Neurophysiological mechanisms of attentional capture and suppression by emotionally salient pictures: Investigations with EEG and MEG

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Abstract

The timing and brain function of attentional capture of emotional distractive stimuli is still unclear. The purpose of current thesis is to examine the effects of physical stimulus properties, emotional salience and voluntary control on attentional capture and brain function. Three sets of experiments were carried out to: (1) examine the effect of emotional salience and spatial frequency on attention capture and event-related potentials (ERPs) in a visual search task; (2) replicate the behavioural and ERP results of an emotion-induced blindness paradigm (Hoffman et al, 2020) that addresses some prominent drawbacks of previous emotional capture paradigms; (3) identify the neuroanatomical sources of MEG responses measured concurrently with the ERP data of Experiment 2. The results of Experiment 1 showed that both high and low anxious people pay more attention to threatening faces compared to neutral pictures. In contrast, only individuals with high anxiety showed a pronounced P1 component (an early visual ERP component) to low-spatial-frequency information. Experiment 2 confirmed that negative pictures capture attention when they are task related, but that attentional capture of emotional pictures was affected by the attention allocated to the pictures. The ERP results point to two important stages of processing: an earlier stage, indexed by an early posterior negativity (EPN) component, in which attention is automatically captured by emotional stimuli; and a subsequent stage, indexed by a P3b component, in which attentional processing can be voluntarily suppressed. The MEG source analyses of Experiment 3 identified neuroanatomical generators active during these two stages. The EPN time window was dominated by a robust activation of the anterior

cingulate cortex during processing of negative pictures, but not neutral pictures. The subsequent P3b epoch was associated with two functionally, temporally and anatomically distinct clusters of activation, first of the insula and, then of anterior cingulate cortex. The anatomical locations, properties and timing of these brain responses are best explained by a "salience network" consisting of the anterior insula and anterior cingulate cortex (Menon and Uddin, 2010; Uddin, 2015), which operate to detect and process emotionally salient stimuli and maintain a task set.

Statement of Originality

I, Xiaofei Dong, certify that the work in this thesis entitled “Neurophysiological mechanisms of attentional capture and suppression by emotionally salient pictures: Investigations with EEG and MEG” is being submitted to Macquarie University and Capital Normal University in accordance with the Cotutelle agreement dated 30th Oct 2020.

To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my work, and the preparation of the thesis itself has been appropriately acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

The research presented in this thesis was approved by the Macquarie University Human Research Ethics Committee, reference number: **5201929799392.**

Signed:

Xiaofei Dong (Student ID: 45063125)

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Related Publications

The research reported in Chapter 3 has been published in:

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Statement of Contributions

All elements of design, testing, analysis and writing are the work of Xiaofei Dong and the supervisor professor Blake Johnson.

Each chapter contains a specific statement of authorship outlining the role the authors played.

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Chapter 1:
General Introduction

CHAPTER 1 GENERAL INTRODUCTION

Accurate processing of the emotional information conveyed by others is essential for social understanding and interactions, and there is considerable evidence that such information is prioritized, in a relatively automatic fashion, for attentive processing and preparation of actions. Attentional control interacts with attention capture of emotional information to ensure accuracy of processing and preparation of adaptive responses. This topic has clear implications for understanding and treatment of individuals who have difficulty understanding and controlling emotion. It is attracting increasing attention in scientific communities studying an attentional bias toward emotional information among socially anxious people. However, inconsistent findings were found in the previous studies about the effect of threat faces and attentional control on attentional bias of socially anxious individuals. Further investigation of the impacts of attentional control and the threat faces in early perceptional and later attentional processing stages among socially anxious individuals is necessary for developing more effective treatments, such as attentional bias modification (ABM) (MacLeod & Mathews, 2012) training. Using behavioural measures of performance and electroencephalogram (EEG) / magnetoencephalography (MEG) measures of brain function, the present thesis examined the effects of physical stimulus properties, emotional salience and voluntary control on emotional capture of attention and brain function.

Chapter 2 provides a review of the literature and discusses concepts and terminologies relevant to social anxiety and attention capture. The review considers methodological issues associated with the study of attentional capture and control, and individual differences associated with social anxiety. The neural mechanisms implicated in emotional attention capture in socially anxious people by neuroimaging studies are reviewed. The chapter

includes a consideration of the role that attentional control plays in emotional attention capture, and the real-world implications for this line of research. Finally, the chapter concludes with several recommendations for future studies of emotional attention capture.

Chapter 3 describes behavioural and event-related potentials (ERP) results from a visual search task, which was designed to measure the effects of emotional salience and spatial frequency content on attention capture in participants with social anxiety. The results of this chapter show that high social anxiety (HSA) individuals showed a general pattern of initial vigilance and later avoidance to low spatial frequency (LSF) faces, reflected by increased P1 amplitudes and reduced P250 amplitudes to LSF relative to HSF faces. Furthermore, our results demonstrate specific attentional avoidance of fearful (vs. disgusted, angry and neutral) faces in social anxiety.

Chapter 4 implemented a modified emotion induced blindness task from Hoffman et al (2020)'s experiment 1 to investigate how attentional allocation affects emotional attention capture. Behavioural and ERP measures were collected in a replication experiment. The results of current study were largely consistent with those of Hoffman et al (2020)'s experiment 1 and indicate that attention capture of negative pictures is more effective than neutral pictures when pictures are task-relevant. However, the emotional attention capture was modulated by attentional allocation to a competing task, and reflecting by reduced amplitude of P3b components. Taken together, the present results and those of Hoffman et al. (2020) indicate that emotional capture attention is not fully automatic and can be suppressed. Further, the ERP results indicate that this suppression of occurs at a relatively late stage of

processing, subsequent to the automatic capture of attention reflected by the early posterior negativity (EPN) component.

Chapter 5 presents the analysis of MEG measurements obtained concurrently with the ERP measurement described in Chapter 4. The results showed significantly greater anterior cingulate activation in motion tracking (MOT) condition compared to picture detecting (PIC) and dual task (DUAL) conditions for negative pictures during EPN time window. The subsequent P3b time window is associated with robust activation of the anterior insula (AI) and anterior cingulate cortex (ACC). for negative pictures. These results are consistent with the notion of a "salience network", composed of AI and ACC, which sequentially detects salient stimuli and maintains a task set. These neuroanatomical processes ultimately account for participants' task performance and electrophysiological responses during performance of an emotional capture rapid serial visual presentation (RSVP) task.

Chapter 6 summarizes the results of the thesis and considers their contribution to the literature.

Chapter 2:
Emotional attention in anxious individuals: A review of the literature

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Author contributions

Xiaofei Dong conducted the literature review and drafted the paper. Both authors discussed the content and edited the manuscript.

Abstract

Social anxiety, involving disproportionate or debilitating fears or worries about social or performance situations, is one of the most common anxiety disorders. In the following, current concepts and terminology of social anxiety are summarized. We then review the neural mechanisms that have been implicated in this disorder by neuroimaging and neuropsychological studies. Cognitive models of social anxiety and experimental methodologies for investigating attentional bias are reviewed. One important point of debate in this field is whether the processing of threatening information is automatic or is susceptible to inhibition by higher level cognitive processes. The review concludes with a summary of the gaps in the literature, real-world implications for this research, and recommendations for future studies.

2.1 Introduction

Anxiety is a diffuse, unpleasant, vague feeling of apprehension (Sadock, Sadock, & Ruiz, 2011). It's a natural response to stress. For example, walking down a dark street alone, going to a job interview, or the first day of school may cause most people to feel fearful and nervous. An important distinction is that anxiety is related to the *possibility* of some potential threat. In contrast, *fear* is associated with a definite or immediate threat (DSM-5). Although the two emotional responses are distinct, fear and anxiety are interrelated. Fear can cause anxiety, and anxiety can cause fear.

Extreme fear and anxiety are associated with many anxiety disorders, such as specific phobias, agoraphobia, social anxiety disorder, and panic disorder. Among these anxiety disorders, social anxiety disorder (SAD), involving fears or concerns about potential embarrassment in social situations, is one of the most common, with a 12-month prevalence of the population about 7% (Kessler et al., 2005b). The concerns and fears of SAD can be disproportionately intense, persistent and debilitating, to the extent that quality of life can be significantly impaired.

Individuals with social anxiety disorder (SAD) are normally worried that their behavior may cause embarrassment or draw negative evaluation from others. Thus, they tend to avoid social interactions and public performance situations (American Psychiatric Association, 2013). SAD has an early age of onset (13 years) and is a risk factor for students dropping out of school (19, drug abuse and other comorbidities (Stein & Stein, 2008). However, public recognition of social anxiety is limited and only about half of people with SAD have attempted to receive treatment (Grant et al., 2005). SAD imposes large costs on individuals, families and

society. People with SAD experience difficulty in getting on with friends (Whisman et al., 2000) and performing everyday activities, have lower than expected incomes (Katzelnick et al., 2001), are more likely to divorce (Wittchen et al., 1999) and are less productive in their work (Stein et al., 1999).

An important area of scientific investigation has aimed to uncover the underlying neural mechanisms of social anxiety. From their meta-analysis of functional magnetic resonance imaging (fMRI) studies, Etkin and Wager (2007) proposed a neurobiological model, comprising brain regions including the amygdala region, insula and the adjacent inferior frontal gyrus, in addition to the fusiform gyrus and superior temporal gyrus, (Etkin and Wager, 2007). These brain regions collectively form a putative "fear circuit" (e.g., Etkin, 2010; LeDoux, 2000; Marek et al.,2013). Results from a number of other neuroimaging studies confirm that fear and anxiety are associated with an increased blood flow in the amygdala (Tillfors et al.,2001; Tillfors et al., 2002), hippocampus (Tillfors et al., 2002) and insula (Warwick et al., 2006).

Another line of research has demonstrated that *information processing biases* play an important role in the development and maintenance of SAD (Bögels & Mansell, 2004; Clark & McManus, 2002; Heinrichs & Hofmann, 2001; Hirsch & Clark, 2004; Morrison & Heimberg, 2013; Wong & Rapee, 2016). Cognitive models posit that individuals with SAD show a persistent cycle of information processing biases, including attentional bias (Bögels & Mansell, 2004), interpretation bias and memory bias (Heinrichs & Hofmann, 2001; Hirsch & Clark, 2004; Morrison & Heimberg, 2013), which accentuate and perpetuate different stages of processing (i.e., automatic and controlled).

CHAPTER 2 LITERATURE REVIEW

Here we will provide a critical overview of behavioral and neural imaging research on social anxiety. Our goal is to focus on important findings on the cognition and the brain function in adult SAD. We will start by sketching a broader context, before considering details of brain and neural mechanisms, and will highlight important experimental paradigms in this area of research.

2.2 Definitions and concepts

2.2.1 Anxiety disorder

Anxiety is characterized by extensive worry, nervousness and uncertainty about a variety of events and domains (Barlow & Cerny, 1988; Raghunathan & Pham, 1999), and is universal in the general population (di Tomasso & Gosch, 2002). The symptoms of anxiety are categorized into behavioral symptoms, physical symptoms and cognitive symptoms (e.g., Rachman, 2004; Albano, Chorpita, & Barlow, 2003). Specifically, the behavioural symptoms include fight or flight response towards certain situations; the physical symptoms include restlessness, difficulties in concentration or sleep, muscle tension, irritability, sweating, and trembling; the cognitive symptoms include attention and memory bias towards threatening information, and negative self-statements or negative thoughts (Watson & Friend, 1969).

2.2.2 Social anxiety disorder and attentional bias

According to DSM-5 (American Psychiatric Association, 2013), anxiety disorders are composed of generalized anxiety disorder (GAD), specific phobias (SP), panic disorder (PD), post-traumatic stress disorder (PTSD), social anxiety disorder, acute stress disorder and obsessive-compulsive disorder (OCD).

Within anxiety disorders, SAD is one of the most common with up to 12% lifetime prevalence (Kessler et al., 2005). Social anxiety is defined as a persistent fear of embarrassment or negative evaluation while engaging in social interaction or public performance. Clinically, patients with SAD are afraid of and avoid situations associated with potential exposure to unfamiliar people or to possible scrutiny by others or endure such situations only with intense anxiety or distress (American Psychiatric Association, 2013).

