjoyment and nonenjoyment smiles. *Psychology and Aging*, 25(1), 246-250.
- Smith, S. D., Most, S. B., Newsome, L. A., & Zald, D. H. (2006). An emotion-induced attentional blink elicited by aversively conditioned stimuli. *Emotion*, 6(3), 523.
- St Jacques, P. L., Bessette-Symons, B., & Cabeza, R. (2009). Functional neuroimaging studies of aging and emotion: fronto-amygdalar differences during emotional perception and episodic memory. *J Int Neuropsychol Soc*, 15(6), 819-825. doi:10.1017/S1355617709990439
- St Jacques, P. L., Dolcos, F., & Cabeza, R. (2010). Effects of aging on functional connectivity of the amygdala during negative evaluation: a network analysis of fMRI data. *Neurobiol Aging*, 31(2), 315-327. doi:10.1016/j.neurobiolaging.2008.03.012
- Sullivan, S., & Ruffman, T. (2004). Social understanding: How does it fare with advancing years? *British Journal of Psychology*, 95, 1-18.
- Suzman, R., & Beard, J. (2011). Global Health and Aging. *National Institute on Aging*.
- Sze, J. A., Goodkind, M. S., Gyurak, A., & Levenson, R. W. (2012). Aging and emotion recognition: Not just a losing matter. *Psychol Aging*, 27(4), 940.
- Thomas, R. C., & Hasher, L. (2006). The Influence of Emotional Valence on Age Differences in Early Processing and Memory. *Psychol Aging*, 21(4), 821-825. doi:10.1037/0882-7974.21.4.821
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cogn Psychol*, 12(1), 97-136. doi:[http://dx.doi.org/10.1016/0010-0285\(80\)90005-5](http://dx.doi.org/10.1016/0010-0285(80)90005-5)
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. G. Ingle, M. A. Goodale, & R. J. Q. Mansfield (Eds.), *Analysis of visual behavior*. Cambridge, MA: MIT Press.
- Von Hippel, W., & Dunlop, S. M. (2005). Aging, inhibition, and social inappropriateness. *Psychology and Aging*, 20, 519. doi:10.1037/0882-7974.20.3.519
- von Hippel, W., & Henry, J. D. (2012). Social cognitive aging. *The handbook of social cognition*. London: Sage, 390-410.
- Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends Cognit. Sci.*, 9(12), 585-594. doi:10.1016/j.tics.2005.10.011

- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of Attention and Emotion on Face Processing in the Human Brain: An Event-Related fMRI Study. *Neuron*, *30*, 829-841.
- Vytal, K., Cornwell, B., Arkin, N., & Grillon, C. (2012). Describing the interplay between anxiety and cognition: from impaired performance under low cognitive load to reduced anxiety under high load. *Psychophysiology*, *49*(6), 842-852. doi:10.1111/j.1469-8986.2012.01358.x
- Wager, T. D., Davidson, M. L., Hughes, B. L., Lindquist, M. A., & Ochsner, K. N. (2008). Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*, *59*(6), 1037-1050. doi:10.1016/j.neuron.2008.09.006
- Wager, T. D., Kang, J., Johnson, T. D., Nichols, T. E., Satpute, A. B., & Barrett, L. F. (2015). A Bayesian model of category-specific emotional brain responses.
- Williams, L. M., Brown, K. J., Palmer, D., Liddell, B. J., Kemp, A. H., Olivieri, G., . . . Gordon, E. (2006). The mellow years?: neural basis of improving emotional stability over age. *The Journal of Neuroscience*, *26*(24), 6422-6430.
- Wolfe, J. M. (1994). Guided search 2.0 a revised model of visual search. *Psychon Bull Rev*, *1*(2), 202-238.
- Wright, C. I., Wedig, M. M., Williams, D., Rauch, S. L., & Albert, M. S. (2006). Novel fearful faces activate the amygdala in healthy young and elderly adults. *Neurobiol Aging*, *27*(2), 361-374. doi:<http://dx.doi.org/10.1016/j.neurobiolaging.2005.01.014>
- Yiend, J. (2010). The effects of emotion on attention: A review of attentional processing of emotional information. *Cognition & Emotion*, *24*(1), 3-47. doi:10.1080/02699930903205698
- Young, M. P., Scanneil, J. W., Burns, G. A., & Blakemore, C. (1994). Analysis of connectivity: neural systems in the cerebral cortex. *Reviews in the Neurosciences*, *5*(3), 227-250.
- Zanto, T. P., & Gazzaley, A. (2014). Attention and ageing. In A. C. Nobre & S. Kastner (Eds.), *The Oxford Handbook of Attention*. (pp. 927-971). Oxford; New York: Oxford University Press.

## **Chapter 2**

# Attention and Memory for Emotional Items: An Eye-tracker Approach

## Preface

In Chapter 1, I outlined and discussed the major findings in the field of emotion and ageing and some of the important issues that remain to be answered. I now move to the empirical section of my thesis in which I examine the emotional processes that occur in aging using various methods targeting more specific research questions. One of the questions that remain to be answered is whether the positivity effect relies on cognitive control or whether it is an automatic process. Several studies have attempted to address this question but the findings have proven inconsistent (for a review see Reed et al., 2014). It has to be noted that automaticity here refers to fast process whereas controlled processing are operationalized as slow which require more cognitive efforts.

The current chapter specifically focuses on this research question by developing a novel paradigm in which pairs of emotional-emotional and emotional-neutral items are presented and participants asked to attend to one target – positive or negative – and ignore the irrelevant items. The use of distractors allowed us to investigate whether the processing of positive items is automatic, if the positive distractors interfere with the memory of the targets and if they require additional cognitive effort. Measuring the pupillary responses during encoding and recognition stages allowed us to investigate the link between encoding and recognition stages for positivity in memory. Therefore, the paradigm used in this study can provide further evidence in order to bridge the gap between attention and memory domains in the emotional ageing literature.

*Note.* This chapter has been published in *PLOS ONE* (see Appendix A).

**Ziaei, M.,** von Hippel, W., Henry, J.D., Becker, S.I. Are age effects in positivity influenced by the valence of distractors? *PLOS one*

## **Abstract**

An age-related ‘positivity’ effect has been identified, in which older adults show an information-processing bias towards positive emotional items in attention and memory. In the present study, we examined this positivity bias by using a novel paradigm in which emotional and neutral distractors were presented along with emotionally valenced targets. Thirty-five older and 37 younger adults were asked during encoding to attend to emotional targets paired with distractors that were either neutral or opposite in valence to the target. Pupillary responses were recorded during initial encoding as well as a later incidental recognition task. Memory and pupillary responses for negative items were not affected by the valence of distractors, suggesting that positive distractors did not automatically attract older adults’ attention while they were encoding negative targets. Additionally, the pupil dilation to negative items mediated the relation between age and positivity in memory. Overall, memory and pupillary responses provide converging support for a cognitive control account of positivity effects in late adulthood and suggest a link between attentional processes and the memory positivity effect.

**Keywords:** Positivity effect, emotional distractors, pupil dilation, cognitive control.

## Introduction

A substantial body of evidence shows age-related decline in many cognitive domains, including speed of processing, memory, and attention [1]. Consistent with the possibility that reduced inhibitory control underlies many of these age-related losses [2], age-related declines in control operations such as inhibition have been shown to disrupt memory [3, 4], decision making [5], and various types of social functioning [6-8].

Despite these cognitive losses in late adulthood, emotion regulation tends to remain stable or show small to moderate gains with aging [9, 10]. A central tenet of socioemotional selectivity theory (SST) is that a sense of limited time among older adults leads to increased prioritization of emotion-focused goals over learning or future rewards [11]. It has been argued that this motivational shift may be responsible for the bias toward positive emotional information in attention, memory, and decision-making seen in late adulthood, a phenomenon that has been referred to as the aging positivity effect. Whatever the cause of this positivity effect might be (e.g., see aging brain hypothesis [12] or immunosenescence hypothesis [13]), the role of effortful processes in these attentional and memory processes remains unclear.

One possibility is that the aging positivity effect is driven by effortful cognitive control on the part of older adults to regulate their negative emotions [14, 15]. In support of this account, older adults' executive functioning predicts the magnitude of their positivity effect in both gaze and memory [16]. Additionally, older adults appear to use positivity in gaze as a regulatory mechanism when they are in a negative mood [17], and positivity effects in memory and visual attention disappear when cognitive resources are constrained by dividing attention [18, 19]. Other evidence, however, has not been consistent with the cognitive control account. For example, using pupillometry (pupil size) as an indicator of cognitive effort, it has been found that older adults exert minimal effort to engage in positively biased gaze when experiencing a negative mood [20]. Additionally, Rosler and colleagues [21] found that the positivity effect emerges among older adults with subcortical vascular dementia, a group characterized by prominent losses in cognitive control. Thomas and Hasher [22] also reported that older adults remembered a higher proportion of positive relative to negative words when they were simultaneously performing a numerical discrimination task. Therefore, it is unclear whether the positivity bias among older adults is relatively automatic, imposing only minimal demands on cognitive resources, or whether it might instead be the result of effortful processing.



In addition to the divided-attention tasks mentioned above, another way to identify the underlying cognitive mechanisms of the positivity effect is to measure the distribution of attention towards emotionally valenced items in the presence of distractors. In one study using negative affective priming, less interference from negative than positive distractors was found for older adults relative to their younger counterparts [23]. On the other hand, Ebner and Johnson [24] reported that older adults' performance was affected by happy emotional distractors more than younger adults. Brassens and colleagues [25] also found that older adults showed increased distractibility to happy faces when more attentional resources were available for processing the distractors. Contrary to these studies, Samanez-Larkin and colleagues [26] found that older adults were more susceptible to interference from a secondary non-emotional task relative to an emotional task. Taken together, the results of these studies indicate that effects of valence on attention may be inconsistent across different methodologies. However, perhaps most importantly in the context of the present study, the primary focus of these studies was on the role of distractors during the early attentional allocation stage, and not how these effects impacted older adults' subsequent memory. Thus, although there is a large literature focused on the impact of distractors on memory in cognitive aging [27-29], there remains a need to explore how selective attentional processes during encoding influence later memory outcomes for emotional items, and whether effort is implicated in these processes.

## **Current study**

Using a novel methodological approach, in this study we presented pairs of emotional-emotional or emotional-neutral pictures during encoding and instructed participants to either attend to positive or negative targets in the presence of emotional or neutral distractors. Simultaneous presentation of the distractors with the emotionally valenced targets has the advantage of allowing us to measure whether emotional distractors capture attention, as the extent to which distractors capture attention may vary as a function of age. Therefore, the memory outcome for the targets and the effort expended during encoding of the targets may be differentially impacted by the distractors' valence.

If positive items automatically attract older adults' attention, then memory for negative information might be worse in the presence of positive relative to neutral distractors, as positive distractors might capture attention despite intentions to attend to the negative targets. In contrast, if positive information is only more memorable via effortful control, then older adults should be

equally capable of ignoring positive and neutral distractors when their task is to focus on negative information. Thus, a cognitive control account of the positivity effect predicts that negative information will be equally well remembered in the presence of positive or neutral distractors.

To further distinguish between these competing accounts, we also measured cognitive effort via pupil dilation during encoding and recognition. Pupil dilation has been shown to function as an indicator of cognitive effort in a number of cognitive and perceptual tasks [30-32]. For instance, increased pupil size in response to enhanced working memory load has been demonstrated in both younger and older adults [33, 34]. Pupil changes were used in the present study to quantify degree of cognitive effort. If the positivity effect relies on effortful control, then older adults should show equivalent pupil dilation when processing negative targets in the presence of positive or neutral distractors. In contrast, the automaticity account predicts that older adults might show larger pupillary responses when processing negative targets in the presence of positive relative to neutral distractors (if positive distractors automatically capture attention and thereby require older adults to exert effortful control over their involuntary tendency to attend to the positive as they attempt to remain focused on the negative targets).

Converging evidence indicates that the positivity effect can emerge from how either positive or negative information is processed (for a review see Reed and Carstensen [35]). That is, people might process the positive information more thoroughly, or alternatively they might engage in effortful suppression processes when attending to negative information. In light of these possibilities, either decreased or increased pupil dilation for the negative items may emerge for older adults, irrespective of the distractors' valence. Increased pupil dilation for negative items could indicate that older adults are trying to suppress negative items from memory, or alternatively that they are trying to down-regulate their response to the negative items to maintain their positivity focus. Although our paradigm does not allow us to tease apart these two potential mechanisms, by measuring both memory and pupillary responses we can assess whether increased or decreased effort while processing positive or negative information mediates the positivity bias in memory. If enhanced pupillary responses to negative items mediate the memory positivity effect, this would suggest that older adults may be trying to suppress negative items at encoding. On the other hand, if enhanced pupillary responses to positive items mediate the memory positivity effect, this would suggest that older adults may be trying to enhance the encoding of positive items.

## **Methods**

### **Ethics statement**

This study was approved by the ethics committee in the School of Psychology at the University of Queensland. All participants were informed of their right to withdraw from the experiment and signed a consent form prior to the experiment. All participants were fully debriefed at the end.

### **Participants**

Forty one older adults (aged 60-83,  $M = 70.54$ ,  $SD = 4.5$ ) and forty-two younger adults (aged 18-29,  $M = 18.97$ ,  $SD = 2.2$ ) participated in this study. Older adults participated in exchange for \$30 AUD and were recruited from the Aging Mind Initiative at the University of Queensland. Younger adults were university students who participated in exchange for course credit. Due to technical issues in acquiring reliable data with an eye tracker, such as glaucoma, multifocal glasses, or excessive blinking during the task, six older adults and five younger adults were excluded. Consequently, 35 older adults (51% male) and 37 younger adults (48% male) contributed to the reported analyses.

All older adults scored 27 or higher on the Mini Mental State Exam [36]. Older adults reported less negative affectivity than younger adults as indexed by the 21-item version of the Depression Anxiety Stress Scales (DASS-21; Lovibond and Lovibond [37]),  $t(68) = 4.78$ ,  $p < .01$ ,  $d = 1.15$ . Older adults also reported fewer difficulties regulating their emotions, as indexed by the Difficulties in Emotion Regulation Questionnaire (DERQ; Gratz and Roemer [38]),  $t(62) = 6.23$ ,  $p < .01$ ,  $d = 1.58$ . Moreover, older adults showed a larger Stroop interference effect than younger adults,  $t(67) = 2.02$ ,  $p < .05$ ,  $d = 0.49$ , suggesting that they were more readily distracted by the incongruent colour words. None of these differences mediated the positivity effect in memory. Descriptive and inferential statistics for these background measures are presented in Table 1.

**Table 1. Descriptive and inferential statistics for the background and experimental measures**

Measure	Older adults		Younger adults		Inferential statistics	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>T</i>	<i>df</i>
Age	70.54	4.53	18.97	2.27		
MMSE	28.50	1.50	-	-	-	-
DERQ	63.91	10.42	84.56	15.83	6.23**	62
DASS-21	4.94	4.27	11.86	7.32	4.78**	68
Interference in Stroop test (%)	27.64	19.80	18.90	15.91	2.02*	67
Memory Positivity Effect	0.12	0.19	0.01	0.18	2.37*	69
FA for negative	0.26	0.19	0.18	0.16	2.01*	69
FA for positive	0.11	0.09	0.13	0.18	0.47	69
Hits for positive	0.77	0.12	0.70	0.20	1.67	69
Hits for negative	0.80	0.14	0.73	0.17	1.78	69

\*=  $p < .05$ , \*\*=  $p < .01$ . MMSE refers to Mini Mental Status Examination; DERQ refers to Difficulties in Emotion Regulation Questionnaire; DASS refers to Depression Anxiety Stress Scales. The percentage of interference in Stroop test refers to  $((RTs \text{ in incongruent} - RTs \text{ in neutral trials}) / RTs \text{ in neutral trials}) * 100$ . The overall positivity effect was operationalized as positive accuracy minus negative accuracy. FA refers to False Alarm rates.

### Materials and procedure

One hundred and ninety images were selected from the International Affective Picture Systems (IAPS, Lang, Bradley [39]). There were no significant differences between positive and negative pictures in arousal ratings based on Lang et al.'s (2008) database ( $t(69) = 1.68$ ,  $p = .09$ ). The arousal level of the pictures was also used as a covariate in the pupil dilation and memory accuracy analyses reported later in the manuscript. Of these pictures, 70 were negative (valence:  $M = 2.87$ ,  $SD = 0.41$ ; arousal:  $M = 4.90$ ,  $SD = 0.68$ ), 70 were positive (valence:  $M = 7.23$ ,  $SD = 0.45$ ; arousal:  $M = 4.68$ ,  $SD = 0.64$ ), and 50 were neutral (valence:  $M = 4.95$ ,  $SD = 0.26$ ; arousal:  $M = 3.02$ ,  $SD = 0.44$ ). Seventy-eight of these pictures (48 presented during the encoding phase and 30 not previously seen) were used for the recognition task. Equal numbers of pictures were selected from each emotional category for the recognition task (24 positive and 24 negative pictures) and an equal number of items were selected from each experimental condition (12 items of each valence

from the conditions with emotional distractors and 12 of each valence from the conditions with neutral distractors). For the not-previously seen pictures, an equal number of items were also selected from each emotional category; positive, negative and neutral (10 items from each category).

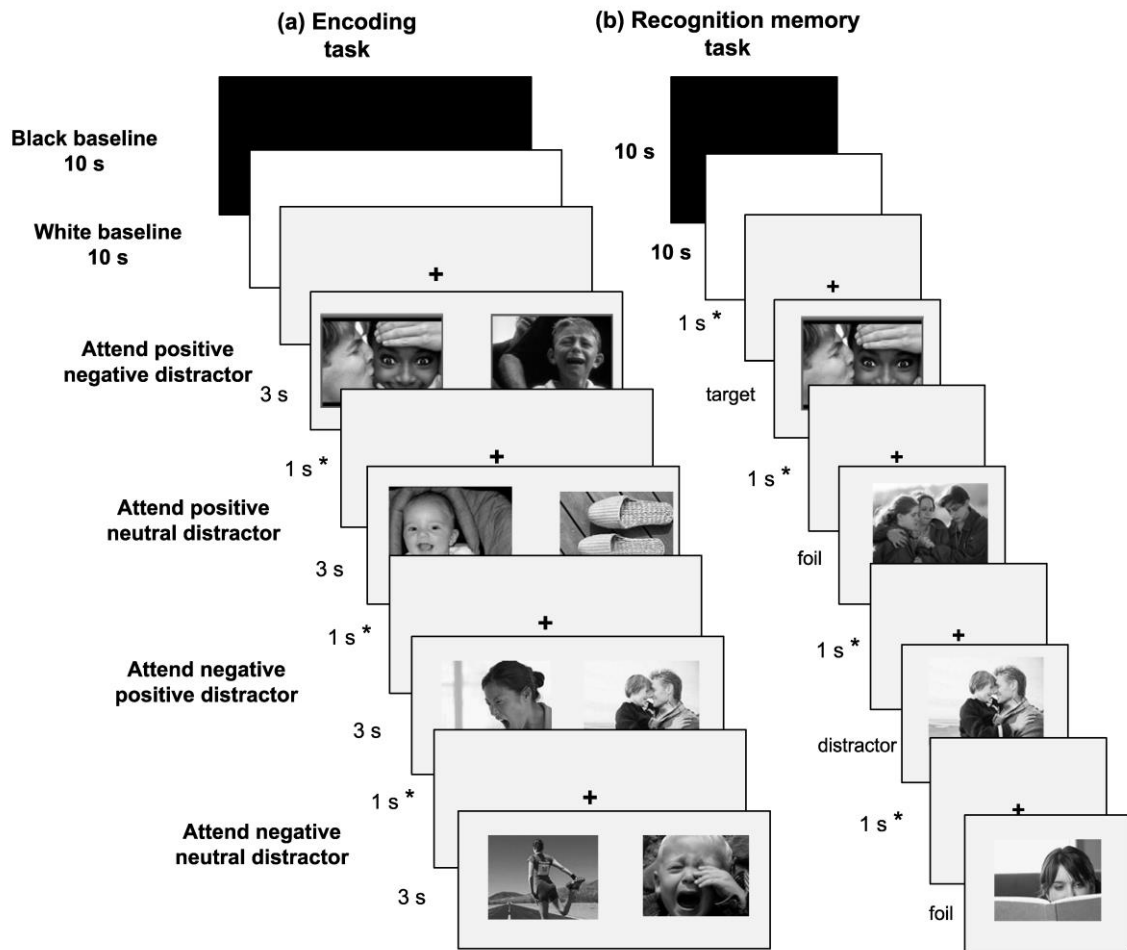
Because of differential sensitivity of the pupils to green, red, and blue light [40], a gray scale transformation of pictures was used and presented against a gray background. Pictures were balanced for luminance using a MATLAB program. The pictures were presented in 512x384 pixels on a 15" Dell computer monitor with 65cm distance from participants' eyes to the middle of the monitor. Fixation ratio and pupil dilation were recorded using a chin-rest SR EyeLink 1000 eye tracker (SR Research, Ontario, Canada) during the encoding and recognition phases. Pupil size measures were restricted to eye-fixations within the pictures' coordinates; pupil dilations outside the pictures' coordinates were excluded from analyses. Prior to the onset of the IAPS pictures, participants performed a 9 - point eye calibration to ensure that the eye-tracker was recording the position of the eyes accurately from different points on the screen. After calibration, the 9 - point validation procedure was applied to ensure that the calibration procedure had been performed correctly. During calibration and validation, participants were asked to focus on each fixation point until it disappeared and then move their eyes to the next fixation point on the screen. This procedure was then followed by presentation of a black and then a white screen for 10 seconds each to provide baseline measures of pupil dilation prior to the encoding phase. Participants' pupil responses were recorded continuously while the pictures were presented. However, only pupillary responses and fixation ratio during the picture presentations were included in the analyses. Eye tracker data recorded outside of the pictures and during the fixation crosses presented between each picture were discarded. Drift correction procedures were applied prior to each trial to ensure that participants' eyes were focused on the center of the screen prior to being shown the experimental stimuli.

## **Experimental design**

**Encoding task.** The encoding tasks used in conjunction with the eye-tracker consisted of four within-subjects conditions. The order of conditions was counterbalanced across participants. Pictures were presented in pairs of emotional-emotional or emotional-neutral stimuli with the target photo randomly placed on either side of the screen. Participants were instructed to attend to the target (positive or negative) and ignore the distractors (emotional or neutral). They were instructed to attend to positive images for 40 trials and to negative images in another 40 trials. Within each of

these conditions, 20 of the distractors were neutral in valence and 20 were of the opposite valence as the target image. Participants received an instruction prior to each condition that was followed by presentation of the pictures. Each pair of pictures was presented for 3 seconds with a minimum of 1 second crosshair between presentations to realign participants' gaze to the center of the screen (Fig. 1a).

**Recognition memory task.** After completion of the encoding and following a ten-minute filler task, participants performed an incidental recognition memory task. They were asked to indicate whether each picture was previously shown during the encoding phase by pressing one of two keys on the keyboard at their own pace (Fig. 1b). During the recognition memory phase, pupil sizes were recorded. Therefore, the calibration procedure was applied again before the recognition task to control for possible memory-load effect on pupil dilations, with baseline measurement of pupil dilations during 10-second presentations of black and white screens. The pupillary responses to these baseline measures were used for the transformation procedure applied to the recognition memory data (see below). Experimental sessions ranged from 90 minutes to 2 hours inclusive of a 15-minute break. Due to the drift correction applied after each trial, the maximum duration of the crosshair varied between subjects during both encoding and recognition tasks.



**Figure 1. Example of experimental design.** Each screen consisted of a pair of pictures presented side by side for 3 seconds during encoding (Panel a). During recognition (Panel b), participants were asked to indicate whether they had seen the picture before. Due to the drift correction applied after each trial, the maximum length of the fixation crosshair varied between subjects. \* indicates the minimum length of 1 second for each fixation crosshair presentation.

## Statistical analyses

**Memory discrimination.** For the recognition data, signal detection analyses were used to calculate accuracy scores by subtracting false alarms (FAs) from hits (as in Ziaei, Peira [41]). Due to the presence of extreme values in hits and FA scores, a loglinear approach was used as proposed by Stanislaw and Todorov [42]. This approach involved adding 0.5 to the number of hits and FAs and adding 1 to the number of signal and noise trials before calculating the hit and FA rates. Thus, memory accuracy scores were computed as loglinear hits minus loglinear false alarms. The false

alarms were subtracted from the hits based on the emotional category of the targets' valence, irrespective of the distractors' valence.

**Pupillary responses.** To control for individual differences between and among younger and older adults in pupil dilation at baseline, we applied transformation procedures similar to those used by Allard et al. [20]. Specifically, pupil diameters to the white screen were subtracted from pupil diameters to each picture, and this difference score was divided by the difference between the pupil diameters to the black and the white screen ( $[\text{current pupil diameter} - \text{minimum overall pupil diameter}] / [\text{maximum overall pupil diameter} - \text{minimum overall pupil diameter}]$ ). Here, higher scores indicate a greater range of change in pupil dilation (larger pupil diameter, thus increased cognitive effort) while viewing a particular image. This transformation procedure was applied for both encoding and recognition memory phases.

**Fixation ratio.** Although participants were instructed to attend to the targets and ignore the distractors, we also calculated the ratio of gaze fixations to targets and distractors, with fixations defined as gaze orientations to a particular point on the screen for at least 100 ms [44]. This ratio reflects the amount of time participants spent viewing the targets relative to the distractors in each condition. The fixation ratio was calculated using the procedure described by Isaacowitz et al. [43]:  $(\text{Target} - \text{distractors}) / (\text{Targets} + \text{distractors})$ .

**Positivity score.** Positivity scores in the presence of emotional and neutral distractors were computed separately by calculating the difference in memory between positive and negative targets in these two conditions. Overall positivity scores were calculated by averaging these two conditions (Table 1). Recognition memory and pupillary responses were subjected to mixed-model analyses of variance (ANOVAs) with age group as between-subjects factors and target valence and distractor types as within-subjects factors.

## Results

### Gaze fixation times for targets relative to distractors

A 2 (distractor type) x 2 (target valence) x 2 (age group) ANOVA on fixation ratios revealed a main effect of target valence,  $F(1,67) = 10.22$ ,  $p < .05$ ,  $\eta_p^2 = .88$ , and a main effect of distractor type,  $F(1,67) = 14.91$ ,  $p < .01$ ,  $\eta_p^2 = .96$ , indicating greater fixation times on negative items than



positive targets and greater fixation times on emotional distractors than neutral distractors (Fig. 2a). The interaction between target valence and distractor type was also significant,  $F(1,67) = 12.74$ ,  $p < .01$ ,  $\eta_p^2 = .94$ . Simple effects analysis revealed that fixation ratios were larger when negative items were presented with positive distractors than with neutral distractors,  $t(68) = 5.52$ ,  $p < .01$ ,  $d = 1.33$ . No significant differences in fixation ratios emerged for positive targets as a function of whether they were presented with negative or neutral distractors,  $t(69) = 0.38$ ,  $p = .70$ ,  $d = 0.09$ . These results suggest that both age groups fixated more on the negative targets when they were presented with positive distractors but the fixation ratio for positive targets was not influenced by the valence of the distractors. A main effect of age group also emerged,  $F(1,67) = 9.84$ ,  $p < .01$ ,  $\eta_p^2 = .87$ , with older adults spending more time fixated on the pictures rather than somewhere else compared to younger adults, independent of the valence of the pictures.

Additional analyses, including the number of switches between the targets and distractors as well as the latency of the initial fixation, are presented in Supporting Information Table S1.

### **Pupillary responses for targets during encoding**

The next stage in the analyses was to assess whether there were differential effects of age on pupil dilation (reflecting the level of cognitive effort) across the different valence and distractor conditions. With regard to pupillary responses during encoding, a 2 (age group) x 2 (target valence) x 2 (distractor type) repeated measures ANOVA on pupil size revealed a main effect of target valence,  $F(1,66) = 99.95$ ,  $p < .01$ ,  $\eta_p^2 = 1.0$ , with larger pupil sizes for negative than positive targets (Fig. 2b). The main effect of age group was also significant,  $F(1,66) = 32.14$ ,  $p < .01$ ,  $\eta_p^2 = 1.0$ , with older adults showing larger pupil dilations compared to younger adults (Fig. 2b). A significant interaction also emerged between target valence and age group,  $F(1,66) = 14.08$ ,  $p < .01$ ,  $\eta_p^2 = .95$ , such that although pupil sizes were larger for negative items than positive items in both groups, the magnitude of this effect was larger in the older group ( $M$  negative = .13,  $SD = .08$  vs.  $M$  positive = .02,  $SD = .04$ ),  $t(31) = 7.27$ ,  $p < .01$ ,  $d = 1.74$ , than the younger group ( $M$  negative = .05,  $SD = .04$  vs.  $M$  positive = .005,  $SD = .02$ ),  $t(35) = 7.28$ ,  $p < .01$ ,  $d = 1.42$ .

The interaction between target valence and distractors was significant,  $F(1,66) = 5.30$ ,  $p = .02$ ,  $\eta_p^2 = .62$ , with larger pupil sizes for positive targets presented with negative distractors relative to neutral distractors,  $t(69) = 2.63$ ,  $p < .01$ ,  $d = 0.42$ , but no significant difference in pupillary responses to the negative targets presented with neutral or positive distractors,  $t(69) = .01$ ,  $p = .99$ ,  $d$

< 0.01. The three way interaction was also significant,  $F(1,66) = 5.77$ ,  $p = .02$ ,  $\eta_p^2 = .65$ , such that older (but not younger) adults showed a significant difference in pupil dilation to positive targets presented with neutral and negative distractors (Fig. 2). None of the other effects were significant, all  $F_s < 1$ . The lack of an effect of positive distractor valence on pupil size suggests that positive distractor images were not automatically attracting older adults' attention. The increased pupil size shown by older relative to younger adults when encoding negative target images suggests a role for effortful processing either in inhibiting the negative items from memory and/or in the regulatory mechanisms recruited during encoding.

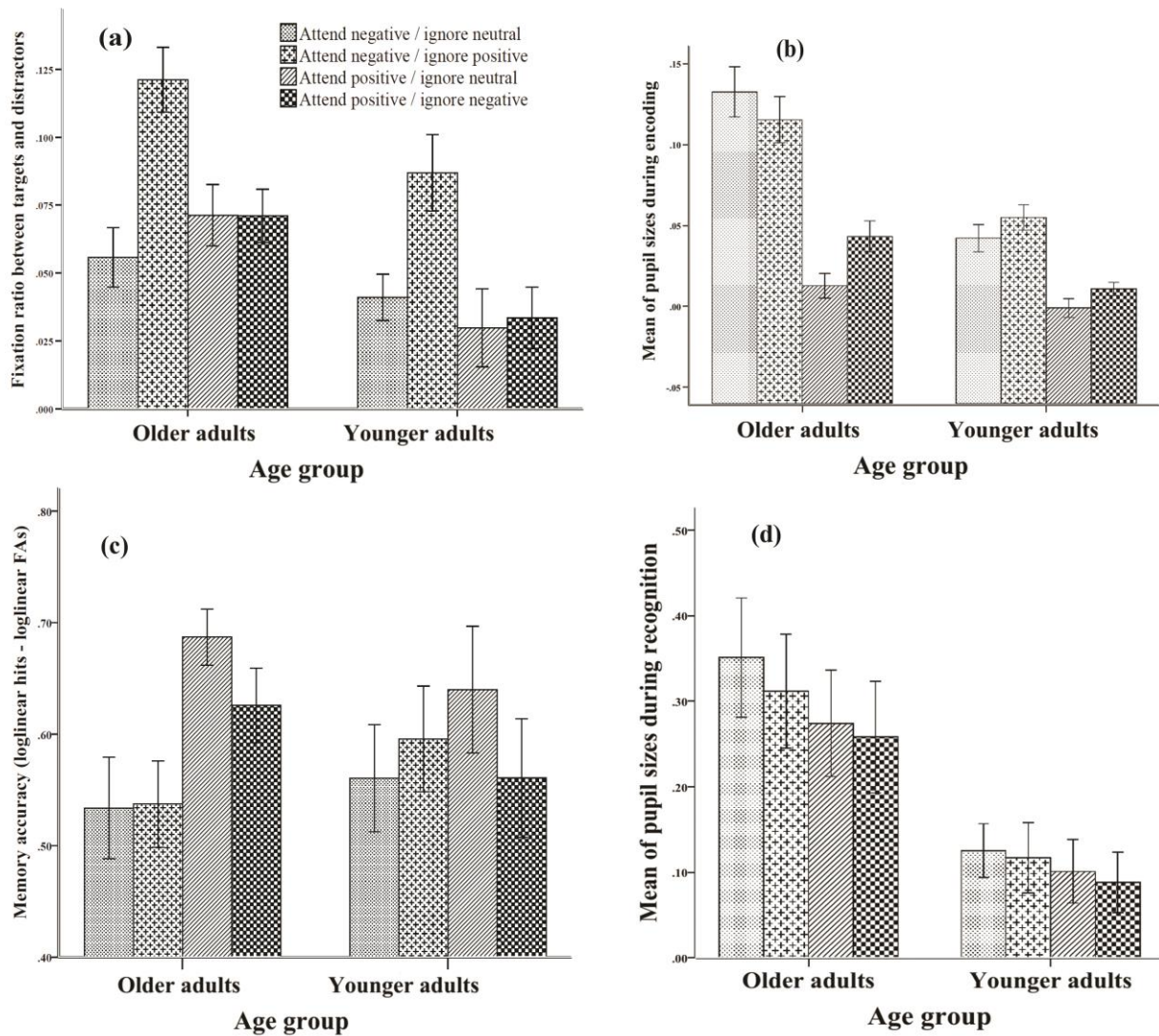
### **Recognition memory for targets**

A 2 (age group) x 2 (target valence) x 2 (distractor type) ANOVA on recognition accuracy scores revealed a main effect of target valence,  $F(1,68) = 10.16$ ,  $p < .01$ ,  $\eta_p^2 = .88$ , with better memory for positive items compare to negative items. This main effect was qualified by the predicted interaction between target valence and age group,  $F(1,68) = 4.81$ ,  $p = .03$ ,  $\eta_p^2 = .06$  (see Fig. 2c). Simple effects analyses revealed greater memory accuracy for positive targets than negative targets among older adults (M positive = .65, SD = .15 vs. M negative = .53, SD = .23),  $t(34) = 3.67$ ,  $p < .01$ ,  $d = 0.61$ , but not among younger adults (M positive = .57, SD = .35 vs. M negative = .55, SD = .30),  $t(35) = 0.69$ ,  $p = .49$ ,  $d = 0.06$ .