Given the ubiquitous nature of social anxiety disorders, it is important to identify possible vulnerability factors of social anxiety. Information processing reflects one's beliefs, thoughts, and modes of thinking (Robinson, Vytal, Cornwell, & Grillon, 2013), can help understand (Wilt, Oehlberg, & Revelle, 2011) and treat social anxiety. Studies have found that individuals with anxiety have a bias towards emotionally salient events compared to individuals with low levels of anxiety. The attentional bias can be defined as faster attentional engagement (e.g., Williams, Watts, MacLeod, & Mathews, 1997) and delayed attentional disengagement towards threatening stimuli (Fox, Russo, Bowles, & Dutton, 2001). This attentional bias towards threatening stimuli has been proposed to play significant role in the maintenance of anxiety (e.g., Beck, 1976; Eysenck & Calvo, 1992; Mathews, 1990; Mathews & MacLeod, 2002; Williams, Watts, MacLeod, & Mathews, 1988). Conversely, the anxious state may optimize detection of threat in certain situation and facilitate response to the environment. Thus, the relation between attentional bias and social anxiety is a bidirectional, maintaining, or mutually reinforcing relation (Van Bockstaele et al., 2014). Studies shows that changes in attentional bias can lead to reduction of distress and symptoms of social anxiety (MacLeod & Clarke, 2015).

2.3 Neural mechanisms of anxiety

Though anxiety and fear are not interchangeable, they have overlapping symptoms and sometimes occur together. Fear relates to a subjective state, a feeling that occur when perceived danger or harm is immediate or imminent, whereas anxiety describe feelings that follows from perceived danger that is poorly defined or distal in space or time (Davis et al., 2010; LeDoux and Pine, 2016; Mobbs, 2018). Research in rodents suggests distinct

mechanisms, with the amygdala mediates phasic responses to fear and the bed nucleus of the stria terminalis (BST) mediates sustained responses to anxiety (e.g., Sylvers et al., 2011; Somerville et al., 2013; Avery et al., 2016; LeDoux and Pine, 2016; Klumpers et al., 2017; Watson et al., 2017).

However, a growing body of research indicates that the brain circuity for fear and anxiety has considerable overlap in human. A "fear network" consisting of amygdala, insula and anterior cingulate cortex (ACC) (Klucken et al., 2009; Hamm & Weike, 2005; Tabbert et al., 2006) was first proposed in human fear conditioning study and is important for processing potentially threatening information (Sehlmeyer et al., 2009). The 'fear network' is also related to inappropriate and prolonged anticipation of negative stimuli or events in anxiety disorders (Sarinopoulos et al., 2010; Straube et al., 2007). Recent fMRI studies in humans indicates that the neural systems recruited by anxiety (uncertain threat anticipation) and fear (certain threat anticipation) are anatomically co-localized in in fronto-cortical regions (including the midcingulate cortex (MCC), anterior insula (AI), and dorsolateral prefrontal cortex (dlPFC) and extended amygdala (including the dorsal amygdala in the region of the central nucleus (Ce) and the BST) (Shackman and Fox, 2016; Fox and Shackman, 2019; Hur et al., 2020).

Anxiety disorder is believed to be related to abnormal brain activations in certain regions, among which the 'fear network' is the core node. Hyperactivation of "fear circuit" will lead to a prioritized processing of threat-related cues over other contextual information in the environment; and a reduced connection to "top-down" mechanisms that serves to modulate and deploy fear responses in a contextually dependent and adaptive manner

(Schmidt et al., 2018). Apart from the core fear network and the prefrontal executive regions, some brain areas associated with perceptual processing have been reported to be over-active in anxiety disorders.

2.3.1 Amygdala

The amygdala is a nucleus found deep within the temporal lobe (Davis & Whalen, 2001; LeDoux, 2007) and recognized as a critical node of the limbic system (Amaral & Price, 1984; LeDoux, 2000). The amygdala has complex functions and play a pivotal role in behavior and emotion (LeDoux, 2007), including the processing of fear, forming fear-related memories and positive memories (Roozendaal et al., 2009; Gallagher et al., 1990), and evaluating the importance of events in the environment (Baxter & Murray, 2002). The amygdala also serves major roles in salience detection, reward learning and unpredictability processing (Adolphs, 2010).

Among all these complex functions, the amygdala is best known for its role in fear processing. Research suggests that there is a subcortical pathway for threatening information to reach the amygdala, even without conscious awareness (Ohman et al., 2007). Through this pathway, fearful sensory information runs from the thalamus to the amygdala before being consciously processed by the cerebral cortex (Ohman et al., 2007).

The amygdala is also one of the most consistently reported regions in anxiety circuitry. Hyperactivation of the amygdala has been related to hypersensitivity to threat stimuli and dysfunction of emotional regulation in a number of anxiety disorders (Whalen et al., 2008; Etkin & Wager, 2007; Holzschneider & Mulert, 2011; Miskovic and Schmidt, 2012). In addition, higher level anxiety in humans is associated with higher amygdala volumes (Qin et

al., 2013; Machado-de-Sousa et al., 2014), and stronger activation of amygdala was found among socially anxious (Boehmeetal., 2013) and general anxiety disorder individuals (Monk et al, 2008; Price et al, 2011; Nitschke et al.,2009) compared to healthy controls during anticipation of anxiety.

2.3.2 Bed nucleus of the stria terminalis

The bed nucleus of the stria terminalis (BST), sometimes referred to as the "extended amygdala", is located at one extremity of the stria terminalis and is important in a range of behaviors such as: the stress response, extended duration fear states and social behavior (Dumont, 2009; Lebow & Chen, 2016).

Together with amygdala (Davis et al., 2010; Dong et al., 2001), dorsal raphe (Hammack et al., 2009), ventral tegmental area (VTA) (Dong & Swanson, 2004a), and medial prefrontal cortex (mPFC) (Radley & Sawchenko, 2011), the BST is involved in mood state and arousal processing. The BST is also a part of the social behavioral network, which consist of lateral septum (Dong & Swanson, 2004b) and medial amygdala (MeA) (Dong et al., 2001; Dong & Swanson, 2004b). In addition, the BST, has an important role in mood and anxiety disorders. Human fMRI studies have reported defensive responses and BST activation during threat anticipation (Straube et al., 2007; Mobbs et al., 2010; Somerville et al., 2010; Grupe et al., 2013; McMenamin et al., 2014)

2.3.3 Insula

The insula is located deep in the lateral sulcus, enclosed by the frontal, parietal, and temporal lobe (Türe et al. 1999). The insula has been proposed to play a pivotal role in sensory, affective (Phillips et al., 2004; Phan et al., 2002; Büchel et al., 1998; Gorno-Tempini

et al., 2001) and cognitive processing (Uddin et al., 2017). It has been suggested that the insular cortex is important to, along with anterior cingulate cortex and limbic structures, identification of salient stimuli in the environment (Menon and Uddin, 2010; Uddin, 2015), and generation and regulation of the affective response (Phillips et al., 2003; Adolphs, 2003). Greater insula activation is thought to be related with dysfunctional anticipatory processing of aversive stimuli among anxious individuals relative to control participants (Stein et al., 2007; Simmons et al., 2006).

2.3.4 Anterior cingulate cortex and midcingulate cortex

The anterior cingulate cortex (ACC), which is composed of subgenual ACC (sACC), the rostral ACC (rACC), and the dorsal ACC (dACC) (Morecraft et al., 2012; Morecraft and Tanji, 2009; Öngür and Price, 2000), has been proposed to involve processing of emotion, motivation, higher cognition, and motor control. The sACC, together with orbitofrontal cortex (OFC) and the amygdala, is involved in the motivation network and is critical for emotional functions (Camille et al., 2011; Jocham et al., 2012; Kolling et al., 2016). Often the actual ACC is called rostral ACC and the rACC is associated with assessing the salience of emotional information (Klumpp et al., 2011), the anticipation of negative outcomes (Sarinopoulos et al., 2010), conflict-monitoring and fear learning (Schmidt et al., 2018; Sehlmeyer et al., 2009). The mid cingulate cortex is also called dorsal ACC. The dACC is involved in proactive and reactive attention control (Jiang et al., 2015), motor planning and action execution (Caruana et al., 2018; Picard and Strick, 1996; Kolling et al., 2018). The dACC also plays a pivotal role in regulating flexibility, adaptation and top-down control by

using value-related information in the environment (Etkin et al., 2015; Kolling et al., 2016; Shenhav et al., 2016).

Excessive activation in the ACC has been found in social anxiety and generalized anxiety disorders for tasks involving aversive stimuli (Etkin & Wager, 2007; Shin & Liberzon, 2010; McClure et al., 2007; Nitschke et al., 2009). In addition, stronger ACC activation and reduced functional connectivity between ACC and lateral prefrontal cortex (LPFC) has been correlated with higher levels of anxiety in an emotional conflict task (Comte et al., 2015).

2.3.5 Prefrontal cortex

Apart from these three core components of the fear network, several other brain regions have been reported to play a role in anxiety disorders. In particular, the prefrontal cortex, regarded as a 'top-down' attentional control region, is considered to play an important role in regulating the activation of the fear network (Quirk and Beer, 2006). Results of surface event-related potential (ERP) and single neuron studies suggest that the prefrontal cortex is responsible for inhibiting the attentional capture of task-irrelevant information (Blair et al., 2007; Cosman et al., 2018; Schall, 2015; Squire et al., 2013) by suppressing representations of distractors in sensory cortex. The prefrontal cortex is composed of dorsolateral prefrontal cortex (DLPFC; Squire et al., 2013), orbitofrontal cortex (OFC; Rolls et al., 1994) and ventromedial prefrontal cortex (vmPFC; Smith et al., 2010). The DLPFC plays a crucial role in top-down modulation of task-relevant processes (Freedman et al., 2001; Duncan, 2013; Erez and Duncan, 2015), such as directing and maintaining attention to task (Squire et al., 2013; Eysenck & Derakshan, 2011; Eysenck et al., 2007), cognitive control adjustments

based on the detection of conflict (Egner and Hirsch, 2005) and inhibiting task-irrelevant information (Bishop et al., 2004).

The OFC, which is closely connected with the limbic system (Carmichael & Price, 1995a; Öngür et al., 1998; Haber et al., 1995), is involved in making decisions based on emotional information (Morrison & Salzman, 2009; Roesch & Olson, 2004; Schoenbaum et al., 1998) and value (Wallis, 2012). This region also plays a major role in integrating information from different modalities, including sensory and emotional information (Romanski et al., 1999; Carmichael & Price, 1995b; Cavada et al., 2000).

Ventromedial prefrontal cortex (vmPFC) plays an important role in reward and value processing as well as emotional regulation, especially in social situations (Hänsel & von Känel, 2008). This region is also associated with learning from mistakes (Bechara et al., 1994), fear extinction (Dunsmoor et al., 2019; Phelps et al., 2004) and stress reactivity (Hänsel & von Känel, 2008).

Decreased activation of prefrontal cortex (Browning et al., 2010) and reduced inhibition have been reported in persons with SAD (Price et al., 2011). Studies have also found reduced functional connectivity between prefrontal cortex and amygdala (Monk et al., 2008) or ACC (Comte et al., 2015) in anxious individuals. DLPFC has been associated with memory processing of affective information (Ferrari & Balconi, 2011) and reduced DLPFC activity has been reported among anxious individuals during threat-related working memory (Balderston et al., 2017).

2.3.6 Visual cortex

Outside of the core fear network and the prefrontal executive regions, brain areas associated with lower-level activities involved in processing of emotional visual stimuli and human faces have been reported to be over-active in anxiety disorders. Pujol et al (2009) reported that the relationship between the amygdala response to threatening faces and social anxiety scores is dependent on the activation of the fusiform gyrus. Task-related functional neuroimaging studies have also reported hyperactivation of occipital regions (secondary visual cortices, Brühl et al., 2014) in SAD (Straube et al., 2004; Straube et al., 2005).

2.4 Cognitive explanations for anxiety

In recent years, several cognitive models have been introduced to interpret the mechanisms underlying threat-related attentional bias in anxiety.

2.4.1 Williams, Watts, Macleod, and Matthews' (1988) model

Williams et al. (1988) proposed a pre-attentional level of processing bias in anxiety, which is explained by an affective decision mechanism (ADM). This model postulates that the ADM determines the threat value of input information. At an initial stage, a decision that whether stimuli are threatening or not is made, which is affected by state anxiety. If a threatening stimulus input is found, a resource allocation mechanism (RAM) would be activated. Then, attention would be allocated to threat. If individuals determine that the input information is low threaten, attention would be maintained to the current task.
According to this model, trait anxiety will cause individuals to allocate attention to threat, which leads to an attentional bias, whereas individuals with low trait anxiety will ignore threatening stimuli.