A significant interaction also emerged between target valence and distractor types,  $F(1,68) = 8.49$ ,  $p < .01$ ,  $\eta_p^2 = .11$ . Simple effects analyses revealed no differences in memory accuracy of negative targets when presented with positive vs. neutral distractors,  $t(69) = 0.86$ ,  $p = .38$ ,  $d = 0.03$ , but greater memory accuracy for positive targets when presented with neutral vs. negative distractors,  $t(70) = 3.66$ ,  $p < .01$ ,  $d = 0.87$ . No main effects emerged for distractor type,  $F(1,68) = 2.93$ ,  $p = .09$ ,  $\eta_p^2 = .04$ , or age group,  $F(1,68) = 0.01$ ,  $p = .90$ ,  $\eta_p^2 = .05$ , nor was there any interaction between distractor type and age group,  $F(1,68) = 0.05$ ,  $p = .81$ ,  $\eta_p^2 = .05$ , nor was there a three-way interaction,  $F(1,68) = 0.65$ ,  $p = .42$ ,  $\eta_p^2 = .12$ . Because positive distractors did not interfere with recognition memory of the negative targets more than neutral distractors, these results suggest that older adults do not differ from younger adults in this regard, and their attention was not automatically attracted to the positive images.

In addition to the analyses focused on memory accuracy, we also analyzed the hits and FA rates separately. The results from a 2 (age group) by 2 (positive vs. negative FAs) mixed model

ANOVA showed a main effect of FA valence,  $F(1,69) = 34.00, p < .01, \eta_p^2 = .33$ , with higher FA rates for negative relative to positive items. The interaction between age group and FA valence was also significant,  $F(1,69) = 9.28, p < .01, \eta_p^2 = .11$ , such that older adults showed more FAs for negative items relative to younger adults,  $F(1,69) = 4.04, p < .05, \eta_p^2 = .05$ , but did not differ from younger adults in positive FAs,  $F(1,69) = 0.22, p = .63, \eta_p^2 = .003$  (see Table 1). Similar analyses were performed for hit rates and none of the effects reached significance, all  $F_s < 1$ .



**Figure 2. Eye-tracker and memory findings during encoding and recognition phases.** Panels a and b represent fixation ratios and pupillary responses for targets, respectively. Panel c represents the memory accuracy for targets from each condition during recognition, and Panel d represents pupillary responses for targets during recognition. Bars represent one standard error of the mean (SEM).

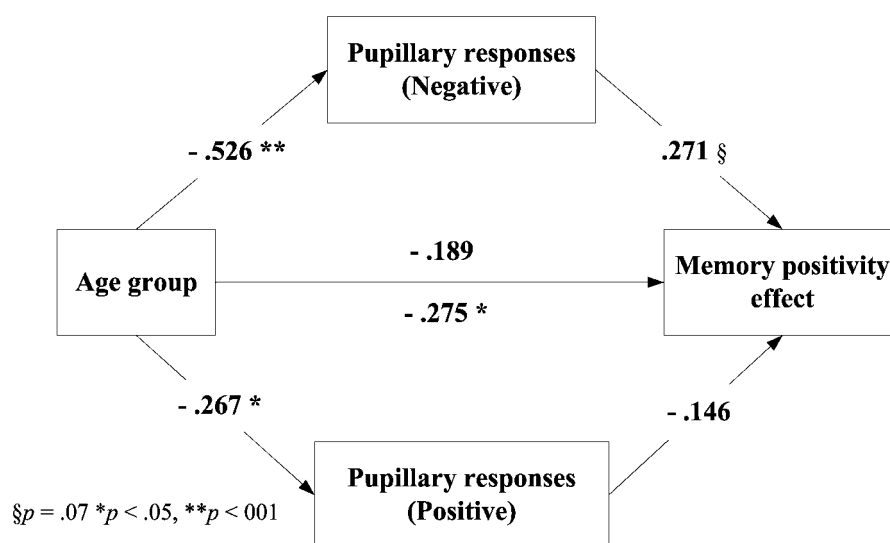
## Covariate analyses with arousal ratings

Given the potential sensitivity of pupil dilation to the arousal level of the pictures, the pupillary analysis was also conducted with the arousal level of the pictures as a covariate. The age by target valence interaction remained significant,  $F(1,63) = 6.03$ ,  $p < .05$ ,  $\eta_p^2 = .12$ , suggesting that the interaction was not a function of different arousal levels of the positive and negative pictures.

A similar analysis was also conducted on memory accuracy scores using the arousal level of the pictures as a covariate. The results continued to reveal a significant age by target valence interaction,  $F(1,63) = 6.87$ ,  $p < .05$ ,  $\eta_p^2 = .13$ , suggesting that the memory positivity effect that emerged among older adults relative to younger adults was also not a function of differential arousal levels of the pictures.

## Mediation analysis

Next, we examined whether the relation between age group and the memory positivity effect is mediated by the pupillary responses obtained from the encoding phase. The results indicated that the relationship between age group and positivity effect in memory was mediated by the cognitive effort exerted during encoding of negative items, but not positive items. The standardized indirect effect was measured using bootstrapping procedure with 10,000 resamples, and found to be  $-.05$ , 95% CI  $[-.13, -.006]$  (see Fig. 3). This result suggests that the memory positivity effect was mediated by the amount of the effort exerted during encoding of negative items, possibly in an effort to suppress negative information from memory.



**Figure 3. Mediation of pupillary responses on the effect of age on the memory positivity effect.** The numbers along the paths represent standardized regression coefficients. The coefficient below the path from age group to memory positivity represents the direct effect with no mediator in the model; the coefficient above the path represents the effect when pupillary dilation was included as a mediator.

### **Pupillary responses for targets during recognition**

Next, we analyzed the pupillary responses during recognition for the target items as a function of the distractor types with which they were presented. A 2 (age group) x 2 (target valence) x 2 (distractor type) ANOVA on pupil sizes during the recognition task revealed a main effect of target valence,  $F(1,66) = 23.69$ ,  $p < .01$ ,  $\eta_p^2 = .99$ , with larger pupil sizes for negative than positive targets. A significant interaction between target valence and age group also emerged,  $F(1,66) = 4.28$ ,  $p = .04$ ,  $\eta_p^2 = .53$ . Simple effects analyses revealed larger pupil dilations in response to negative than positive targets, and this effect was larger among older adults ( $M$  negative = .33,  $SD = .38$  vs.  $M$  positive = .26,  $SD = .36$ ),  $t(32) = 4.55$ ,  $p < .01$ ,  $d = 0.18$ , than younger adults ( $M$  negative = .12,  $SD = .20$  vs.  $M$  positive = .09,  $SD = .20$ ),  $t(33) = 2.17$ ,  $p = .03$ ,  $d = 0.15$  (Fig. 2d). Given that the pattern of pupillary responses during recognition resembled the pattern of results from encoding, it seems that greater cognitive effort was required during encoding and recognition of negative items relative to positive items for older adults.

### **Discussion**

The present study investigated the effect of instructed attention towards emotional targets in the presence of emotional versus neutral distractors during encoding, and examined the impact of these distractors on the subsequent recognition memory performances of older and younger adults. Consistent with prior research, older adults showed a memory positivity effect such that they were more accurate in their recognition of positive than negative items, whereas younger adults did not show this effect. The present study also extends the prior literature by showing that this memory positivity effect was independent of the valence of distractors during encoding. In particular, memory for negative information was not influenced by whether the distractors were positive or neutral, which suggests that positive items do not automatically capture the attention of older adults when they are intentionally directing attention to negative items. The results also provide evidence

that the cognitive effort older adults exert while encoding negative items mediates the relation between age and the memory positivity effect.

Previous studies have tested the role of cognitive control in the processing of emotionally valenced items using a range of experimental designs. Here we used a novel approach to examine the link between attention and memory and to assess whether distractors that vary in emotional valence differentially impact attention and memory for targets. The amount of effort required for processing positive distractors in particular, allowed us to infer whether cognitive control or automaticity accounts most readily explain positivity effects in memory. By presenting emotional-emotional and emotional-neutral pairs of stimuli during encoding, we were able to compare the effect of emotional versus neutral distractors on two dependent measures (i) participants' memory of the targets, and (ii) their pupillary responses. The lack of a significant difference in memory for negative targets when presented with positive or neutral distractors suggests that the presence of positive distractors did not automatically interfere with participants' encoding of the negative targets. These results therefore suggest that cognitive control plays a role in the aging positivity effect in memory. Additionally, negative distractors had a more detrimental effect than neutral distractors on memory for positive targets across both age groups. Taken together, these results are consistent with previous findings showing the resource-dependency of the positivity effect in participants who recruit brain regions known to be particularly important for cognitive control (e.g., frontal regions Brassens, Gamer [25]).

Consistent with the memory data, older adults did not show differential pupillary responses as a function of distractor valence when viewing negative pictures. These results indicate that positive distractors did not automatically attract older adults' attention away from negative targets, and thus did not require older adults to inhibit this automatic response in an effort to stay focused on the target items. Although the usefulness of pupillary responses to detect subtle changes in cognitive effort apparently decreases with age [33], pupillary responses in the current experiment were sensitive to target valence among older adults. Thus, these data are consistent with the recognition memory data in supporting a cognitive control account of the memory positivity effect.

It remains unclear, however, exactly why older adults showed a larger pupillary response to negative relative to positive targets. There are at least two possible interpretations of this pattern of findings. First, the processing of negative items might have required greater cognitive effort to down regulate negative emotions by older adults. Second, greater effort during the encoding of

negative items may have reflected older adults' efforts to suppress their memory for the negative images, resulting in better memory for the positive images during the recognition task. The increased FA rates and the mediation results support this latter interpretation.

We should note, however, that although the results remained unchanged when the arousal ratings of the pictures were used as a covariate in the analyses, it is still possible that pupillary responses for negative items might be related to differences in arousal levels. According to the negativity bias principle, “negative events are more salient, potent, and dominant than positive events [44]” and therefore, a stronger reaction may be elicited by negative items relative to positive items. Thus, the impact of arousal on pupil dilation and memory would benefit from further investigation, although it seems unlikely that the results of the current research reflect differences in arousal between negative and positive items.

Alternatively, the larger pupillary responses during encoding of negative items by older adults might reflect emotion-regulatory mechanisms. Such a possibility would be in line with previous studies suggesting that pupillary responses reflect regulation during negative moods [17, 20]. As regulatory mechanisms often demand cognitive effort, it is possible that the pupillary responses reflected the cognitive effort exerted for down-regulating negative emotions. This interpretation is consistent with three other research findings. First, previous studies in the emotion regulation literature indicate that emotion regulation imposes substantial demands on cognitive control operations [45, 46]. Second, older adults appear to be well equipped to regulate their emotions in the earliest stages of the emotion-generative process [10, 47, 48]. Third, a number of functional neuroimaging studies suggest that older adults use their cognitive control regions – prefrontal cortex regions – when encoding or processing negative items [49], which could reflect an effort to down-regulate negative emotions.

With regard to the fixation ratios, greater fixation time was spent on the negative targets presented with positive rather than neutral distractors across both age groups. Older adults were able to attend to the relevant items and ignore the irrelevant ones when instructed to do so, despite the fact that this ability tends to be impaired in late adulthood [50]. The converging results from fixation ratio, pupil dilations, and memory suggest that older adults were able to follow the instruction to attend to the targets. Although previous studies suggest that the positivity effect emerges when no experimental constraints are applied [35], our current findings suggest that the type of instruction might have an impact on the positivity effect. Goal-directed instructions to

process the relevant targets in this study might have supported the involvement of top-down processes in the positivity effect [35]. It remains for future studies to investigate how different types of regulatory mechanisms during encoding are linked to the positivity bias in memory.

One limitation of this study was that we did not include neutral targets. Future studies are therefore needed that investigate memory for neutral targets in the presence of emotional distractors. Moreover, further investigation using participants' own subjective ratings of arousal and valence is needed. Evidence indicates that there are some differences between older and younger participants in arousal rating of IAPS pictures [51]. Therefore, future studies should investigate whether participants' own subjective ratings of arousal for emotionally valenced items influence pupillary responses. Different methodological tools such as EEG or fMRI will also be important for capturing the underlying neural mechanisms of the aging positivity effect (for example see Brassens, Gamer [25]).

In conclusion, three primary findings emerged: 1) Older adults' recognition memory for negative items was not affected by the valence of distractors during encoding; suggesting that greater attention to positive information among older adults is not a result of automatic attention capture. 2) Consistent with these memory findings, no pupillary changes emerged as a function of distractor valence at either encoding or recognition of negative targets, again suggesting that positive distractors did not automatically capture attention from its intended target. 3) Pupillary responses to negative items mediated the relationship between age and the memory positivity effect, suggesting that older adults may have suppressed the negative items from their memory during encoding. Taken together, these data provide further insights into the link between attentional processes and later recognition memory, and provide support for a cognitive control account during encoding that leads to a memory positivity effect in late adulthood.



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## References

1. Reuter-Lorenz PA, Park DC. Human neuroscience and the aging mind: A new look at old problems. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*. 2010; 65B: 405-15.
2. Hasher L, Zacks RT. Working memory, comprehension, and aging: A review and a new view. In: Bower GH, editor. *The Psychology of Learning and Motivation*. 22: New York: Academic Press; 1988. p. 193-225.
3. Gazzaley A, Cooney JW, Rissman J, D'Esposito M. Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience*. 2005; 8: 1298-300.
4. Gazzaley A, Clapp W, Kelley J, McEvoy K, Knight RT, D'Esposito M. Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proc Natl Acad Sci U S A*. 2008; 105: 13122-6.
5. Lockenhoff CE, Carstensen LL. Aging, emotion, and health-related decision strategies: motivational manipulations can reduce age differences. *Psychology and aging*. 2007; 22: 134-46.
6. Henry JD, von Hippel W, Baynes K. Social inappropriateness, executive control, and aging. *Psychology and aging*. 2009; 24: 239-44.
7. von Hippel W, Silver LA, Lynch ME. Stereotyping against your will: The role of inhibitory ability in stereotyping and prejudice among the elderly. *Personality and Social Psychology Bulletin*. 2000; 26: 523-32.
8. von Hippel W, Dunlop SM. Aging, inhibition, and social inappropriateness. *Psychology and aging*. 2005; 20: 519.
9. Mather M, Carstensen LL. Aging and motivated cognition: the positivity effect in attention and memory. *Trends in cognitive sciences*. 2005; 9: 496-502.
10. Phillips LH, Henry JD, Hosie JA, Milne AB. Effective regulation of the experience and expression of negative affect in old age. *Journal of Gerontology: Psychological Sciences*. 2008; 63B: P138-P45.
11. Carstensen LL. The influence of a sense of time on human development. *Science*. 2006; 312: 1913-5.
12. Cacioppo JT, Berntson GG, Bechara A, Tranel D, Hawkey LC. Could an aging brain contribute to subjective well-being? The value added by a social neuroscience perspective. In: Todorov A, Fiske S, Prentice D, editors. *Social neuroscience*. Oxford; New York: Oxford University Press; 2011. p. 249-62.

13. Kalokerinos EK, von Hippel W, Henry JD, Trivers R. The aging positivity effect and immune function: Positivity in recall predicts higher CD4 counts and lower CD4 activation. *Psychology and aging*. 2014; 29: 636.
14. Nashiro K, Sakaki M, Mather M. Age differences in brain activity during emotion processing: reflections of age-related decline or increased emotion regulation? *Gerontology*. 2012; 58: 156-63.
15. Mather M. The emotion paradox in the aging brain. *Ann N Y Acad Sci*. 2012.
16. Allard ES, Isaacowitz DM. Are preferences in emotional processing affected by distraction? Examining the age-related positivity effect in visual fixation within a dual-task paradigm. *Neuropsychology, development, and cognition Section B, Aging, neuropsychology and cognition*. 2008; 15: 725-43.
17. Isaacowitz DM, Toner K, Neupert SD. Use of gaze for real-time mood regulation: Effects of age and attentional functioning. *Psychology and aging*. 2009; 24: 989-94.
18. Mather M, Knight M. Goal-directed memory: the role of cognitive control in older adults' emotional memory. *Psychology and aging*. 2005; 20: 554-70.
19. Knight M, Seymour TL, Gaunt JT, Baker C, Nesmith K, Mather M. Aging and goal-directed emotional attention: distraction reverses emotional biases. *Emotion*. 2007; 7: 705-14.
20. Allard ES, Wadlinger HA, Isaacowitz DM. Positive gaze preferences in older adults: assessing the role of cognitive effort with pupil dilation. *Neuropsychology, development, and cognition Section B, Aging, neuropsychology and cognition*. 2010; 17: 296-311.
21. Rosler A, Ulrich C, Billino J, Sterzer P, Weidauer S, Bernhardt T, et al. Effects of arousing emotional scenes on the distribution of visuospatial attention: changes with aging and early subcortical vascular dementia. *Journal of the neurological sciences*. 2005; 229-230: 109-16.
22. Thomas RC, Hasher L. The Influence of Emotional Valence on Age Differences in Early Processing and Memory. *Psychology and aging*. 2006; 21: 821-5.
23. Goeleven E, De Raedt R, Dierckx E. The positivity effect in older adults: the role of affective interference and inhibition. *Aging & mental health*. 2010; 14: 129-37.
24. Ebner NC, Johnson MK. Age-Group Differences in Interference from Young and Older Emotional Faces. *Cogn Emot*. 2010; 24: 1095-116.
25. Brassens S, Gamer M, Buchel C. Anterior cingulate activation is related to a positivity bias and emotional stability in successful aging. *Biological psychiatry*. 2011; 70: 131-7.
26. Samanez-Larkin GR, Robertson ER, Mikels JA, Carstensen LL, Gotlib IH. Selective attention to emotion in the aging brain. *Psychology and aging*. 2009; 24: 519-29.
27. Zanto TP, Gazzaley A. Neural suppression of irrelevant information underlies optimal working memory performance. *J Neurosci*. 2009; 29: 3059-66.

28. Clapp WC, Gazzaley A. Distinct mechanisms for the impact of distraction and interruption on working memory in aging. *Neurobiology of aging*. 2012; 33: 134-48.
29. Gazzaley A. Influence of early attentional modulation on working memory. *Neuropsychologia*. 2011; 49: 1410-24.
30. Hyönä J, Tommola J, Alaja A-M. Pupil dilation as a measure of processing load in simultaneous interpretation and other language tasks. *The Quarterly Journal of Experimental Psychology*. 1995; 48: 598-612.
31. Steinhauer SR, Siegle GJ, Condray R, Pless M. Sympathetic and parasympathetic innervation of pupillary dilation during sustained processing. *International Journal of Psychophysiology*. 2004; 52: 77-86.
32. Taylor JS. Pupillary response to auditory versus visual mental loading: A pilot study using super 8-mm photography. *Perceptual and Motor Skills*. 1981; 52: 425-6.
33. Van Gerven PWM, Paas F, Van Merriënboer JGG, Schmidt HG. Memory load and the cognitive pupillary response in aging. *Psychophysiology*. 2004; 41: 167-74.
34. Piquado T, Isaacowitz D, Wingfield A. Pupillometry as a measure of cognitive effort in younger and older adults. *Psychophysiology*. 2010; 47: 560-9.
35. Reed AE, Carstensen LL. The theory behind the age-related positivity effect. *Frontiers in psychology*. 2012; 3: 339.
36. Folstein MF, Folstein SE, McHugh PR. "Mini-Mental State": a practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*. 1975; 12: 189-98.
37. Lovibond PF, Lovibond SH. The structure of negative emotional states: Comparison of the Depression Anxiety Stress Scales (DASS) with the Beck Depression and Anxiety Inventories. *Behaviour research and therapy*. 1995; 33: 335-43.
38. Gratz KL, Roemer L. Multidimensional assessment of emotion regulation and dysregulation: Development, factor structure, and initial validation of the difficulties in emotion regulation scale. *Journal of Psychopathology and Behavioral Assessment*. 2004; 26: 41-54.
39. Lang PJ, Bradley MM, Cuthbert BN. International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Technical report A-8. 2008.
40. Bradley MM, Miccoli L, Escrig MA, Lang PJ. The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*. 2008; 45: 602-7.
41. Ziaei M, Peira N, Persson J. Brain systems underlying attentional control and emotional distraction during working memory encoding. *NeuroImage*. 2014; 87: 276-86.
42. Stanislaw H, Todorov N. Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*. 1999; 31: 137-49.

43. Isaacowitz DM, Wadlinger HA, Goren D, Wilson HR. Selective preference in visual fixation away from negative images in old age? An eye-tracking study. *Psychology and aging*. 2006; 21: 40-8.
44. Charles ST, Mather M, Carstensen LL. Aging and emotional memory: the forgettable nature of negative images for older adults. *Journal of Experimental Psychology General*. 2003; 132: 310-24.
45. Wager TD, Davidson ML, Hughes BL, Lindquist MA, Ochsner KN. Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*. 2008; 59: 1037-50.
46. Ochsner KN, Gross JJ. The cognitive control of emotion. *Trends in cognitive sciences*. 2005; 9: 242-9.
47. John OP, Gross JJ. Healthy and unhealthy emotion regulation: personality processes, individual differences, and life span development. *Journal of Personality*. 2004; 72: 1301-33.
48. Larcom MJ, Isaacowitz DM. Rapid emotion regulation after mood induction: age and individual differences. *J Gerontol B Psychol Sci Soc Sci*. 2009; 64: 733-41.
49. St Jacques PL, Bessette-Symons B, Cabeza R. Functional neuroimaging studies of aging and emotion: fronto-amygdalar differences during emotional perception and episodic memory. *Journal of the International Neuropsychological Society : JINS*. 2009; 15: 819-25.
50. Gazzaley A, Nobre AC. Top-down modulation: bridging selective attention and working memory. *Trends in cognitive sciences*. 2012; 16: 129-35.
51. Gröhn D, Smith J, Baltes PB. No aging bias favoring memory for positive material: Evidence from a heterogeneity-homogeneity list paradigm using emotionally toned words. *Psychology and aging*. 2005; 20: 579-88.

## Supporting Information

**Table S1.** Descriptive and inferential statistics for the additional analyses on the eye-tracker data

Measure	Older adults		Younger adults		Inferential statistics	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>t</i>	<i>df</i>
<b><i>Gaze switches</i></b>						
Attend negative/ignore neutral	1.80	0.34	1.84	0.32	0.51	70
Attend negative/ignore positive	1.68	0.23	1.78	0.33	1.49	70
Attend positive/ignore neutral	2.07	0.32	2.06	0.32	0.13	70
Attend positive/ignore negative	2.10	0.44	2.02	0.37	0.90	70
<b><i>Initial fixation duration in ms. (latency)</i></b>						
Attend negative/ignore neutral	1081.80	364.58	1661.57	479.16	5.75**	70
Attend negative/ignore positive	1060.39	357.36	1689.64	509.54	6.03**	70
Attend positive/ignore neutral	1055.60	355.85	1634.87	478.76	5.80**	70
Attend positive/ignore negative	1040.10	358.65	1663.04	471.87	6.28**	70

\*\*=  $p < .005$

## **Chapter 3**

### **Attention and Memory for Emotional Items: A Multivariate Approach**

## Preface

Chapter 2 describes a study in which we investigated the underlying cognitive mechanisms during memory encoding of emotionally valenced items. We were able to demonstrate that the positivity effect relies on cognitive control processes, and that attending to positive information requires cognitive resources in older adults. It was also found that the cognitive effort for processing negative items mediate the relation between age and the positivity effect. However, there is still lack of understanding of age-differences in the underlying neural networks associated with encoding of emotionally valenced items. Therefore, this chapter describes a study that aimed to examine the functional brain networks connected to the amygdala and ventrolateral prefrontal cortex two key regions involved in processing emotional items, during working memory encoding of emotional targets in young and older adults. I employed a multivariate method, partial least squares analysis, in order to identify age-related differences in functional brain networks engaged during encoding of positive and negative targets, and the importance of these networks in behavioural performance. Using the same paradigm that I have used in my previous publication (Ziaei et al., 2014, *Neuroimage*<sup>1</sup>), age-related differences during working memory encoding of emotionally valenced items was investigated in older and younger adults.

*Note.* The paper incorporated in this chapter is now under review in journal of *Neuropsychologia*.

<sup>1</sup> **Ziaei, M.**, Peira, N. & Persson, J. (2014), Brain systems underlying attentional control and emotional distraction during working memory encoding, *NeuroImage*, 87, 276-286



## **Abstract**

Previous findings indicate age-related differences in frontal-amygdala connectivity during emotional processing. However, direct evidence for age differences in brain functional activation and connectivity during emotional processing and concomitant behavioural implications is lacking. In the present study, we examined the impact of ageing on the neural signature of selective attention to emotional information during working memory (WM) encoding. Participants completed an emotional WM task in which they were asked to attend to emotional targets and ignore irrelevant distractors. Despite an overall reduction in accuracy for older relative to younger adults, no behavioural age effect was observed as a function of emotional valence. The functional connectivity pattern of left ventrolateral prefrontal cortex showed that two distinct networks were recruited by older adults for encoding of positive and negative emotional targets. The functional connectivity analysis using left amygdala further demonstrated that older adults recruited one single network during encoding of positive as well as negative targets, and that engagement of this network also contributed to higher memory performance and faster response times in this cohort. Our findings provide novel insights into the differential roles of functional brain networks connected to the PFC and amygdala during encoding of emotional items with advancing age.

**Keywords:** Ageing, Emotion, Working Memory, Functional Connectivity, PLS, fMRI

## Introduction

Ageing is characterized by an overall decline in several cognitive domains, including working memory (WM) and episodic memory. Behavioural and neural evidence has suggested that attentional deficits in suppressing task-irrelevant information underlie decline in WM performance with advancing age (Gazzaley and D'Esposito, 2007). However, despite overall age-related cognitive impairment in inhibiting task-irrelevant information, emotional processing is typically well preserved in ageing (Reuter-Lorenz and Lustig, 2005). According to one dominant theory, the socioemotional selectivity theory (SST), limited time perception in late adulthood leads to a motivational shift, and subsequent changes in processing of emotional information (Carstensen et al., 1999). Consistent with this account, a number of behavioural studies have demonstrated that older adults show a processing bias for positive, compared to negative information in attention (Allard and Isaacowitz, 2008; Mather and Carstensen, 2003, 2005; Samanez-Larkin et al., 2009), decision making (Lockenhoff and Carstensen, 2007; Löckenhoff and Carstensen, 2004), and memory (Charles et al., 2003; Mather and Knight, 2005; Ziaei et al., 2015). This processing bias is often referred to as the positivity effect (For a review see Reed et al. (2014)). It has been argued that the positivity effect relies on top-down attentional control subserved by the prefrontal cortex (Mather, 2012). However, there is limited understanding of the underlying neural correlates involved in the positivity effect.

In addition to behavioural support for a positivity effect in ageing, neuroimaging studies have reported age-related brain activation differences in regions involved in emotional processing, such as the amygdala and lateral PFC. More specifically, age-related increased recruitment of PFC, along with decreased amygdala activity is the most consistent finding across studies (for reviews see Mather (2012); Nashiro et al. (2012)). In addition to regional activation differences, age-related alterations in the functional connectivity between amygdala and PFC regions have been observed. For instance, St Jacques et al. (2010) showed that the functional connectivity between amygdala and the ventral anterior cingulate was greater during evaluation of negative items in older, compared to younger adults. Moreover, during the processing of positive relative to negative stimuli, older adults showed a stronger connectivity between medial PFC and retrosplenial cortex during deep processing (semantic elaboration), whereas younger adults demonstrated the opposite pattern (Ritchey et al., 2011a). The findings of PFC - amygdala functional connectivity during processing of emotional items suggest that older adults, more so than their younger counterparts,

may engage in regulatory mechanisms, particularly during processing of negative emotions. In light of these previous findings, and given the complex nature of emotional processes, it seems reasonable to assume that age-differences in these processes can be linked to changes in interactions among a set of functionally related nodes, rather than activation of discrete regions. Investigations on how brain regions interact may be critical for understanding how emotional and cognitive operations are affected by increasing age. Given that only a handful of studies have investigated age-related alteration in functional connectivity during emotional processing, and that the results have been inconclusive, the impact of ageing on the connectivity pattern between PFC and amygdala with the rest of the brain during WM encoding of emotional items needs to be further examined.

Here, we investigated age-related differences in neural activation and functional connectivity associated with selective attention during encoding of emotional items in WM. Both univariate and multivariate (spatial-temporal partial-least-squares, PLS) analyses were applied to 1) investigate age-related differences in behaviour and brain activation by instructed attention to emotional targets during WM encoding, 2) examine the functional connectivity pattern between *lateral PFC* and the rest of the brain in response to task-relevant emotional items, and 3) explore the functional connectivity pattern between the *amygdala* and the rest of the brain during instructed attention to task-relevant emotional items.

In order to achieve these aims, we first identified activity patterns associated with instructed attention to emotional target items across age groups using whole-brain univariate statistics. Key regions implicated in selective attention during WM encoding were subsequently used for seed-behavioural PLS to examine whether functional connectivity involved in WM encoding were modulated by emotional valence, if functional connectivity differed between age groups, and whether functional connectivity was related to task performance. Given previous evidence for a positivity effect in older adults, we hypothesized that younger and older adults would show differential recruitment of brain networks in response to positive and negative target items. If younger and older adults show age-invariant functional network engagement from each of the seed regions, results from the seed PLS analysis should reveal a common circuitry with a possibility for quantitative differences. Alternatively, if younger and older adults engage distinct networks that support emotional processing, then results from the seed PLS analysis should reveal separate networks that are differentially connected to the seed regions as a function of emotional valence.

## Methods and Materials

### Participants

Sixteen healthy younger adults and 15 healthy older adults participated in this study. Three younger and two older participants were excluded from the analysis due to extensive movement in the scanner and brain signal losses. Therefore, analyses were conducted on the data from 13 younger adults (9 females;  $M = 22.6$ ,  $SD = 1.69$ ; range = 23-26 years) and 13 older adults (9 females;  $M = 68.23$ ,  $SD = 3.7$  years; age range = 64-74). Younger participants were undergraduate students recruited from Stockholm University and older adults were community volunteers. All participants were right-handed, Swedish speakers, with no history of neurological or psychiatric problems, and had normal or corrected-to-normal vision using MRI compatible glasses. All participants were screened for claustrophobia, neurological and psychiatric medications, and MRI contraindications. Additionally, older adults were screened for cognitive impairments using Mini Mental State Examination (MMSE; Folstein et al. (1975)). All participants took part in two separate test sessions; one for behavioural assessment, and one for the fMRI scanning session. Informed consent was obtained from all participants. The investigation was approved by the Ethics Committee in Stockholm. Participants were paid 800 SEK (~ \$95 USD) for their participation. Descriptive and inferential statistics for these background measures are presented in Table 1.

**Table 1.** Descriptive and inferential statistics for the background measures for younger and older adults.

Measures	Older adults	Younger adults	Inferential statistics	
	<i>Mean (SD)</i>	<i>Mean (SD)</i>	<i>t</i>	<i>df</i>
<i>Age</i>	68.23(3.7)	22.53(1.71)		
<i>Gender</i>	9 females, 4 males	9 females, 4 males		
<i>MMSE</i>	27.61(1.19)	-		
<i>ERQ</i>				
Reappraisal	24.30(9.25)	30.23(7.06)	1.83	24
Suppression	10.00(3.87)	11.38(5.28)	0.76	24
<i>Stroop test</i>				
Congruent (ms.)	1428(261.11)	842.72(183.60)	6.62*	24
Incongruent (ms.)	1650.95(308.76)	1034.30(209.60)	5.98*	24
Neutral (ms.)	1313.85(184.80)	817.99(168.19)	7.15*	24

\*=  $p < .05$ ; MMSE = Mini Mental State Examination, ERQ = Emotion Regulation Questionnaire Stroop effect in ms. refers to incongruent minus congruent trials. RTs in incongruent – RTs in neutral trials) / RTs in neutral trials)\*100

## Materials

Stimuli consisted of seven hundred eighty six pictures that were drawn from the International Affective Pictures Systems (IAPS; Lang et al., 2008). Of these pictures, 312 were rated as negative (valence:  $M = 2.83$ ,  $SD = 1.7$ , arousal:  $M = 5.54$ ,  $SD = 2.17$ ), 312 as positive (valence:  $M = 6.79$ ,  $SD = 1.73$ ; arousal:  $M = 4.83$ ,  $SD = 2.3$ ), and 162 as neutral (valence:  $M = 4.87$ ,  $SD = 1.26$ ; arousal:  $M = 2.79$ ,  $SD = 2.0$ ). No significant differences were found between the arousal levels of positive and negative pictures ( $p > .05$ ). Pictures were presented against a black background using E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA, USA), and were presented at a  $600 \times 800$  pixel resolution.

## Procedure

The study consisted of two sessions; first a behavioural testing session which took place at the Department of Psychology at Stockholm University, and second, an fMRI session which took place at the MRI facility at the Karolinska hospital on a separate day. Both sessions were conducted within a week. During the behavioural testing session, participants completed the color-word Stroop test (Jensen and Rohwer, 1966), a complex short-term memory tests (operation span; Unsworth et al. (2005), and an emotion regulation questionnaire (Gross and John, 2003). Older adults also completed the MMSE. In addition, practice runs of the scanner tasks were performed in preparation for the scanning session. During the second session, and prior to MR scanning, participants were again instructed on how to perform the task, and also performed a practice run until they were familiarized with the task.

## Experimental Design

A modified version of a visual WM task developed by Gazzaley et al. (2005a) was used to investigate age-related changes in brain networks involved during selective attention to emotional items. Participants first received an instruction to either attend to negative or positive pictures (5 sec). Then, three sequential screens, each composed of a pair of pictures were presented (2.5 sec for

each pair separated by a 0.5 sec fixation cross). Presentation of all three screens were followed by a fixation cross (maintenance phase; 4 sec), and finally a WM probe (retrieval phase; 2 sec). Trials were separated by an intertrial interval (ITI) with a variable length (42% ITIs of 1.5 sec, 28% ITIs of 3 sec, 14% ITIs of 4.5 sec, 12% ITIs of 6 sec, and 4% ITIs of 7.5 sec), allowing for an independent estimation of the BOLD response on a trial-by-trial basis.

A full description of the task is provided elsewhere (Ziaei et al., 2014). In short, five different conditions were used: (1) attend to negative pictures/ignore positive pictures, (2) attend to negative pictures/ignore neutral pictures, (3) attend to positive pictures/ignore negative pictures, (4) attend to positive pictures/ignore neutral pictures, (5) and passive viewing (Figure 1). During encoding, pairs of emotional-neutral (positive-neutral or negative-neutral pairs) or emotional-emotional (positive-negative or negative-positive) pictures were presented, and participants were instructed to focus on the relevant target and ignore the irrelevant item. During retrieval, an emotional picture (with either positive or negative valence) was presented. Participants were instructed to respond with their index finger if the probe matched one of the previously presented pictures, and press with their middle finger if the probe did not match any of the previously presented pictures. All responses were collected using a scanner compatible response box (Lumitouch, Inc.). The valence of the retrieval cue (probe) and the target always matched. Thus, if participants were instructed to attend to positive picture (target), the probe also had positive valence. Fifty novel and 50 previously-shown images were used as probes. For the passive viewing condition, 50 % of the probes were positive and 50% were negative. Neutral pictures were never used as probes. For each condition, participants performed 20 trials in four different blocks (5 trials in each block) in two separate runs. The order of conditions was counterbalanced between participants.



**Figure 1. Example of experimental design.** The task includes five conditions; (1) attend negative pictures/ignore neutral pictures, (2) attend negative pictures/ignore positive pictures, (3) attend positive pictures/ignore neutral pictures, (4) attend positive pictures/ignore negative pictures, and (5) passive viewing of the pictures included in the target set. During retrieval, participants were asked to decide whether the probe was a part of the previously presented target set.

*Incidental recognition memory task:* After scanning, participants performed a self-paced incidental recognition memory task that included images that were included in the WM target set, but were not used as probes in the WM task. One-hundred and thirty pictures (100 previously shown pictures; 20 pictures from each condition) intermixed with 30 novel stimuli (10 from each of positive/negative/neutral categories) were chosen for the incidental recognition memory task. For each picture, participants were asked to indicate whether the picture had been presented previously

during the WM scanning task, and also, for each picture, were asked to rate the confidence of their responses using a 4-point scale (one of four responses: sure old, unsure old, unsure new, sure new).

### **Image Acquisition, Preprocessing, and Analyses**

Magnetic resonance imaging was performed using a 3-Tesla General Electric scanner MR750 equipped with a 32 channel head coil. Acquisition of functional data was achieved using a gradient echo-planar imaging sequence (37 transaxial slices, odd–even interleaved, 2 mm in plane resolution, gap: 0.5 mm, repetition time [TR]: 2000 ms, echo time [TE]: 30 ms, flip angle: 80°, field of view: 25 × 25 cm, voxel size: 2 × 2 × 2 mm). In order to allow for progressive saturation of the fMRI-signal, 10 dummy scans were collected, and discarded prior to experimental image acquisition. High-resolution T1-weighted structural images were also collected with a 3D fast spoiled gradient echo sequence (180 slices, with a 1 mm thickness, TR = 8.2 ms, TE = 3.2 ms, flip angle: 12°, field of view: 25 × 25 cm). The scanner task was presented to the participants on a computer screen, seen through a mirror mounted on the head coil. Participants were using headphones and earplugs to dampen scanner noise, and cushions inside the head coil minimized head movements.

All fMRI data were preprocessed using the statistical parametric mapping software (SPM8, Wellcome Department of Imaging Neuroscience, University College London, UK) implemented in MATLAB 2010b (Mathworks Inc., MA). Following slice timing correction, motion correction was done using the INRIAlign toolbox (Freire et al., 2002). Following coregistration, the “New Segment” procedure was used to segment the T1 image into gray matter (GM) and white matter (WM). The “DARTEL” toolbox was used to create a custom group template from the segmented GM and WM images (Ashburner, 2007). In addition, deformation from the group-specific template to each of the subject-specific GM/WM images was computed (i.e. flow field). Finally, the coregistered fMRI images and segmented GM/WM images were nonlinearly normalized, subject by subject, to the sample-specific template (using a subject-specific flow field), affine aligned into the Montreal Neurological Institute (MNI) template, and finally smoothed using an 8 mm FWHM Gaussian kernel. At the end, a correction was applied to remove noise in the data using the voxel-level linear model (Macey et al., 2004). The artifact repair toolbox (<http://cibsr.stanford.edu/tools/human-brain-project/artrepair-software.html>) was also utilized to correct for movement. None of the participants required more than 3% repair from all volumes.



*Whole-brain univariate analysis:* Functional MRI data was collected in two separate runs. Each run contained 10 trials of each condition (see above) with a total time of approximately 30 min. Given our aim of investigating brain networks involved during encoding and corresponding memory performance, only the encoding phase was modelled in the framework of the general linear model (GLM) as implemented in SPM8. Blocked sustained responses were modelled with a boxcar function, whereas event-related transient responses were modelled as delta functions based on trial onset. All regressors of interest were convolved with the hemodynamic response function (HRF). Only onsets of trials with correct responses were used in the analyses. In addition, in order to account for in-scanner movement, three translational [x y z] and three rotational (pitch, roll, and yaw) regressors obtained from the realignment step were included as covariates of no interest in the individual fixed effect analyses. Single-subject statistical contrasts were set up using the GLM, and group data were analysed in a random-effects model that differentiated between conditions and effects of age. Statistical parametric maps were generated using  $t$  statistics to identify regions activated according to the model. All results are reported in MNI space. Unless otherwise specified, whole-brain analyses were employed when no regional a-priori hypothesis was considered; in these cases, only effects surviving a family-wise error (FWE) corrected (cluster and/or height) level of  $P = .05$ .

*Voxel-Based Morphometry (VBM):* The VBM8 toolbox for SPM was used to examine age-related changes in the gray matter volume. The segmented modulated gray matter images from the DARTEL analysis were subjected to a between group  $t$ -test. Given that we were specifically interested in examining age-related structural changes in the amygdala and VLPFC, an explicit mask of each ROI was used to perform age comparisons of gray matter volume.

*Partial least squares (PLS) analyses:* To investigate multivariate relations between brain activation and behavioural performance, along with experimentally induced brain-brain functional connectivity in relation to ageing, seed-PLS analysis was conducted (McIntosh et al., 1996; McIntosh et al., 2004). For a detailed tutorial of PLS, see Krishnan et al. (2011). PLS analyses were used to extend the univariate analyses by using a network-level approach. In contrast to univariate analyses, which assess the significance of each voxel separately, PLS identifies activity patterns across the brain in relation to the experimental manipulation of interest. As the activation patterns identified by PLS reflects activity changes across all regions of the brain simultaneously, there is no need for multiple comparison correction. Moreover, PLS is a data-driven approach which

decomposes the data into a set of patterns that capture the most amount of variance in the data, rather than using prior assumptions by imposing contrasts between conditions of interest.

For this study, we were primarily interested in identifying brain networks involved in WM encoding of emotional targets. Therefore, we collapsed across conditions with emotional and neutral distractors resulting in three conditions; instructed attention to positive target items (positive condition), instructed attention to negative target items (negative condition), and passive viewing (passive). A cross-correlation matrix was computed as the correlation between behaviour (accuracy and RT), the temporal signature of the seed region, and activity in all other brain voxels across participants within each experimental condition (young-positive, young-negative, young-passive, old-positive, old-negative, and old-passive). This cross-correlation matrix was then subjected to Singular Value Decomposition (SVD) to identify a set of orthogonal latent variables (LVs), which represent linear combinations of the original variables. The first LV accounts for the largest covariance of the data, with progressively smaller amount for each subsequent LV. The first set of saliencies of each LV represent the pattern of covariance of behavioural performance, seed voxel, and the rest of the brain across experimental conditions. Additionally, the brain score reflects how strong each subject contributes to the pattern expressed in each LV.

The statistical significance of each LV was assessed using permutation tests that involve reordering the rows of the data matrix and recalculating the LVs of the reordered matrix using a SVD approach. The number of times a singular value exceeds the original singular value yields the probability of significance of original LVs. In the present study, 500 permutations were performed. In addition, stability of voxel saliencies contributing to each LV was determined using bootstrap estimation of standard errors (SEs), using 100 bootstrap samples. The Bootstrap Ratio (BR) was computed, and voxels with  $BR > 3$  (approximately a Z-score of 3, corresponding to  $p < 0.0001$ , two-tailed) were considered as reliable. All reliable clusters comprised at least 50 contiguous voxels. In addition, the upper and lower percentiles of the bootstrap distribution were used to generate 95% confidence intervals (CIs) around the brain and correlation scores respectively to facilitate interpretation. For example, brain/correlation scores were considered unreliable when CIs crossing zero and two groups were considered significantly different from each other if the CIs did not overlap.

We identified two seed regions for seed-behaviour PLS analysis; the left amygdala (-30 -6 -10) and the left VLPFC (-38 16 26). The selection of both of these seeds was based on two criteria;

first they need to show reliable task-related activation for instructed attention to emotional items in the univariate whole-brain analysis, and, second, there needs to be converging evidence from previous studies demonstrating the role of each region in emotional processing. In addition to being activated in the univariate analysis in the instructed attention vs. passive viewing contrast, the selection of the VLPFC region was based on the converging evidence supporting the role of this region in emotion regulation (Buhle et al., 2014), attention to emotional stimuli (Lindquist et al., 2012), and deep processing of emotional stimuli among older adults (Ritchev et al., 2011a). The amygdala has been reported as a key region involved in emotional processes in a number of neuroimaging and brain lesion studies (for instance see Adolphs (1999); Lindquist et al. (2012); Pessoa and Adolphs (2010)).

## **Results**

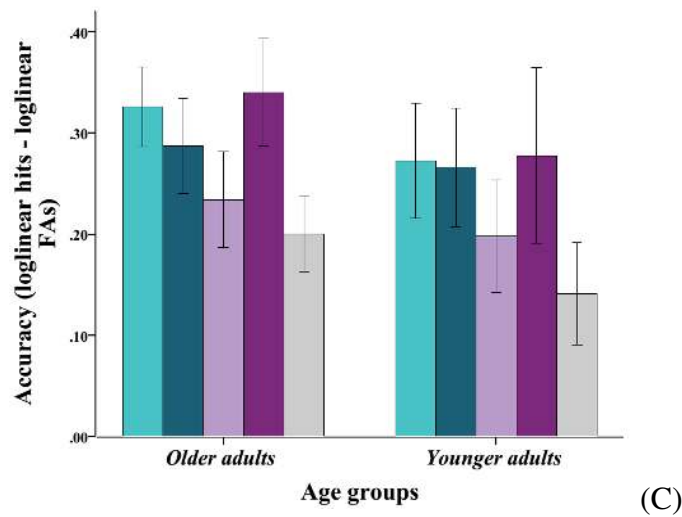
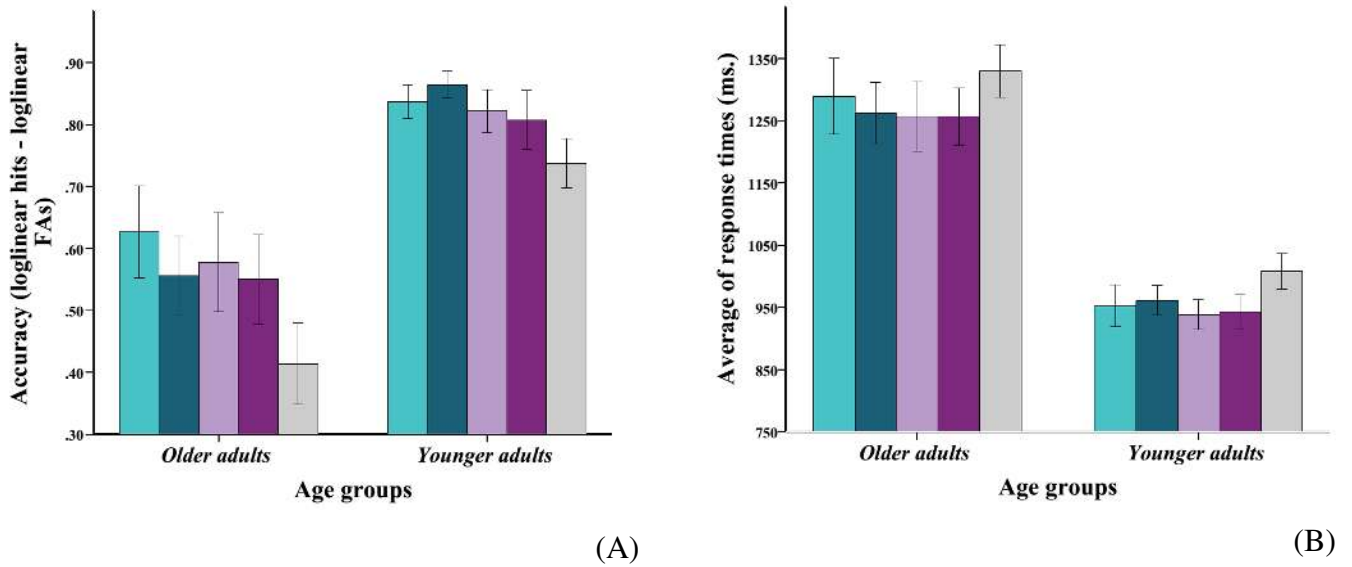
### **Behavioural Findings**

Signal detection theory was used to calculate memory accuracy scores by subtracting false alarms from hits. Due to extreme values (1- extreme bias in favour of yes to all conditions or 0 - extreme bias in favour of no responses), all data were put through loglinear transformation using the approach proposed by Stanislaw and Todorov (1999). The loglinear approach involved adding 0.5 to the number of hits and FAs and adding 1 to the number of signal and noise trials before calculating the hit and FA rates. Thus, memory accuracy scores were computed as loglinear hits – loglinear false alarms.

*Working memory performance:* First, we tested whether instructed attention to specific emotional targets had an impact on WM accuracy. As predicted, results from a 5 (condition) by 2 (age group) repeated measure ANOVA revealed a significant main effect of condition ( $F(4,96) = 7.36, p < .01, \eta_p^2 = .23$ ), showing higher WM accuracy in conditions with instructed attention, compared to passive viewing (all  $ps < .05$ ). No significant differences were found between instructed attention conditions (all  $ps > .05$ ). The main effect of age was also significant, showing that older adults had lower accuracy compared to young adults ( $F(1,24) = 15.27, p < .01, \eta_p^2 = .38$ ; Figure 2). The age group by condition interaction did not reach significance ( $F(4,96) = 1.09, p = .36, \eta_p^2 = .04$ ).

Next, we examined the role of instructed attention on reaction times (RTs) using a 5 (condition) by 2 (age group) repeated measure ANOVA. There was a significant reduction in RTs for instructed attention compared to passive viewing in across age groups ( $F(4,88) = 3.07, p = .02, \eta_p^2 = .12$ ), but the age by condition interaction was not significant ( $F(4,88) = .14, p = .96, \eta_p^2 = .01$ ). As expected, older adults responded slower relative to younger adults ( $F(1,22) = 44.72, p < .01, \eta_p^2 = .67$ ). No significant differences were found between instructed attention conditions (all  $ps > .05$ ).

*Incidental recognition memory performance:* We further investigated whether instructed attention during encoding influenced off-line recognition memory performance. First, a 5 (conditions) by 2 (age group) repeated measure ANOVA analysis revealed a significant main of condition ( $F(4,88) = 4.52, p < .05, \eta_p^2 = .17$ ), showing that recognition memory accuracy was higher for instructed attention conditions compared to passive viewing (all  $ps < .05$ ), with the exception of the condition where participants selectively attended to positive items while ignoring neutral items ( $p = .17$ ). Neither the main effect of age nor the age by condition interaction was significant ( $F_s < 1$ ).



■ *Attend negative / ignore neutral*     ■ *Attend positive / ignore negative*  
■ *Attend negative / ignore positive*     ■ *Passive viewing*  
■ *Attend positive / ignore neutral*

**Figure 2. Working memory and incidental recognition memory performance in both age groups.** Panel (A) represents accuracy during working memory (WM) retrieval. Panel (B) represents average of response times during WM retrieval. Panel (c) represents accuracy of responses during off-line recognition memory task administered outside scanner. Accuracy performance is based on loglinear hits – loglinear false alarms (FA). Bars represent 1 standard error of the mean (SEM).

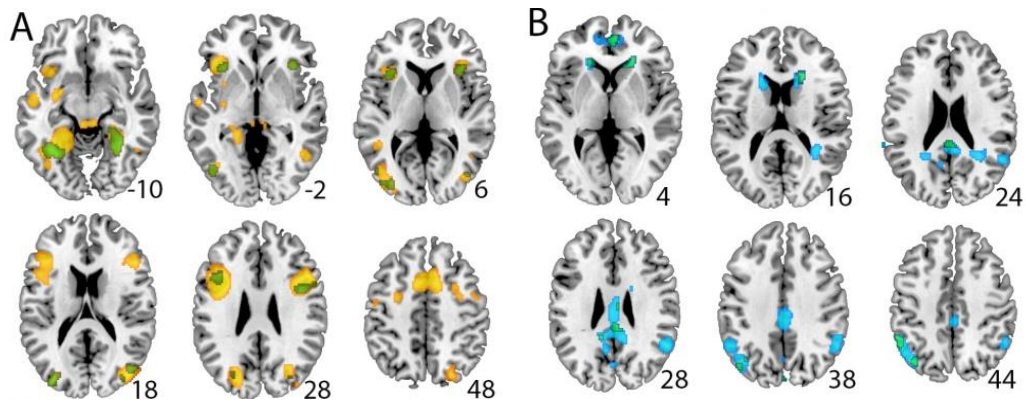
## fMRI Findings

### Univariate Whole-Brain Analyses

To investigate brain correlates associated with processing of emotional items during selective attention, we contrasted all conditions in which participants were instructed to attend to emotional targets with the passive viewing condition (*instructed attention* > *passive viewing*) across both groups using a full factorial model in SPM. A network of fronto-parietal regions, including bilateral ventrolateral prefrontal cortex (VLPFC), anterior cingulate cortex (ACC), insula, bilateral parietal cortex, and left amygdala was found to be associated with instructed attention to emotion during WM encoding. These findings are consistent with prior literature reporting increased fronto-parietal activation during instructed attention (Corbetta and Shulman, 2002b; Desimone and Duncan, 1995; Gazzaley and Nobre, 2012). The reverse contrast (*passive viewing* > *instructed attention*) showed significant deactivation in a set of regions known to be part of the default-mode network (DMN); including angular gyrus, inferior parietal cortex, , midcingulate cortex, precuneus, and posterior cingulate cortex (Buckner et al., 2008; Raichle et al., 2001). Enhanced suppression of the DMN has repeatedly been associated with task difficulty/effort across a variety of cognitive tasks e.g. (Buckner et al., 2008; Mazoyer et al., 2001; Shulman et al., 1997).

Next, we investigated age-related differences in brain activation identified from the whole-brain analysis across participants. These comparisons were masked by the overall activation pattern for task-positive (*instructed attention* > *passive viewing*) and task-negative (*passive viewing* > *instructed attention*) brain activation patterns across participants. Brain activation associated with instructed attention conditions to emotion for younger adults was compared to the corresponding pattern for older adults. Older adults showed less recruitment in a sub-set of the task-positive fronto-parietal regions, along with reduced DMN deactivation compared to younger adults (Figure 3).

To further investigate the role of amygdala, this region showed to be significant at a peak-level threshold during all instructed attention conditions relative to passive viewing. Therefore, for the following functional connectivity analysis, the coordinates acquired from univariate analysis were used (-30 -6 -10).



**Figure 3. Whole-brain univariate analysis.** (A) Represents the activation in all conditions vs. passive viewing (yellow color). Regions in green represent areas with reduced activation in older adults compared to younger adults. (B) Regions in blue color shows increased activation in passive viewing vs. all conditions (i.e. deactivation). Areas in green reflect reduced deactivation in older adults relative to younger adults.

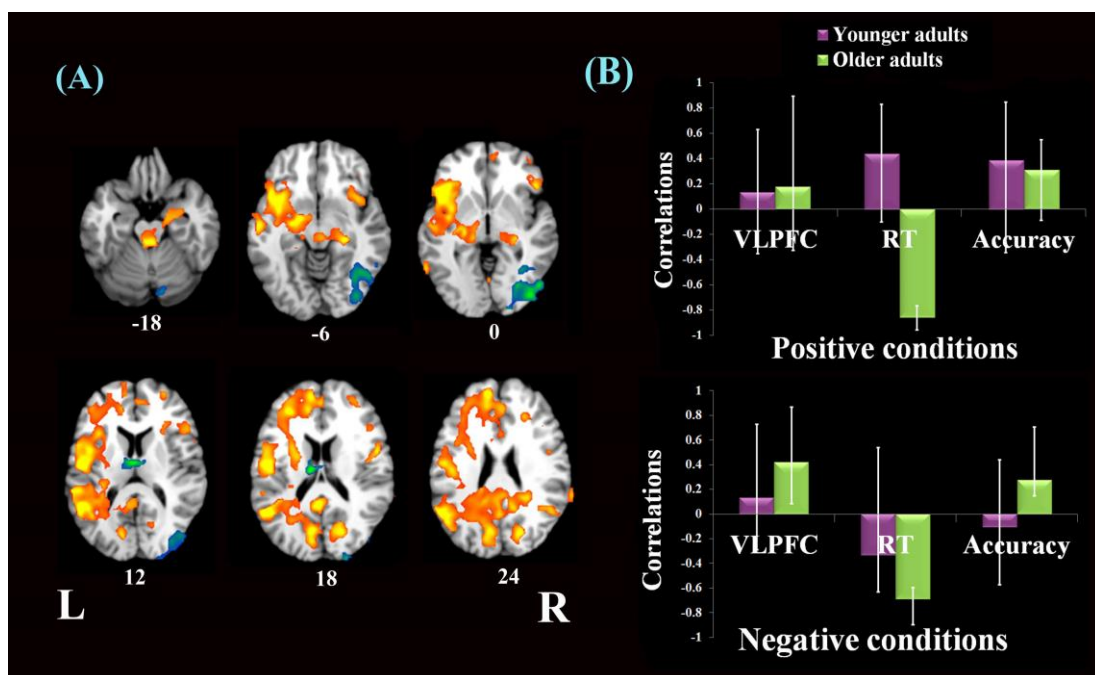
### Seed-Behavioural PLS Findings

Although results from the univariate analysis revealed that the left amygdala and the VLPFC was part of the network which was more activated during the instructed attention conditions relative to passive viewing across the two age groups, it is still plausible that the networks functionally connected to these regions might differ between age groups. Using seed-behavioural PLS, we therefore mapped brain network functional connectivity with each seed region (VLPFC and amygdala), and examined potential modulation of these networks as a function of target item emotional valence, and whether age-related changes in functional connectivity, as well as brain – behaviour correlations differed between younger and older adults.

#### Left VLPFC (-38 16 26)

The left VLPFC seed analysis resulted in two significant LVs. LV1 ( $p = .000$ ) accounted for 34% of the covariance in the data, and showed a positive seed and positive memory accuracy correlation during encoding of negative items among older adults. Although both younger and older adults engaged the network (LV1; Figure 4B, overlapping CIs across green and purple bars for VLPFC during negative condition), the correlation with seed was reliable among older adults, but not for the younger adults' group (i.e. purple bar's CI in the younger group crosses zero). This network also revealed a negative correlation with WM reaction time for both positive and negative

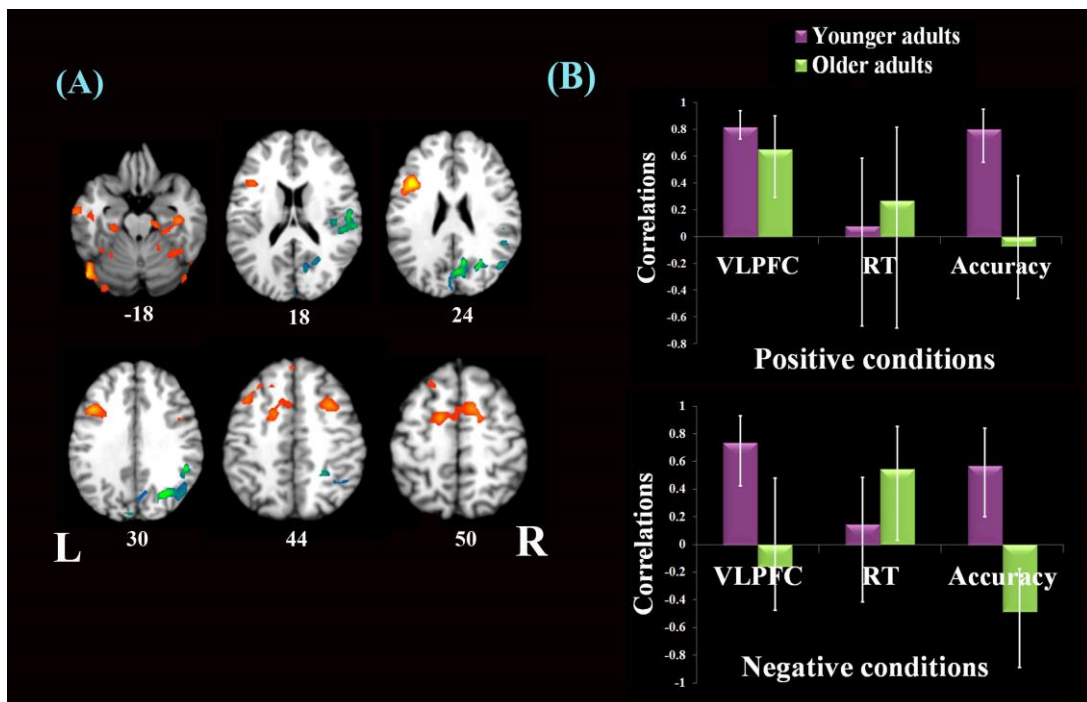
items among older adults, indicating that older adults who responded faster engaged this network (yellow regions) to a larger extent. Critically, the correlation with RT was remarkably different across the two groups (non-overlapping CIs across purple and green bars of RT). Regions that were positively connected to the seed region (and facilitated faster response in older group; regions in yellow) included right insula, right inferior parietal cortex, bilateral inferior frontal gyrus (IFG), right superior frontal gyrus, and right middle temporal gyrus (Figure 4 & Table 2). Regions with a negative functional connectivity (anticorrelated; regions in blue) with the seed region included right cerebellum, right middle occipital gyrus, and right precentral gyrus. No reliable correlation were found for seed, memory accuracy, or RT in the younger group in any of the conditions (CIs cross zero).



**Figure 4. Seed-PLS results using left VLPFC as a seed (LV1).** Panel A represents a pattern of whole brain activity in LV1. For LV1, regions shown in yellow indicate greater activity during negative condition in older adults only. Panel B represents brain scores from LV1 indicating significant correlations between the brain regions connected to the left VLPFC and behavioural performances, such as RTs and accuracy, during negative conditions among older group (Green bars). Error bars denote 95% confidence intervals for the correlations calculated using the bootstrap procedure.



The second LV ( $p = .010$ ) accounted for 14% of the covariance, and revealed a network which was positively correlated with the VLPFC during encoding of both positive and negative items among younger adults. This network also facilitated WM accuracy for positive and negative items in this group. This network which was positively connected to the seed region among younger adults for both conditions (regions in yellow) included left IFG, left superior medial gyrus, right hippocampus, right parahippocampus, bilateral fusiform gyrus (FG), right cerebellum, left middle temporal gyrus, left middle frontal gyrus, left inferior temporal gyrus, left superior parietal lobule (SPL), and the left thalamus. This particular network was also engaged during encoding of positive, but not negative items, in older adults' group. The engagement of this network was related to slower response time and lower WM accuracy for negative items in older adults (Figure 5 & Table 2). Note that, although both younger and older adults reliably and similarly engaged the network for positive conditions (LV2; Figure 5B, overlapping CIs across purple and green bars for positive conditions), the correlation with accuracy differed considerably between the two groups (non-overlapping CIs across purple and green bars for accuracy). Regions that were anticorrelated with the seed (regions in blue) included right IFG, right superior temporal gyrus (STG), and right occipital gyrus (Figure 5 & Table 2).



**Figure 5. Seed-PLS results using left VLPFC as a seed (LV2).** Panel A represents the whole brain functional connectivity associated with LV2. For LV2, regions depicted in yellow color

reflect areas with greater activity during encoding of positive conditions in older adults, and both positive and negative conditions in the younger group. Panel B represents the brain scores indicating the positive correlation between the brain networks connected to VLPFC during encoding of both emotional items and higher accuracy during retrieving of positive and negative items among younger adults (Purple bars).

Taken together, results from the left VLPFC seed functional connectivity analyses showed that, for older adults, VLPFC was connected to two separate networks during WM encoding of positive and negative items. One network facilitated faster response times in older adults in both conditions (LV1), and memory accuracy for negative items only. Younger adults, on the other hand, engaged one network for both encoding of positive and negative items, and this network was positively correlated with performance (LV2).

**Table 2.** Peak coordinates for clusters from the functional connectivity analysis using VLPFC (-38 16 26) as a seed region.