2.4.2 Mogg and Bradley's cognitive-motivational model

In the cognitive-motivational model, Mogg and Bradley (2018) propose that anxiety and attention bias emerges from the influences of salience-driven and goal-directed cognitive control on multiple processes (Mogg & Bradley, 2016; Cisler & Koster, 2010), including evaluation, inhibition, switching, and orienting functions. Salience evaluation is a fast, preconscious process of stimuli appraisal. Factors, such as state anxiety, prior learning, and contextual information, can have an influence on the evaluation and reactivity to threatening stimuli. Specifically, high state anxiety can sensitize the salience evaluation to appraise mild threat cues as high threat.

The goal-directed cognitive control determines the allocation of processing resources to the stimulus, which receives input from salience evaluation. If a stimulus is assessed as threatening after the valence evaluation, current goals will be interrupted, and more attention will be paid to the salient stimulus. However, if the stimulus input is tagged as being of low threat, the attention will be maintained at the ongoing activities without any interruption. Accordingly, a more sensitive salience evaluation system can be found among individuals with high trait anxiety who tend to regard ambiguously and mildly threatening information as highly threatening. On this account, the threat-related attentional biases in anxiety are relegated to later stages of processing.

2.4.3 Eysenck et al.'s attentional control theory

Attentional control theory posits that anxiety impairs both the goal-driven attentional system and the stimulus-driven attentional system. Eysenck et al. (2007) added that anxiety disrupts inhibition and shifting, which are two central functions of attentional control.

Inhibition refers to a top-down process, which can regulate automatic responses. Individuals with anxiety showed impairment in top-down regulatory control, and have difficulty disengaging attention from threatening information (Cisler & Koster, 2010; Eysenck et al., 2007). Shifting refers to a bottom-up process, which shifts attention between tasks according to context. Anxiety facilitates shifting and heightens stimulus-driven bottom-up processing. Individuals with high anxiety has been found to detect threatening stimuli faster.

2.5 Experimental paradigms for studying attentional bias in anxiety

Several spatial attention tasks have been used to measure attentional bias. Abundant data has been collected using these tasks, which have provided a description and prediction of the attention of anxious individuals.

2.5.1 Emotional Stroop paradigm

In the emotional Stroop task, threating and neutral words are presented in different colors (for a review, see Williams, Mathews, & MacLeod, 1996). The colors of the words are targets, whereas the meaning of the words are distractors. The response time for threating words are longer than neutral words. The common interpretation of this effect is that attention is allocated to the threatening meaning of the word and hinders the naming of the color.

However, there are criticisms of this task. Firstly, the distracting threating information is not dissociable with the targets. Secondly, a number of studies have reported that the test-retest reliability of emotional Stroop effect is low (Eide, Kemp, Silberstein, Nathan, & Stough, 2002; Strauss, Allen, Jorgensen, & Cramer, 2005; but see Dresler, Mériau, Heekeren, & van der Meer, 2009). Study have also found that the emotional Stroop effect is absent

when neutral and emotional words are presented in a mixed block (Algom et al., 2004). Finally, the emotional Stroop effect can be interpreted in terms of *either* an attentional engagement bias or an attentional disengagement bias (Clarke, MacLeod, & Guastella, 2013).

2.5.2 Dot probe task

The dot probe task (Macleod et al., 1986; Mogg and Bradley, 1999) is another popular measure for assessing attentional bias for threating information. In this task, a target stimulus will appear at one of the locations of two cues (typically one threating and one neutral). The response time to the target stimulus is recorded. The task can reflect how fast the attention is drawn to or away from emotional cues compared to neutral cues (e.g., Koster, Crombez, Verschuere, & De Houwer, 2004).

However, researchers found that both versions (pictorial or verbal) of dot probe task had low split-half reliability or test-retest reliability (Cooper et al., 2011; Van Bockstaele et al., 2011). Some studies using dot-probe have found a bias away from threat (Brown et al., 2013; Monk et al., 2006; Salum et al., 2013; Thai, Taber-Thomas, & Pérez-Edgar, 2016). Several investigators have failed to find evidence of any significant bias at all (Britton et al., 2012; Fu, Taber-Thomas, & Pérez-Edgar, 2017). Although the dot probe task provides an index for attentional engagement bias, the bias can be well explained by attentional engagement or attentional disengagement (Clarke, MacLeod, & Guastella, 2013).

2.5.3 Emotional spatial cueing paradigm

In this task, either a threatening cue or a nonthreatening cue is presented in one of two possible positions. A brief interval later, the target appears in the same or opposite position of the cue. Participants need to identity the location of the target as fast and as accurately as

possible. A cue validity index is defined as the subtraction of reaction time between invalid trials and valid trials. Attentional bias can be reflected by the response time to the target (Fox, Russo, Bowles, & Dutton, 2001), which is longer with a threatening cue compared to nonthreatening cue. Similar to the dot probe task, this task cannot distinguish between the effect of attentional engagement and attentional disengagement.

2.5.4 Visual search task

In a visual search task (Öhman, Flykt, & Esteves, 2001), participants are required to search for a target stimulus among a search array with distracting stimuli. In this paradigm, the valence of target is manipulated, whereas the valence of distractors normally is neutral. Attentional bias is inferred either when the reaction times is faster for threatening targets among neutral distractors compared to neutral targets or when the reaction times is slower for neutral target among threatening distractors compared to neutral distractors. Typically, the faster detection of emotional stimuli is attributed to a pop-out effect. In other versions of this task, the target is neutral, the threat value of distractors is manipulated. In this case, attentional bias is inferred from slower reaction times on trials with threatening distractors compared to trials with neutral distractors.

However, the slower reaction time for neutral targets among threatening distractors maybe also because there are more threat images. Unfortunately, as there is no baseline condition in this task, it is difficult to decide whether the findings from the visual search task are due to speeded detection of emotional stimuli or interference in detection of neutral stimuli (Lipp, 2006).

2.5.5 Attentional blink task

The paradigms discussed above are all spatial attention tasks. An attentional blink paradigm instead measures attention in the time domain. In the attentional blink task, participants are required to search for two targets (T1 and T2) in a rapidly presented stream of pictures. Normally, the search performance of the first target is better. However, the performance of T2 depends on the time interval between T1 and T2. T2 performance is hampered when the interval is short (i.e., between 200 and 400 ms) compared to long. This phenomenon is interpreted such that the identification of T1 consumes limited attentional resources and there are no sufficient resources for the identification of T2 in short interval.

In some emotional versions of this task, the threat value of one target is manipulated (see Yiend, 2010). Normally the threat value of T2 is manipulated, while the threat value of T1 is neutral. In this case, the attentional blink would be diminished as the threatening T2 stimuli are processed more efficiently (e.g., Anderson, 2005; Keil & Ihssen, 2004). Attentional bias toward threatening T2 stimuli in this version of task is inferred from a smaller attentional blink effect. Another emotional version of attentional blink task has threat value manipulated T1 and neutral T2. In this version of task, the attentional blink effect would increase as participants are assumed to have difficulty disengaging their attention away from threatening T1 stimuli (e.g., Ihssen & Keil, 2009; Mathewson, Arnell, & Mansfield, 2008). In this case, an attentional bias toward threatening stimuli is inferred from a larger attentional blink effect.

The third version of this task is called emotion-induced blindness study (EIB; Most, Chun, Widders, & Zald, 2005), which presents only one target (a rotated picture) in a stream.

Sometimes, a task-irrelevant emotional or neutral picture is presented before the target picture. The impairment of target detecting performance is larger for emotional distractors compared to neutral ones. The impairment of target detecting performance also depends on the time interval between target and distractor, which appears when time interval is short. The findings of this paradigm are interpreted in terms of the automatic capture of emotional picture. Even through participant already have a perceptual set to allocate their attention to the targets, the top-down attentional control does not prevent emotional attention capture.

This task has some important advantages compared to those described previously. Firstly, the targets and distractors are spatially and temporally separate. Secondly, this task is sensitive to the different effects of emotional distractors on target detection compared to other tasks (the probe and spatial cueing tasks), even in a non-clinical sample (Sigurjónsdóttir, Sigurðardóttir, Björnsson, & Kristjánsson, 2015). Finally, the EIB paradigm have a baseline condition, which allows for direct comparison between the effect of emotional and neutral distractors on target detection.

However, only a few studies have applied this paradigm to investigate attentional bias of anxious individuals. Behavioural studies found that individuals with anxiety disorder (compared to healthy controls) showed impaired target detection following emotional distractors (Olatunji, Ciesielski, Armstrong, Zhao, & Zald, 2011; Van Dam, Earleywine, & Altarriba, 2012). Another behavioural study using an attentional blink task found that high anxiety children demonstrated better detection performance for threatening targets compared to low anxiety children (Kelly, Maratos, Lipka, & Croker, 2016). One ERP study used this paradigm to investigate how anxiety and N2 amplitude contribute to emotional eating

behaviour but not attentional bias (Denke, Rawls, & Lamm, 2018). A variant of this paradigm is used in the current thesis to investigate the attentional capture effect.

2.6 ERP components related to attentional bias

Electroencephalography (EEG) is the non-invasive measurement of the brain's electrical activity using electrodes placed on the scalp (Sur & Sinha, 2009). Event-related potentials (ERPs) are EEG changes that are time locked to specific events or stimuli (Blackwood and Muir, 1990). ERPs can be elicited by a wide variety of sensory, cognitive or motor events, here we review the visual processing related ERPs.

2.6.1 P1

The visual P1, an early positive ERP component that is observed 90–110 ms after stimulus onset, peaks at scalp locations over the lateral occipital lobe and lateral occipitotemporal cortex (Luck & Kappenman, 2013). The amplitude of P1 is affected by attention and emotion processing (Luck & Kappenman, 2013). The generator of P1 may be related to the amygdala (Jetha, Zheng, Schmidt, and Segalowitz ,2012; Rotshtein et al., 2010) as patients with amygdala damage have showed reduced P1 amplitude during emotional faces processing (Rotshtein et al., 2010). Other study found that P1 amplitude may also affected by the medial prefrontal cortex during emotional face processing (Mattavelli et al., 2016).

Enhanced P1 to facial expressions was found among high anxious participants compared to low anxious participants in a modified Stroop task and in an emotional oddball paradigm (Peschard, Philippot, Joassin, & Rossignol, 2013; Rossignol, Campanella et al., 2012).

2.6.2 N2

The N2, which is a negative component peaking at about 200–350 m after stimulus onset, has two visual subcomponents: one frontocentral component related to response inhibition and error monitoring, termed error related negativity (ERN) (Gehring, Goss, Coles, & Meyer, 1993) or feedback-related negativity (FRN) (Hajcak, Holroyd, Moser, & Simons, 2005; Dong et al., 2016); and a posterior component associated with visual attention and which is larger to targets than to non-targets (Folstein & Van Petten, 2008), which is a companion of P3b (Ritter, Simson, Vaughan, & Friedman,1979; Ritter, Simson, Vaughan, & Macht, 1982).

Our study focusses on the posterior N2 component, which have been extensively studied in attention paradigms, including visual search (N2pc; Luck & Hillyard, 1994) and attention to relevant stimulus features (selection negativity or SN; Anllo-Vento, Luck, & Hillyard, 1998). Both the N2pc and SN are largest contralateral to those stimulus elements when they are presented lateral to fixation (Anllo-Vento & Hillyard, 1996). The N2pc is a negative component peaks around 200 ms after stimulus onset, which is observed at posterior and contralateral area (e.g., Hickey, McDonald, & Theeuwes, 2006; Kappenman et al., 2014; Kiss et al., 2008; Luck & Hillyard, 1994; Woodman and Luck, 2003). N2pc reflects selective attention to certain location and larger N2pc amplitudes to threatening faces were found in the dot-probe task (Grimshaw, Foster, & Corballis, 2014; Osinsky, Wilisz, Kim, Karl, & Hewig, 2014) and visual search tasks (Ikeda, Sugiura, & Hasegawa, 2013; Weymar et al., 2011). Studies also found individuals with high level anxiety had greater N2pc for

threatening faces compared to healthy individuals (Fox, Derakshan, & Shoker, 2008; Buodo, Sarlo, & Munafò, 2010; Weymar, Gerdes, Löw, Alpers, & Hamm, 2013).

Another component reflecting automatic attention capture of emotional stimuli (e.g., Holmes, Nielsen, Tipper, & Green, 2009; Rellecke, Sommer, & Schacht, 2012), is termed early posterior negativity (EPN), also overlapping with the posterior N2 component. Several studies have found increased EPN for emotional pictures compared to neutral pictures among anxiety disorders and healthy controls (e.g., Li et al., 2008; Lamm et al., 2012).

Greater EPN amplitudes to emotional and unemotional stimuli have been reported for anxious individuals. Some studies using go/no-go task found more negative EPN amplitude for individuals with high trait anxiety (Sehlmeyer et al, 2010), generalized anxiety disorder, social anxiety disorder, or separation anxiety disorder compared to non-clinical controls (Hum et al, 2013).