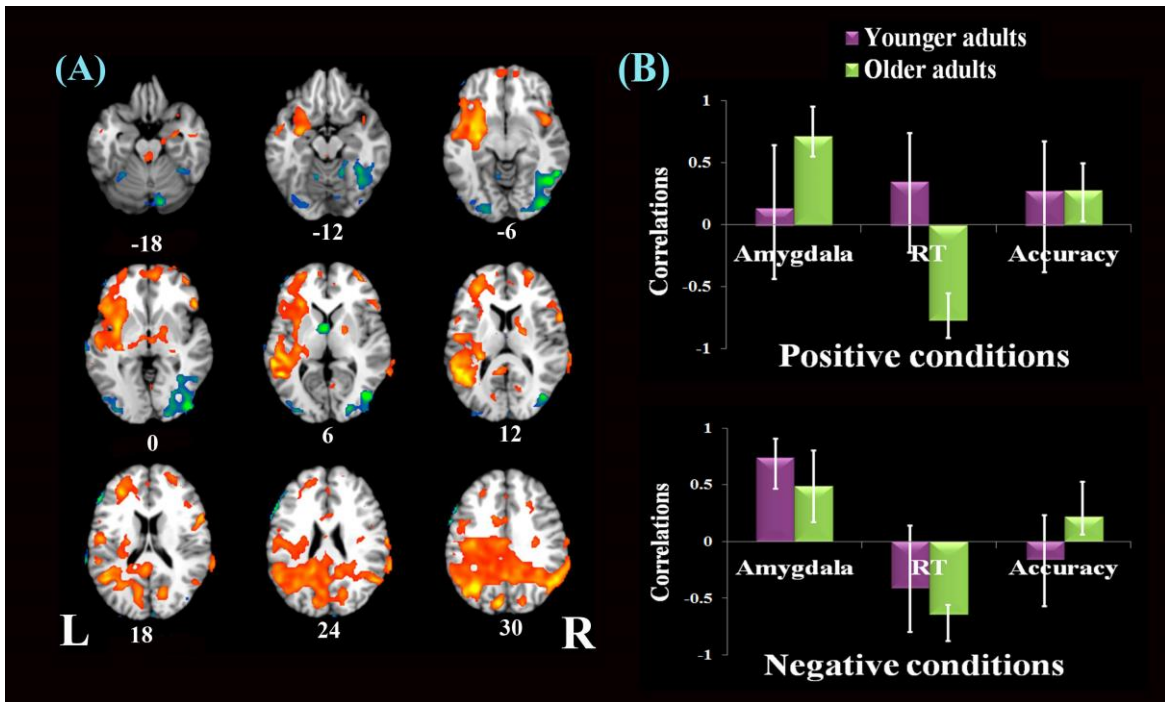
Regions	Hem	BA	MNI coordinates	BR
			XYZ	
<i><b>LV1</b></i>				
Middle Occipital Gyrus	R		[42 -80 0]	4.95
Cerebellum	R		[40 -66 -24]	4.74
Precentral Gyrus	R	6	[14 -22 72]	4.29
Cerebellum	R		[12 -74 -16]	3.90
Inferior Frontal Gyrus	R	45	[46 26 2]	-5.88
Medial Temporal Gyrus	R		[64 -46 8]	-5.58
Rolandic Operculum	R	44	[52 4 16]	-5.23
Inferior Parietal Cortex	R	40	[52 -52 30]	-5.08
Insula lobe	R		[38 12 -6]	-4.50
Superior Frontal Gyrus	R		[28 56 10]	-4.36
<i><b>LV2</b></i>				
Inferior Frontal Gyrus	L	44/45	[-40 18 26]	8.19
Superior Medial Gyrus	L		[-2 50 38]	6.17
Parahippocampus	R		[20 -22 -24]	5.26

Middle Frontal Gyrus	R		[32 30 38]	4.76
Hippocampus	R		[28 -24 -8]	4.75
Cerebellum	R		[44 -64 -26]	4.69
Fusiform Gyrus	L	37	[-34 -48 -22]	4.68
Middle Temporal Gyrus	L		[-48 -20 -14]	4.54
Middle Frontal Gyrus	L		[-38 16 46]	4.49
Superior Parietal Lobe	L	40	[-20 -78 52]	4.46
Thalamus	L		[-14 -30 -2]	4.45
Middle Frontal Gyrus	L		[-20 28 52]	4.42
Inferior Temporal Gyrus	L		[-54 -54 -6]	4.13
Fusiform Gyrus	R	37	[20 -48 -14]	3.94
Superior Occipital Gyrus	R		[28 -68 32]	-5.42
Superior Temporal Gyrus	R		[52 -26 8]	-5.00
Inferior Frontal Gyrus	R	44/45	[54 20 10]	-4.14

Hem = hemisphere, BA = Brodmann Area, BR = Bootstrap Ratio.

#### **Left Amygdala (-30 -6 -10)**

One significant LV was identified when the left amygdala was used as a seed. This LV ( $p = .0001$ ) accounted for 44% of the covariance in the data and exhibited a network that showed a positive seed correlation during encoding of both positive and negative items in the older group and only negative for the younger group. This network, including left middle temporal gyrus, right IFG, right superior and middle frontal gyrus, right insula, right hippocampus and right superior medial gyrus (yellow regions), was also engaged by older adults who showed higher accuracy and faster RTs during retrieving of both positive and negative items. Note that, although both younger and older adults engaged the network (LV1; Figure 6, overlapping CIs across green and purple bars for amygdala during positive condition), the correlation with seed was reliable in the old, but not for the younger adults (i.e. purple bar's CI in the younger adults crosses zero). For younger adults, however, this network was only correlated with the seed during encoding of negative items (Figure 6 & Table 3). No reliable correlation was found for RT or memory accuracy among younger adults (CIs cross zero).



**Figure 6. Seed-PLS results using left amygdala as a seed.** Panel A represents the functional connectivity pattern for LV1. Panel B represents a correlation between activity in left amygdala, RTs, accuracy, and the scores representing activity in regions seen in panel A. Error bars denote 95% confidence intervals for the correlations calculated using the bootstrap procedure.

**Table 3.** Peak coordinates for clusters from the functional connectivity analysis using amygdala (-30 -6 -10) as a seed region.

Regions	Hem	BA	MNI coordinates		BR
			XYZ		
<i>LV1</i>					
Middle Temporal Gyrus	L		[-50 -50 6]		9.06
Inferior Frontal Gyrus	R	44	[58 12 14]		6.44
Postcentral Gyrus	R		[64 -14 24]		6.41
Superior Frontal Gyrus	R		[26 16 38]		6.04
Middle Frontal Gyrus	R		[36 54 6]		5.89
Superior Medial Gyrus	R	9	[6 56 0]		5.15
Insula Lobe	R	13	[44 8 -6]		4.91
Hippocampus	R		[28 -8 -18]		4.37

Superior Medial Gyrus	R		[0 48 18]	3.20
Precentral Gyrus	L	6	[-60 8 28]	-6.46
Middle Temporal Gyrus	R	22	[42 -72 8]	-5.84
Cerebellum	R		[14 -80 -20]	5.09
	L		[-12 -52 -10]	-4.60
Middle Frontal Gyrus	L		[-42 56 4]	-3.90
Middle Occipital Gyrus	L		[-32 -88 8]	-3.87
Fusiform Gyrus	L	37	[-28 -50 -18]	-3.56
Cuneus	R		[8 -94 24]	-3.55
Middle Temporal Gyrus	L		[-68 -22 0]	-3.50

Hem = hemisphere, BA = Brodmann Area, BR = Bootstrap Ratio.

We were also interested to examine gray matter volume of the two seed regions used in the PLS analysis by utilizing VBM: the left VLPFC and left amygdala. The results from these analyses revealed that there were no significant age differences in gray matter volume in either of the ROIs at an FWE corrected threshold ( $p = .05$ ), suggesting that any age-related changes in the functional connectivity in these particular regions are not driven by gray matter atrophy in older adults' cohort.

## Discussion

The present study was designed to investigate age-related changes in brain functional activity and connectivity associated with instructed attention to emotional valence during WM encoding. We aimed specifically at identifying functional brain networks connected to the left VLPFC and the left amygdala. The behavioural results showed that instructed attention to items with a specific emotional valence, relative to passive viewing, resulted in enhanced WM and incidental recognition memory accuracy, along with faster reaction times. Whole-brain analyses across age groups demonstrated increased activation of a fronto-parietal network during instructed attention, relative to passive viewing, and deactivation of the default-mode network. Older adults exhibited reduced activation in a subset of the fronto-parietal task positive regions, along with reduced DMN deactivation relative to their younger counterparts. Functional connectivity analyses using VLPFC as a seed was related to activation in two separate networks, which were involved during processing of positive and negative items among older adults. Amygdala functional connectivity was associated with network engagement during encoding of both positive and negative items in older

adults. These results indicate that specific brain networks are differentially engaged by young and older adults, and are also differently modulated by emotional valence.

### **Behavioural Findings**

In line with previous findings (Gazzaley et al., 2005b), enhanced memory performance during instructed attention compared to passive viewing was found both for working and incidental recognition memory in both age groups, while older adults had overall worse performance compared to young adults. This finding suggests that enhanced attention to task-relevant information during encoding improves performance both in the short- and long-term and indicate beneficial effects from instructed attention during WM encoding.

While there was a general effect of improved performance for instructed attention, we did not find any evidence for a positivity effect in older adults. While this was somewhat unexpected, this finding is in line with some previous evidence that have not been able to demonstrate a positivity effect (Grühn et al., 2005; Kensinger et al., 2002). Reed et al. (2014) have argued that the lack of positivity effect in some experiments could be due to the experimental instructions and task characteristic. Using a similar paradigm with a larger sample size, Ziaei et al. (2015) recently reported a significant positivity effect in older, relative to younger adults in incidental recognition memory. Thus, one potential explanation for the lack of a positivity effect in the current study may be lack of statistical power due to the small sample size. Indeed, the positivity effect is typically rather small (Ruffman et al., 2008), and a small sample size might reduce the possibility for detecting this effect in the behavioural data.

### **Whole-Brain Analyses**

In line with previous neuroimaging studies, instructed attention compared to passive viewing, revealed increased activation in a fronto-parietal network, including IFG, ACC, insula, and the parietal cortex (Yarkoni et al., 2009). The role of fronto-parietal network engagement during top-down modulation of attention is well documented in studies of selective attention (Corbetta and Shulman, 2002a; Yarkoni et al., 2009). A likely role for fronto-parietal network engagement is in directing attention to and processing of relevant items, and filtering out task irrelevant information. Similar to the present findings, a number of studies have also linked fronto-parietal network engagement to top-down attentional processes during WM encoding, which may result in

subsequent enhancement of WM accuracy and faster RTs (for a review, see Gazzaley and Nobre (2012). Our findings corroborate and extend these previous observations to the emotional domain by showing the role of fronto-parietal circuit during encoding of emotional information.

Within the fronto-parietal network, older adults exhibited reduced activation in a sub-set of these regions, such as bilateral IFG, bilateral parietal cortex, bilateral anterior insula, and bilateral fusiform gyrus. While reduced frontal engagement in older adults during WM *retrieval* has been suggested to account for age-related decline in WM performance (e.g. (Rypma and D'Esposito, 2000), the link between frontal activation during *encoding* and age-related decline in WM performance is relatively unknown. Given the importance of fronto-parietal activation for selective attention in WM tasks, the observed age-related reduction of activity in task relevant regions suggest a link between impaired encoding-related attentional processes, and emotional WM performance in older adults, which is supported by prior findings (Ferri et al., 2013; Gazzaley et al., 2005b).

Similarly, the reverse contrast (passive viewing > instructed attention) yielded an activation in regions which are known to be parts of the DMN. In line with previous WM and episodic memory findings (Ferri et al., 2013; Persson et al., 2007; Sambataro et al., 2010), reduced default-mode deactivation in older adults might indicate impaired ability in suppressing task-irrelevant information during WM encoding.

### **Functional Connectivity with VLPFC**

The functional connectivity analysis with left VLPFC as a seed revealed that this region was functionally connected to one network during instructed attention to negative items during WM encoding among older adults. The first network (LV1) which was functionally connected to VLPFC for encoding of negative items in older adults included left amygdala, right middle frontal gyrus, bilateral IFG, right superior frontal gyrus, and bilateral middle temporal gyrus. This finding is in line with number of studies in younger adults' cohort suggesting the role of VLPFC in regulation of negative emotion (Ochsner and Gross, 2005; Phan et al., 2005), and that such regulatory functions may engage cognitive control processes. For instance, Wager and colleagues (2008) demonstrated that VLPFC – subcortical connectivity predicted reappraisal success. St Jacques et al. (2010) also showed increased activity of the PFC in response to the evaluation of negative items and stronger connectivity between PFC, amygdala, and hippocampus was found for subsequently remembered

negative items. The involvement of PFC regions during instructed attention to negative emotion is also in line with findings from a recent meta-analysis on emotion regulation (Buhle et al., 2014) reporting increased activity in cognitive control regions, including medial and lateral PFC, posterior parietal cortex, along with modulation of amygdala activation in emotion regulation tasks. Although there were no explicit regulatory instructions in this experiment, in a process model of emotion regulation, attentional deployment has been highlighted as a core function of emotion regulation strategies, and may influence emotional responding by redirecting attention within a given situation (Gross and Thompson, 2007). Consequently, recruitment of a cognitive control network during WM encoding of negative emotions by older adults might indicate that they were engaged in regulatory processes, and that this recruitment is selective for negative emotions. Thus, the present result provides neuroimaging support for previous behavioural findings showing enhanced ability for older adults in regulating negative emotions (Charles and Carstensen, 2007; Scheibe and Carstensen, 2010).

Moreover, another network, that included left IFG, left superior medial frontal gyrus, right hippocampus, left FG, right cerebellum, left middle temporal gyrus, left SPL, and the left thalamus was functionally connected to the VLPFC during encoding of positive items for both age groups (LV2). Although some regions did overlap with the brain regions from LV1 (see above), most of the regions were uniquely associated with instructed attention to positive items. This suggests that in older adults, two, at least partially separate networks were involved for WM encoding of negative and positive items respectively. The finding of frontal and hippocampal involvement during encoding of positive information is in line with previous studies on episodic memory indicating age-differential connectivity for encoding of positive and negative information (Addis et al., 2010). It has been found that effective connectivity between the amygdala and other task-relevant regions, such as the hippocampus and PFC, were enhanced for positive, but not negative items, in older compared to younger adults. Also, Ritchey et al. (2011b) showed that, during a task which required semantic elaboration, older adults had more pronounced brain activation in medial and VLPFC for positive than negative stimuli. These findings indicate that, unlike younger adults, older adults recruit specific anterior PFC regions for processing of positive items which might result in increased memory performance.

Younger adults, on the other hand, recruited one single network for encoding of both positive and negative items (LV2). This finding suggests that younger adults may be less influenced by



emotional target valence during encoding. Although there was no significant effect of a positivity bias at the behavioural level among older adults, the engagement of differential brain networks for processing of positive and negative items in the older group suggest that at the brain network level, older adults engage two separate functional networks connected to VLPFC during encoding of positive and negative items. Possibly, the lack of behavioural evidence for a positivity bias along with a brain functional segregation between positive and negative information suggest that the neural changes might provide a more sensitive measures relative to behavioural performance in identifying age by valence interactions (Ritchey et al., 2011b).

### **Functional Connectivity with Amygdala**

Functional network connectivity with the amygdala was characterized by engagement in superior temporal gyrus, ACC, superior medial gyrus, angular gyrus, and the thalamus for older adults during encoding of both positive and negative items. Most likely, recruitment of this network is influenced by the increased cognitive control effort required for instructed attention during WM encoding, regardless of emotional valence. The lack of age-related differences in amygdala volume, along with no age differences in modulation by valence in amygdala network connectivity among older adults provide converging evidence of functional preservation of amygdala functionality in ageing (Ritchey et al., 2011a; St Jacques et al., 2010; Wright et al., 2006). Although the dominant view on the amygdala advocates the engagement of this region for negative or fear-relevant stimuli, several authors have suggested that amygdala activity might be related to arousal rather than valence (Anderson et al., 2003; Hamann, 2003). Although individual differences play a fundamental role in understanding the role of amygdala, there are not enough studies to investigate the impact of ageing on the amygdala engagement in response to different emotionally valenced items. The current results do not seem to support the results from St Jacques et al. (2010) showing altered activation in the amygdala in response to different emotionally valenced information. Moreover, the results from the current study are not in line with an ageing brain model that attributes amygdala functional changes in response to emotional stimuli to age-related amygdala atrophy (Cacioppo et al., 2011), and seem to suggest that amygdala and by extension, its network, is engaged during encoding of emotional items irrespective of valence.

Taken together, the results from the VLPFC and amygdala functional connectivity analyses suggest that there are distinguishable functional connectivity patterns during WM encoding of emotionally valenced items, mainly among older adults. While the amygdala is functionally

connected to one network engaged during encoding of both positive and negative items, VLPFC is differentially responsive to emotional valence of target items by recruiting two distinct networks for encoding of positive and negative information. Interestingly, the network of regions connected to VLPFC during encoding of negative emotions resembles the emotion regulation network, which possibly involves down regulating negative emotions, and thus supporting a cognitive control account of the positivity effect. This finding is in line with previous suggestions that older adults might recruit different brain regions as a function of emotional valence and that they rely more on cognitive control for processing of negative items (Mather, 2012; Nashiro et al., 2012).

### **Brain-Behaviour Relationships**

Ventrolateral PFC functional network connectivity was associated with faster response time and higher accuracy for negative items in older adults. The fact that faster and more accurate older adults recruited a wide-spread network that included frontal and parietal regions to a larger extent, adhere to the view that frontal regions are core components of an executive control network that are also involved in effortful emotionally task-related activity. This is also in line with prior findings showing recruitment of frontal regions during cognitive effortful tasks (Cabeza, 2002; Davis et al., 2008). One possibility for this pattern of activity is that RTs reflect effort or time-on-task effects (Yarkoni et al., 2009), and faster individuals and individuals with higher accuracy may engage this fronto-parietal brain regions in order to perform the task appropriately.

Moreover, another VLPFC-related functional network was found to be related to memory accuracy in younger adults for WM encoding of positive and negative items. This particular network included lateral and medial frontal regions that have a known role in cognitive control (such as left IFG and ACC), and memory processes (such as the hippocampus). Increased functional connectivity between VLPFC and ACC region as well as hippocampus was associated with enhanced performance for both positive and negative conditions among younger adults. The ACC plays a critical role in executive control via a distributed attentional network. Indeed, it has been suggested that the ACC is part of a core system for maintaining a task-set relevant for goal-directed behaviour (Dosenbach et al., 2008). Previous studies have also shown that ACC activation is positively correlated with successful attention shifting (Kondo et al., 2004). At a more general level, activation in these regions has repeatedly been associated with behavioural performance across task domains (Eriksson et al., 2011; Kim, 2011; Walsh et al., 2011). Therefore, it seems that younger adults, relative to older adults, recruited a less distributed network during WM encoding of

emotional targets, irrespective of valence, although the cognitive processes associated with functional connectivity in this network remains to be specified.

One limitation of this study was the small sample size. Future studies will be required to investigate the functional brain networks during processing emotionally valenced items in a larger sample. Evidence also indicates that there are age-related differences in arousal ratings of IAPS pictures, and future studies will be required to investigate how brain activation and memory performance is modulated by subjective ratings of the pictures. Moreover, the use of eye-tracking during the task would provide helpful insights into the attentional mechanisms underlying instructed attention during WM encoding.

Taken together, while older adults performed at a lower level compared to younger adults, instructed attention to encode relevant emotional items resulted in enhanced working memory performance in both age groups. Age-related differences in fronto-parietal and default-mode engagement during WM encoding may indicate that older adults are less efficient in selecting task-relevant emotional information, and ignoring irrelevant information. The seed PLS analyses demonstrated differential frontal functional connectivity networks for WM encoding of positive and negative items in older adults, while younger adults recruited a single network regardless of emotional valence. Amygdala functional connectivity reveals a single network which was engaged during encoding of both positive and negative items among older adults, suggesting that this network subserves different function relative to the networks connected to VLPFC seed. Although there was lack of a behavioural positivity effect, the functional connectivity findings highlight the engagement of cognitive control regions during encoding of negative items and a separate and more localized network during encoding of positive items among older adults. These findings imply that older adults' preference for positive items might stem differential functional engagement during processing of both positive and negative items. Mapping age differences in frontal-amygdala functional connectivity may contribute to further understanding changes in emotion-cognition interactions that occur in normal ageing.

## References

- Adolphs, R. (1999). The human amygdala and emotion. *Neuroscientist*, 5, 125-137.
- Allard, E. S., & Isaacowitz, D. M. (2008). Are preferences in emotional processing affected by distraction? Examining the age-related positivity effect in visual fixation within a dual-task paradigm. *Neuropsychol Dev Cogn B Aging Neuropsychol Cogn*, 15, 725-743.
- Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D., Glover, G., Gabrieli, J., & Sobel, N. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature neuroscience*, 6(2), 196-202.
- Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *Neuroimage*, 38(1), 95-113.
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.*, 1124, 1-38.
- Buhle, J. T., Silvers, J. A., Wager, T. D., Lopez, R., Onyemekwu, C., Kober, H., Weber, J., & Ochsner, K. N. (2013). Cognitive reappraisal of emotion: a meta-analysis of human neuroimaging studies. *Cerebral Cortex*, bht154.
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychology and Aging*, 17(1), 85-100.
- Cacioppo, J. T., Berntson, G. G., Bechara, A., Tranel, D., & Hawkley, L. C. (2011). Could an aging brain contribute to subjective well-being? The value added by a social neuroscience perspective. In A. Todorov, S. Fiske & D. Prentice (Eds.), *Social Neuroscience* (pp. 249-262). Oxford; New York: Oxford University Press.
- Carstensen, L. L., Isaacowitz, D. M., & Charles, S. T. (1999). Taking time seriously: A theory of socioemotional selectivity. *American Psychologist*, 54(3), 165.
- Charles, S. T., & Carstensen, L. L. (2007). Emotion regulation and aging. *Handbook of emotion regulation*, 6, 307-327.
- Charles, S. T., Mather, M., & Carstensen, L. L. (2003). Aging and emotional memory: the forgettable nature of negative images for older adults. *Journal of Experimental Psychology. General*, 132(2), 310-324.
- Corbetta, M., & Shulman, G. L. (2002a). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci*, 3(3), 201-215.
- Corbetta, M., & Shulman, G. L. (2002b). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci*, 3, 201-215.
- Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The posterior-anterior shift in aging. *Cerebral Cortex*, 18(5), 1201-1209.

- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, 18(1), 193-222.
- Dosenbach, N. U., Fair, D. A., Cohen, A. L., Schlaggar, B. L., & Petersen, S. E. (2008). A dual-networks architecture of top-down control. *Trends in Cognitive Science*, 12(3), 99-105.
- Eriksson, J., Kalpouzos, G., & Nyberg, L. (2011). Rewiring the brain with repeated retrieval: a parametric fMRI study of the testing effect. *Neuroscience Letter*, 505(1), 36-40.
- Ferri, J., Schmidt, J., Hajcak, G., & Canli, T. (2013). Neural correlates of attentional deployment within unpleasant pictures. *Neuroimage*, 70(0), 268-277.
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-Mental State": a practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, 12(3), 189-198.
- Freire, L., Roche, A., & Mangin, J.-F. (2002). What is the Best Similarity Measure for Motion Correction in fMRI Time Series? *IEE Transaction on Medical Imaging*, 21.
- Gazzaley, A., Cooney, G. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005a). Top-down Enhancement and Suppression of the Magnitude and Speed of Neural Activity. *Journal of Cognitive Neuroscience*, 17, 507-517.
- Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005b). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature neuroscience*, 8, 1298-1300.
- Gazzaley, A., & D'Esposito, M. (2007). Top-down modulation and normal aging. *Ann. N. Y. Acad. Sci.*, 1097, 67-83.
- Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: bridging selective attention and working memory. *Trends in Cognitive Science*, 16(2), 129-135.
- Gross, J. J., & John, O. P. (2003). Individual differences in two emotion regulation processes: implications for affect, relationships, and well-being. *Journal of personality and social psychology*, 85(2), 348.
- Gross, J. J., & Thompson, R. A. (2007). Emotion Regulation: conceptual foundation. *Handbook of emotion regulation*.
- Grühn, D., Smith, J., & Baltes, P. B. (2005). No aging bias favoring memory for positive material: Evidence from a heterogeneity-homogeneity list paradigm using emotionally toned words. *Psychol Aging*, 20(4), 579-588.
- Hamann, S. (2003). Nosing in on the emotional brain. *Nature neuroscience*, 6, 106-108.
- Jensen, A. R., & Rohwer, W. D. (1966). The Stroop color-word test: A review. *Acta psychologica*, 25, 36-93.

- Kensinger, E. A., Brierley, B., Medford, N., Growdon, J. H., & Corkin, S. (2002). Effects of normal aging and Alzheimer's disease on emotional memory. *Emotion*, 2, 118-134.
- Kim, H. (2011). Neural activity that predicts subsequent memory and forgetting: a meta-analysis of 74 fMRI studies. *Neuroimage*, 54(3), 2446-2461.
- Kondo, H., Morishita, M., Osaka, N., Osaka, M., Fukuyama, H., & Shibasaki, H. (2004). Functional roles of the cingulo-frontal network in performance on working memory. *Neuroimage*, 21(1), 2-14.
- Krishnan, A., Williams, L. J., McIntosh, A. R., & Abdi, H. (2011). Partial Least Squares (PLS) methods for neuroimaging: A tutorial and review. *Neuroimage*, 56(2), 455-475.
- Lang, P., Bradley, M. M., & Cuthbert, B. N. (2008). International affective picture system (IAPS): Affective ratings of pictures and instruction manual.: University of Florida, Gainesville, FL.
- Lindquist, K. A., Wager, T. D., Kober, H., Bliss-Moreau, E., & Barrett, L. F. (2012). The brain basis of emotion: a meta-analytic review. *Behavioral and Brain Sciences*, 35(3), 121-143.
- Lockenhoff, C. E., & Carstensen, L. L. (2007). Aging, emotion, and health-related decision strategies: motivational manipulations can reduce age differences. *Psychol Aging*, 22, 134-146.
- Löckenhoff, C. E., & Carstensen, L. L. (2004). Socioemotional selectivity theory, aging, and health: The increasingly delicate balance between regulating emotions and making tough choices. *Journal of Personality*, 72(6), 1395-1424.
- Macey, P. M., Macey, K. E., Kumar, R., & Harper, R. M. (2004). A method for removal of global effects from fMRI time series. *Neuroimage*, 22(1), 360-366.
- Mather, M. (2012). The emotion paradox in the aging brain. *Ann. N. Y. Acad. Sci.*
- Mather, M., & Carstensen, L. L. (2003). Aging and Attentional Biases for Emotional Faces. *Psychological Science*, 14(5), 409-415.
- Mather, M., & Carstensen, L. L. (2005). Aging and motivated cognition: the positivity effect in attention and memory. *Trends in Cognitive Science*, 9, 496-502.
- Mather, M., & Knight, M. (2005). Goal-directed memory: the role of cognitive control in older adults' emotional memory. *Psychol Aging*, 20(4), 554-570.
- Mazoyer, B., Zago, L., Mellet, E., Bricogne, S., Etard, O., Houde, O., Crivello, F., Joliot, M., Petit, L., & Tzourio-Mazoyer, N. (2001). Cortical networks for working memory and executive functions sustain the conscious resting state in man. *Brain Research Bulletin*, 54(3), 287-298.
- McIntosh, A. R., Bookstein, F. L., Haxby, J. V., & Grady, C. L. (1996). Spatial Pattern Analysis of Functional Brain Images Using Partial Least Squares. *Neuroimage*, 3(3), 143-157.

- McIntosh, A. R., Chau, W. K., & Protzner, A. B. (2004). Spatiotemporal analysis of event-related fMRI data using partial least squares. *Neuroimage*, *23*(2), 764-775.
- Nashiro, K., Sakaki, M., & Mather, M. (2012). Age differences in brain activity during emotion processing: reflections of age-related decline or increased emotion regulation? *Gerontology*, *58*(2), 156-163.
- Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Science*, *9*(5), 242-249.
- Persson, J., Lustig, C., Nelson, J. K., & Reuter-Lorenz, P. A. (2007). Age differences in deactivation: a link to cognitive control? *Journal of Cognitive Neuroscience*, *19*(6), 1021-1032.
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, *11*(11), 773-783.
- Phan, K. L., Fitzgerald, D. A., Nathan, P. J., Moore, G. J., Uhde, T. W., & Tancer, M. E. (2005). Neural substrates for voluntary suppression of negative affect: a functional magnetic resonance imaging study. *Biological psychiatry*, *57*(3), 210-219.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *PNAS*, *98*(2), 676-682.
- Reed, A. E., Chan, L., & Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: Age differences in preferences for positive over negative information. *Psychol Aging*, *29*, 1-15.
- Reuter-Lorenz, P. A., & Lustig, C. (2005). Brain aging: reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology*, *15*(2), 245-251.
- Ritchey, M., Bessette-Symons, B., Hayes, S. M., & Cabeza, R. (2011a). Emotion processing in the aging brain is modulated by semantic elaboration. *Neuropsychologia*, *49*(4), 640-650.
- Ritchey, M., Dolcos, F., Eddington, K. M., Strauman, T. J., & Cabeza, R. (2011b). Neural correlates of emotional processing in depression: changes with cognitive behavioral therapy and predictors of treatment response. *Journal of Psychiatric Research*, *45*(5), 577-587.
- Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: implications for neuropsychological models of aging. *Neurosci Biobehav Rev*, *32*(4), 863-881.
- Rypma, B., & D'Esposito, M. (2000). Isolating the neural mechanisms of age-related changes in human working memory. *Nature neuroscience*, *3*(5), 509-515.
- Samanez-Larkin, G. R., Robertson, E. R., Mikels, J. A., Carstensen, L. L., & Gotlib, I. H. (2009). Selective attention to emotion in the aging brain. *Psychol Aging*, *24*(3), 519-529.

- Sambataro, F., Murty, V. P., Callicott, J. H., Tan, H.-Y., Das, S., Weinberger, D. R., & Mattay, V. S. (2010). Age-related alterations in default mode network: impact on working memory performance. *Neurobiol Aging*, *31*(5), 839-852.
- Scheibe, S., & Carstensen, L. L. (2010). Emotional aging: recent findings and future trends. *J Gerontol B Psychol Sci Soc Sci*, *65B*(2), 135-144.
- Shulman, G. L., Corbetta, M., Buckner, R. L., Raichle, M. E., Fiez, J. A., Miezin, F. M., & Petersen, S. E. (1997). Top-down modulation of early sensory cortex. *Cereb Cortex*, *7*(3), 193-206.
- St Jacques, P., Dolcos, F., & Cabeza, R. (2010). Effects of aging on functional connectivity of the amygdala during negative evaluation: a network analysis of fMRI data. *Neurobiol Aging*, *31*(2), 315-327.
- St Jacques, P. L., Dolcos, F., & Cabeza, R. (2009). Effects of Aging on Functional Connectivity of the Amygdala for Subsequent Memory of Negative Pictures A Network Analysis of Functional Magnetic Resonance Imaging Data. *Psychological Science*, *20*(1), 74-84.
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*, 137-149.
- Unsworth, N., Heitz, R. P., Schrock, J. C., & Engle, R. W. (2005). An automated version of the operation span task. *Behav Res Methods*, *37*(3), 498-505.
- Wager, T. D., Davidson, M. L., Hughes, B. L., Lindquist, M. A., & Ochsner, K. N. (2008). Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*, *59*(6), 1037-1050.
- Walsh, B. J., Buonocore, M. H., Carter, C. S., & Mangun, G. R. (2011). Integrating conflict detection and attentional control mechanisms. *Journal of Cognitive Neuroscience*, *23*(9), 2211-2221.
- Wright, C. I., Wedig, M. M., Williams, D., Rauch, S. L., & Albert, M. S. (2006). Novel fearful faces activate the amygdala in healthy young and elderly adults. *Neurobiol Aging*, *27*(2), 361-374.
- Yarkoni, T., Barch, D. M., Gray, J. R., Conturo, T. E., & Braver, T. S. (2009). BOLD correlates of trial-by-trial reaction time variability in gray and white matter: a multi-study fMRI analysis. *PLoS One*, *4*(1), 23.
- Ziaei, M., Peira, N., & Persson, J. (2014). Brain systems underlying attentional control and emotional distraction during working memory encoding. *Neuroimage*, *87*, 276-286.
- Ziaei, M., von Hippel, W., Henry, J. D., & Becker, S. I. (2015). Are Age Effects in Positivity Influenced by the Valence of Distractors? *PLoS One*, *10*(9), e0137604.



## **Chapter 4**

# Emotional Expressions and Eye Gaze: A Multivariate Approach

## Preface

During the final year of my PhD, I became more interested in the potential implications of age-related changes in emotional processing on everyday social function. Because the ability to respond quickly and appropriately to facial cues is particularly critical for our ability to communicate effectively with others in everyday life, I decided to focus on the neural correlates of age-related differences processing and integrating two specific types of facial cues: cues to emotional state, and cues to eye gaze focus (eye gaze orientation).

The final empirical Chapter aims to understand the age-related changes that occur at the neural level when processing and integrating these facial cues. Behaviourally, previous literature has shown that older adults have deficits integrating eye gaze and emotional expression cues, with these deficits particularly pronounced for angry expressions. However, the neural mechanisms involved in this process have not yet been explored. Moreover, a further novel contribution of this work was to assess whether older adults' difficulties recognising emotional expressions presented with different eye gaze cues were associated with their difficulties in other important aspects of social-cognitive function, including theory of mind. Therefore, the following chapter has two broad aims; to investigate the underlying neural correlates involved in integrating socially relevant cues, and to assess the relation between task performance with other important aspects of social-cognitive function.

*Note.* This manuscript has been submitted to the *Neurobiology of Aging*.

## **Abstract**

Normal adult ageing is associated with difficulties integrating important social cues to emotion, including facial affect and eye gaze cues, but there is limited understanding of the neural substrates underpinning age-related differences in perceiving these cues. The main aim of the present study was to delineate activity in brain regions underlying age differences in recognition of emotional expressions as a function of eye gaze. Younger and older adults completed an fMRI experiment in which they were asked to identify happy, angry, and neutral expressions displayed either with direct or averted gaze. Results indicated that while younger adults showed neural sensitivity to eye gaze during recognition of angry expressions, older adults demonstrated neural dedifferentiation to these stimuli. Additionally, younger (but not older) adults' performance on a measure of theory of mind (TOM) and recognition of angry expressions was differentially correlated with activation in two sets of brain regions as a function of eye gaze. In contrast, and unlike younger adults, older adults showed neural sensitivity to eye gaze for happy expressions. Older adults' TOM performance was also differentially correlated with the key node of mentalizing brain network during happy expressions as a function of eye gaze. For the first time, these data provide evidence for age-related differences in the neural substrates underlying the capacity to integrate facial affect and eye-gaze cues. The results of this study suggest that age-related differences in integrating facial cues may be related to engagement of the mentalizing network, with potentially important implications for social-cognitive functioning in late adulthood.