2.6.3 P2

The visual P2 is a positive ERP component that peaks 190-290 ms after stimulus onset at occipital sites (Van Voorhis & Hillyard, 1977; Hillyard & Mangun, 1986; Schupp, Junghoefer, Weike, & Hamm, 2003; Schupp et al., 2004). The P2 component is early electrocortical index of attentional resources allocation and emotional significance processing. For example, increased P2 amplitude was found in response to negative versus positive-arousing pictures (Carretié et al., 2001; Correll et al., 2006; Schutter et al., 2004; Dennis and Chen, 2007). The P2 component has also been associated with anxiety and is enhanced in the anxious relative to non-anxious group (Bar-Haim et al., 2005; Eldar, Yankelevitch, Lamy, & Bar-Haim, 2010).

2.6.4 P300

The visual P3 component is normally divided to two subcomponents: P3a, a frontocentral component, is evoked by novel stimuli in oddball task (Friedman, Cycowicz, & Gaeta, 2001; Herrmann & Knight, 2001); P3b usually peaks 300-700 ms after stimuli onset and is broadly distributed over posterior, central and temporal areas. P3b reflects the voluntary shift in attention towards target stimuli (Herrmann & Knight, 2001) and is sensitive to the amount of attention given to a stimulus (Luck & Kappenman, 2013; Polich, 2013). Studies have also found that P3b amplitude is larger for negative compared to neutral pictures (Hajcak, Weinberg, MacNamara, & Foti, 2012; Kennedy, Rawding, Most, & Hoffman, 2014).

Although there have been conflicting findings, patients with anxiety disorders tend to show some reduction of parietal P3b to target stimuli in oddball tasks (Howe, Pinto, & De Luca, 2014; Sachs et al., 2004), emotional flanker task (Yu et al., 2018) and dot probe task (Bechor et al., 2019). Only one study has found increased frontal P3b (Bruder et al., 2002) in an anxiety group compared to healthy controls.

2.7 MEG studies related to anxiety

Magnetoencephalography (MEG) is a non-invasive neurophysiological technique that measures magnetic fields produced in the brain due to neuronal activity, using very sensitive magnetometers (Baillet, 2017). MEG has excellent temporal and reasonable amount of spatial resolution (Cohen, 1968). Studies have used MEG data to investigate anxiety in resting state and task-based experiments.

2.7.1 Resting state

Resting state MEG data is recorded when a subject is awake and alert but not performing any task (Verdoorn et al., 2011). Brain regions may have different roles when activate in resting state compared to evoked study (Daianu et al., 2013).

MEG resting-state study have found that patients with obsessive compulsive disorder (OCD) demonstrated significantly lower phase synchronization among the insula, orbitofrontal cortex, and cortical regions of the limbic lobe than healthy controls in all band frequencies, except in the delta band (Koh et al., 2018). Study also found that veterans with posttraumatic stress disorder (PTSD) had significantly stronger neural activity in prefrontal, sensorimotor, bilateral amygdalae, parahippocampal, hippocampal and temporal areas compared to those without PTSD (Badura-Brack et al., 2017).

2.7.2 Event-related response

Oscillatory neuronal activity (Engel et al., 2001), event related fields and source reconstruction are used to investigate attentional processing in evoked studies.

Some studies used spectral analyses and beamforming (Sekihara et al., 2001) for the source reconstruction of MEG data. One study found that anxiety is related with greater gamma-band response and reduced beta response in the fusiform gyrus (FFG) and the amygdala during fearful face processing (Schneider et al., 2018). Another study found that anxious individuals showed greater negative oscillatory in ventrolateral prefrontal cortex (vlPFC) compared to heathy controls when processing of neutral faces (Britton et al., 2012). A reduced MEG response (M170) and activation in the right insula during early-stage processing of emotional faces was observed in socially anxious individuals (Riwkes et al.,

2015), but an over-activation in the right dorsolateral prefrontal cortex was found in late stage.

Enhanced activation in visual cortical regions during early threat processing and reduced activation in the right dorsolateral prefrontal cortex during late threat processing was found in children with anxiety disorder (Wessing et al., 2017) using the minimum norm estimates method (Hämäläinen & Ilmoniemi, 1994).

2.8 Thesis statements

Attentional bias toward threatening information has been associated with behaviour or symptoms of anxiety (Shechner et al., 2012) and used as an assessment of treatment (MacLeod & Mathews, 2012). Attentional Bias Modification (ABM) (MacLeod & Mathews, 2012) was designed to modulate attentional biases using different spatial attentional tasks (McNally, 2019) to reduce anxiety. The basic assumptions of ABM training are that threat information automatically capture attention of anxious individuals (Williams et al., 1988), and reduction of this attention bias (AB) can lead to changes of anxiety (MacLeod et al., 2002; MacLeod & Clarke, 2015). However, empirical research indicates that both facilitated attention (Amir et al., 2003; Harrewijn, Schmidt, Westenberg, Tang, & van der Molen, 2017; Eastwood & Smilek, 2005; Gilboa-Schechtman, Foa, & Amir, 1999) and attentional avoidance (Bögels & Mansell, 2004; Garner, Mogg, & Bradley, 2006) for threatening information was found among socially anxious individuals. Another study found that individuals with high social anxiety did not show attentional bias to threat faces compared to positive faces (Wieser, Hambach, and Weymar, 2018).

One possibility for the inconsistencies in the previous findings about the attentional bias of socially anxious individuals is that different types of threat faces (disgust, anger, and fear) might have different modulation on attentional processing. For example, differences in neural responses to different types of emotions (e.g., fear, disgust, and anger) have been found in healthy individuals (You & Li, 2016; Zhang, Liu, Wang, Ai, & Luo, 2017). In addition, studies found that socially anxious individuals show particular biases toward low-spatial-frequency (LSF) information when processing faces (Langner, Becker, & Rinck, 2009, 2012). However, the modulation of spatial-frequency and threat faces on temporal dynamics of attentional bias among individuals with social anxiety remain unclear. Further investigation of the attentional modulation of spatial-frequency and threat faces (fear, disgust, and anger faces) in early perceptional and later attentional processing stages among socially anxious individuals is necessary for developing more effective ABM training procedures. ***This is the first aim of the present study***.

The spatial frequency information and the threat value of the facial expressions are bottom-up factors that affect attention. Whether goal-directed attention control can mediate biased attention toward threat among socially anxious individuals remain relatively unknown. The normative attention literature suggests that goal-directed attention can override the attentional capture by threatening information. The threatening faces captures attention via bottom-up mechanisms when searching target is face, this capture can be overridden if top-down attentional goal is letters or objects (Barratt & Bundesen, 2012; Burra & Kerzel, 2019). Studies argued that distractors can be more efficiently inhibited when target is facilitated (Noonan et al., 2018) and precisely defined (Sylvester et al., 2008).

However, whether goal-directed attention control can mediate biased attention toward threat among socially anxious individuals remain relatively unknown. To develop treatments and strategy that may reduce threat bias and levels of social anxiety, it is essential to understand the underlying inhibition mechanism that suppressing this threat bias.

According to attentional control theory (Eysenck, Derakshan, Santos, & Calvo, 2007) and cognitive-motivational model (Mogg & Bradley, 2018), the goal-directed attentional control is impaired among socially anxious individuals, with prioritized processing for threat-related stimuli.

However, given the paradigms used by previous research, there is still an important gap in the social anxiety literature. Firstly, a number of the paradigms used in the attentional bias literature do not actually index emotional attention capture, but attention shifting. Furthermore, the effect of goal-directed attention to threat bias was not directly measured as there is no manipulation of attention control. Third, emotional information is presented, as targets or distractors, is processed at an early stage of attention. It is still not clear that whether distractor processing can be suppressed when the load involved in the processing of goal-relevant information is high.

The variance of EIB paradigm developed by Hoffman et al. (2020) is a well-designed task to test the effect of attention control on emotional attention capture. This task (1) has a baseline condition to reveal the attention capture of emotional and neutral information directly; (2) manipulate the attention resources involved in the processing of goal-relevant information that occurs before the appearance of emotional distractors. It is important to

confirm that this paradigm can provide robust measure of the influence of attention control on emotional attention capture. ***This is the second aim of the present study***.

As identification of structural and functional characteristics underlying social anxiety have been the recent focus, future research into neurocognitive mechanisms of attention capture should seek to explore when and where the attention capture is modulated. This remains unknown even in non-anxious population as lacking a robust behavioural task, which can distinguish the influence of attention control ability on attention capture, to be associated with measures of brain activity. ***The third aim of the present study*** is using Hoffman et al. (2020) paradigm to explore the neurocognitive mechanisms of attention modulation on attention capture.

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Chapter 3:
Time course of attentional bias in social anxiety: the effects of spatial frequencies and individual threats

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Chapter 4: Experimental paradigm and neurophysiological markers: Replication of Hoffman et al. (2020)

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Abstract

The notion of selective attention toward threatening information has long been associated with individuals with social anxiety. Numerous studies have investigated how emotionally salient stimuli impairs the attention of socially anxious people, the impact of top down control on the visual attention is still unclear. Previous studies using spatial attention tasks cannot reveal how emotional distractors capture attention due to the limitations of the experimental paradigms. First, targets and distractors are not separated temporally and spatially. Second, the tasks are not sensitive to emotional capture due to too many ongoing processing. Finally, there is no baseline condition, the attentional bias is inferred from subtraction of response time between negative and neutral pictures. The present study adapted an experimental task which addresses these limitations. We aimed to (1) replicate the behavioural of Hoffman et al. (2020) to demonstrate that emotional capture of attention can be voluntarily suppressed; (2) replicate the ERP results of Hoffman et al. (2020) to determine the timing of neural processes associated with suppression of emotional capture; (3) carry out concurrent MEG recordings to provide further specification of the anatomical sources of the ERP components. Our results confirm the main results of Hoffman et al. (2020). Both sets of results support the conclusion that emotional capture of attention can be voluntarily suppressed; and specify the timing of this suppression to a relatively late stage of processing. The neural sources associated these processes are examined in the following Chapter 5.

4.1 Introduction

For most of us social anxiety, involving fears or worries about social or performance situations, is a common and to greater or lesser extent, manageable part of everyday life. For a significant minority -- about 7% of the population (Kessler et al., 2005) – such fears are disproportionately intense, persistent and debilitating, to the extent that quality of life can be significantly impaired. People with social anxiety disorder (SAD) excessively worry that their behaviour may cause embarrassment or draw negative evaluation from others. Individuals with SAD fear social interactions and public performance situations to the extent they avoid most such encounters or endure them with intense discomfort (American Psychiatric Association, 2013). SAD has an early age of onset (13 years), and is a risk factor for depressive illnesses, drug abuse and other comorbidities (Stein & Stein, 2008). SAD imposes large costs on individuals, families and society. SAD sufferers have difficulty getting on with friends (Whisman et al., 2000), performing everyday activities, have lower than expected incomes (Katzelnick et al., 2001), are more likely to divorce (Wittchen et al., 1999) and are less productive in their work (Stein et al., 1999). Public recognition of social anxiety is low and only about half of SAD persons ever seek treatment (Grant et al., 2005).

Most ably functioning individuals can readily identify with both the evoking stimuli (social and performance situations) and the basic emotional responses to these stimuli (anxiety) experienced in social anxiety disorders. Clinical SAD and its debilitating consequences are set apart by the low triggering thresholds,

disproportionate intensity and enduring persistence of the response that is evoked. These amplified/dysregulated response characteristics seem to point to a dysfunction in neurocognitive systems that serve to identify, process, and prepare us to respond to potentially threatening circumstances. The present EEG/MEG neuroimaging study (together with the analyses described in the following Chapter 5), was designed to identify, in a group of healthy adult participants, brain mechanisms and systems that are operative under such circumstances.

Previous neuroimaging studies

A number of functional neuroimaging studies have reported abnormal activations of specific brain mechanisms and systems by threatening stimuli in persons with social anxiety. Current theoretical formulations propose that abnormal brain activations of SAD are centered on a hyperactivation of a "fear circuit", in a manner that prioritizes the processing of threat-related cues over other contextual information in the environment; and reduces the efficacy of connections to "top-down" mechanisms that serve to modulate and deploy fear responses in a contextually-dependent and adaptive manner (Schmidt et al., 2018).

Neuroimaging studies using a human fear conditioning paradigm provide evidence for a "fear network" consisting of brain structures including the amygdala, insula, and anterior cingulate cortex (ACC) (Klucken et al., 2009; Hamm & Weike, 2005; Tabbert et al., 2006). This 'fear network' is proposed to process and elaborate potentially threatening information (Sehlmeyer et al., 2009), and has been implicated in inappropriate and prolonged anticipation of negative stimuli or events in anxiety

disorders (Sarinopoulos et al., 2010; Straube et al., 2007). The amygdala serves major roles in salience detection, reward learning and unpredictability processing (Adolphs, 2010). Hyperactivation of the amygdala has been related to hypersensitivity to threat stimuli and dysfunction of emotional regulation in a number of anxiety disorders (Whalen et al., 2008; Etkin & Wager, 2007; Holzschneider & Mulert, 2011; Miskovic and Schmidt, 2012).

The insula has been proposed to play a pivotal role in dysfunctional anticipatory processing of aversive stimuli. Greater insula activation among anxious individuals relative to control participants has been reported during the anticipation of aversive stimuli (Stein et al., 2007; Simmons et al., 2006). Excessive activation in the ACC has been found in social anxiety and generalized anxiety disorders for tasks involving aversive stimuli (Etkin & Wager, 2007; Shin & Liberzon, 2010; McClure et al., 2007; Nitschke et al., 2009). The ACC has been related to conflict-monitoring and fear learning (Schmidt et al., 2018).

In addition to these three core components of the fear network, a number of other brain regions have been reported to play a role in anxiety disorders. In particular, the prefrontal cortex, regarded as a ‘top-down’ attentional control region, is considered to play an important role in regulating the activation of the fear network (Quirk and Beer, 2006). Results of surface event-related potential (ERP) and single neuron studies suggest that the prefrontal cortex is responsible for inhibiting the attentional capture of task-irrelevant information (Blair et al., 2007; Cosman et al., 2018; Schall, 2015; Squire et al., 2013) by suppressing representations of distractors in sensory cortex.

Decreased activation of prefrontal cortex (Browning et al., 2010) and reduced inhibition have been reported in persons with SAD (Price et al., 2011). Studies have also found reduced functional connectivity between prefrontal cortex and amygdala (Monk et al., 2008) or ACC (Comte et al., 2015) in anxious individuals.

Outside of the core fear network and the prefrontal executive regions, brain areas associated with lower-level activities involved in processing of emotional visual stimuli and human faces have been reported to be over-active in anxiety disorders. Pujol et al (2009) reported that the relationship between the amygdala response to threatening faces and social anxiety scores is dependent on the activation of the fusiform gyrus. Task-related functional neuroimaging studies have also reported hyperactivation of occipital regions (secondary visual cortices, Brühl et al., 2014) in SAD (Straube et al., 2004; Straube et al., 2005).

Electrophysiological indices of emotional capture

Electroencephalographic (EEG) studies have demonstrated that emotional tasks reliably modulate event-related potentials in (at least) two distinct time windows: An earlier epoch occurs over a time window of about 200-300 ms after stimulus onset in which the N2 component is enhanced by negatively-valenced images. A difference component obtained by subtracting the N2 obtained in experimental and control conditions is termed the early posterior negativity (EPN) (Wiens & Syrjänen, 2013; Schupp et al., 2003; Schupp et al., 2006) and is maximal in amplitude at temporo-occipital electrode sites (Schupp et al., 2006; Schupp, Stockburger, Bublatzky et al., 2007; Schupp, Stockburger, Codispoti et al., 2007). The EPN is regarded as an index

of selective attention, reflecting the evaluation of features of images according to their perceptual qualities and emotional salience (Dolcos and Cabeza, 2002; Schupp et al., 2004a, b). Another posterior N2 component termed N2pc is elicited by target or salient non-target in attention paradigms (Luck & Hillyard, 1994). The N2pc is elicited over the hemisphere contralateral to the visual field in which stimulus elements are presented (Eimer, 2015) and is typically followed by a positive component with a similar scalp topography. This positive component, known as PD component, has been proposed to reflect inhibition of the distractor object (Sawaki, Geng, & Luck, 2012). The non-lateralized EPN and lateralized N2pc components have similar scalp topographies and latencies and both index attention. Whether they are the same component still lack evidence.

A second and later timeframe for emotional processing occurs during a window of about 300-700 ms and is marked by the enhancement of the P3b component (for a review, Schindler & Bublatzky, 2020). The P3b peaks over posterior-central and temporal areas and is normally elicited by task relevant stimuli (for a review, see Hajcak, MacNamara, & Olvet, 2010) but has also been demonstrated to be elicited by task irrelevant emotional stimuli (Conroy & Polich, 2007; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). The P3b is a robust neurophysiological response, and had been proposed to reflect the allocation of limited attentional resources toward stimuli with motivational salience: Target stimuli fail to elicit a P3b when attention is allocated to another task, or when the targets are ignored (Duncan-Johnson & Donchin, 1977; Hillyard, Hink, Schwent, & Picton, 1973).

An important next step toward a more complete understanding of emotional capture requires that the neuroanatomical substrates implicated by functional neuroimaging, and the temporal processing stages marked by electrophysiological measurements, be reconciled into an integrated picture of which functional-anatomical networks are activated during which temporal processing stages. Some initial progress has been made towards this goal using electrophysiological source localisation techniques, and concurrent fMRI-EEG measurements (Schindler & Kissler, 2016; Crottaz-Herbette & Menon, 2006; Albert et al, 2011). Source localisation studies have found that the EPN elicited by emotion perception is associated with activity in extrastriate visual areas (Frühholz et al., 2011; Schettino et al., 2016), fusiform gyri (Schindler et al., 2015), visual cortex (Schindler & Kissler, 2016) and anterior cingulate cortex (ACC) (Carretie et al., 2004). Source localisation and fMRI-EEG studies have implicated anterior cingulate cortex in the attentional modulation of the EPN (Schindler & Kissler, 2016; Crottaz-Herbette & Menon, 2006) and the P3b (Albert et al, 2011).

At the current time, however, the evidence bases from fMRI and EEG studies remains largely separate and unconnected. This is in part due to fundamental differences between the temporal resolving powers and aspects of brain function that are captured by these two classes of brain measurements (low time resolution hemodynamics, versus high time resolution electrophysiology); and the relative difficulty and lack of precision associated with current techniques for deriving

neuroanatomical inferences from electrophysiological data (the "inverse problem" of electrophysiology, Dassios et al., 2007).

Another major source of difficulty for functional-anatomical-temporal integration derives from the use of widely differing experimental paradigms in the study of emotional capture and/or suppression of emotional capture. The most prominent and widely used paradigms include emotional Stroop (Williams, Mathews, & MacLeod, 1996), dot probe task (Macleod et al., 1986), visual search task (Öhman, Flykt, & Esteves, 2001) and emotional spatial cues task (Fox, Russo, Bowles, & Dutton, 2001). These tasks all focus on the suppression of task-irrelevant and distractive emotional information, but the targeted modes of inhibition vary between tasks. Some tasks require *attentional inhibition*, whereby participants must ignore concurrent emotional distractor features in order to respond to orthogonal target features, as in emotional Stroop tasks (Williams, Mathews, & MacLeod, 1996). In contrast in other attentional inhibition tasks the emotional stimuli and the target are separated spatially or temporally (Öhman, Flykt, & Esteves, 2001), as when the emotional stimuli serve as a cue presented before target (Macleod et al., 1986) in the dot probe task.

Thus, task-related differences can be expected to contribute substantial variance to the activation and timing of anatomical components of an emotional salience network. This variance presents significant additional difficulties for reconciling outcomes from separately conducted electrophysiological and functional neuroimaging studies. Taken together with the fundamental differences between the two classes of techniques described above, these pose significant barriers to

integration of anatomico-functional and temporal processing insights. Thus, the linkages between the neuroimaging and electrophysiological evidence bases remain highly underspecified in regards to emotional capture of attention.

The current study was designed to address this gap in our understanding. We used an established emotion-induced blindness (EIB) paradigm which has been demonstrated to have particular potency in eliciting both emotional capture effects (indexed by behavioural measures) and in modulating ERP components associated with emotional processing (Hoffman et al., 2020). To gain insights into brain generators of ERP components we employed magnetoencephalographic (MEG) measures of brain function and source analytic techniques.

Relative to other emotional capture paradigms described above, the EIB task, in which participants are required to detect a target picture (a scene picture that has been rotated to the right or left) presented after a task-irrelevant emotional or neutral picture in a stream of upright images (Most, Chun, Widders, & Zald, 2005), is considered to elicit particularly robust capture effects. A recent modification (Hoffman et al., 2020) further increases the utility of basic EIB paradigm by adding an attentional manipulation (a concurrent motion tracking task) that directly probes the effects of voluntary attention on emotional processing.

Further advances in our understanding of social anxiety require more specificity of these mechanisms. The approach adopted in the present experiment was to replicate the Hoffman et al. (2020) experiment with the addition of MEG recordings of brain activity. MEG has the same temporal precision as EEG, but in principle, has

greater spatial precision for neural generators (Baillet, 2017). MEG source localization is highly robust to errors in modelling of the volume conductor as MEG measures magnetic fields of brain, which are largely unaffected by electrically conductive inhomogeneities (Lopes da Silva, 2013; Baillet, 2017). In addition, MEG measures are reference-free (since magnetic flux density is an absolute measure and therefore bypasses the problem of selecting a reference site on the head (required for relative measurements of electrical potential differences) and which complicates the spatial interpretation of EEG responses (Biasiucci et al., 2019; Baillet, 2017).

The current study used the Hoffman et al. (2020) version of the EIB paradigm in conjunction with concurrent EEG and MEG measures of brain function. EEG measures were used as a bridge to the extant literature, to confirm the ERP modulation and timing effects reported by Hoffman et al. (2020); while concurrent MEG measurements were used to derive inferences about the neuroanatomical generator sources of the electromagnetic measurements. Chapter 4 describes the behavioural and ERP results; Chapter 5 describes the MEG source analysis.

4.2 Method

Procedures and methods were adapted from Hoffman et al. (2020, Experiment 1). The primary modifications to the original experiment were:

(1) porting of experimental code from Blitz 3D (Sibly, 2005) to Presentation (Neurobehavioral Systems, San Francisco, CA);

(2) participants in supine rather than upright position;

(3) stimulus presentation on a projection screen rather than a computer monitor;

(4) Concurrent EEG and MEG measurements rather than EEG measurements alone.

4.2.1 Participants

Twenty-three participants were recruited. Three participants were excluded from the final analysis due to excessive artifacts during the EEG recording (> 25% rejection of total epochs), resulting in a final sample of 20 (9 women) with a mean age of 25.95 years (*SD* = 4.38). All participants were right-handed (by self-report), had normal or corrected-to-normal vision and reported no history of neurological injury. All participants provided written informed consent. All procedures were approved by the Macquarie University Human Ethics Review Committee (Ref #5201929799392).

4.2.2 Apparatus

EEG and MEG data were measured concurrently in a magnetically shielded room (Fujihara Co. Ltd., Tokyo, Japan) with participants in a supine position. Electroencephalogram (EEG) was recorded with a MEG-compatible EEG system (BrainProducts GmbH, Gilching, Germany) with 64 electrodes placed in accordance

with the 10-10 system (Acharya et al., 2016). Magnetoencephalography (MEG) data were measured using a whole-head MEG system (Model PQ1160R-N2, KIT, Kanazawa, Japan) consisting of 160 axial gradiometers with a 50 mm baseline. The experiment was controlled by a Dell 3.60 GHz computer and programmed using Presentation software (Neurobehavioral Systems, San Francisco, CA). Visual stimuli were projected onto a screen by video projectors (Sharp Note vision Model PG10S, Japan) at a viewing distance of 106 cm. MEG and EEG were sampled continuously at a rate of 1000 Hz and MEG data were filtered online with a bandpass of 0.03-200 Hz.

4.2.3 Stimuli

Images were from Hoffman et al. (2020), taken from the International Affective Picture System (IAPS, Lang, Bradley, & Cuthbert, 2008) and 16 additional pictures from the internet. A sample of 25 participants had made valence and arousal ratings for the additional internet pictures on a nine-point scale (Hoffman et al., 2020).

Each trial started with a fixation point, followed by an image stream and terminated with a button-press response. The fixation point was presented for a random duration between 900-1100 ms. There were 20 image presentations per stream. Each image subtended a visual angle of 9.6° * 6.4°. Each image had a duration of 100 ms and was followed immediately by the next image in the stream.

Each sequence contained at most one animate picture. One third of the streams contained only background pictures, which were randomly selected from a set containing 252 landscape and architectural photographs. Two thirds of the streams contained one person or animal picture, replacing one of the background pictures in

the sequence. These person or animal pictures were referred as “animate pictures” and were either negatively or neutrally valanced. The animate picture could appear in any position among stimuli 6-12 of the picture stream (see Figure 1).