**Key words:** Emotion recognition, gaze perception, social-cognition, theory of mind, ageing, dedifferentiation.

## Introduction

People rely on eye gaze and emotional expressions to form expectations about others' mental states (Graham and Labar, 2012). For example, the personal significance of an angry expression depends on whether it is accompanied by direct or averted gaze. Aging diminishes the ability to process information from eye gaze (Slessor et al., 2008) and emotional expressions (Ruffman et al., 2008), as well as the integration of these cues (particularly for angry facial expressions; Slessor et al. (2010b)). Reduced sensitivity to expression and eye-gaze cues may be indicative of underlying neural changes in old age and may have potential consequences for social interaction in late adulthood.

Angry expressions in the context of direct gaze signal immediate threat to the observer. Neural responses to such threatening cues are automatic (Shepherd, 2010) and reflexive (Adams et al., 2012). In contrast, angry expressions accompanied by averted gaze signal that the anger is directed towards something else in the environment, so are less likely to be interpreted as personal threat, and may invoke social-cognitive brain regions to determine the intentions of the angry individual (Pfeiffer et al., 2013). However, because older adults show a lack of sensitivity to eye gaze in angry expressions (Slessor et al., 2010b), they may also show similar neural patterns when observing angry faces with direct and averted gaze. Additionally, age-related changes in integrating facial cues may reflect a lack of recruitment of mentalizing networks, which are most critical for the condition that requires understanding the mental state of others, angry faces with averted gaze.

Although happy expressions presented with eye-gaze orientations might convey different meanings, being targeted with happiness is less critical for survival than being targeted with anger. Thus, at a neural level, there may be less differentiation in the brain regions activated for direct versus averted gaze accompanied by a happy expression relative to angry expressions, especially among younger adults. Because older adults are particularly motivated to attend to and process positive information such as happy faces (Carstensen, 2006; Mather and Carstensen, 2003), they may actually show greater neural differentiation when processing happy expressions with different eye-gaze directions compared to their younger counterparts.

The aim of this study was to identify age differences in the neural substrates involved in processing happy and angry facial expressions with different eye-gaze cues. We predicted that in younger adults, distinct brain substrates would be activated in response to angry expressions with

differing gaze cues. For angry faces with direct gaze, activity in the salience network involved in identifying the most relevant stimuli in the environment and orienting attention towards them in order to adaptively guide behaviour (Barrett and Satpute, 2013; Menon, 2015) should be more prominent, while in averted gaze conditions additional brain regions involved in mentalizing, e.g., medial prefrontal cortex (Frith and Frith, 2006; Van Overwalle, 2009; Van Overwalle and Baetens, 2009), should be engaged in decoding intentions. However, because older adults make less distinction between angry direct and averted eye gaze cues, it is expected that the neural differentiation between these conditions should be attenuated among older adults.

Finally, we anticipated that the neural differentiation between direct and averted gaze should be smaller for happy expressions, at least amongst younger people. In contrast, older adults might show greater differentiation in processing facial expressions of happiness, because of their high motivation to attend to positive stimuli. We expected to observe increased activity in reward-based brain regions, e.g., ventromedial PFC (Kringelbach and Rolls, 2004; O'Doherty et al., 2001), during recognition of happy expressions. Such activity is less likely to be influenced by the eye-gaze orientations relative to angry expressions.

## **Methods**

### **Participants**

Twenty-one healthy older adults (aged 65-75 years;  $M = 69.75$ ,  $SD = 2.97$ ; 10 females) and 21 healthy younger adults (aged 17-27 years;  $M = 20.65$ ,  $SD = 2.66$ ; 10 females) participated in this study. One older and one younger adult were excluded from the analysis due to brain signal loss, leaving 20 participants in each group. Younger adults were undergraduate students at the University of Queensland who were reimbursed either course credits or \$15 AUD per hour. All of the older adults were community volunteers who were reimbursed \$20 AUD per hour. All participants were right-handed English speakers who had normal or corrected-to-normal vision using MRI compatible glasses and no history of neurological impairment or psychiatric illnesses. All participants were screened for claustrophobia, neurological and psychiatric medication, and MRI compatibility before the recruitment. All older adults scored above the recommended cut-off of 27 on a widely used dementia screen ( $M = 28.38$ ,  $SD = 1.28$ ), the Mini Mental State Examination (Folstein et al., 1975). All participants took part in two separate sessions of testing, the first involving fMRI scanning and the second involving behavioural/neuropsychological assessment. All participants were provided

with written consent forms approved by the Human Research Ethics Committee at the University of Queensland and were debriefed upon the completion of the second session.

## **Materials**

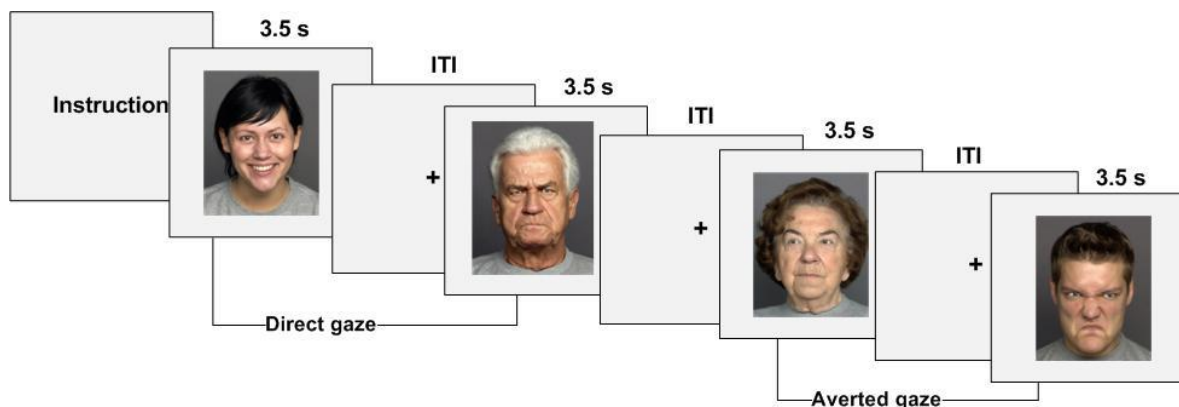
One hundred angry, 100 happy, and 100 neutral faces were drawn from the FACES database (Ebner et al., 2010). All faces were coloured, front-view, and high quality (300 Dots per Inch). The presented faces comprised two age groups (young posers: 18-31 years and old posers: 69-80 years). The gazes of the posers were photoshopped so that an equal number of direct and averted gazes were used for the scanner task. All faces were categorized into 5 lists, using MATLAB, according to four selection criteria: age of the posers, gender of the posers, gaze direction, and emotional expression. The lists consisted of equal number of male and female posers (30 males), old and young posers (30 old posers), and emotional expressions (20 in each category) presented in each run. To control for any potential role of different features of the faces in recognition of emotional expressions, faces in each list were also matched based on their attractiveness ratings ( $M = 41.66$ ,  $SD = 13.08$ ). The order of the runs presented in the scanner was counterbalanced among participants. All of the stimuli were presented against a gray background using E-prime software, which were adjusted to be standardized in size (600 x 450 pixels) prior to presentation in the scanner.

## **Experimental Design**

The 50-minute scanner session consisted of 3 components: structural magnetic resonance imaging (sMRI), functional MRI (fMRI), and a face localizer task. Prior to the scanning, participants were verbally and visually instructed about the emotion recognition task and subsequently asked to practice it until they were completely familiarized with the instructions and timing of the task. Faces that were different to those used in the scanner stimuli were presented during the practice run. In the scanner, participants performed two runs of an emotion recognition task (described below), followed by an sMRI acquisition, followed by another three runs of the emotion recognition task, and finally the face localizer task.

During the emotion recognition task (Figure 1), each face was presented one at a time for 3.5 sec and followed by a fixation cross. Presentation of the fixation cross was jittered using three time intervals: 0.5 sec, 1 sec, and 1.5 sec. In total, the task consisted of 5 runs, 4.5 minutes each. During

the scan, participants were required to indicate, as fast and as accurately as possible, whether each face displayed a happy, angry, or neutral emotional expression by pressing the relevant button on an MRI-compatible response box – using index finger for either angry or happy, middle finger for neutral, and ring finger for either happy or angry. The order of the fingers was counterbalanced among participants to account for a possible interaction between responding with a specific finger and specific emotional expressions.



**Figure 1. Example of experimental design.** Each trial consisted of a presentation of a face with happy, angry, or neutral expressions for 3.5 seconds. Equal number of males and females, direct and averted gaze were presented. Fixation crosses were jittered using 0.5 second, 1 second, and 15 second time intervals. In total, the task consisted of 5 runs, 4.5 minutes each. During the task, participants were required to indicate the emotional expressions of each face by using a MRI compatible response buttons. Abbreviation: ITI = Inter-Trial Interval.

*Face localizer task:* At the end of the scanner session, participants performed a functional face localizer task, which consisted of four blocks of faces, houses, and words, with a total number of 16 blocks. Each block consisted of four images from each category presented for 3 sec with a fixation cross (0.5 sec) in between images. To allow for the hemodynamic response to reach the baseline level, 16 sec of fixation cross was also presented between each block of images. Participants were instructed to press the relevant button on the response box using their index finger when the stimulus was the same as the previous image. A detailed description of the task is presented in Burianová et al. (2013).

## Neuropsychological Measures

During the behavioural sessions, all participants were asked to complete a range of background measures assessing executive control, intelligence, emotion recognition, social functioning, personality, empathy, and theory of mind (TOM) ability. Descriptive and inferential statistics of background measures are reported in Table 1. Descriptions of the measures are as follow:

***National Adult Reading Test (NART):*** The NART (Nelson, 1982) is a valid and reliable measure of crystallized intelligence that consists of 50 irregular words. Participants were required to read each word aloud and their responses were scored by two independent coders.

***Trail Making Test:*** The Trail Making Test consists of two parts, A and B (Reitan and Wolfson, 1986). In part A, participants were instructed to connect the circled numbers in sequential orders. In Part B, they were instructed to alternate between numbers and letters (e.g., 1-A-2-B).

***Ekman Emotion Recognition test:*** The faces used in this experiment were drawn from the “Facial Expressions of Emotion: Stimuli and Test” stimulus set (Young et al., 2002). Sixty black and white images from six basic emotional categories: anger, sadness, surprise, happiness, disgust, and fear, were presented for 3.5 secs. Participants were required to choose the best label that describes each face and press the relevant key on the keyboard. Reaction times and responses were recorded.

***Peer-Report Social Functioning Scale (PRSF):*** This scale is a peer-report assessment of social functioning (Henry et al., 2009a). A 10-item subscale assesses socially inappropriate behaviour (e.g., “enquires about potentially embarrassing issues in public” or “comments negatively on someone else’s physical appearance”). A 17-item subscale assesses socially appropriate behaviour (e.g., “speaks positively about others” or “lets other people have their say”). A 3-item subscale taps assesses prejudicial and stereotyping behaviour (e.g., “ignores stereotypes when making decision about people”). Participants’ peers provided their responses on a 4-point scale with labels, *never*, *rarely*, *occasionally*, *frequently*. Higher scores indicate a higher level of socially inappropriate behaviour, socially appropriate behaviour, or prejudicial behaviour on the three subscales.



**Big Five Personality Inventory (BFI):** A 44-item self-report personality inventory was used (John, 1991). This test comprises of 5 subscale measuring 5 personality dimensions including *extraversion* (8 items; e.g., “I am someone who is talkative”), *agreeableness* (9 items; e.g., “I am someone who is helpful and unselfish with others”), *Conscientiousness* (9 items; e.g., “I am someone who does a thorough job”), *Neuroticism* (8 items; e.g., “I am someone who is depressed, blue”), and *openness* (10 items; e.g., “I am someone who is original, comes up with new ideas”). Participants were provided their responses on a scale from 1 (*strongly disagree*) to 5 (*strongly agree*) for each item indicating the extent they agree or disagree with each statement. The reliability of this test has been reported 0.83 (John and Srivastava, 1999).

**Empathy Quotient (EQ):** A 40-item adult version of the empathy quotient developed by Baron-Cohen and Wheelwright (2004) was used in this study to measure the level of empathy between two age groups. Participants responded to this questionnaire by choosing one of the 4-scale response options; *strongly agree*, *slightly agree*, *slightly disagree*, and *strongly disagree*. On each item, a person can obtain 2, 1, or 0, so the EQ score has a maximum score of 80 and a minimum of zero. High test–retest reliability was reported for this measure as well as moderate concurrent validity between this measure and perspective subscale of Interpersonal Reactivity Index (Lawrence et al., 2004).

**Eye-movements:** In the behavioural session, participants’ eye movements were recorded using a chin-rest SR EyeLink 1000 eye tracker (SR Research, Ontario, Canada) while they viewed a series of faces selected from the FACES database. One-hundred and twenty of these were selected from the lists previously presented in the fMRI task and 60 were novel photos that were included to control for the impact of familiarity of the face. Equal numbers of male and female posers, old and young posers, emotional expressions, and averted vs. direct eye gaze were presented to all participants.

**Reading the Mind in the Eye Test (RMET):** This is a measure of theory of mind, which broadly refers to the ability to understand the mental states of others (Baron-Cohen et al., 2001). This test consists of a series of 36 photographs of the eye region of a person’s face. Participants are required to choose which word (out of 4 words) best describes what the person in the picture is feeling or thinking. The RMET assesses how well people can decode others’ mental states, and is one of the best-validated measures of this construct (Henry et al., 2015). Younger adults performed significantly better on this task relative to older adults,  $t(35) = 2.69, p < .05$ .

**Table 1.** Descriptive and inferential statistics for the background cognitive measures

Measure	Older adults		Younger adults		Inferential statistics	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>t</i>	<i>df</i>
<b>NART FSIQ</b>	118.33	2.93	113.75	3.84	3.76	38
<b>Trail Making Test</b>						
<i>Trail A in ms.</i>	2780.0	635.94	1789.17	667.67	4.74**	37
<i>Trail B in ms.</i>	5830.19	2103.62	3758.26	1971.73	3.20**	38
<b>RMET</b>	23.65	5.54	27.47	1.94	2.69*	35
<b>Emotion recognition test</b>						
<i>Sadness</i>	7.71	1.48	7.78	1.81	0.14	38
<i>Disgust</i>	7.85	1.79	7.68	1.56	0.32	38
<i>Happiness</i>	9.85	0.35	9.60	0.58	1.14	38
<i>Surprise</i>	8.66	1.71	9.15	1.06	1.07	38
<i>Fear</i>	7.57	2.11	7.21	2.55	0.48	38
<i>Anger</i>	8.00	1.54	7.36	1.64	1.25	38
<b>PRSF</b>						
<i>Social Inappropriateness</i>	17.28	5.44	19.73	4.90	1.49	38
<i>Social Appropriateness</i>	61.57	5.38	58.10	6.90	1.78	38
<i>Prejudice</i>	6.71	0.90	6.84	1.06	0.41	38
<b>Empathy Quotient</b>	46.57	14.04	42.16	10.35	1.12	38
<b>Big five personality</b>						
<i>Extraversion</i>	25.61	6.25	27.89	6.05	1.16	38
<i>Agreeableness</i>	33.33	2.72	31.31	3.41	2.07*	38
<i>Conscientiousness</i>	36.80	5.17	30.78	5.66	3.51**	38
<i>Neuroticism</i>	19.05	6.26	21.10	6.17	1.03	37
<i>Openness</i>	36.76	6.43	33.36	6.29	1.68	38

*Note.* \* =  $p < .05$ , \*\* =  $p < .005$ . NART IQ = National Adult Reading Test Intelligence Quotient, RMET = Reading the Mind in the Eye Test, PRSF = Peer-Report Social Functioning Scale, ms. = millisecond

## Image Acquisition, Preprocessing, and Analyses

Functional images were acquired using a Siemens scanner equipped with a 32-channel head coil. The acquisition of functional data was achieved by using a whole-brain T2\*-weighted echo-planar image (EPI) sequence (93 interleaved slices, repetition time (TR) = 3000ms, echo time (TE) = 45ms, flip angle = 90°, field of view (FOV) = 192mm, voxel size = 2x2x2 mm). High resolution T1-weighted images were acquired with a MPRAG sequence (126 slice with 1mm thickness, TR = 1900ms, TE = 2.3ms, inversion time (TI) = 900ms, FOV = 230mm, voxel size = 0.9mm<sup>3</sup>, flip angle = 90°). The tasks were presented to participants on a computer screen through a mirror mounted on top of the head coil. Participants were using earplugs and cushions inside the head coil to dampen the noise and minimize the head movement.

For functional analysis, the images were preprocessed with Statistical Parametric Mapping Software (SPM8; <http://www.fil.ion.ucl.ac.uk/spm>) implemented in MATLAB 2010b (Mathworks Inc., MA). Following the realignment to a mean image for head-motion correction, the images were segmented to gray matter and white matter, and then spatially normalized into a standard stereotaxic space with a voxel size of 2mm<sup>3</sup> using the Montreal Neurological Institute (MNI) template, and finally spatially smoothed with a 6-mm Gaussian Kernel.

The procedure of the fMRI analysis was twofold. First, we examined the impact of age on whole-brain activity during the recognition of emotional faces presented with different eye gaze direction. For this purpose, we conducted a whole-brain analysis of brain activity during angry and happy conditions, which were compared between the two age groups. Neutral faces were included in the experimental design as a control condition to remove the effects of the visual perception component (for a review see Sabatinelli et al. (2011)). However, the ambiguity of neutral faces may lead to uncertainty and heightened vigilance, which in turn may increase amygdala activation (Blasi et al., 2009). Therefore, all analyses were conducted only on happy and angry facial expressions in order to avoid activation confounds due to the presence of neutral pictures.

Second, to explore any age-related differences in integrating facial cues, we conducted a brain-behaviour analysis, examining the relationship between the neural activation involved in gaze and emotion processes and the scores obtained on the RMET. For angry expressions, we included the accuracy of behavioural performance in the scanner task and correlated them with the TOM scores. Because accuracy for recognition of happy expressions was at ceiling for both age groups,

TOM scores were correlated with the brain activity in the two happy experimental conditions without including the behavioural performance accuracy from the emotion recognition task.

The imaging data were analysed using a multivariate analytical technique Partial Least Squares analysis (PLS; McIntosh et al. (1996); McIntosh et al. (2004); for a detailed tutorial and review of PLS, see Krishnan et al. (2011), as implemented in PLS software ([http://research.baycrest.org/pls\\_software](http://research.baycrest.org/pls_software)) running on MATLAB 2010b (The MathWorks Inc., MA). PLS decomposes all images into a set of patterns that capture the greatest amount of covariance in the data, rather than making assumptions about conditions or imposing contrasts for each pattern. PLS analysis uses singular value decomposition (SVD) of a single matrix that contains all participants' data to find a set of orthogonal latent variables (LVs), which represent linear combinations of the original variables. Therefore, PLS enables one to differentiate the degree of contribution of different brain regions associated with task demands, behavioural or anatomical covariates, or functional seed activity.

The first LV usually accounts for the largest covariance of the data, with progressively smaller amount of covariance for subsequent LVs. Each LV delineates cohesive patterns of brain activity related to experimental conditions. Additionally, brain scores are calculated as the dot product of a participant's image volume of each LV. The brain score reflects how strongly each participant contributes to the pattern expressed in each LV. Therefore, each LV consists of a singular image of voxel saliences (*i.e.*, a spatiotemporal pattern of brain activity), a singular profile of task saliences (*i.e.*, a set of weights that indicate how brain activity in the singular image is related to the experimental conditions, functional seeds, or behavioural/anatomical covariates), and a singular value (*i.e.*, the amount of covariance accounted for by the LV). Given that the task was event-related, the analysis was conducted on the 15-sec period (5 TRs), starting at the onset of the faces to account for the duration of the BOLD response. Activity at each time point in the analysis was normalized to activity in the first TR.

The statistical significance of each LV was assessed using a permutation test, which determines the probability of a singular value from 500 random reordering and resampling (McIntosh et al., 1996). In addition to the permutation test, to determine the reliability of the saliences for each brain voxel, a standard error of each voxel's salience on each LV was estimated by 100 bootstrap resampling steps (Efron and Tibshirani, 1985). Peak voxels with a bootstrap ratio (BSR; *i.e.*, salience/standard error) > 3.0 were considered to be reliable, as this approximates  $p <$

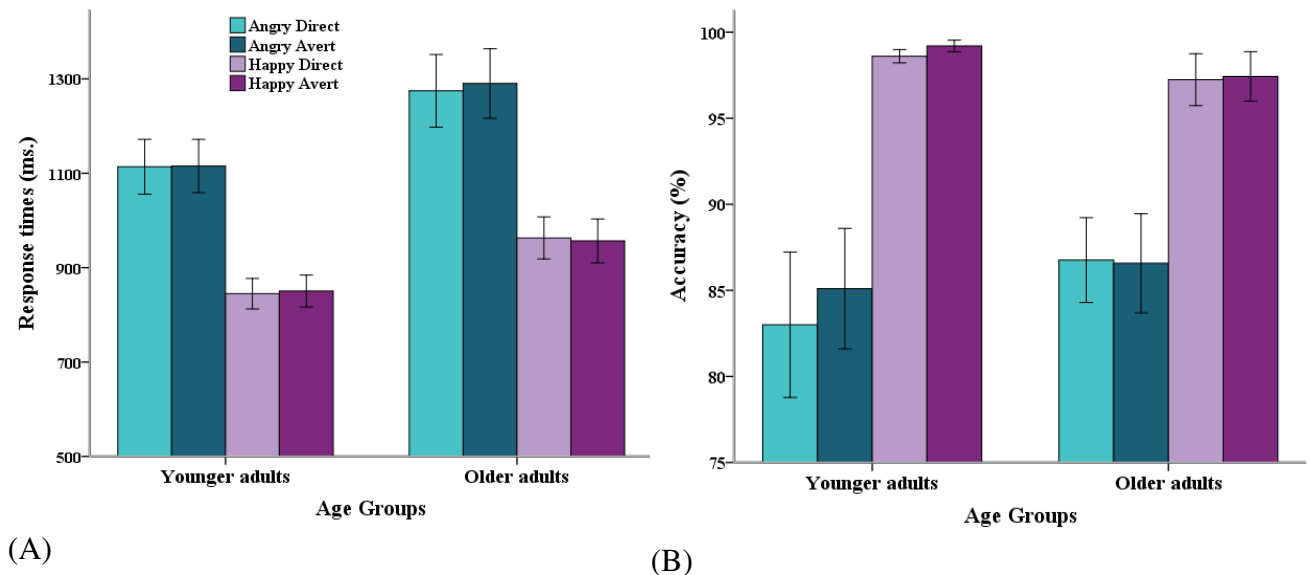
0.01 (Sampson et al., 1989). In the current study, we used task PLS and brain-behaviour PLS, to examine the whole-brain activity pattern for processing each emotional category as a function of eye gaze and to assess the link between performance in the emotion recognition task and TOM ability.

## Results

### Emotion Recognition Performance

A 2 (eye gaze: direct, averted) by 2 (emotional expression: angry, happy) by 2 (age group: young, older) repeated-measures ANOVA with response accuracy as the dependent measure showed that there was a significant main effect of emotion,  $F(1, 38) = 34.85, p < .01, \eta_p^2 = 1.0$ . This reflected greater accuracy in recognising happy relative to angry facial expressions in both age groups (Figure 2). No other main effects or interactions were significant (all  $F$ s  $< 1$ ).

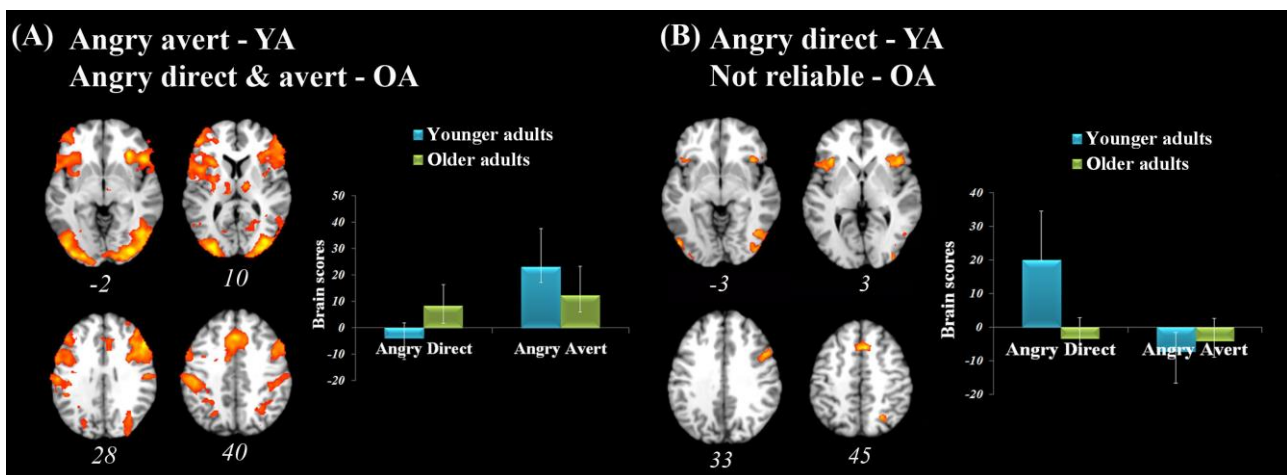
A similar analysis on response times (RTs) of accurate responses revealed a main effect of emotion,  $F(1,35) = 83.27, p < .01, \eta_p^2 = 1.0$ , with faster RTs for happy relative to angry facial expressions. None of the other main or interaction effects were significant (all  $F$ s  $< 1$ ).



**Figure 2. Behavioural performance in emotion recognition task.** Panel A represents response times in milliseconds and Panel B represents the percentage of accurate responses in recognition of emotional expressions for each condition. Abbreviation: ms. = milliseconds.

## Whole-Brain Analyses

*Angry expressions.* The results from the whole-brain analyses delineated two significant and distinct LVs for recognition of angry expressions as a function of eye gaze among younger but not older adults. The first LV accounted for 33% of the covariance in the data and included brain regions such as inferior frontal gyrus (IFG), anterior cingulate cortex (ACC), inferior parietal lobule (IPL), posterior cingulate cortex (PCC), and amygdala. This pattern of brain activities was found in younger adults only when angry expressions with averted gaze were present. In contrast, older adults recruited these regions during recognition of angry expressions with *both* direct and averted gaze (Figure 3, Panel A & Table 2). LV2, which accounted for 25% of the covariance in the data, yielded a pattern that was related to the recognition of angry expressions with direct gaze only among younger adults. This pattern included insula and medial prefrontal gyrus, the main nodes of salience network (Menon, 2015). In older adults there was no reliable recruitment of these regions in any of the conditions (Figure 3, Panel B & Table 2). These results indicate that social-cognitive brain regions (Frith and Frith, 2006; Van Overwalle, 2009) were engaged among younger adults during recognition of angry expressions with averted gaze in which the understanding of the intention of expresser was required. The salience network, in contrast, was activated in young participants when recognizing angry expressions with possible threatening signals to themselves, i.e. direct gaze. These data further demonstrate that at the neural level, younger, but not older adults, are differentiating between angry facial expressions with direct versus averted gaze.



**Figure 3. Whole-brain results for angry expressions.** Patterns of whole-brain activity during the recognition of angry expressions with averted gaze among younger adults (YA) and both eye-gaze directions among older adults (OA) (A), angry expressions with direct gaze among YA, without any

reliable effects among OA (B), relative to the other conditions. Error bars denote 95% confidence intervals for the correlations calculated from the bootstrap procedure. All reported regions have  $BSR \geq 2.5$  and cluster size  $\geq 100$  voxels. Abbreviations: L = left hemisphere, R = right hemisphere, OA = older adults, YA = younger adults.

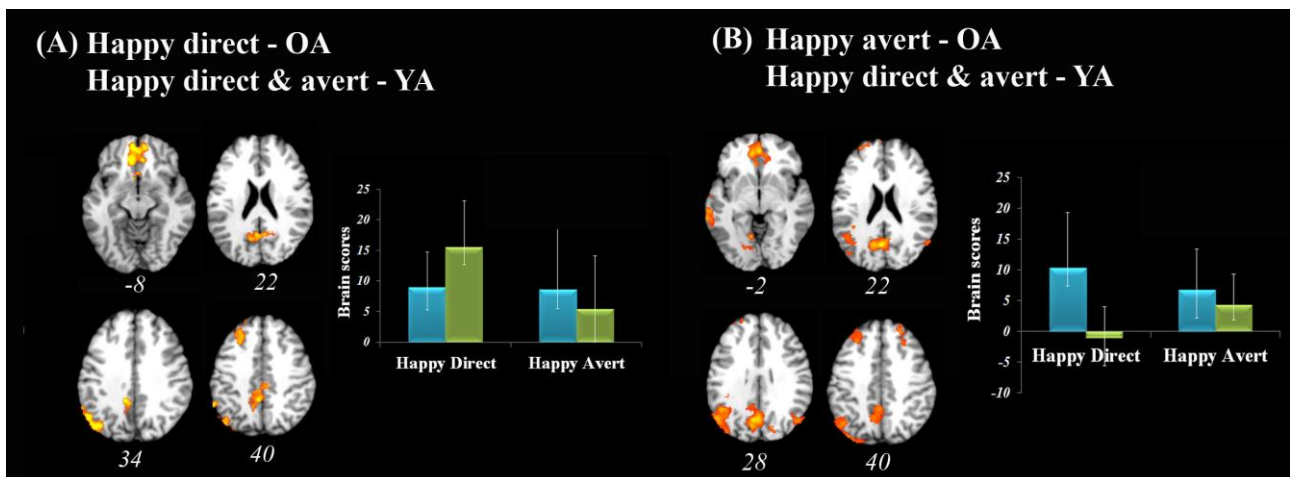
**Table 2.** Peak coordinates for clusters from whole-brain analyses for angry facial expressions

Regions	Hem	BA	MNI	BSR
			coordinates XYZ	
<b>Angry averted gaze – Younger adults</b>				
<b>Angry direct and averted gaze – Older adults</b>				
Middle frontal gyrus	R	9	[51 26 27]	7.77
	L	9	[-58 8 26]	5.10
Inferior frontal gyrus	R	45/47	[46 22 -1]	6.77
	L	45/47	[-44 20 -6]	5.13
	L	46/10	[-43 45 10]	5.17
Anterior cingulate cortex	R	32	[0 24 41]	6.86
Insula	L	13	[-31 17 10]	5.42
	R	13	[46 21 -1]	6.63
Postcentral gyrus	L	3	[-36 -24 55]	5.81
	R	2	[54 -14 29]	4.60
Inferior parietal lobule	L	40	[-45 -26 41]	6.03
	R	40	[47 -27 41]	4.06
Posterior cingulate cortex	R	31	[32 -68 30]	4.28
Precuneus	R	7	[36 -52 48]	5.55
	L	7	[-26 -54 50]	2.97
Fusiform gyrus	R	37	[48 -64 -9]	6.83
	L	37	[-39 -67 -9]	4.40
Cerebellum	L		[-9 -76 -22]	6.60
	R		[9 -74 -22]	5.03
Middle occipital gyrus	R	18	[32 -82 3]	7.80
	L	18	[-34 -88 3]	7.44
Occipital gyrus	R	19	[32 -77 -9]	5.72
	L	19	[-34 -75 -9]	5.73
Thalamus	R		[14 -12 9]	5.07
	L		[-9 -20 9]	3.80
Amygdala	R		[23 -7 -13]	4.97
<b>Angry direct gaze – Younger adults</b>				
Insula	R	13	[42 22 4]	4.51

	L	13	[-34 22 4]	4.83
Medial prefrontal gyrus	R	6	[6 20 46]	5.82
Precentral gyrus	R	9	[43 12 30]	3.94

Hem = hemisphere, BA = Broadmann Area, BR = Bootstrap Ratio

*Happy expressions.* During the recognition of happy expressions, results from the whole-brain analyses revealed two LVs. The first LV included brain regions such as ACC, PCC, precuneus, angular gyrus, middle temporal gyrus (MTG), and hippocampus – known as major nodes of default mode network (DMN; Buckner et al. (2008); Raichle et al. (2001)). These brain regions were engaged by older adults for happy facial expressions with direct gaze. In contrast, younger adults recruited these regions for happy expressions with both direct and averted gaze (Figure 4, Panel A & Table 3). LV2 yielded a network of brain regions including medial and middle PFC, ACC, MTG, superior temporal gyrus (STG), PCC, and precuneus. These regions were engaged by older adults for happy expression with averted gaze and by younger adults for both direct and averted gaze (Figure 4, Panel B & Table 3). Overall, the whole-brain analyses for happy expressions indicate that older, but not younger adults, recruit two networks during recognition of happy expressions as a function of eye gaze while younger adults showed no sensitivity to the eye-gaze orientations in terms of their neural activity patterns.