Negative pictures were randomly drawn from a set of 43 images of medical trauma, predators or violence. Neutral pictures were randomly drawn from a set of 52 images of people or animals. A dependent measures t-tests conducted by Hoffman et al. (2020) showed the valence ratings of the negative pictures (M = 7.92, SE = .15) differed significantly from those of the neutral pictures (M = 4.83, SE =.06), t (93) = 19.91, $p < .001$. There were also significant differences in the arousal scores of the negative (M = 6.26, SE = .49) and neutral (M = 4.04, SE = .07) pictures, t (93) = 26.04, $p < .001$.

Streams containing only landscape or architectural pictures were regarded as “baseline condition” streams.

A set of six identical moving disks (1° in diameter) was superimposed on the pictures. The disks consisted of two concentric rings, one black and one white, which made them visible on both light and dark areas of the pictures. The trajectories of the disks were independent and random. They moved with a constant velocity of 7.2 degrees/s and “bounced” (reversed trajectory) when they hit each other or the sides of the picture frame.

4.2.4 Procedure

Prior to each recording, the five head position indicators (HPI) were attached to an elastic cap placed on participants’ head. The participant's head shape, 3D locations

of the HPIs and fiducial landmarks were recorded using a pen digitizer (Polhemus Fastrack, Colchester, VT) and tracked by the MEG system before and after each block to determine head movement. If head movement exceeded 5 mm, the recording would terminate and repeat again.

Before entering the shielded room, participants completed 9 practice trials (3 per task condition). Participants were instructed to avoid unnecessary movements and blinks and maintain fixation at the center of the screen during experimental trials. Participants pressed the left mouse button to start the trial and initiate the picture stream. In the picture only (PIC) task, participants were required to detect the animate picture among the background pictures in the stream, prompted by the text 'Was there a picture of person or animal?'. Feedback was provided to indicate correct or incorrect responses. If there was an animate image in the sequence, participants would be required to choose the matching picture among 4 pictures. This choice was required whether or not they had correctly detected the animate picture. The location of the matching picture was random and balanced across the trials. The three incorrect choices were from the same picture set as the matching picture (i.e., neutral or negative). A colored box (green for correct and red for incorrect) was presented around the selected picture to provide feedback. The trial finished after the feedback a new trial was initiated.

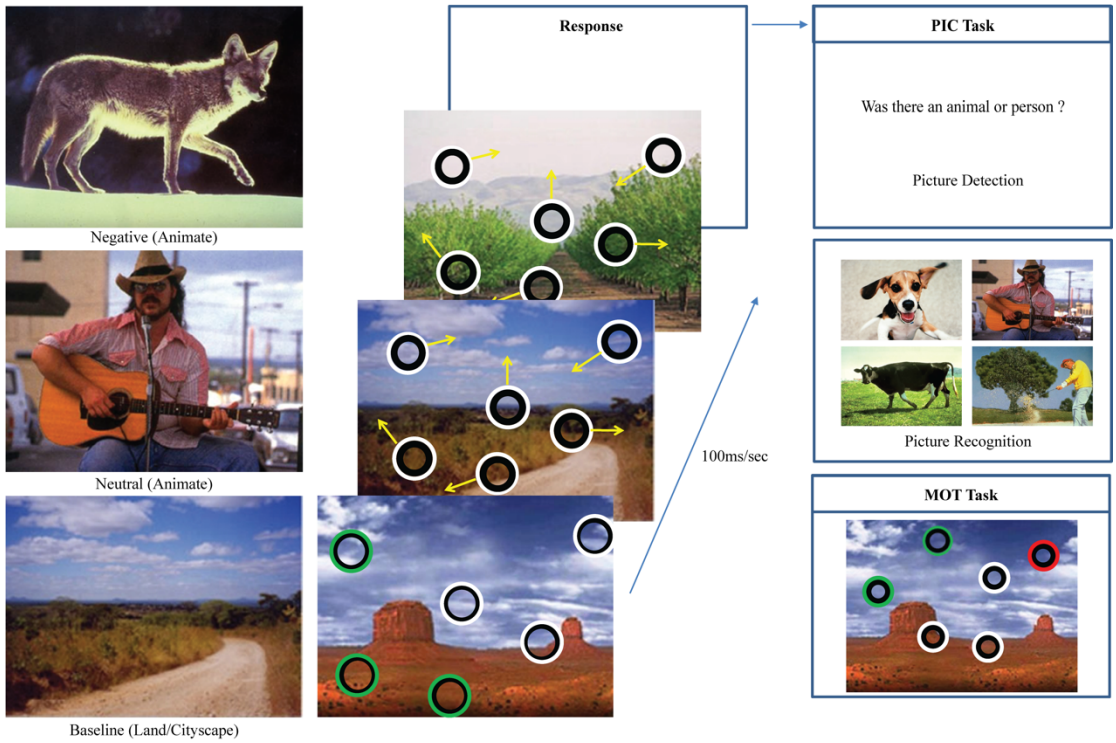

Figure 1: Experimental paradigm. Each trial was initiated with a mouse click. Six disks (three marked as green) were displayed moved in front of the RSVP stream for 500 ms. The stream contained landscape and city-scape pictures and a maximum of one distractor. The distractors could be a negative or neutral image of people or animals, or a baseline image. For the PIC task, participants were required to detect and recognize the distractors. For MOT task, they were asked to track three disks (shown in green) while ignoring the distractors. For DUAL, they were asked to perform both tasks but to give priority to the motion tracking task.

In the motion tracking (MOT) task, six stationary disks were presented for 500 ms with three of them are green. Then, all disks began moving along random trajectories until the trial ended with the three green disks turn white. Participants were required to attend to the moving circles and ignore the background pictures. After all pictures in the stream were presented, participants selected the target circles with a mouse click. The chosen disks would change colour (green for correct and red

for incorrect) to provide feedback. A correct response was defined as correct selection of three circles.

In the dual task (DUAL) condition, participants were required to perform both tasks with instructions that the motion tracking task had priority over the picture detection. Participants were instructed to reach 100% accuracy of the MOT task and would be reminded during the break if the performance of MOT task reach 50%. At the end of the trial, participants were asked to choose the target circles and then respond to the detection and recognition questions.

459 trials were presented in nine blocks (51 trials each block) with PIC, MOT and DUAL tasks repeated three times, resulting in 51 trials per condition. Participants were given short breaks between each block.

4.2.5 EEG

Electrode impedances were maintained under 5 kΩ during data recording. EEG recordings were referenced to the FCz electrode, and signals were subsequently re-referenced off-line to the average reference. The vertical electrooculogram (VEOG) and electrocardiogram (ECG) were recorded using two additional electrodes (one electrode was placed below the right eye to monitor vertical electrooculogram; another electrode was placed at the back to monitor electrocardiogram). EEG pre-processing and analysis were performed offline using BESA Research Version 7.0 software (BESA Research GmbH: Grafelfing, Germany). Signals from all channels were filtered using .1 Hz low cut-off filter (forward, 6 dB/oct) and 40 Hz high cut-off filter (zero phase, 24 dB/oct). Bad (flat) channels were identified by visual inspection

and interpolated from adjacent recording channels. Artifact correction was performed using spatial filters based on artifact (including eye blink and heartbeat) and brain signal topographies (Ille et al., 2002). Trials with voltages exceeding ±75 μV were excluded from analyses. ERPs were epoched from -200 ms to +1,000 ms from target picture onset and baseline-corrected to the pre-stimulus interval according to the timing of photodetector triggers.

The mean amplitudes of the N2, EPN (calculated at the electrode sites of TP7, TP9, P7, TP8, TP10, and P8) and P3b components (calculated at the electrode sites of C1, CZ, C2, CP1, CPZ, and CP2) were measured. All electrodes included in a given ERP component were given equal weight. The time windows of N2, EPN and P3b were centered on the peak of the group mean amplitude. Time windows were determined based on a collapsed localizer technique (Luck & Gaspelin, 2017).

The EPN was obtained through subtraction of N2 component elicited by negative and neutral pictures. The time window of EPN was adjusted to the peak of the subtraction waveform, 276-391ms (see Kennedy et al., 2014).

Repeated measures Analysis of Variance (ANOVAs) were performed using Greenhouse-Geisser corrections where appropriate. Following a significant result of the ANOVAs, post hoc comparisons using Fisher's Least Significant Difference (LSD) test were applied to the group means. The LSD test was performed using t-test and t distribution was referred to retrieve a p-value.

4.3 Results

4.3.1 Behavioral results

4.3.1.1 Picture detection

Picture detection performance was not analyzed, because they are close to ceiling (ranging from 86.3% to 97.6%) in all conditions and are not important for our examining of the automaticity of attention capture.

4.3.1.2 Picture recognition

Generalized linear mixed modelling (GLMM) using a binomial distribution with a logit link was applied to the accuracy data for within factors of *valence* (Negative vs Neutral) and *task* (PIC vs DUAL). Analysis was conducted in R (R Core Team, 2014) with lme4 (Bates et al., 2015), and the subject was used as random intercept. The denominator degrees of freedom were estimated by LRT methods and were based on the number of observed trials.

There were significant main effects of *task*, $X^2(1, N = 4074) = 181.14$, $p < .001$, and *valence* $X^2(1, N = 4074) = 11.92$, $p < .001$. The two-way interaction was not significant, $X^2(1, N = 4074) < 1$ (see Figure 2).

4.3.1.3 Motion tracking

A correct response was defined as correctly selecting all three targets. Generalized linear mixed modelling using a binomial distribution with a logit link was applied to these data with factors of picture type (Negative, Neutral, Baseline) and

task (MOT, DUAL). Analysis was conducted in R (R Core Team, 2014) with lme4 (Bates et al., 2015), and the subject was used as random intercept. The denominator degrees of freedom were estimated by LRT methods and were based on the number of observed trials.

There was a significant main effect of *task*, $X^2(1, N = 6113) = 11.44$, $p < .001$.

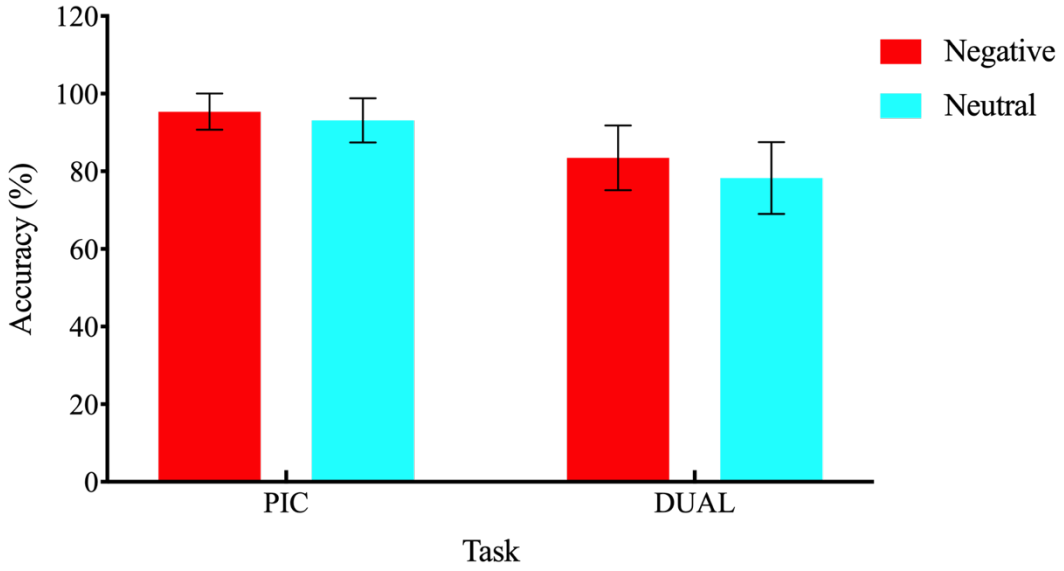

Figure 2: Picture recognition accuracy. Error bars represent standard errors of means.