**Figure 4. Whole-brain results for happy expressions.** Patterns of whole-brain activity during the recognition of happy expressions with direct gaze among older adults (OA) and both eye-gaze directions among younger adults (YA) (A), and happy expressions with averted gaze among OA and both eye-gaze directions among YA (B), relative to the other conditions. Error bars denote 95% confidence intervals for the correlations calculated from the bootstrap procedure. All reported



regions have  $BSR \geq 2.5$  and cluster size  $\geq 100$  voxels. Abbreviations: L = left hemisphere, R = right hemisphere, OA = older adults, YA = younger adults.

**Table 3.** Peak coordinates for clusters from whole-brain analyses for happy expressions

Regions	Hem	BA	MNI	BSR
			coordinates XYZ	
<b>Happy direct gaze – Older adults</b>				
<b>Happy direct &amp; averted gaze – Younger adults</b>				
Anterior cingulate cortex	L	24	[-7 36 -8]	4.83
	L	10	[-3 63 8]	3.91
Supramarginal gyrus	L	40	[-58 -50 38]	3.83
Angular gyrus	L	39	[-44 -73 38]	3.64
Middle temporal gyrus	L	21	[-54 -8 -19]	3.63
Posterior cingulate cortex	L	31	[-2 -32 44]	4.45
	L	30	[-12 -56 20]	4.23
Precuneus	R	7	[32 -66 39]	3.89
	L	23	[-4 -58 16]	4.38
Middle occipital gyrus	R	19	[36 -87 12]	4.48
Hippocampus	R		[35 -35 -9]	3.79
<b>Happy averted gaze – Older adults</b>				
<b>Happy direct &amp; averted gaze – Younger adults</b>				
Medial prefrontal cortex	R	9	[4 60 13]	4.42
Anterior cingulate cortex	R	24	[2 28 -14]	4.69
	R	32	[0 46 -5]	5.91
Middle frontal gyrus	L	8	[-25 35 43]	3.81
	R	8	[27 30 43]	4.11
Middle temporal gyrus	R	39	[50 -66 26]	3.88
Superior temporal gyrus	L	22/42	[-64 -31 6]	5.07
	L	39	[-47 -54 26]	4.39
Posterior cingulate cortex	L	31	[-2 -45 43]	3.84
Precuneus	L	31/23	[-2 -64 25]	5.42
Cerebellum	L		[-11 -57 -5]	4.61

Hem = hemisphere, BA = Brodmann Area, BR = Bootstrap Ratio

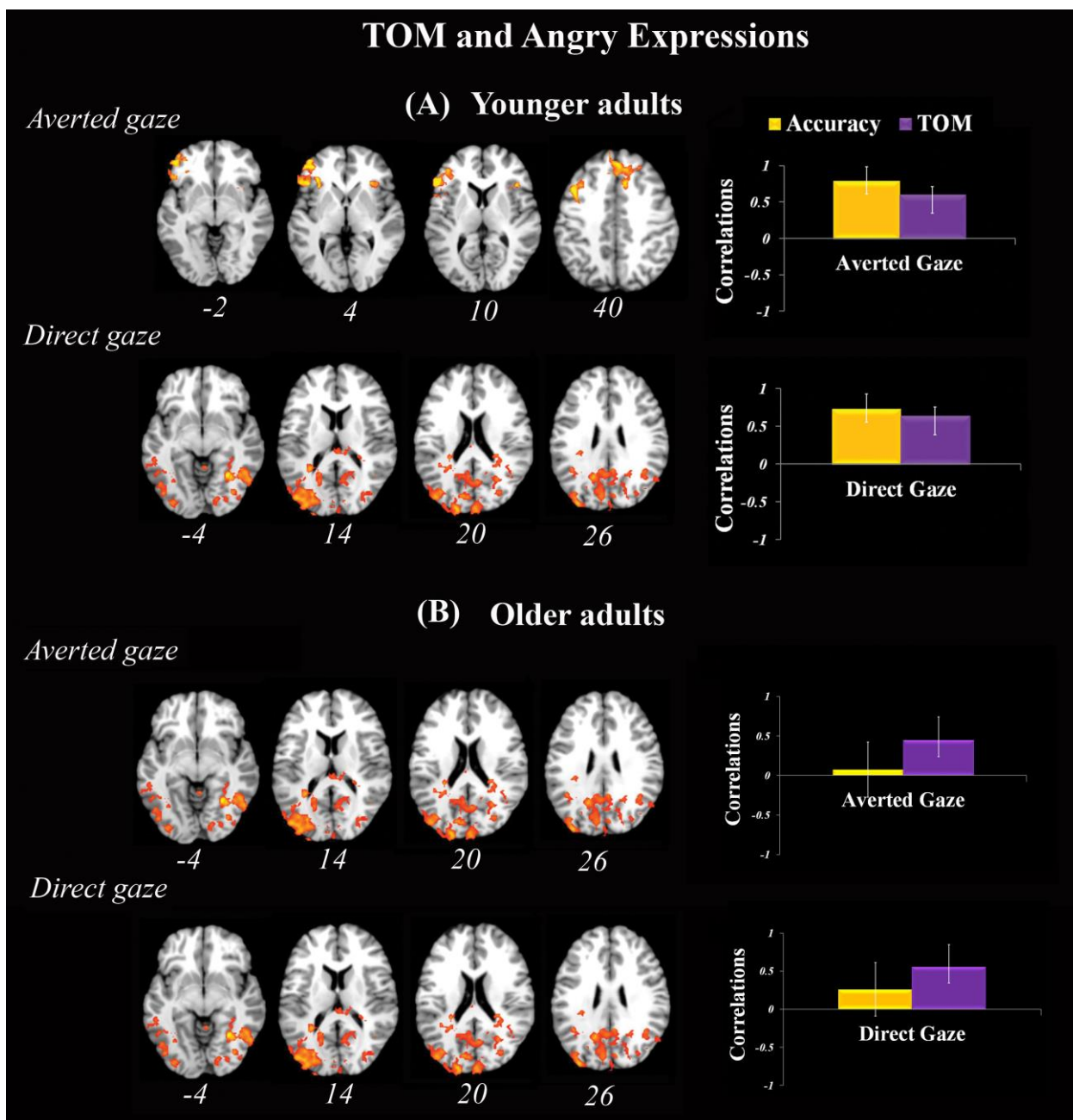
## Brain-Behaviour Analyses

Insensitivity to eye-gaze cues during recognition of angry expressions might have consequences for social-cognitive abilities. Thus, if the capacity to integrate facial cues declines in late adulthood, such age-related changes might be related to the differential engagement of mentalizing or social-cognitive brain regions. Brain-behaviour analyses were thus conducted to assess the correlation between brain activity during the angry and happy recognition conditions with TOM scores obtained on the Reading the Mind in the Eye Test (administered outside the scanner). As noted, accuracy scores from the angry conditions in the scanner task were included in the brain-behaviour analysis with the scores from TOM task. For the happy conditions, however, accuracy scores did not contribute, because these were at ceiling. Instead, only the correlations between TOM scores and brain activation during the recognition of happy expressions were considered.

*Angry expressions.* Brain-behaviour analyses focused on angry expressions revealed one significant LV, which accounted for 36% of the covariance in the data and yielded two patterns of brain activity. The first of these patterns included superior, middle, and inferior PFC regions as well as insula. This network subserved recognition of angry expressions with *averted* gaze among younger adults and correlated positively with TOM scores and accuracy during the recognition of angry averted gazes. That is, those younger adults who performed better on the TOM task and the recognition of angry averted gazes engaged the frontal brain regions to a larger extent (Figure 5, Panel A & Table 4). The second brain pattern mainly included posterior brain regions such as PCC, precuneus, cuneus, middle occipital gyrus, inferior temporal gyrus, MTG as well as medial PFC and caudate. This network subserved recognition of angry expressions with *direct* gaze among younger adults and was correlated positively with TOM scores and accuracy during recognition of angry faces with direct gaze in this cohort. In other words, younger adults who obtained higher scores on the TOM task and were better at recognizing angry faces with direct gaze recruited a set of posterior brain regions when processing angry direct gaze faces (Figure 5, Panel A & Table 4).

In older adults group, brain-behaviour analyses revealed two important findings. First, activity of the posterior brain regions; PCC, precuneus, cuneus, middle occipital gyrus, inferior temporal gyrus, MTG as well as medial PFC and caudate, was correlated with TOM scores during recognition of angry expressions, irrespective of eye-gaze directions. Moreover, these regions were only correlated with TOM scores – and not with accuracy of recognizing angry faces as seen in younger adults group. In other words, there were no reliable association between TOM scores and

task performance in the scanner in this age group. Older adults who obtained higher scores on TOM task engaged only the posterior areas while recognizing angry expressions with both direct and averted eye-gaze orientation. However, activity in these regions was not related to older adults' behavioural performance in the recognition of angry expressions in the scanner (Figure 5, Panel B & Table 4).



**Figure 5. Brain-behaviour results for angry expressions and theory of mind measure. (A)** Left panel: a pattern of whole-brain activity during recognition of angry expressions with averted gaze (top row) and direct gaze (bottom row) that correlated with scores on Reading the Mind in the

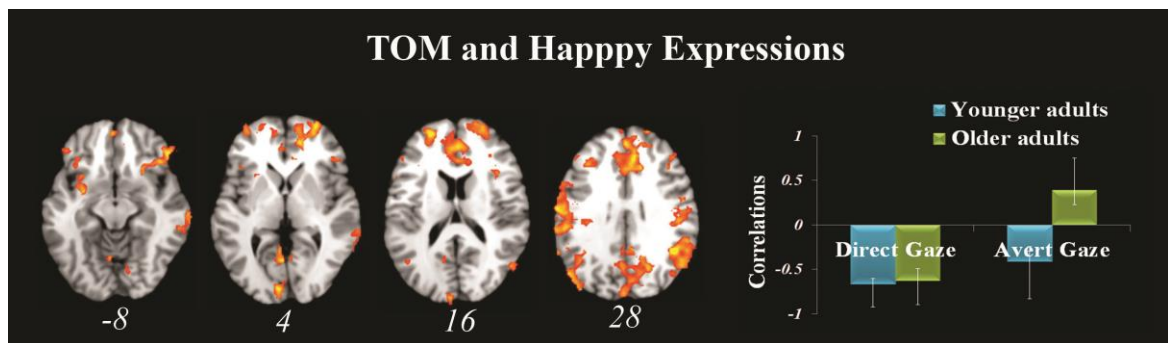
Eye Test (RMET) among younger adults. Right panel: correlations between RMET scores and performance on the scanner task during recognition of angry expressions. (B) Left panel: a pattern of whole-brain activity during recognition of angry expressions with averted gaze (top row) and direct gaze (bottom row) that correlated with scores on Reading the Mind in the Eye Test among older adults. Right panel: correlations between RMET scores and performance on the scanner task during recognition of angry expressions. Error bars denote 95% confidence intervals for the correlations calculated from the bootstrap procedure. All reported regions have BSR  $\geq 2.5$  and cluster size  $\geq 100$  voxels. Abbreviations: L = left hemisphere, R = right hemisphere.

**Table 4.** Peak coordinates for clusters from brain-behaviour analyses for angry expressions and Reading the Mind in the Eye Test (RMET) performance

Regions	Hem	BA	MNI	BSR
			coordinates XYZ	
<b>Angry averted – Younger adults</b>				
Superior frontal gyrus	R	8	[0 42 41]	3.92
	L	6	[-3 14 59]	4.41
Middle frontal gyrus	L	8/9	[-44 14 43]	5.39
Inferior frontal gyrus	L	45	[-51 27 6]	4.50
Middle frontal gyrus	L	10/46	[-40 44 4]	4.15
Insula	L	13	[-32 22 4]	4.77
<b>Angry direct – Younger adults</b>				
<b>Angry direct and averted – Older adults</b>				
Medial prefrontal gyrus		6	[3 7 61]	4.70
Inferior temporal gyrus	R	37	[50 -54 -4]	4.51
	R	19	[29 -56 -4]	5.23
Middle temporal gyrus	L	39	[-41 -79 20]	4.61
	L	22	[-49 -49 0]	5.49
Middle occipital gyrus	L	19	[-34 087 12]	5.77
PCC	L	30	[-18 -62 15]	3.87
	R	31	[0 -50 33]	5.05
Precuneus	R	7	[26 -63 33]	4.66
	L	31/7	[-12 -64 33]	3.50
Cuneus	R	7	[23 -71 38]	3.75
	L	7	[-24 -81 38]	4.34
Thalamus	R		[0 -27 15]	3.23
Caudate	R		[25 -33 15]	3.75
	L		[-26 -35 20]	4.38

Hem = hemisphere, BA = Broadmann Area, BR = Bootstrap Ratio

*Happy expressions.* The corresponding analyses for happy expressions revealed one significant LV. This LV accounted for 32% of the covariance in the data and yielded a set of regions that were activated during the recognition of happy averted gaze among older adults and positively correlated with TOM scores. This network included superior, middle, and inferior PFC, ACC, STG, IPL, and precuneus regions. Older adults who obtained higher scores on the TOM task recruited these areas during recognition of happy expressions with averted gaze more than direct gaze, and more than younger adults (Figure 6 & Table 5).



**Figure 6. Brain-behaviour results for happy expressions and theory of mind measure.** Left panel: a pattern of whole-brain activity during recognition of happy expressions with averted gaze that correlated with the scores on Reading the Mind in the Eye Test (RMET) among older adults. Right panel: correlations between RMET scores and performance on the scanner task during recognition of happy expressions. All reported regions have BSR  $\geq 2.5$  and cluster size  $\geq 100$  voxels. Abbreviations: L = left hemisphere, R = right hemisphere.

**Table 5.** Peak coordinates for clusters from brain-behaviour analyses for happy expressions and Reading the Mind in the Eye Test (RMET) performance

Regions	Hem	BA	MNI	BSR
			coordinates XYZ	
<b>Happy averted gaze – Older adults</b>				
Superior frontal gyrus	R	10	[28 60 5]	5.11
	L	10	[-21 54 18]	7.10
Anterior cingulate cortex	L	32	[-4 41 9]	4.42
Middle frontal gyrus	R	6/8	[44 15 41]	5.32
Insula	L	13	[-56 -36 24]	4.06

Inferior frontal gyrus	L	9	[-57 12 24]	5.11
	L	45/47	[-36 27 -4]	6.55
Postcentral gyrus	L	3	[-44 -17 44]	4.74
Precentral gyrus	L	4/6	[-47 -4 49]	5.10
Cingulate gyrus	L	23	[-4 -11 33]	4.07
Superior temporal gyrus	R	39	[44 -48 27]	6.63
	L	39	[-42 -56 25]	4.63
IPL	L	40	[-54 -23 31]	5.14
	R	40	[52 -48 35]	7.01
Angular gyrus	L	39	[-44 -66 33]	5.11
Precuneus	R	31	[22 -64 27]	4.62
	L	31	[-4 -60 25]	4.44
Cuneus	R	18	[0 -87 25]	4.24
Cerebellum	L		[-4 -62 -4]	4.84

Hem = hemisphere, BA = Brodmann Area, BR = Bootstrap Ratio

Taken together, these brain-behaviour correlations indicate that older adults' lack of neural sensitivity to eye gaze with angry expressions is related to the decreased likelihood of recruiting some of the main nodes of the mentalizing network in situations in which interpreting the intentions of the expresser is important; e.g., angry expressions with averted gaze. For happy expressions a different pattern emerged, with older adults recruiting the mentalizing brain regions for averted gaze conditions more than in the direct gaze condition, as well as relative to their younger counterparts. This finding was not predicted but it is in line with the results from the whole-brain analyses, and might reflect well-documented motivational changes known to occur with age.

## Discussion

The present results provide insight into the neural substrates underlying age-related differences in integrating facial affect and eye gaze cues. First, the whole-brain results showed that, in contrast to younger adults, older adults' brain activity was not modulated by eye-gaze direction during the recognition of angry expressions. Second, the brain-behaviour results showed that the ability to integrate angry expression and gaze cues was related to TOM ability; for younger, but not older adults. TOM ability was differentially correlated with two distinct networks of brain regions activated as a function of eye-gaze direction in the presence of an angry expression. The brain-behaviour correlations indicate that older adults' lack of neural sensitivity to eye gaze with angry expressions was related to the decreased recruitment of the main nodes of the mentalizing network

in situations in which interpreting the intentions of the expresser is important; angry expressions with averted gaze.

#### *Eye-gaze modulation to angry expression*

The present results provide insight into the neural substrates underlying age-related differences in integrating facial affect and eye gaze cues. First, the whole-brain results showed that, in contrast to younger adults, older adults' brain activity was not modulated by eye-gaze direction during the recognition of angry expressions. Second, the brain-behaviour results showed that the ability to integrate angry expression and gaze cues was related to TOM ability; for younger, but not older adults. TOM ability was differentially correlated with two distinct networks of brain regions activated as a function of eye-gaze direction in the presence of an angry expression. The brain-behaviour correlations indicate that older adults' lack of neural sensitivity to eye gaze with angry expressions was related to the decreased recruitment of the main nodes of the mentalizing network in situations in which interpreting the intentions of the expresser is important; angry expressions with averted gaze.

#### *Eye- gaze modulation to angry expression*

Younger adults recruited areas of a more localized brain network including insula and anterior cingulate regions – major nodes of a salience network – during recognition of angry expression with direct relative to averted gaze. The engagement of the salience network is in line with the notion that angry expressions with direct gaze are considered to be more self-relevant (N'Diaye et al., 2009; Sander et al., 2007; Sander et al., 2005) and important for survival. Therefore, a less distributed neural activation and fewer executive control regions should be required to recognize angry expressions with direct gaze. On the other hand, younger adults recruited a more distributed network of regions, including more fronto-parietal regions during averted gaze. Because angry expressions with averted gaze convey ambiguous signals to the observer (Adams et al., 2003; Adams and Kleck, 2005), it was anticipated that angry expressions with averted gaze would impose greater demands on cognitive operations such as executive control and core social-cognitive brain regions to understand the mental states of the expresser. Whole-brain results are therefore aligned with our predictions that two different networks of brain regions should be involved among young adults for processing angry expressions, one involved in encoding threatening signals with direct

gaze and one engaged social-cognitive processes when the expressions were presented with averted gaze.

Older adults, on the other hand, recruited a distributed and large-scale pattern of brain activity, during recognition of angry expressions irrespective of the eye gaze supporting the age-related neural dedifferentiation hypothesis, whereby older adults show reduced distinctiveness of neural representation in domain-specific areas (Li et al., 2001). Dedifferentiation has been evidenced in a variety of cognitive tasks in late adulthood, including memory processing (Carp et al., 2010; Carp et al., 2011; St-Laurent et al., 2011), visual perception (Park et al., 2004), as well as cognitive load-dependent processes (Burianová et al., 2015; Grady, 2008). The pattern of dedifferentiation among older adults suggests that they might exert greater executive control than needed (Dirnberger et al., 2010). The lack of specificity in recruiting brain networks for angry expressions with different eye gaze among older cohorts is also consistent with behavioural findings showing less distinction between interpreting angry expressions with direct and averted gaze (Slessor et al., 2010b) and may therefore reflect a neural inefficiency in processing threatening stimuli. This pattern of response may be related to the greater cognitive control resources older adults might recruit while processing angry expressions or the regulatory effort they employ during processing of these emotions (Ebner et al., 2012b) Although in the present study such inefficiency did not manifest at a behavioural level.

#### *Angry expressions and TOM*

Younger adults who were better at recognizing angry faces with averted gaze and who also obtained higher scores on the measure of TOM, showed greater recruitment of anterior prefrontal cortex regions, such as medial prefrontal cortex and inferior frontal gyrus. In revealing a correlation between activity in medial prefrontal cortex, TOM score, and emotion recognition, the present data suggests that the recognition of angry expressions with averted gaze (relative to direct gaze) may impose greater social-cognitive demands relying on medial prefrontal cortex and inferior frontal gyrus, which are key regions in mentalizing network (Schurz et al., 2014). Task-related activation differences also emerged, whereby angry expressions with averted gaze engaged anterior brain regions and angry expression with direct gaze engaged more posterior regions, supporting functional specialization of the mentalizing network (Schurz et al., 2014).



In contrast to their younger counterparts, older adults showed no reliable association between task performance and TOM scores. In addition, their TOM capacity was only correlated with activity in the posterior parts of the mentalizing network, such as parietal region, when they were making explicit judgments about emotional expression of the angry faces in the scanner task. The absence of an association between anterior prefrontal cortex activity and TOM scores in this group is consistent with the results of Moran et al. (2012), who also found age-related decline in recruitment of dorsal medial prefrontal cortex during various social-cognitive tasks. The age-related decline in integrating facial cues during recognition of angry expressions could potentially be associated with older adults' difficulties in reorienting social attention or higher-order mentalizing processes during the condition when the social-cognitive ability is mostly needed, e.g. averted gaze.

#### *Eye-gaze modulation to happy expression*

For happy expressions, whole-brain analyses revealed that older adults recruited two networks of brain regions as a function of direct vs. averted gaze. This gaze-dependent differentiation was unique to older adults, as no neural modulation was found for younger adults in response to eye-gaze direction. Older adults' greater sensitivity to eye gaze when processing happy expressions coupled with older adult's *insensitivity* to eye-gaze cues when processing angry expressions, align with findings on the positivity effect in aging (Reed and Carstensen, 2012; Reed et al., 2014), showing age-related biases in attention, memory, and decision-making towards positive emotional information. The current data provide evidence that these motivational shifts in late adulthood might also be reflected in the recruitment of differential neural substrates to positive expressions with direct and averted gaze.

Additionally, the brain regions involved during recognition of happy expressions support the motivational shift toward positive information. Brain areas mainly included the parietal lobes, medial PFC, and PCC, superior temporal gyrus - the main nodes of default mode network (DMN; Raichle et al. (2001)). Previous studies found increased activity of ventromedial prefrontal cortex during happy relative to angry expressions (Ebner et al., 2012b). Activity of this region is thought to reflect affective responses to cues which are probably associated with reward and demand lower cognitive resources. In other words, happy expressions seem to be more easily accessible and require lower cognitive demand, which consequently engage DMN more than angry expressions. Furthermore, engagement of DMN during recognition of happy expression is consistent with studies of theory of mind that reveal activity of DMN components. One of the subregions of this

network, medial prefrontal cortex, is activated when “thinking about the complex interactions among people that are conceived of as being social, interactive, and emotive like oneself” (Buckner et al., 2008). Correlation between DMN activity and TOM scores during recognition of happy expressions, suggest that older adults may be motivated to engage in social-cognitive processing when the facial cues are of particular interest to them.

In conclusion, the present study for the first time provides evidence that the brain networks that subserve the recognition of angry expressions are modulated by eye-gaze direction for younger but not older adults. For happy expressions, the reverse pattern of neural specificity emerged, with older (but not younger) adults showing neural sensitivity to eye gaze direction. These results are consistent with a broader motivational shift toward positive emotional information known to occur in late adulthood. Moreover, the pattern of brain-behaviour correlations showed that two networks of brain regions were differentially correlated with TOM scores and the ability to recognize angry expressions as a function of eye gaze, but only among younger adults. Taken together, these findings suggest that the age-related differences in neural regions involved in integrating facial cues relate to age-related difficulties in social-cognitive functioning.

## References

- Adams, R. B., Jr., Franklin, R. G., Jr., Kveraga, K., Ambady, N., Kleck, R. E., Whalen, P. J., . . . Nelson, A. J. (2012). Amygdala responses to averted vs direct gaze fear vary as a function of presentation speed. *Soc Cogn Affect Neurosci*, 7(5), 568-577. doi:10.1093/scan/nsr038
- Adams, R. B., Jr., Gordon, H. L., Baird, A. A., Ambady, N., & Kleck, R. E. (2003). Effect of gaze on amygdala sensitivity to anger and fear faces. *Science*, 300(1536-1536).
- Adams, R. B., Jr., & Kleck, R. E. (2005). Effects of direct and averted gaze on the perception of facially communicated emotion. *Emotion*, 5(1), 3-11. doi:10.1037/1528-3542.5.1.3
- Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of autism and developmental disorders*, 34(2), 163-175.
- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The “Reading the Mind in the Eyes” test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of child psychology and psychiatry*, 42(2), 241-251.
- Barrett, L. F., & Satpute, A. B. (2013). Large-scale brain networks in affective and social neuroscience: towards an integrative functional architecture of the brain. *Current Opinion in Neurobiology*, 23(3), 361-372.
- Blasi, G., Hariri, A. R., Alce, G., Taurisano, P., Sambataro, F., Das, S., . . . Mattay, V. S. (2009). Preferential amygdala reactivity to the negative assessment of neutral faces. *Biological psychiatry*, 66(9), 847-853.
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.*, 1124, 1-38. doi:10.1196/annals.1440.011
- Burianová, H., Marstaller, L., Choupan, J., Sepelband, F., Ziaei, M., & Reutens, D. (2015). The relation of structural integrity and task-related functional connectivity in the aging brain. *Neurobiol Aging*, 36(10), 2830-2837. doi:10.1016/j.neurobiolaging.2015.07.006
- Carp, J., Gmeindl, L., & Reuter-Lorenz, P. A. (2010). Age differences in the neural representation of working memory revealed by multi-voxel pattern analysis. *Front Hum Neurosci*, 4.
- Carp, J., Park, J., Polk, T. A., & Park, D. C. (2011). Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. *Neuroimage*, 56(2), 736-743.
- Carstensen, L. L. (2006). The influence of a sense of time on human development. *Science*, 312, 1913-1915. doi:10.1126/science.1127488

- Dirnberger, G., Lang, W., & Lindinger, G. (2010). Differential effects of age and executive functions on the resolution of the contingent negative variation: a reexamination of the frontal aging theory. *Age*, 32(3), 323-335.
- Ebner, N. C., & Johnson, M. K. (2010). Age-Group Differences in Interference from Young and Older Emotional Faces. *Cogn Emot*, 24(7), 1095-1116. doi:10.1080/02699930903128395
- Ebner, N. C., Johnson, M. K., & Fischer, H. (2012). Neural mechanisms of reading facial emotions in young and older adults. *Front Psychol*, 3, 223. doi:10.3389/fpsyg.2012.00223
- Ebner, N. C., Riediger, M., & Lindenberger, U. (2010). FACES--a database of facial expressions in young, middle-aged, and older women and men: development and validation. *Behav Res Methods*, 42(1), 351-362. doi:10.3758/BRM.42.1.351
- Efron, B., & Tibshirani, R. (1985). The bootstrap method for assessing statistical accuracy. *Behaviormetrika*, 12(17), 1-35.
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-Mental State": a practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, 12(3), 189-198. doi:DOI: 10.1016/0022-3956(75)90026-6
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 50(4), 531-534.
- Grady, C. L. (2008). Cognitive neuroscience of aging. *Ann N Y Acad Sci*, 1124, 127-144. doi:10.1196/annals.1440.009
- Graham, R., & Labar, K. S. (2012). Neurocognitive mechanisms of gaze-expression interactions in face processing and social attention. *Neuropsychologia*, 50(5), 553-566. doi:10.1016/j.neuropsychologia.2012.01.019
- Henry, J. D., von Hippel, W., & Baynes, K. (2009). Social inappropriateness, executive control, and aging. *Psychol Aging*, 24(1), 239-244. doi:10.1037/a0013423
- Henry, J. D., von Hippel, W. H., Molenberghs, P., Lee, T., & Sachdev, P. (2015). Clinical assessment of social cognitive function in neurological disorders. *Nature Reviews Neurology*, *In Press*.
- John, O. P., Donahue, E. M., & Kentle, R. L. (1991). The Big Five Inventory--Versions 4a and 54. . Berkeley, CA: University of California, Berkeley, Institute of Personality and Social Research.
- John, O. P., & Srivastava, S. (1999). The Big Five trait taxonomy: History, measurement, and theoretical perspectives. *Handbook of personality: Theory and research*, 2(1999), 102-138.
- Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in neurobiology*, 72(5), 341-372.

- Krishnan, A., Williams, L. J., McIntosh, A. R., & Abdi, H. (2011). Partial Least Squares (PLS) methods for neuroimaging: A tutorial and review. *Neuroimage*, *56*(2), 455-475. doi:10.1016/j.neuroimage.2010.07.034
- Lawrence, E., Shaw, P., Baker, D., Baron-Cohen, S., & David, A. (2004). Measuring empathy: reliability and validity of the Empathy Quotient. *Psychological medicine*, *34*(05), 911-920.
- Li, S.-C., Lindenberger, U., & Sikström, S. (2001). Aging cognition: from neuromodulation to representation. *Trends Cognit. Sci.*, *5*(11), 479-486.
- Mather, M., & Carstensen, L. L. (2003). Aging and Attentional Biases for Emotional Faces. *Psychological Science*, *14*(5), 409-415. doi:10.1111/1467-9280.01455
- McIntosh, A. R., Bookstein, F. L., Haxby, J. V., & Grady, C. L. (1996). Spatial Pattern Analysis of Functional Brain Images Using Partial Least Squares. *Neuroimage*, *3*(3), 143-157. doi:10.1006/nimg.1996.0016
- McIntosh, A. R., Chau, W. K., & Protzner, A. B. (2004). Spatiotemporal analysis of event-related fMRI data using partial least squares. *Neuroimage*, *23*(2), 764-775. doi:10.1016/j.neuroimage.2004.05.018
- Menon, V. (2015). Salience Network. 597-611. doi:10.1016/b978-0-12-397025-1.00052-x
- Moran, J. M., Jolly, E., & Mitchell, J. P. (2012). Social-cognitive deficits in normal aging. *J Neurosci*, *32*(16), 5553-5561. doi:10.1523/jneurosci.5511-11.2012
- N'Diaye, K., Sander, D., & Vuilleumier, P. (2009). Self-relevance processing in the human amygdala: gaze direction, facial expression, and emotion intensity. *Emotion*, *9*(6), 798-806. doi:10.1037/a0017845
- Nelson, H. E. (1982). National Adult Reading Test (NART): Test manual. *Windsor, UK: NFER Nelson*.
- O'Doherty, J., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature neuroscience*, *4*(1), 95-102.
- Park, D. C., Polk, T. A., Park, R., Minear, M., Savage, A., & Smith, M. R. (2004). Aging reduces neural specialization in ventral visual cortex. *Proc Natl Acad Sci U S A*, *101*(35), 13091-13095.
- Pfeiffer, U. J., Vogeley, K., & Schilbach, L. (2013). From gaze cueing to dual eye-tracking: Novel approaches to investigate the neural correlates of gaze in social interaction. *Neuroscience & Biobehavioral Reviews*, *37*, 2516-2528.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *PNAS*, *98*(2), 676-682.

- Reed, A. E., & Carstensen, L. L. (2012). The theory behind the age-related positivity effect. *Front Psychol*, 3, 339. doi:10.3389/fpsyg.2012.00339
- Reed, A. E., Chan, L., & Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: Age differences in preferences for positive over negative information. *Psychol Aging*, 29, 1-15. doi:10.1037/a0035194
- Reitan, R. M., & Wolfson, D. (1986). The Halstead-Reitan Neuropsychological Test battery and aging. *Clinical Gerontologist: The Journal of Aging and Mental Health*, 5, 39 – 61. doi:doi:10.1300/J018v05n01\_03
- Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: implications for neuropsychological models of aging. *Neurosci Biobehav Rev*, 32(4), 863-881. doi:10.1016/j.neubiorev.2008.01.001
- Sabatinelli, D., Fortune, E. E., Li, Q., Siddiqui, A., Krafft, C., Oliver, W. T., . . . Jeffries, J. (2011). Emotional perception: meta-analyses of face and natural scene processing. *Neuroimage*, 54(3), 2524-2533.
- Sampson, P. D., Streissguth, A. P., Barr, H. M., & Bookstein, F. L. (1989). Neurobehavioral effects of prenatal alcohol: Part II. Partial Least Squares analysis. *Neurotoxicology and Teratology*, 11(5), 477-491. doi:10.1016/0892-0362(89)90025-1
- Sander, D., Grandjean, D., Kaiser, S., Wehrle, T., & Scherer, K. R. (2007). Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. *European Journal of Cognitive Psychology*, 19(3), 470-480. doi:10.1080/09541440600757426
- Sander, D., Grandjean, D., & Scherer, K. R. (2005). A systems approach to appraisal mechanisms in emotion. *Neural networks : the official journal of the International Neural Network Society*, 18(4), 317-352. doi:10.1016/j.neunet.2005.03.001
- Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: a meta-analysis of functional brain imaging studies. *Neurosci Biobehav Rev*, 42, 9-34. doi:10.1016/j.neubiorev.2014.01.009
- Shepherd, S. V. (2010). Following gaze: gaze-following behavior as a window into social cognition. *Front Integr Neurosci*, 4, 5. doi:10.3389/fnint.2010.00005
- Slessor, G., Phillips, L. H., & Bull, R. (2008). Age-related declines in basic social perception: evidence from tasks assessing eye-gaze processing. *Psychol Aging*, 23(4), 812-822. doi:10.1037/a0014348
- Slessor, G., Phillips, L. H., & Bull, R. (2010). Age-related changes in the integration of gaze direction and facial expressions of emotion. *Emotion*, 10(4), 555-562. doi:10.1037/a0019152

- St-Laurent, M., Abdi, H., Burianová, H., & Grady, C. L. (2011). Influence of aging on the neural correlates of autobiographical, episodic, and semantic memory retrieval. *Journal of Cognitive Neuroscience*, 23(12), 4150-4163.
- Van Overwalle, F. (2009). Social cognition and the brain: a meta-analysis. *Human brain mapping*, 30(3), 829-858.
- Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage*, 48(3), 564-584.
- Young, A. W., Perrett, D. I., Calder, A. J., Sprengelmeyer, R., & Ekman, P. (2002). Facial expression of emotion: Stimuli and tests (FEEST). . *Suffolk, UK: Thames Valley Test*.