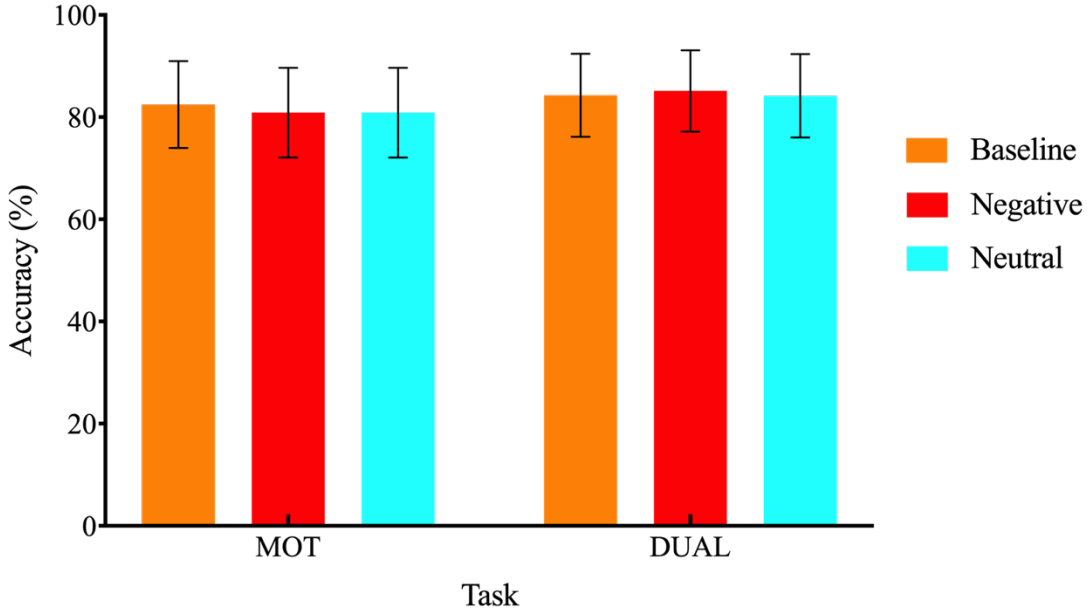

Figure 3: Motion tracking accuracy. Error bars represent standard error of means.

Neither the main effect of *valence*, $X^2(2, N = 6113) < 1$, nor its interaction with *task* were significant, $X^2(2, N = 6113) = 1.10$. Fig. 3 shows tracking accuracy as a function of task and image valence. Motion tracking accuracy was higher in the DUAL than MOT (see Figure 3).

4.3.2 ERP results

4.3.2.1 N2 and EPN component

Figure 4 shows grand mean N2 responses, averaged over left hemisphere (TP10, TP8, P8) and right hemisphere (TP9, TP7, P7) electrode clusters (Kennedy et al., 2014; Hoffman et al., 2020). The analysis time window was a 60 ms interval from 245 to 305 ms centered on the N2 grand mean peak latency (see Kennedy et al., 2014).

A three-way repeated measures ANOVA was computed using factors of *valence* (Negative vs Neutral), *hemisphere* (Left vs Right) and *task* (DUAL, MOT, & PIC). There was no significant main effect of *hemisphere* F (1, 19) = 1.01, η^2_p = .05. However, there were significant main effects of *valence*, F (1,19) = 7.219, $p < .05$, η^2_p = .275 and *task*, F (2, 38) = 41.328, $p < .001$, η^2_p = .685. Post-hoc comparisons revealed that the N2 amplitude for PIC condition was significantly greater than that of MOT condition ($p < .001$) and DUAL condition ($p < .001$). The difference between MOT and DUAL was not significant, (p = .368).

In addition, the *task* x *valence* interaction was significant F (2, 38) = 3.658, p = .035, η^2_p = .161, reflecting that the N2 amplitude for negative pictures was significantly larger than that of neutral pictures in the PIC and DUAL task, but not in the MOT task (see Fig. 4). The peak latency and posterior topography are in accord with previous results (e.g., Kennedy et al., 2014). Two-way interactions of hemisphere by task, F (2, 38) < 1, η^2_p = .011, and hemisphere by valence, F (1, 19) < 1, $\eta^2_p < .001$, were not significant. The three-way interaction between image valance, hemisphere, and task did not reach significance, F (2, 38) < 1, η^2_p = .046.

To confirm the presence of the EPN we applied one-sample t-tests comparing EPN amplitude to zero. The results showed a significant EPN (see Figure 5) for PIC and DUAL conditions in both hemispheres (all p's < .01) and a marginal significant EPN for MOT condition in right hemisphere (p = .051). However, this comparison was not significant for MOT condition in left hemisphere (p >.05).

A two factor repeated measures ANOVA using factors of *hemisphere* (Left vs Right) and *task* (DUAL, MOT, & PIC) was computed. There was no significant main effect of *hemisphere* F (1, 19) = 1.92, η^2_p = .09 or *task* F (2, 38) = 2.30, η^2_p = .11. The *task* x *hemisphere* interaction was also not significant F (2, 38) = .43, η^2_p = .02.

To examine the strength of evidence favouring the null hypothesis for the effect of *hemisphere* and *task* on EPN activation, we conducted a Bayesian repeated-measures ANOVA on EPN amplitude using JASP (JASP Team, 2018), with default priors (i.e., r = 0.5 for fixed effects; r = 1 for random effects; r = 0.354 for covariates) (Rouder, Morey, Speckman, & Province, 2012). This analysis produces a Bayes Factor (BF) consisting of the ratio of evidence in favour of the null compared to the alternative hypothesis. The BF_{01} (inverse BF) statistic, used in this analysis, favours the null model when it is greater than 1 with higher BF_{01} values indicating stronger evidence in favour of the null model. Results (BF_{01} =1.21) showed that the EPN amplitude across the three tasks are approximately 1.2 times more likely to be observed under the null model compared to the alternative model. Results (BF_{01} = 2.32) also showed that EPN amplitude in the left and right hemisphere are approximately 2.3 times more likely to be observed under the null model compared to the alternative model.

We also conducted a Bayesian one-sample t-test comparing EPN amplitude to zero in MOT condition in both hemispheres using JASP (JASP Team, 2018), with default priors (Cauchy prior distribution with r = 0.707) (Rouder, Morey, Speckman, & Province, 2012). Results showed that in the left hemisphere (BF_{01} =3.24), the EPN

activation was approximately 3 times more likely to be observed under the null model compared to the alternative model. However, in the right hemisphere (BF_{01} = .73), the EPN activation was more likely to be observed under alternative model.

4.3.2.2 P3b and P3b(N-N) component

Figure 6 shows grand mean P3b ERPs averaged over a cluster of six central-parietal electrodes (C1, Cz, C2, CP1, CPz, CP2). Analyses were computed over a 592ms time-window (450-992 msec determined using a collapsed localizer technique; Luck & Gaspelin, 2017).

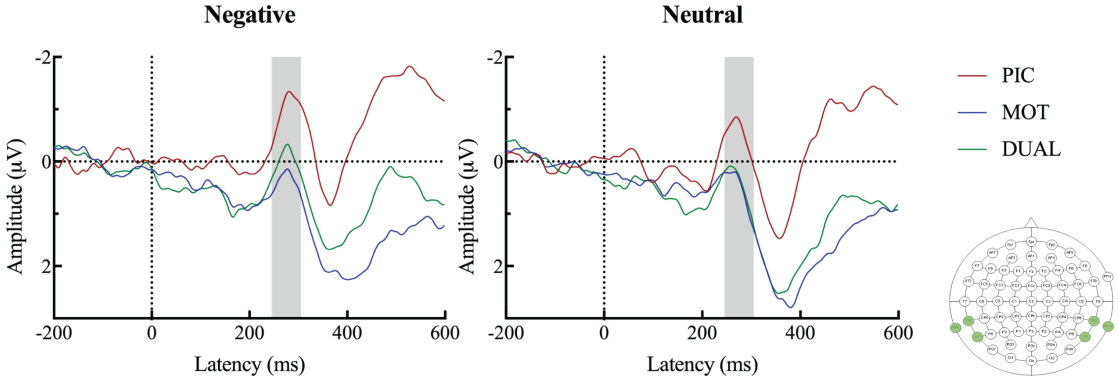

Figure 4: N2 ERP. The shaded region (245-305 ms) represents the time window used for measuring mean N2 amplitude.

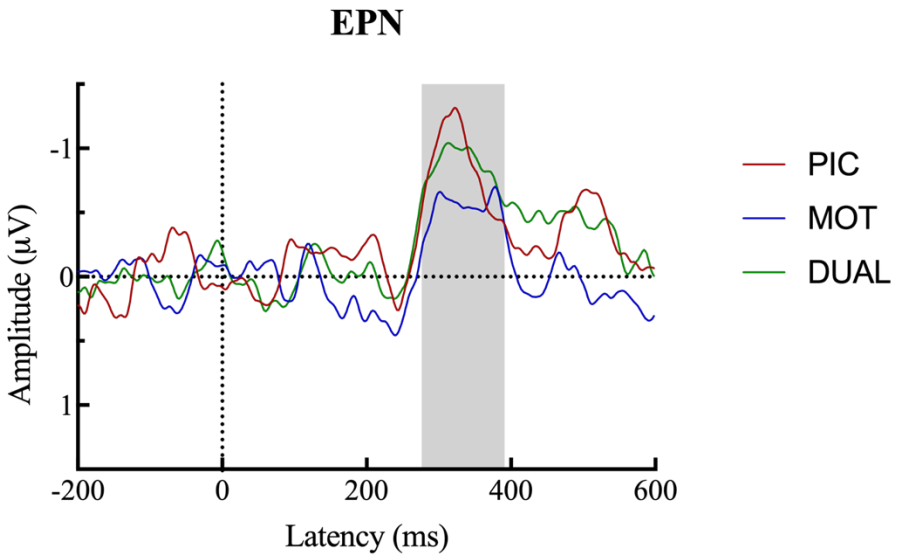

Figure 5: EPN ERP. The shaded region (276-391 ms) represents the time window used for measuring mean EPN amplitude.

A two-factor repeated measures ANOVA was conducted with factors of image *valence* (Negative vs Neutral) and *task* (MOT, DUAL, & PIC). There were significant main effects of *task* F (2, 38) = 68.118, $p < .001$, $\eta^2_p = .782$ and *valence* F (1, 19) = 18.400, $p < .001$, $\eta^2_p = .492$, as well as their interaction, F (2, 38) = 6.419, $p < .01$, $\eta^2_p = .253$. Pairwise LSD tests were applied to the main effect of *task*, revealing that the P3b amplitude of three different tasks were significantly different from each other: PIC versus MOT ($p < .001$), PIC versus DUAL ($p < .001$) and MOT versus DUAL ($p < .05$). The significant effect of *task* reflects that the P3b amplitude increase as more attention was allocated to the animate pictures. In accord with previous studies (e.g., Foti, Hajcak, & Dien, 2009; Kennedy et al., 2014), the main effect of *valence* shows that the P3b amplitude for negative pictures is greater compared to neutral pictures.

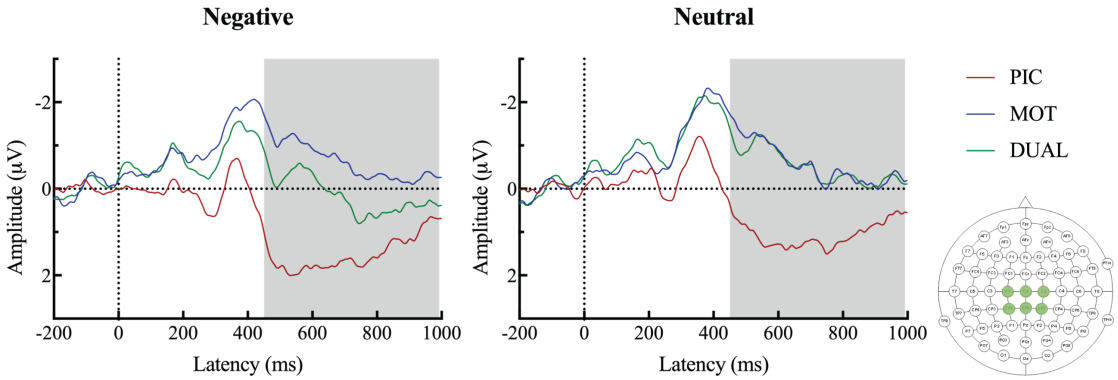

Figure 6: P3b component elicited by negative and neutral pictures. The shaded region (450-992 ms) represents the time window used for calculating the mean amplitude of the P3b component.