# **Chapter 5**

## **General Discussion**



## Summary of research findings

The overarching aim of this thesis was to investigate the underlying cognitive and neural mechanisms involved in processing emotional information in late adulthood. Specifically, I explored the cognitive and neural mechanisms involved in attention towards emotionally valenced items as well as the neural correlates of processing facial cues in relation to social-cognitive functions. In this chapter, I first review the main findings from my empirical Chapters (2-4) and then discuss the implications and contributions of each study incorporated in those chapters. I will then conclude this chapter by providing some recommendations for future research and describing the overall contribution of this thesis.

The main aims of **Study 1** (Ziaei et al., 2015) were twofold: first, to investigate the role of cognitive control in understanding the age-related memory positivity effect and second, to explore how selective attentional processes during encoding influence later memory outcomes for emotional items in late adulthood. As discussed previously in the General Introduction chapter, the positivity effect broadly refers to the processing bias older, but not younger, adults exhibit towards positive relative to negative items, which has been studied using many different types of paradigms (for a review see Reed et al. (2014). Although several studies have suggested that the positivity effect requires cognitive control resources (Knight et al., 2007; Mather and Knight, 2005), some studies have failed to support this position (Allard et al., 2010; Rosler et al., 2005; Thomas and Hasher, 2006). Additionally, several important questions remain unanswered with respect to how later memory for emotional items is influenced by early selective attentional processing. To address these issues, in Study 1, older and younger participants were presented with pairs of emotional-emotional and emotional-neutral pictures and asked to attend to either positive or negative targets and ignore the distractors during the encoding. They subsequently performed a recognition memory task. Pupillary responses were also recorded during both encoding and recognition memory stages.

The first aim of **Study 1** was to explore how cognitive resources are distributed to emotional targets in the presence of distractors. Confirming prior literature, the positivity effect in memory was found, with older adults recognising positive items with higher accuracy than negative items, relative to younger adults. However, of particular interest was the finding that, participants' memory for negative targets was not influenced by the presence of positive distractors. This finding suggests that positive distractors did not automatically capture older adults' attention during encoding for negative items. Second aim was to explore the relation between attentional processes

involved during encoding and the link with memory performance. Importantly, we found that participants' pupillary responses to negative items mediated the relationship between age and the memory positivity effect. Collectively, these two findings provide converging support for the cognitive control account of the positivity effect.

**Study 2** (presented in Chapter 3) aimed to explore neural correlates underlying encoding of positive and negative items during working memory (Ziaei, Salami & Persson, Submitted). Although a few studies have directly examined PFC-amygdala interaction (Ritchey et al., 2011a; St Jacques et al., 2010), there is still limited knowledge of brain network changes that take place during the processing of emotionally valenced items with advancing age. To directly examine the neural correlates that underlie emotional encoding, a similar task to Study 1 was used in which pairs of images, one target and one distractor, were presented during working memory encoding. Participants were asked to attend to either positive or negative items and ignore distractors. During the retrieval phase, participants were asked to identify whether they had seen the picture/probe during encoding.

In **Study 2**, I employed a multivariate method to investigate functional brain connectivity in two brain areas with the rest of the brain, the vIPFC and amygdala. This study also aimed to explore the behavioural relevance of these networks in both age groups. Analyses showed that two distinct functional brain networks were connected to the vIPFC. One of these networks that included a set of fronto-parietal brain areas was engaged during processing of negative items. These networks contributed to performance, both accuracy and response times, in older adults' group as well. This finding indicates that older adults may recruit this network to suppress the impact of negative emotions from their memory. This idea is in line with previous studies suggesting involvement of cognitive control processes during negative emotions. A brain network connected to the amygdala, on the other hand, was not differentially modulated by the emotional valence of targets among older adults. This network contributed to higher accuracy and faster response time in both conditions among older adults. Taken together, the results from these functional connectivity analyses with the vIPFC and amygdala suggest that there is differential engagement of brain networks connected to these two regions, which are modulated by the emotional valence. While two separate brain networks underlying the encoding of emotionally valence targets are connected to the vIPFC region, one distinct network is functionally connected to the amygdala and subserves the processing of both positive and negative targets.

In **Study 3** (presented in Chapter 4), I examined neural correlates of integration of facial cues, focusing specifically on emotional expression and eye-gaze cues. This study was predicated on prior empirical research indicating that older adults have difficulties detecting changes in eye-gaze (Slessor et al., 2008), they show poorer recognition of some facial expressions such as anger (Ruffman et al., 2008), and have greater difficulties integrating these facial cues (Slessor et al., 2010b). It has also been proposed that any breakdown in the capacity to integrate these cues may have important implications for social functioning in late adulthood. However, there is limited understanding of neural networks that underlie age-related differences in integrating facial cues and how difficulties in integrating facial cues are related to social-cognitive abilities.

To address these questions, **Study 3** used neuroimaging to assess older and younger adults' brain activity while engaged in a task in which they were required to identify emotional expression of faces presented with either direct or averted gaze. Results showed that while younger adults demonstrated neural sensitivity to eye-gaze orientation during recognition of angry expressions, older adults showed dedifferentiation towards eye-gaze cues for angry expressions at neural level. However, older adults, unlike younger adults, showed sensitivity to eye gaze orientation during recognition of happy expressions. Furthermore, the brain regions recruited by younger adults during processing angry expressions with averted gaze included a more distributed network which included fronto-parietal regions, suggesting that the processing angry expressions with averted gaze imposes demands on social-cognitive resources. Older adults, however, recruited this large-scale network during recognition of angry expressions with *both* direct and averted gaze, in line with the over-recruitment hypothesis. The over-recruitment pattern may suggest the neural inefficiency in processing angry expressions among older adults.

Final analyses in **Study 3** focused on the relationship between scores obtained from a measure of theory of mind (the Reading the Mind in the Eyes Test, RMET) and brain activation during recognition of happy and angry expressions. Results showed that more posterior parts of the mentalizing network (e.g. parietal cortices and posterior cingulate regions) underlie the relation between theory of mind (TOM) ability and recognising angry expressions with direct gaze. More frontal regions underpin the relationship between TOM and recognition of angry expression with averted gaze. However, older adults' TOM ability was only correlated with posterior parts of the mentalizing network. For happy expressions, however, older adults recruited the main nodes of the mentalizing network during recognition of happy expressions with averted gaze, whereas younger

adults did not show this effect. These results indicate that older adults differentially recruit their mentalizing network based on their motivation to process socially relevant stimuli.

## **Implications of findings**

Several theoretical and methodological implications can be inferred from studies presented in this thesis. Findings from the cognitive ageing literature suggest that memory difficulties in older adults might stem from poor inhibitory control, and importantly, difficulties in suppressing distractors encountered in their environment (for a review see Gazzaley and Nobre (2012)). However, our understanding of how older adults' memory for emotionally valenced items is influenced by underlying attentional processes remains very limited. Results from **Study 1** contribute to the existing literature by demonstrating that the memory positivity bias seen in older adults may be mediated by cognitive efforts that are evident during encoding of emotional items, specifically for negative items. Investigating the link between cognitive processes and outcome measures is an important issue for future research to explore how older adults' affective experience could be associated with various underlying cognitive processes such as attentional biases (for a review see Isaacowitz and Blanchard-Fields (2012)). In line with previous arguments in cognitive ageing literature (Burianová et al., 2013; Davis et al., 2008; Grady, 2008), investigating early stages of emotional processes are critical as any age-related deficit at this stage may cascade downstream manifesting itself differently at both neural and cognitive level.

Findings from **Study 1** have further theoretical implications for our understanding of cognitive and emotional interaction in late adulthood. A growing body of evidence suggests the impact of emotion on various cognitive functions, such as attention, perception, working memory, long-term memory, and decision making (for a review see Dolcos et al. (2011)) and provides important insights into the age-related changes occur in emotion and cognition interaction. The finding that older adults' memory performance was not affected by the presence of emotional distractors, specifically positive ones, add to the previous literature by suggesting that older adults employ top-down regulatory mechanisms to down regulate the impact of negative emotions - as well as distractors - to be able to perform the task.

Furthermore, results from **Study 1** have potential practical and methodological contribution in introducing a novel method that can be used in emotional control training to help clinical population or patients with neurodegenerative disorders. In line with this idea, it has been shown that

attentional training in multitasking among older adults have an impact on participants' memory and cognitive control performance (Anguera et al., 2013). In another study, Berry et al. (2010) showed that perceptual attentional training increased older adults' working memory performance. Therefore, understanding how attentional processes are linked to other outcome measures will help to identify the targeted processes that could cause long-lasting effects in therapeutic settings. Future research is needed to examine the association between the attentional processes during encoding and memory performances among older adults with clinical symptoms, e.g. depressions or anxiety, or neurodegenerative disorders.

Findings in **Study 2** extend current discussions about age-related changes in processing emotional items. The ageing brain model (Cacioppo et al., 2011) posits that the lack of activity of amygdala is the main factor explaining the positivity effect. Results from Study 1 and 2 support the view that older adults not only process negative items, but also spend more effort during encoding negative items. This might be because of suppressing negative items from their memory or down-regulating their responses to negative items to remain positive. As Mather (2012) argues, reduced activity of the amygdala is not an indication of poor functioning. When considering the functional connectivity between the amygdala and PFC regions, previous studies showed age-related differences in connectivity between amygdala and anterior cingulate regions in perceiving the emotional content of negative pictures (St Jacques et al., 2010). Older adults' pattern of increased activity of the PFC region along with decreased activity in the amygdala reflects the spontaneous regulatory mechanisms they employ while processing negative emotions. This finding is in line with previous studies that used explicit emotion regulation paradigms (Urry et al., 2006; Winecoff et al., 2011). Findings in Study 2 align with previous claim of preservation of emotional processing as well as anatomical and functional preservation of the amygdala in ageing (Dolcos et al., 2011). Our findings extend prior literature and further suggest that different brain networks might be engaged depending on the emotional valence of the stimuli. In other words, ageing positivity effect in memory may stem from the recruitment of two distinct brain networks, one engages in processing negative and one involves in processing positive emotions.

**Study 3** extends Studies 1 and 2 to a more socially-relevant context, and demonstrates that the processing of emotional expressions from faces relies on at least two distinct networks, dependent on the valence of the faces. The main contribution of Study 3 was that older adults' difficulties in integrating angry facial expressions are reflected at neural level. This finding is

important in social situations in which threat or negative emotions might be involved. Specifically, older adults might behave inappropriately when they encounter a person displaying anger simply because of difficulties detecting and integrating relevant cues. This finding has potential practical implications for older adults' ability to negotiate complex social situations, and ultimately their personal safety. This finding builds on previous studies of age-related difficulties in social functioning (Henry et al., 2009a; von Hippel and Dunlop, 2005a) by suggesting that integrating facial cues might be the precedence of complex social-cognitive behaviours and social functioning.

The finding that older – unlike younger adults – do not recruit anterior parts of the mentalizing network when processing angry expressions with averted gaze was also interesting and potentially very important. These data suggest that older adults' difficulties integrating facial cues may underlie their reduced capacity to infer the mental states of others. These findings have theoretical implications for debates about how emotion recognition and social cognitive processes are linked. The two existing theories, mind-reading and the information processing systems, have been influential in clarifying the importance of emotion perception for more complex social-cognitive processes, such as theory of mind (TOM) in autistic and schizophrenic individuals (for a review see Mitchell and Phillips (2015)). Findings from **Study 3** provide empirical evidence on how emotion perception and TOM are interrelated in late adulthood. Older adults who have higher TOM ability recruit their mentalizing network during recognition of happy expressions but not angry expressions. Thus, in addition to the social-cognitive theories, these findings contribute to the emotional ageing theories, such as SST, by indicating that motivational shift toward positive information and away from negative information may also manifest itself in a way that older adults recruit their mentalizing network while recognising communicative cues such as emotional expressions.

## **Future research**

Results from Study 2 suggest that the brain network connectivity, rather than isolated region, provides further insights for our understanding of the underlying neural substrates associated with encoding of emotional targets in ageing. Higher cognitive functions, such as emotional processes, are not presumably localized to the isolated regions, such as the amygdala, but rather they rely on functionally related neural networks. With advancement of technological and theoretical approaches, the cognitive processes are considered as the results of “collective and coordinated phenomena which unfolding within a complex network” (Sporns, 2012). Therefore, complexity and

multidimensional nature of emotional responses necessitate investigating the interaction between brain regions and covarying activity within a network subserving these functions as a function of age in future.

Previous studies have shown increased attention to faces of own-age group relative to other-age faces (Ebner and Johnson, 2010; He et al., 2011) as well as enhanced memory for own-age faces (Rhodes and Anastasi, 2012). A neuroimaging study also showed age-related differences in engaging specific brain regions such as the insula, medial PFC, and amygdala for own-age relative to other-age faces mainly for happy and neutral expressions but not for angry expressions (Ebner et al., 2013). They proposed an “overriding effect” suggesting that negative facial emotions may override own-age bias. Further research is needed to investigate this effect and examine how own-age versus other-age faces may influence the integration of facial features. I have started to investigate this idea by analysing the current dataset I acquired in Study 3, based on the age of the posers. The aim here is to examine whether age of the poser is related to neural correlates involved in processing emotional expressions displayed with different eye-gaze orientations. According to the “overriding effect”, older adults should show lack of sensitivity to the eye-gaze for angry expressions irrespective of the age of the faces. That is because angry expressions will override the effect of own-age bias. However, their preference for own-age relative to other-age faces should be evident for happy expressions. On the other hand, if the emotional expressions of the faces are irrelevant in demonstrating own-age bias, then the lack of sensitivity to eye-gaze we observed in Study 3 may be reduced as a function of own-age relative to other-age faces. This has theoretical importance as it demonstrates that age-related differences in integrating emotional cues, posited by SST, may be mediated by older adults’ preference in spending time with their desirable partners. In other words, shifts in social motivation may be a contributing factor in the way older adults integrate communicative facial cues (Moran et al., 2012).

In Study 3, I explored neural correlates underlying angry and happy facial expressions presented with direct and averted gaze. Future studies are needed to investigate how older adults integrate other types of emotional cues, such as fear, disgust, surprise and sadness when faces are presented with different eye-gaze orientations. Indeed, Slessor et al. (2010b) tested three emotions - angry, fear, and joy - and showed that older adults also exhibit difficulties integrating eye-gaze cues and emotional expressions for fearful faces as well as angry faces. Future research is needed to explore whether older adults would show lack of neural sensitivity in recognising fearful faces

presented with different eye-gaze orientations similar to what we observed for angry expressions in Study 3. Fearful faces with averted gaze are considered to signal a threat in the environment (Adams et al., 2003). Therefore, it is likely that different strategies and processes might be engaged when individuals perceive immediate threat to themselves (in case of an angry face) or in the environment (in case of a fearful face). Consequently, such differences in cognitive processes may activate different brain networks when processing fearful faces relative to angry expressions, displayed with different eye gaze.

Future studies will also benefit from investigating factors mediating the relation between emotion recognition and TOM. One possibility is that executive control operations mediate the relation between these two constructs at neural level. Previous studies have shown that both emotion recognition and TOM impose demands on executive processes. In line with this idea, Bailey and Henry showed that executive control mediates the relation between age and TOM ability (Bailey and Henry, 2008). Additionally, other evidence also suggests that deficit in emotion recognition in ageing might be associated with deficits in executive control processes (Ruffman et al., 2008). Therefore, it is possible that executive functions might be a mediating factor in the relationship between emotion recognition and TOM, which needs to be addressed in future research. Understanding factors that mediate the relationship between emotion recognition and TOM have potential importance for training and therapeutic programs. Training programs can be developed to enhance emotional or social-cognitive functioning among patients with severe impairments in these functions, such as patients with fronto-temporal dementia (Kumfor et al., 2014; Kumfor and Piguet, 2012).

It would also be interesting to investigate the relation between emotion recognition and other types of TOM tasks. Moran et al. (2012) examined older and younger adults using three different TOM tasks that involved animated movement, moral judgment, and false belief. Their results showed that in all of these tasks the medial PFC, a critical region for understanding the mental states of others, was less involved among older relative to younger adults. However, Castelli et al. (2010) used another TOM task, RMET, and did not find any differences in terms of brain activation among older and younger adults related to the performance on the RMET. One potential reason for such discrepancy in the results is related to the nature of these tasks that may involve different brain regions, as in Castelli et al. (2012), the lateral PFC, a region that is not typically associated with social cognition, was engaged during performing the RMET. This may suggest that older adults



recruit additional brain regions such as dlPFC to compensate for their impairments in social-cognitive processes. However, this potential explanation remains speculative as there are only a few studies on neural correlates of social cognition in normal ageing. Future research should investigate underlying neural substrates involved in processing different TOM tasks and the extent that the performance in other forms of TOM tasks will explain age-related difficulties in integrating facial cues.

It has been argued that structural changes in some specific regions such as the ACC or insula might be the main factor contributing to age-related difficulties in emotion recognition (Ruffman, 2011). Future research is required to examine this idea by investigating the regional gray matter volume as well as structural connectivity between critical nodes of emotion recognition processing. One recent study examined the relationship between the structural integrity of the white matter in longitudinal fasciculus track and functional connectivity of the working memory network in healthy ageing (Burianová et al., 2015). Their findings suggest that behavioural performance and functional connectivity depend on structural integrity of white matter. Previous studies also showed a relation between gray matter thinning and functional connectivity reduction (Thomsen et al., 2004). Furthermore, structural connection can shape the functional interaction on multiple time scale (Honey et al., 2007). Thus, these results indicate that there is an intricate interplay between brain structure and function in which age-related changes in structure may mediate changes in functional activation. Future research in the emotional ageing literature should adopt a multimodal perspective to examine structural and functional changes in processing emotional and social-cognitive information. In the current research I have started to pursue this strategy by investigating the relations between amygdala-PFC tracts, functional connectivity, and behavioural performance associated with processing social cues across age groups. The goal is to obtain a better understanding of the extent to which structural changes can explain the degree of age-related functional changes that occur in emotional processing. Gaining better understanding of interplay between structure and function and identifying changes in functional networks as well as structural integrity measures is crucial in early diagnoses of neurodegenerative disorders. Discerning changes and differences across healthy and neurodegenerative patients may facilitate early diagnosis of neurodegenerative disorder which in turn may provide a preventive program.

Finally, Ebner et al. (2014) has proposed a model in which the hormones including neuropeptide oxytocin may be important in understanding cognitive and social-cognitive

performance in ageing. However, no study to date has examined the modulatory role of oxytocin on brain activity involved in facial recognition. Future research is needed in order to investigate the role of the oxytocin genotype in emotion recognition processes. Although there are some inconsistencies in the literature, the role of oxytocin has been identified as a neuropeptide that enhances the salience of social stimuli, reducing social anxiety, and prompting social approach in human and animals (for a review see Ebner et al. (2014)), known as “social neuropeptide”. Further experimental studies using oxytocin are needed to examine how older and younger adults respond to emotional stimuli following exogenous administration of oxytocin. Given the importance of interpersonal and social relationship on cognitive functions in ageing (Ellwardt et al., 2013), it seems critical to understand the underlying mechanisms by which oxytocin has an impact on cognitive and emotional functions.

## **Limitations**

There are some limitations in the studies presented in this thesis that should be recognised and addressed in future research. First, although the arousal level of images used for Study 1 was controlled, we did not include participants’ own subjective ratings of arousal and valence in Study 1 and 2. Evidence indicates that there are some differences between older and younger participants in arousal rating of IAPS pictures (Grühn et al., 2005). Therefore, future studies should investigate whether participants’ own subjective ratings of arousal for emotionally valenced items influence pupillary responses. Future studies are needed to control for the arousal difference between positive and negative stimuli more closely and assess other factors could be accounted for the cognitive control effort older adults exhibited during encoding negative items.

One of the major limitations of this thesis is lack of concurrent eye-tracker during the scanner task. Having eye-tracker measure while participants were encoding the emotional items (Study 2) or recognising emotional expressions (Study 3) would have been helpful in understanding the age-related differences in eye movement patterns. In Study 3, I also measured the eye gaze fixation towards faces in a separate task administered in the behavioural session (Neuropsychological Measures in Chapter 4). However, Future studies should consider having concurrent eye-tracker and fMRI measures while studying emotional processes in late adulthood.

Another limitation of Study 2 of this thesis is its limited sample size. The positivity effect is typically rather small (Ruffman et al., 2008), and a small sample size might reduce the possibility

for detecting this effect in the behavioural data. In line with this, using larger sample size with similar paradigm in Study 1, I was able to detect a memory positivity effect among older relative to younger adults.

## **Contribution of the thesis**

In Study 1, the relation between encoding and memory for emotionally valenced items was directly examined in younger and older adults. Importantly, cognitive efforts required during encoding of negative items mediated the memory positivity effect. In Study 2, brain networks connected to the amygdala and vIPFC regions during encoding of positive and negative items have been explored. These findings extend previous literature by showing that there are age-related differences in recruitment of brain networks connected to the amygdala and vIPFC as a function of emotional valence of stimuli. In Study 3, for the first time the age-related lack of sensitivity to eye-gaze cues for angry expressions were identified. The engagement of mentalizing network during recognition of emotional expressions is an important factor contributing to age-related changes in integrating facial cues. Overall, a major contribution of this thesis is in applying Multivariate, instead of Univariate methodology, in order to gain a deeper and more comprehensive understanding of the underlying neural networks, rather than isolated brain regions, involved during emotional processing in late adulthood.

## **Conclusion**

Despite the fact that older adults show deficit in many cognitive domains, their ability to process emotional items seems often to be preserved, and in some cases, even enhanced. However, our understanding of underlying neural correlates involved in emotional processing in late adulthood remains very limited. In this thesis, I used various measures and techniques including behavioural assessment, eye-tracking and neuroimaging to investigate the underlying neural and cognitive correlates of emotional processes in attention and memory as well as facial recognition domains. The key findings are threefold. First, cognitive processes invoked during early encoding mediated subsequent memory for emotional items, and more specifically, the positivity effect. Second, two distinct brain networks underlie the processing emotionally valenced targets were connected to the vIPFC region among older adults. However, only one network was functionally connected to the amygdala and subserved the processing both positive and negative targets in the older adults' group. Remarkably, these networks facilitated behavioural performance among both

older and younger adults. Third, older adults showed sensitivity to eye-gaze cues for happy expressions but demonstrate lack of sensitivity to the eye gaze for angry expressions. The engagement of mentalizing network was found when older adults recognised happy expressions with averted gaze, but not during recognition of angry expressions.

## References

- Adams RB, Jr., Franklin RG, Jr., Kveraga K, Ambady N, Kleck RE, Whalen PJ, Hadjikhani N, Nelson AJ (2012) Amygdala responses to averted vs direct gaze fear vary as a function of presentation speed. *Soc Cogn Affect Neurosci* 7: 568-577.
- Adams RB, Jr., Gordon HL, Baird AA, Ambady N, Kleck RE (2003) Effect of gaze on amygdala sensitivity to anger and fear faces. *Science* 300.
- Adams RB, Jr., Kleck RE (2005) Effects of direct and averted gaze on the perception of facially communicated emotion. *Emotion* 5: 3-11.
- Addis DR, Leclerc CM, Muscatell KA, Kensinger EA (2010) There are age-related changes in neural connectivity during the encoding of positive, but not negative, information. *Cortex; a journal devoted to the study of the nervous system and behavior* 46: 425-433.
- Adolphs R (1999) The human amygdala and emotion. *Neuroscientist* 5: 125-137.
- Adolphs R, Tranel D, Damasio AR (2003) Dissociable neural systems for recognizing emotions. *Brain Cogn* 52: 61-69.
- Allard ES, Isaacowitz DM (2008) Are preferences in emotional processing affected by distraction? Examining the age-related positivity effect in visual fixation within a dual-task paradigm. *Neuropsychol Dev Cogn B Aging Neuropsychol Cogn* 15: 725-743.
- Allard ES, Wadlinger HA, Isaacowitz DM (2010) Positive gaze preferences in older adults: assessing the role of cognitive effort with pupil dilation. *Neuropsychol Dev Cogn B Aging Neuropsychol Cogn* 17: 296-311.
- Anderson AK, Christoff K, Stappen I, Panitz D, Ghahremani D, Glover G, Gabrieli J, Sobel N (2003) Dissociated neural representations of intensity and valence in human olfaction. *Nature neuroscience* 6: 196-202.
- Anguera JA, Boccanfuso J, Rintoul JL, Al-Hashimi O, Faraji F, Janowich J, Kong E, Larraburo Y, Rolle C, Johnston E, Gazzaley A (2013) Video game training enhances cognitive control in older adults. *Nature* 501: 97-101.
- Ashburner J (2007) A fast diffeomorphic image registration algorithm. *Neuroimage* 38: 95-113.
- Bailey PE, Henry JD (2008) Growing less empathic with age: Disinhibition of the self-perspective. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences* 63: P219-P226.
- Bailey PE, Henry JD, Nangle MR (2009) Electromyographic evidence for age-related differences in the mimicry of anger. *Psychology and Aging*, 24: 224-229.

- Baltes PB, Baltes MM (1990) Psychological perspectives on successful aging: The model of selective optimization with compensation. *Successful aging: Perspectives from the behavioral sciences* 1: 1-34.
- Baron-Cohen S, Wheelwright S (2004) The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of autism and developmental disorders* 34: 163-175.
- Baron-Cohen S, Wheelwright S, Hill J, Raste Y, Plumb I (2001) The “Reading the Mind in the Eyes” test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of child psychology and psychiatry* 42: 241-251.
- Barrett LF, Satpute AB (2013) Large-scale brain networks in affective and social neuroscience: towards an integrative functional architecture of the brain. *Current Opinion in Neurobiology* 23: 361-372.
- Bergerbest D, Gabrieli JDE, Whitfield-Gabrieli S, Kim H, Stebbins GT, Bennett DA, Fleischman DA (2009) Age-associated reduction of asymmetry in prefrontal function and preservation of conceptual repetition priming. *Neuroimage* 45: 237-246.
- Berntson GG, Bechara A, Damasio H, Tranel D, Cacioppo JT (2007) Amygdala contribution to selective dimensions of emotion. *Soc Cogn Affect Neurosci* 2: 123-129.
- Berry AS, Zanto TP, Clapp WC, Hardy JL, Delahunt PB, Mahncke HW, Gazzaley A (2010) The influence of perceptual training on working memory in older adults. *PLoS One* 5: e11537.
- Blasi G, Hariri AR, Alce G, Taurisano P, Sambataro F, Das S, Bertolino A, Weinberger DR, Mattay VS (2009) Preferential amygdala reactivity to the negative assessment of neutral faces. *Biological psychiatry* 66: 847-853.
- Boraston ZL, Corden B, Miles LK, Skuse DH, Blakemore S-J (2008) Brief report: Perception of genuine and posed smiles by individuals with autism. *Journal of autism and developmental disorders* 38: 574-580.
- Buchanan TW, Adolphs R. (2002). The role of the human amygdala in emotional modulation of long-term declarative memory. In S. Moore, M. Oaksford (Eds.), *Emotional cognition: From brain to behavior* (pp. 9-34). London, UK.: Benjamins.
- Buckner RL, Andrews-Hanna JR, Schacter DL (2008) The brain's default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.* 1124: 1-38.
- Buhle JT, Silvers JA, Wager TD, Lopez R, Onyemekwu C, Kober H, Weber J, Ochsner KN (2014) Cognitive reappraisal of emotion: a meta-analysis of human neuroimaging studies. *Cerebral Cortex* 24: 2981-2990.
- Burianová H, Lee Y, Grady CL, Moscovitch M (2013) Age-related dedifferentiation and compensatory changes in the functional network underlying face processing. *Neurobiol Aging* 34: 2759-2767.

- Burianová H, Marstaller L, Choupan J, Sepehrband F, Ziaei M, Reutens D (2015) The relation of structural integrity and task-related functional connectivity in the aging brain. *Neurobiol Aging* 36: 2830-2837.
- Cabeza R (2002) Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychology and Aging*, 17: 85-100.
- Cabeza R, Anderson ND, Locantore JK, McIntosh AR (2002) Aging Gracefully: Compensatory Brain Activity in High-Performing Older Adults. *Neuroimage* 17: 1394-1402.
- Cacioppo JT, Berntson GG, Bechara A, Tranel D, Hawkley LC. (2011). Could an aging brain contribute to subjective well-being? The value added by a social neuroscience perspective. In A. Todorov, S. Fiske, D. Prentice (Eds.), *Soc Neurosci* (pp. 249-262). Oxford; New York: Oxford University Press.
- Calvo MG, Nummenmaa L (2008) Detection of emotional faces: salient physical features guide effective visual search. *Journal of Experimental Psychology: General* 137: 471.
- Carp J, Gmeindl L, Reuter-Lorenz PA (2010) Age differences in the neural representation of working memory revealed by multi-voxel pattern analysis. *Front Hum Neurosci* 4.
- Carp J, Park J, Polk TA, Park DC (2011) Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. *Neuroimage* 56: 736-743.
- Carstensen LL (2006) The influence of a sense of time on human development. *Science* 312: 1913-1915.
- Carstensen LL, Fung HH, Charles ST (2003) Socioemotional Selectivity Theory and the regulation of emotion in the second half of the life *Motivation and Emotion* 27: 103-123.
- Carstensen LL, Isaacowitz DM, Charles ST (1999) Taking time seriously: A theory of socioemotional selectivity. *American Psychologist* 54: 165.
- Carstensen LL, Turan B, Scheibe S, Ram N, Ersner-Hershfield H, Samanez-Larkin GR, Brooks KP, Nesselroade JR (2011) Emotional experience improves with age: evidence based on over 10 years of experience sampling. *Psychol Aging* 26: 21-33.
- Castelli I, Baglio F, Blasi V, Alberoni M, Falini A, Liverta-Sempio O, Nemni R, Marchetti A (2010) Effects of aging on mindreading ability through the eyes: an fMRI study. *Neuropsychologia* 48: 2586-2594.
- Charles ST, Carstensen LL (2007) Emotion regulation and aging. *Handbook of emotion regulation* 6: 307-327.
- Charles ST, Carstensen LL (2010) Social and emotional aging. *Annu Rev Psychol* 61: 383-409.
- Charles ST, Mather M, Carstensen LL (2003) Aging and emotional memory: the forgettable nature of negative images for older adults. *Journal of Experimental Psychology. General* 132: 310-324.

- Corbetta M, Shulman GL (2002a) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3: 201-215.
- Corbetta M, Shulman GL (2002b) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3: 201-215.
- Davis SW, Dennis NA, Daselaar SM, Fleck MS, Cabeza R (2008) Que PASA? The posterior-anterior shift in aging. *Cerebral Cortex* 18: 1201-1209.
- Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. *Annual review of neuroscience* 18: 193-222.
- Dirnberger G, Lang W, Lindinger G (2010) Differential effects of age and executive functions on the resolution of the contingent negative variation: a reexamination of the frontal aging theory. *Age* 32: 323-335.
- Dolcos F, Jordan AD, Dolcos S (2011) Neural correlates of emotion-cognition interactions: A review of evidence from brain imaging investigations. *J Cogn Psychol (Hove)* 23: 669-694.
- Dolcos F, LaBar KS, Cabeza R (2004) Dissociable effects of arousal and valence on prefrontal activity indexing emotional evaluation and subsequent memory: an event-related fMRI study. *Neuroimage* 23: 64-74.
- Dolcos F, McCarthy G (2006) Brain systems mediating cognitive interference by emotional distraction. *The Journal of neuroscience : the official journal of the Society for Neuroscience* 26: 2072-2079.
- Dolcos S, Katsumi Y, Dixon RA (2014) The role of arousal in the spontaneous regulation of emotions in healthy aging: a fMRI investigation. *Front Psychol* 5: 681.
- Dosenbach NU, Fair DA, Cohen AL, Schlaggar BL, Petersen SE (2008) A dual-networks architecture of top-down control. *Trends in Cognitive Science* 12: 99-105.
- Ebner NC, He Y, Johnson MK (2011) Age and emotion affect how we look at a face: Visual scan patterns differ for own-age versus other-age emotional faces. *Cognition & Emotion* 25: 983-997.
- Ebner NC, Johnson MK (2010) Age-Group Differences in Interference from Young and Older Emotional Faces. *Cogn Emot* 24: 1095-1116.
- Ebner NC, Johnson MK, Fischer H (2012a) Neural mechanisms of reading facial emotions in young and older adults. *Emotion Science* 3: 223.
- Ebner NC, Johnson MK, Fischer H (2012b) Neural mechanisms of reading facial emotions in young and older adults. *Front Psychol* 3: 223.
- Ebner NC, Johnson MR, Rieckmann A, Durbin KA, Johnson MK, Fischer H (2013) Processing own-age vs. other-age faces: neuro-behavioral correlates and effects of emotion. *Neuroimage* 78: 363-371.



- Ebner NC, Kamin H, Diaz V, Cohen RA, MacDonald K (2014) Hormones as "difference makers" in cognitive and socioemotional aging processes. *Front Psychol* 5: 1595.
- Ebner NC, Riediger M, Lindenberger U (2010) FACES--a database of facial expressions in young, middle-aged, and older women and men: development and validation. *Behav Res Methods* 42: 351-362.
- Efron B, Tibshirani R (1985) The bootstrap method for assessing statistical accuracy. *Behaviormetrika* 12: 1-35.
- Ekman P. (2009). *Telling Lies: Clues to Deceit in the Marketplace, Politics, and Marriage (Revised Edition)*: WW Norton & Company.
- Ekman P, Friesen WV. (1978). *The Facial Action Coding System*.
- Ellwardt L, Aartsen M, Deeg D, Steverink N (2013) Does loneliness mediate the relation between social support and cognitive functioning in later life? *Social science & medicine* 98: 116-124.
- Emery L, Hess TM (2008) Viewing instructions impact emotional memory differently in older and young adults. *Psychology and Aging*, 23: 2-12.
- Eriksson J, Kalpouzos G, Nyberg L (2011) Rewiring the brain with repeated retrieval: a parametric fMRI study of the testing effect. *Neuroscience Letter* 505: 36-40.
- Ferri J, Schmidt J, Hajcak G, Canli T (2013) Neural correlates of attentional deployment within unpleasant pictures. *Neuroimage* 70: 268-277.
- Fischer H, Nyberg L, Backman L (2010) Age-related differences in brain regions supporting successful encoding of emotional faces. *Cortex* 46: 490-497.
- Fischer H, Sandblom J, Gavazzeni J, Fransson P, Wright CI, Backman L (2005) Age-differential patterns of brain activation during perception of angry faces. *Neuroscience letters* 386: 99-104.
- Folstein MF, Folstein SE, McHugh PR (1975) "Mini-Mental State": a practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research* 12: 189-198.
- Folster M, Hess U, Werheid K (2014) Facial age affects emotional expression decoding. *Front Psychol* 5: 30.
- Freire L, Roche A, Mangin J-F (2002) What is the Best Similarity Measure for Motion Correction in fMRI Time Series? *IEE Transaction on Medical Imaging* 21.
- Frith CD, Frith U (2006) The neural basis of mentalizing. *Neuron* 50: 531-534.
- Gallo DA, Foster KT, Johnson EL (2009) Elevated false recollection of emotional pictures in young and older adults. *Psychol Aging* 24: 981-988.

- Gazzaley A (2011) Influence of early attentional modulation on working memory. *Neuropsychologia* 49: 1410-1424.
- Gazzaley A. (2012). Top-down modulation deficit in the aging brain: an emerging theory of cognitive aging. In D. T. Stuss, R. T. Knight (Eds.), *Principles of Frontal Lobe Function* (second ed.). Oxford; New York: Oxford University Press.
- Gazzaley A, Clapp W, Kelley J, McEvoy K, Knight RT, D'Esposito M (2008) Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proc. Natl. Acad. Sci. U. S. A.* 105: 13122-13126.
- Gazzaley A, Cooney GW, McEvoy K, Knight RT, D'Esposito M (2005a) Top-down Enhancement and Suppression of the Magnitude and Speed of Neural Activity. *Journal of Cognitive Neuroscience* 17: 507–517.
- Gazzaley A, Cooney JW, Rissman J, D'Esposito M (2005b) Top-down suppression deficit underlies working memory impairment in normal aging. *Nature neuroscience* 8: 1298-1300.
- Gazzaley A, D'Esposito M (2007) Top-down modulation and normal aging. *Ann. N. Y. Acad. Sci.* 1097: 67-83.
- Gazzaley A, Nobre AC (2012) Top-down modulation: bridging selective attention and working memory. *Trends in Cognitive Science* 16: 129-135.
- Goh JO, Park DC (2009) Neuroplasticity and cognitive aging: the scaffolding theory of aging and cognition. *Restorative neurology and neuroscience* 27: 391-403.
- Grady C (2012) The cognitive neuroscience of ageing. *Nature Reviews Neuroscience* 13: 491-505.
- Grady CL (2008) Cognitive neuroscience of aging. *Ann N Y Acad Sci* 1124: 127-144.
- Graham R, Labar KS (2012) Neurocognitive mechanisms of gaze-expression interactions in face processing and social attention. *Neuropsychologia* 50: 553-566.
- Gross JJ, John OP (2003) Individual differences in two emotion regulation processes: implications for affect, relationships, and well-being. *Journal of personality and social psychology* 85: 348.
- Gross JJ, Thompson RA (2007) Emotion Regulation: conceptual foundation. *Handbook of emotion regulation*.
- Grühn D, Smith J, Baltes PB (2005) No aging bias favoring memory for positive material: Evidence from a heterogeneity-homogeneity list paradigm using emotionally toned words. *Psychol Aging* 20: 579-588.
- Gunning-Dixon FM, Gur RC, Perkins AC, Schroeder L, Turner T, Turetsky BI, Chan RM, Loughead JW, Alsop DC, Maldjian J, Gur RE (2003) Age-related differences in brain activation during emotional face processing. *Neurobiol Aging* 24: 285-295.

- Gutchess AH, Kensinger EA, Schacter DL (2007) Aging, self-referencing, and medial prefrontal cortex. *Soc Neurosci* 2: 117-133.
- Halberstadt J, Ruffman T, Murray J, Taumoepeau M, Ryan M (2011) Emotion perception explains age-related differences in the perception of social gaffes. *Psychology and Aging*, 26: 133-136.
- Hamann S (2003) Nosing in on the emotional brain. *Nature neuroscience* 6: 106-108.
- Hasher L, Zacks RT. (1988). Working memory, comprehension, and aging: A review and a new view. In G. H. Bower (Ed.), *The Psychology of Learning and Motivation* (Vol. 22, pp. 193-225): New York: Academic Press.
- He Y, Ebner NC, Johnson MK (2011) What predicts the own-age bias in face recognition memory? *Social Cognition* 29: 97-109.
- Henry JD, von Hippel W, Baynes K (2009a) Social inappropriateness, executive control, and aging. *Psychol Aging* 24: 239-244.
- Henry JD, Von Hippel W, Baynes K (2009b) Social inappropriateness, executive control, and aging. *Psychol Aging* 24: 239.
- Henry JD, von Hippel WH, Molenberghs P, Lee T, Sachdev P (2015) Clinical assessment of social cognitive function in neurological disorders. *Nature Reviews Neurology*. In Press.
- Honey CJ, Kötter R, Breakspear M, Sporns O (2007) Network structure of cerebral cortex shapes functional connectivity on multiple time scales. *Proceedings of the National Academy of Sciences* 104: 10240-10245.
- Iidaka T, Okada T, Murata T, Omori M, Kosaka H, Sadato N, Yonekura Y (2002) Age-related differences in the medial temporal lobe responses to emotional faces as revealed by fMRI. *Hippocampus* 12: 352-362.
- Iordan AD, Dolcos S, Dolcos F (2013) Neural signatures of the response to emotional distraction: a review of evidence from brain imaging investigations. *Front Hum Neurosci* 7: 200.
- Isaacowitz DM, Allard ES, Murphy NA, Schlangel M (2009a) The time course of age-related preferences toward positive and negative stimuli. *J. Gerontol. B Psychol Sci Soc Sci*, 64B: 188-192.
- Isaacowitz DM, Blanchard-Fields F (2012) Linking Process and Outcome in the Study of Emotion and Aging. *Perspect Psychol Sci* 7: 3-17.
- Isaacowitz DM, Löckenhoff CE, Lane RD, Wright R, Sechrest L, Riedel R, Costa PT (2007) Age differences in recognition of emotion in lexical stimuli and facial expressions. *Psychol Aging* 22: 147.
- Isaacowitz DM, Toner K, Goren D, Wilson HR (2008) Looking while unhappy: mood-congruent gaze in young adults, positive gaze in older adults. *Psychological Science* 19: 848-853.

- Isaacowitz DM, Toner K, Neupert SD (2009b) Use of gaze for real-time mood regulation: Effects of age and attentional functioning. *Psychol Aging* 24: 989-994.
- Isaacowitz DM, Wadlinger HA, Goren D, Wilson HR (2006) Selective preference in visual fixation away from negative images in old age? An eye-tracking study. *Psychol Aging* 21: 40-48.
- Itier RJ, Batty M (2009) Neural bases of eye and gaze processing: the core of social cognition. *Neurosci Biobehav Rev* 33: 843-863.
- Jensen AR, Rohwer WD (1966) The Stroop color-word test: A review. *Acta psychologica* 25: 36-93.
- John OP, Donahue, E. M., & Kentle, R. L. (1991) *The Big Five Inventory--Versions 4a and 5a*. . Berkeley, CA: University of California, Berkeley, Institute of Personality and Social Research.
- John OP, Srivastava S (1999) The Big Five trait taxonomy: History, measurement, and theoretical perspectives. *Handbook of personality: Theory and research* 2: 102-138.
- Kapucu A, Rotello CM, Ready RE, Seidl KN (2008) Response bias in "remembering" emotional stimuli: a new perspective on age differences. *J Exp Psychol Learn Mem Cogn* 34: 703-711.
- Kensinger EA (2008) Age differences in memory for arousing and nonarousing emotional words. *J. Gerontol. B Psychol Sci Soc Sci*, 63B: 13-18.
- Kensinger EA, Brierley B, Medford N, Growdon JH, Corkin S (2002) Effects of normal aging and Alzheimer's disease on emotional memory. *Emotion* 2: 118-134.
- Kensinger EA, Corkin S (2004) Two routes to emotional memory: distinct neural processes for valence and arousal. *Proc. Natl. Acad. Sci. U. S. A.* 101: 3310-3315.
- Kensinger EA, Garoff-Eaton RJ, Schacter DL (2007a) Effects of emotion on memory specificity in young and older adults. *J. Gerontol. B Psychol Sci Soc Sci*, 62: P208-P215.
- Kensinger EA, Garoff-Eaton RJ, Schacter DL (2007b) Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of memory and language* 56: 575-591.
- Kensinger EA, Schacter DL. (2007). Memory and emotion. In M. Lewis, J. M. Haviland-Jones, L. F. Barrett (Eds.), *The handbook of emotions* (3rd ed., pp. 601-617). New York: Guilford.
- Kensinger EA, Schacter DL (2008) Neural processes supporting young and older adults' emotional memories. *Journal of Cognitive Neuroscience* 20: 1161-1173.
- Kim H (2011) Neural activity that predicts subsequent memory and forgetting: a meta-analysis of 74 fMRI studies. *Neuroimage* 54: 2446-2461.
- Knight M, Seymour TL, Gaunt JT, Baker C, Nesmith K, Mather M (2007) Aging and goal-directed emotional attention: distraction reverses emotional biases. *Emotion* 7: 705-714.

- Kondo H, Morishita M, Osaka N, Osaka M, Fukuyama H, Shibasaki H (2004) Functional roles of the cingulo-frontal network in performance on working memory. *Neuroimage* 21: 2-14.
- Koster EH, Crombez G, Verschuere B, De Houwer J (2004) Selective attention to threat in the dot probe paradigm: Differentiating vigilance and difficulty to disengage. *Behaviour research and therapy* 42: 1183-1192.
- Krendl AC, Ambady N (2010) Older adults' decoding of emotions: role of dynamic versus static cues and age-related cognitive decline. *Psychology and Aging*, 25: 788-793.
- Kringelbach ML, Rolls ET (2004) The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in neurobiology* 72: 341-372.
- Krishnan A, Williams LJ, McIntosh AR, Abdi H (2011) Partial Least Squares (PLS) methods for neuroimaging: A tutorial and review. *Neuroimage* 56: 455-475.
- Krumhuber EG, Kappas A, Manstead ASR (2013) Effects of Dynamic Aspects of Facial Expressions: A Review. *Emotion Review* 5: 41-46.
- Kumfor F, Irish M, Leyton C, Miller L, Lah S, Devenney E, Hodges JR, Piguet O (2014) Tracking the progression of social cognition in neurodegenerative disorders. *Journal of Neurology, Neurosurgery & Psychiatry* 85: 1076-1083.
- Kumfor F, Piguet O (2012) Disturbance of Emotion Processing in Frontotemporal Dementia: A Synthesis of Cognitive and Neuroimaging Findings. *Neuropsychology Review* 22: 280-297.
- LaBar KS, Cabeza R (2006) Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience* 7: 54-64.
- Lang P, Bradley MM, Cuthbert BN. (2008). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual.*: University of Florida, Gainesville, FL.
- Larcom MJ, Isaacowitz DM (2009) Rapid emotion regulation after mood induction: age and individual differences. *J. Gerontol. B Psychol Sci Soc Sci* 64: 733-741.
- Lawrence E, Shaw P, Baker D, Baron-Cohen S, David A (2004) Measuring empathy: reliability and validity of the Empathy Quotient. *Psychological medicine* 34: 911-920.
- Leclerc CM, Kensinger EA (2008) Age-related differences in medial prefrontal activation in response to emotional images. *Cognitive, Affective, & Behavioral Neuroscience* 8: 153-164.
- Leclerc CM, Kensinger EA (2011) Neural processing of emotional pictures and words: A comparison of young and older adults. *Developmental neuropsychology* 36: 519-538.
- Levine LJ, Edelman RS (2009) Emotion and memory narrowing: A review and goal-relevance approach. *Cognition & Emotion* 23: 833-875.

- Li S-C, Lindenberger U, Sikström S (2001) Aging cognition: from neuromodulation to representation. *Trends Cognit. Sci.* 5: 479-486.
- Lindquist KA, Wager TD, Kober H, Bliss-Moreau E, Barrett LF (2012) The brain basis of emotion: a meta-analytic review. *Behavioral and Brain Sciences* 35: 121-143.
- Lockenhoff CE, Carstensen LL (2007) Aging, emotion, and health-related decision strategies: motivational manipulations can reduce age differences. *Psychol Aging* 22: 134-146.
- Löckenhoff CE, Carstensen LL (2004) Socioemotional selectivity theory, aging, and health: The increasingly delicate balance between regulating emotions and making tough choices. *Journal of Personality* 72: 1395-1424.
- Macey PM, Macey KE, Kumar R, Harper RM (2004) A method for removal of global effects from fMRI time series. *Neuroimage* 22: 360-366.
- Marsiske M, Lang FB, Baltes PB, Baltes MM (1995) Selective optimization with compensation: life-span perspectives on successful human development.
- Mather M (2012) The emotion paradox in the aging brain. *Ann. N. Y. Acad. Sci.*
- Mather M, Canli T, English T, Whitfield S, Wais P, Ochsner KN, Gabrieli JD, Carstensen LL (2004) Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science* 15: 259-263.
- Mather M, Carstensen LL (2003) Aging and Attentional Biases for Emotional Faces. *Psychological Science* 14: 409-415.
- Mather M, Carstensen LL (2005) Aging and motivated cognition: the positivity effect in attention and memory. *Trends in Cognitive Science* 9: 496-502.
- Mather M, Knight M (2005) Goal-directed memory: the role of cognitive control in older adults' emotional memory. *Psychol Aging* 20: 554-570.
- Mather M, Knight MR (2006) Angry faces get noticed quickly: Threat detection is not impaired among older adults. *J. Gerontol. B Psychol Sci Soc Sci*, 61: P54-P57.
- Mather M, Sutherland MR (2011) Arousal-biased competition in perception and memory. *Perspect Psychol Sci* 6: 114-133.
- Mazoyer B, Zago L, Mellet E, Bricogne S, Etard O, Houde O, Crivello F, Joliot M, Petit L, Tzourio-Mazoyer N (2001) Cortical networks for working memory and executive functions sustain the conscious resting state in man. *Brain Research Bulletin* 54: 287-298.
- McIntosh AR, Bookstein FL, Haxby JV, Grady CL (1996) Spatial Pattern Analysis of Functional Brain Images Using Partial Least Squares. *Neuroimage* 3: 143-157.
- McIntosh AR, Chau WK, Protzner AB (2004) Spatiotemporal analysis of event-related fMRI data using partial least squares. *Neuroimage* 23: 764-775.

- Menon V (2015) Salience Network. Arthur W. Toga, editor. *Brain Mapping: An Encyclopedic Reference*, vol. 2, pp. 597-611. Academic Press: Elsevier.
- Mitchell RLC, Phillips LH (2015) The overlapping relationship between emotion perception and theory of mind. *Neuropsychologia*.
- Moran JM, Jolly E, Mitchell JP (2012) Social-cognitive deficits in normal aging. *J Neurosci* 32: 5553-5561.
- Murphy NA, Lehrfeld JM, Isaacowitz DM (2010) Recognition of posed and spontaneous dynamic smiles in young and older adults. *Psychology and Aging*, 25: 811-821.
- Murty VP, Ritchey M, Adcock RA, LaBar KS (2011) Reprint of: fMRI studies of successful emotional memory encoding: A quantitative meta-analysis. *Neuropsychologia* 49: 695-705.
- Murty VP, Sambataro F, Das S, Tan H-Y, Callicott JH, Goldberg TE, Meyer-Lindenberg A, Weinberger DR, Mattay VS (2009) Age-related alterations in simple declarative memory and the effect of negative stimulus valence. *Journal of Cognitive Neuroscience* 21: 1920-1933.
- N'Diaye K, Sander D, Vuilleumier P (2009) Self-relevance processing in the human amygdala: gaze direction, facial expression, and emotion intensity. *Emotion* 9: 798-806.
- Nashiro K, Sakaki M, Mather M (2012) Age differences in brain activity during emotion processing: reflections of age-related decline or increased emotion regulation? *Gerontology* 58: 156-163.
- Nelson HE. (1982). *National Adult Reading Test (NART): Test manual*. Windsor, UK: NFER Nelson.
- O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C (2001) Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature neuroscience* 4: 95-102.
- Ochsner KN, Gross JJ (2005) The cognitive control of emotion. *Trends in Cognitive Science* 9: 242-249.
- Öhman A, Lundqvist D, Esteves F (2001) The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of personality and social psychology* 80: 381-396.
- Park DC, Polk TA, Park R, Minear M, Savage A, Smith MR (2004) Aging reduces neural specialization in ventral visual cortex. *Proc Natl Acad Sci U S A* 101: 13091-13095.
- Persson J, Lustig C, Nelson JK, Reuter-Lorenz PA (2007) Age differences in deactivation: a link to cognitive control? *Journal of Cognitive Neuroscience* 19: 1021-1032.
- Persson J, Pudas S, Nilsson L-G, Nyberg L (2014) Longitudinal assessment of default-mode brain function in aging. *Neurobiol Aging* 35: 2107-2117.

- Pessoa L (2008) On the relationship between emotion and cognition. *Nature Reviews Neuroscience* 9: 148-158.
- Pessoa L (2010) Emergent processes in cognitive-emotional interactions. *Dialogues in Clinical Neuroscience* 12: 433-448.
- Pessoa L, Adolphs R (2010) Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, 11: 773-783.
- Pessoa L, McKenna M, Gutierrez E, Ungerleider LG (2002) Neural processing of emotional faces requires attention. *Proc. Natl. Acad. Sci. U. S. A.*, 99: 11458-11463.
- Pfeiffer UJ, Vogeley K, Schilbach L (2013) From gaze cueing to dual eye-tracking: Novel approaches to investigate the neural correlates of gaze in social interaction. *Neuroscience & Biobehavioral Reviews* 37: 2516-2528.
- Phan KL, Fitzgerald DA, Nathan PJ, Moore GJ, Uhde TW, Tancer ME (2005) Neural substrates for voluntary suppression of negative affect: a functional magnetic resonance imaging study. *Biological psychiatry* 57: 210-219.
- Phelps EA (2004) Human emotion and memory: interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology* 14: 198-202.
- Phillips LH, Slessor G, Bailey PE, Henry JD (2014) Older Adults' Perception of Social and Emotional Cues. *The Oxford Handbook of Emotion, Social Cognition, and Problem Solving in Adulthood* 9.
- Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001) A default mode of brain function. *PNAS* 98: 676-682.
- Reed AE, Carstensen LL (2012) The theory behind the age-related positivity effect. *Front Psychol* 3: 339.
- Reed AE, Chan L, Mikels JA (2014) Meta-analysis of the age-related positivity effect: Age differences in preferences for positive over negative information. *Psychol Aging* 29: 1-15.
- Reitan RM, Wolfson D (1986) The Halstead-Reitan Neuropsychological Test battery and aging. *Clinical Gerontologist: The Journal of Aging and Mental Health* 5: 39 – 61.
- Reuter-Lorenz PA, Lustig C (2005) Brain aging: reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology* 15: 245-251.
- Reuter-Lorenz PA, Park DC (2010) Human neuroscience and the aging mind: A new look at old problems. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences* 65B: 405-415.
- Rhodes MG, Anastasi JS (2012) The own-age bias in face recognition: a meta-analytic and theoretical review. *Psychological Bulletin* 138: 146-174.



- Riediger M, Studtmann M, Westphal A, Rauters A, Weber H (2014) No smile like another: adult age differences in identifying emotions that accompany smiles. *Front Psychol* 5.
- Ritchey M, Bessette-Symons B, Hayes SM, Cabeza R (2011a) Emotion processing in the aging brain is modulated by semantic elaboration. *Neuropsychologia* 49: 640-650.
- Ritchey M, Dolcos F, Eddington KM, Strauman TJ, Cabeza R (2011b) Neural correlates of emotional processing in depression: changes with cognitive behavioral therapy and predictors of treatment response. *Journal of Psychiatric Research* 45: 577-587.
- Rosler A, Ulrich C, Billino J, Sterzer P, Weidauer S, Bernhardt T, Steinmetz H, Frolich L, Kleinschmidt A (2005) Effects of arousing emotional scenes on the distribution of visuospatial attention: changes with aging and early subcortical vascular dementia. *Journal of Neurological Sciences* 229-230: 109-116.
- Ruffman T (2011) Ecological Validity and Age-Related Change in Emotion Recognition. *Journal of Nonverbal Behavior* 35: 297-304.
- Ruffman T, Henry JD, Livingstone V, Phillips LH (2008) A meta-analytic review of emotion recognition and aging: implications for neuropsychological models of aging. *Neurosci Biobehav Rev* 32: 863-881.
- Ruffman T, Murray J, Halberstadt J, Taumoepeau M (2010) Verbosity and emotion recognition in older adults. *Psychology and Aging*, 25: 492-497.
- Ruffman T, Murray J, Halberstadt J, Vater T (2012) Age-related differences in deception. *Psychol Aging* 27: 543.
- Ruffman T, Ng M, Jenkin T (2009) Older adults respond quickly to angry faces despite labeling difficulty. *J. Gerontol. B Psychol Sci Soc Sci* 64: 171-179.
- Rypma B, D'Esposito M (2000) Isolating the neural mechanisms of age-related changes in human working memory. *Nature neuroscience* 3: 509-515.
- Sabatinelli D, Fortune EE, Li Q, Siddiqui A, Krafft C, Oliver WT, Beck S, Jeffries J (2011) Emotional perception: meta-analyses of face and natural scene processing. *Neuroimage* 54: 2524-2533.
- Sakaki M, Gorlick MA, Mather M (2011) Differential interference effects of negative emotional states on subsequent semantic and perceptual processing. *Emotion* 11: 1263-1278.
- Samanez-Larkin GR, Robertson ER, Mikels JA, Carstensen LL, Gotlib IH (2009) Selective attention to emotion in the aging brain. *Psychol Aging* 24: 519-529.
- Sambataro F, Murty VP, Callicott JH, Tan H-Y, Das S, Weinberger DR, Mattay VS (2010) Age-related alterations in default mode network: impact on working memory performance. *Neurobiol Aging* 31: 839-852.

- Sampson PD, Streissguth AP, Barr HM, Bookstein FL (1989) Neurobehavioral effects of prenatal alcohol: Part II. Partial Least Squares analysis. *Neurotoxicology and Teratology* 11: 477-491.
- Sander D, Grandjean D, Kaiser S, Wehrle T, Scherer KR (2007) Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. *European Journal of Cognitive Psychology* 19: 470-480.
- Sander D, Grandjean D, Scherer KR (2005) A systems approach to appraisal mechanisms in emotion. *Neural networks : the official journal of the International Neural Network Society* 18: 317-352.
- Santangelo V, Ho C, Spence C (2008) Capturing spatial attention with multisensory cues. *Psychonomic Bulletin & Review* 15: 398-403.
- Scheibe S, Carstensen LL (2010) Emotional aging: recent findings and future trends. *J Gerontol B Psychol Sci Soc Sci* 65B: 135-144.
- Schultz J, Pilz KS (2009) Natural facial motion enhances cortical responses to faces. *Experimental Brain Research* 194: 465-475.
- Schurz M, Radua J, Aichhorn M, Richlan F, Perner J (2014) Fractionating theory of mind: a meta-analysis of functional brain imaging studies. *Neurosci Biobehav Rev* 42: 9-34.
- Shafer AT, Matveychuk D, Penney T, O'Hare AJ, Stokes J, Dolcos F (2012) Processing of emotional distraction is both automatic and modulated by attention: Evidence from an Event-related fMRI investigation. *Journal of Cognitive Neuroscience* 24: 1233-1252.
- Shepherd SV (2010) Following gaze: gaze-following behavior as a window into social cognition. *Front Integr Neurosci* 4: 5.
- Shulman GL, Corbetta M, Buckner RL, Raichle ME, Fiez JA, Miezin FM, Petersen SE (1997) Top-down modulation of early sensory cortex. *Cereb Cortex* 7: 193-206.
- Slessor G, Bailey PE, Rendell PG, Ruffman T, Henry JD, Miles LK (2014) Examining the time course of young and older adults' mimicry of enjoyment and nonenjoyment smiles. *Emotion* 14: 532-544.
- Slessor G, Miles LK, Bull R, Phillips LH (2010a) Age-related changes in detecting happiness: discriminating between enjoyment and nonenjoyment smiles. *Psychology and Aging*, 25: 246-250.
- Slessor G, Phillips LH, Bull R (2008) Age-related declines in basic social perception: evidence from tasks assessing eye-gaze processing. *Psychol Aging* 23: 812-822.
- Slessor G, Phillips LH, Bull R (2010b) Age-related changes in the integration of gaze direction and facial expressions of emotion. *Emotion* 10: 555-562.

- Smith SD, Most SB, Newsome LA, Zald DH (2006) An emotion-induced attentional blink elicited by aversively conditioned stimuli. *Emotion* 6: 523.
- Sporns O. (2012). *Discovering the Human Connectome*. Cambridge: MIT Press.
- St-Laurent M, Abdi H, Burianová H, Grady CL (2011) Influence of aging on the neural correlates of autobiographical, episodic, and semantic memory retrieval. *Journal of Cognitive Neuroscience* 23: 4150-4163.
- St Jacques PL, Bessette-Symons B, Cabeza R (2009) Functional neuroimaging studies of aging and emotion: fronto-amygdalar differences during emotional perception and episodic memory. *J Int Neuropsychol Soc* 15: 819-825.
- St Jacques PL, Dolcos F, Cabeza R (2010) Effects of aging on functional connectivity of the amygdala during negative evaluation: a network analysis of fMRI data. *Neurobiol Aging* 31: 315-327.
- Stanislaw H, Todorov N (1999) Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers* 31: 137-149.
- Sullivan S, Ruffman T (2004) Social understanding: How does it fare with advancing years? *British Journal of Psychology* 95: 1-18.
- Suzman R, Beard J (2011) *Global Health and Aging*. National Institute on Aging.
- Sze JA, Goodkind MS, Gyurak A, Levenson RW (2012) Aging and emotion recognition: Not just a losing matter. *Psychol Aging* 27: 940.
- Thomas RC, Hasher L (2006) The Influence of Emotional Valence on Age Differences in Early Processing and Memory. *Psychol Aging* 21: 821-825.
- Thomsen T, Specht K, Rimol LM, Hammar A, Nytingnes J, Ersland L, Hugdahl K (2004) Brain localization of attentional control in different age groups by combining functional and structural MRI. *Neuroimage* 22: 912-919.
- Treisman AM, Gelade G (1980) A feature-integration theory of attention. *Cogn Psychol* 12: 97-136.
- Ungerleider LG, Mishkin M. (1982). Two cortical visual systems. In D. G. Ingle, M. A. Goodale, R. J. Q. Mansfield (Eds.), *Analysis of visual behavior*. Cambridge, MA: MIT Press.
- Unsworth N, Heitz RP, Schrock JC, Engle RW (2005) An automated version of the operation span task. *Behav Res Methods* 37: 498-505.
- Urry HL, van Reekum CM, Johnstone T, Kalin NH, Thurow ME, Schaefer HS, Jackson CA, Frye CJ, Greischar LL, Alexander AL, Davidson RJ (2006) Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. *Journal of Neuroscience* 26: 4415-4425.

- Van Overwalle F (2009) Social cognition and the brain: a meta-analysis. *Human brain mapping* 30: 829-858.
- Van Overwalle F, Baetens K (2009) Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage* 48: 564-584.
- von Hippel W, Dunlop SM (2005a) Aging, inhibition, and social inappropriateness. *Psychology and Aging* 20: 519.
- Von Hippel W, Dunlop SM (2005b) Aging, inhibition, and social inappropriateness. *Psychology and Aging*, 20: 519.
- von Hippel W, Henry JD (2012) Social cognitive aging. *The handbook of social cognition*. London: Sage 390-410.
- Vuilleumier P (2005) How brains beware: neural mechanisms of emotional attention. *Trends Cognit. Sci.* 9: 585-594.
- Vuilleumier P, Armony JL, Driver J, Dolan RJ (2001) Effects of Attention and Emotion on Face Processing in the Human Brain: An Event-Related fMRI Study. *Neuron* 30: 829-841.
- Vytal K, Cornwell B, Arkin N, Grillon C (2012) Describing the interplay between anxiety and cognition: from impaired performance under low cognitive load to reduced anxiety under high load. *Psychophysiology* 49: 842-852.
- Wager TD, Davidson ML, Hughes BL, Lindquist MA, Ochsner KN (2008) Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron* 59: 1037-1050.
- Wager TD, Kang J, Johnson TD, Nichols TE, Satpute AB, Barrett LF (2015) A Bayesian model of category-specific emotional brain responses.
- Walsh BJ, Buonocore MH, Carter CS, Mangun GR (2011) Integrating conflict detection and attentional control mechanisms. *Journal of Cognitive Neuroscience* 23: 2211-2221.
- Williams LM, Brown KJ, Palmer D, Liddell BJ, Kemp AH, Olivieri G, Peduto A, Gordon E (2006) The mellow years?: neural basis of improving emotional stability over age. *The Journal of Neuroscience* 26: 6422-6430.
- Wincoff A, Labar KS, Madden DJ, Cabeza R, Huettel SA (2011) Cognitive and neural contributors to emotion regulation in aging. *Soc Cogn Affect Neurosci* 6: 165-176.
- Wolfe JM (1994) Guided search 2.0 a revised model of visual search. *Psychon Bull Rev* 1: 202-238.
- Wright CI, Wedig MM, Williams D, Rauch SL, Albert MS (2006) Novel fearful faces activate the amygdala in healthy young and elderly adults. *Neurobiol Aging* 27: 361-374.

- Yarkoni T, Barch DM, Gray JR, Conturo TE, Braver TS (2009) BOLD correlates of trial-by-trial reaction time variability in gray and white matter: a multi-study fMRI analysis. *PLoS One* 4: 23.
- Yiend J (2010) The effects of emotion on attention: A review of attentional processing of emotional information. *Cognition & Emotion* 24: 3-47.
- Young AW, Perrett DI, Calder AJ, Sprengelmeyer R, Ekman P (2002) Facial expression of emotion: Stimuli and tests (FEEST). . Suffolk, UK: Thames Valley Test.
- Young MP, Scanneil JW, Burns GA, Blakemore C (1994) Analysis of connectivity: neural systems in the cerebral cortex. *Reviews in the Neurosciences* 5: 227-250.
- Zanto TP, Gazzaley A. (2014). Attention and ageing. In A. C. Nobre, S. Kastner (Eds.), *The Oxford Handbook of Attention*. (pp. 927-971). Oxford; New York: Oxford University Press.
- Ziaei M, Peira N, Persson J (2014) Brain systems underlying attentional control and emotional distraction during working memory encoding. *Neuroimage* 87: 276-286.
- Ziaei M, von Hippel W, Henry JD, Becker SI (2015) Are Age Effects in Positivity Influenced by the Valence of Distractors? *PLoS One* 10: e0137604.

## **Appendix A**

Here is the link for the published version of Study 1:

<http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0137604>