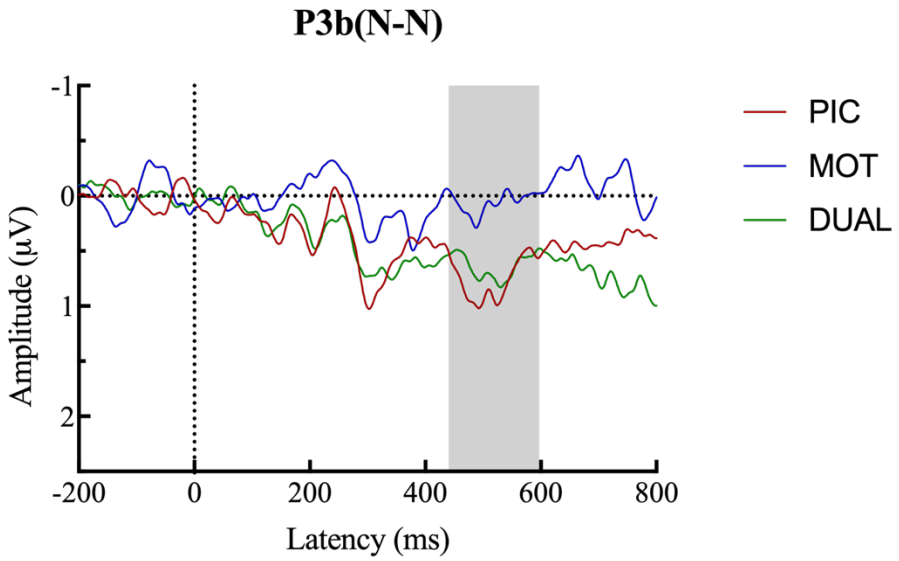

Figure 7: Negative-Neutral difference scores of P3b component. The shaded region (440-597 ms) represents the time window used for calculating the mean amplitude of the difference scores.

Simple effect analysis of the *task* by *valence* interaction indicated that the P3b amplitude evoked by negative pictures was significantly larger than neutral pictures in PIC ($p < .01$) and DUAL ($p < .001$), but not MOT ($p < 1$).

A Negative-Neutral difference scores of P3b, in the following we refer this as P3b(N-N), was created to examine the *task* by *valence* interaction in detail. The time window was adjusted to 440-597 msec based on the average half amplitude of P3b(N-N) across the three task conditions. A one-way repeated-measures ANOVA was

applied to these amplitudes using *task* as factors. The main effect of task was significant, F (2, 38) = 3.45, $p < .05$, $\eta^2_p = .15$. LSD comparisons revealed that the MOT condition was significantly different from PIC and DUAL condition ($p < .05$) (see Figure 7). To confirm this result, a single-sample t-tests was performed to determine whether the P3b(N-N) for three conditions were significantly different from zero. We found significant P3b components in PIC and DUAL conditions (all ps < .01) but not MOT condition ($p > .05$).

We also applied a Bayesian one-sample t-test comparing P3b(N-N) amplitude to zero in MOT condition using JASP (JASP Team, 2018), with default priors (Cauchy prior distribution with r = 0.707) (Rouder, Morey, Speckman, & Province, 2012). Results showed that the P3b(N-N) activation ($BF_{01} = 3.17$) is approximately 3 times more likely to be observed under the null model compared to the alternative model, providing "substantial" evidence (Jeffreys, 1961) that there are no differences in P3b amplitude between negative and neutral pictures in MOT condition.

Table 1: Comparison of main results and interpretation between current study and Hoffman (2020) experiment 1.

Measure	Hoffman	Interpretation	Present Study	Interpretation
Picture recognition accuracy	*Lower* accuracy for neg pics in PIC and DUAL	Neg pics more homogenous, more difficult to distinguish	*Higher* accuracy for neg pics in PIC and DUAL	Neg pics capture attention
	Lower accuracy for DUAL than PIC	Reduced attention in DUAL condition	Lower accuracy for DUAL than PIC	Reduced attention in DUAL condition
Motion tracking accuracy	NEG = NEU = Baseline	Motion tracking not affected by picture valence	NEG = NEU = Baseline	Motion tracking not affected by picture valence
	MOT > DUAL		DUAL > MOT	Participants prioritised the MOT task
N2 amplitude	NEG > NEU	Neg pics capture	NEG>NEU in	In MOT task,

		attention	PIC DUAL Not MOT *(task* x *valence* interaction)	attention was occupied by moving circled. Attention capture of emotional pic was inhibited.
	PIC > DUAL > MOT	Attention is (parametrically) allocated from PIC to MOT task	PIC > DUAL > MOT	Attention is (parametrically) allocated from PIC to MOT task
P3b amplitude	NEG > NEU	Neg pics capture attention	Main effect of *valence* Main effect of *task* *Task* x *valence* interaction	In MOT task, attention was occupied by moving circled. Attention capture of emotional pic was inhibited.
	PIC > DUAL > MOT	Attention is (parametrically) allocated from PIC to MOT task	PIC > DUAL > MOT	Attention is (parametrically) allocated from PIC to MOT task
EPN visual	PIC = DUAL = MOT ("remarkably similar", no explicit valence test)	EPN elicited in all conditions, conflicts with behavioral results	PIC = DUAL >MOT	
EPN 2 factor ANOVA	Main effect of hemisphere	Larger EPN in Right Hem	None	No difference
EPN one sample t-tests, both hems	all significant (note: unclear if corrected for multiple comparisons)	EPN elicited in all conditions and both hems	all significant but MOT left hemi (marginal significant in MOT right hemi)	EPN is not affected by task
EPN Bayesian ANOVA	"Substantial" evidence for no differences in EPN amplitude across the three tasks	Confirms EPN Visual	no differences in EPN amplitude across the three tasks	Negative pics captures more attention in three conditions

4.4 Discussion

This study was designed to replicate Experiment 1 of Hoffman et al. (2020), with methodological adaptations to include MEG recordings of brain activity. In the present chapter we focus on the behavioural and ERP results. MEG results are presented in Chapter 5.

Comparison to results of Hoffman et al. 2020 Experiment 1

Behavioural results

The behavioural results of the current study were consistent with those of Hoffman et al (2020)'s experiment 1, with some discrepancies in details (see Table 1). One such discrepancy is the present finding of higher recognition accuracy for negative than neutral pictures. This result is in accord with previous studies (Dennis and Chen, 2007; Eldar, Yankelevitch, Lamy, & Bar-Haim, 2010), and supports the interpretation that processing of threatening information is facilitated relative to neutral information. In contrast, and against their expectations, Hoffman et al. (2020) reported the reverse effect, i.e. that recognition accuracy was significantly lower for negative than neutral pictures, an unexpected result that they attributed to a possibly greater visual homogeneity of negative pictures relative to neutral pictures. It is worth noting that the facilitated processing of negative pictures may also cause by the arousal as the arousal of the negative pictures is significantly higher than neutral pictures. Previous studies found that both positive and negative high arousal (Anderson, 2005; Milders et al., 2006) verbs have preferential access in the limited capacity system of attention.

Since the present experiment used identical pictures and produced results that are consistent both with previous work and with theoretical considerations of attentional capture outlined in the introduction, the homogeneity explanation seems unlikely. Since our results are otherwise generally consistent with those of Hoffman et al. (2020) (see below), we have no compelling reasons to believe that the methodological differences between the two studies (e.g. supine versus upright positioning, concurrent MEG recordings) should contribute to this. Thus, it is difficult to reconcile these two sets of results. If the methodological differences are of minor significance, the discrepancy may be most likely attributable to some unknown difference(s) in the characteristics of the participant samples in the two studies.

In accord with the results of Hoffman et al. (2020) the present results show that mean picture recognition performance was significantly attenuated in the DUAL task condition (80.88%) relative to the PIC condition (94.27%). These findings support the conclusion that the secondary motion tracking task was effective in modulating allocation of attention to the primary picture recognition task.

A second discrepancy was that motion tracking accuracy in the present experiment was significantly higher for DUAL (84.54%) than MOT (81.40%) tasks in the present experiment, while Hoffman et al. (2020) reported the opposite (DUAL 90.8%; MOT 93.5%). In this case the results of Hoffman (2020) are more consistent with expectations and support the conclusion that the DUAL task requirements had a detrimental effect on performance on the primary motion tracking task. It is somewhat unclear how to account for this effect. However, participants were instructed to

prioritize the motion tracking task, and it is conceivable that these instructions may have provided some small advantage over the MOT task. We note however that the mean task differences reported in both studies are relatively small in magnitude, and the anomaly is not critical to inferences concerning performance on the picture task. Further, both sets of results are consistent in their findings of no main effect or interaction of picture valence in the motion task.

In summary, the present results show greater recognition accuracy for negative pictures than neutral pictures, replicating previous work (Dennis and Chen, 2007; Eldar, Yankelevitch, Lamy, & Bar-Haim, 2010) but not the anomalous results of Hoffman et al. (2020). These results support the interpretation that negative pictures are more salient and capture attention more readily than neutral pictures. We also observed some results in motion tracking task which are not consistent with Hoffman et al. (2020), showing that motion tracking accuracy was significantly higher in DUAL than MOT condition. Our finding of no significant valence effect on motion tracking performance is consistent with Hoffman et al. (2020)'s finding, supporting the interpretation that the negative pictures did not get access to the limited capacity system of attention (Lavie, 2005) when participants' attention was engaged in another difficult task in the MOT condition.

ERP Results

The ERP results of current study replicated the main effect of valence reported by Hoffman et al (2020), such that N2 and P3b amplitudes were larger for negative than neutral pictures. This result is in accord with prior research (Foti et al., 2009;

Kennedy et al., 2014) and is consistent with our behavioural results showing greater accuracy for recognition of negatively-valenced pictures. Taken together, the behavioural and ERP results support the interpretation that negative pictures were allocated more attention than neutral pictures. In line with Hoffman et al. (2020) and previous studies, the current study found that N2 (Schupp, Stockburger, Bublatzky et al., 2007; Wiens & Syrjänen, 2013) and P3b (Duncan-Johnson & Donchin, 1977; Hillyard, Hink, Schwent, & Picton, 1973) amplitudes were reduced in the DUAL and MOT tasks which required sharing of attention between picture recognition and motion tracking. These results support the contention that attentional capture and subsequent processing of emotional information is susceptible to secondary inhibition that controlled by target facilitation (Noonan et al., 2018).

However, some of our ERP results were discrepant from those of Hoffman et al (2020). One discrepancy is the present finding of a *task* x *valance* interaction, due to the fact that negative pictures elicited greater N2 and P3b amplitudes in the PIC and DUAL condition but not in the MOT condition. The ERP results are consistent with our observation of greater accuracy for recognition of negative pictures in the PIC and DUAL conditions. In contrast, Hoffman et al. (2020)'s found that negative pictures elicited greater N2 and P3b amplitudes in all three task conditions, indicating that attention to picture valence was not fully suppressed in the MOT condition by participants of that study. We do not wish to overinterpret the lack of a picture valence statistical effect in our MOT ERP's, as it is possible that this is simply an issue of lower signal-to-noise ratios in our data.

In line with Hoffman et al. (2020), our Bayesian test found no significant task effect for the EPN component, indicating that this component was not affected by the amount of attention allocated to the picture stream. In addition, the current study found that the EPN in the MOT condition was significant only in the right hemisphere, whereas Hoffman et al. (2020) found that EPN was elicited in all three tasks, in both hemispheres but with a significantly higher amplitude for the right hemisphere. Both sets of results support the contention that EPN reflect the pre-attentive (e.g., Holmes, Nielsen, Tipper, & Green, 2009; Rellecke, Sommer, & Schacht, 2012) and automatic (Holmes, Kiss, & Eimer, 2006; Holmes, Nielsen, Tipper & Green, 2009) attention capture of emotional salient stimuli compared to neutral stimuli. However, it is worth noting that EPN is the Negative-Neutral subtraction of N2, which eliminates a small overlapping PD component that may index attentional control or inhibition (Gaspar & McDonald, 2014; Hickey, Di Lollo, & McDonald, 2009). Therefore, the effect of attentional suppression may not be directly indexed by the EPN.

Surprisingly, the absence of attentional capture effect in MOT condition is in conflict with the finding that the EPN component was not affected by the amount of attention allocated to the picture stream. One plausible explanation is that the motion tracking task is insensitive to brief interruptions. Hoffman et al (2020) assumed that attentional capture is caused by *physical salience* rather than *emotional salience*: the larger capture effect for negative pictures than neutral pictures is related to the later processes that occurs after the early visual processes. In other words, neutral pictures

are effectively suppressed during early visual processes. In contrast, negative pictures are assessed and suppressed in later stages.

The EPN component has been demonstrated to reflect the pre-attentive (e.g., Holmes, Nielsen, Tipper, & Green, 2009; Rellecke, Sommer, & Schacht, 2012) and automatic (Holmes, Kiss, & Eimer, 2006; Holmes, Nielsen, Tipper & Green, 2009) attention capture of emotional salient stimuli relative to neutral stimuli. However, there is increasing evidence that the N2pc, and possibly EPN as well, reflect later processes that occurs after attention has been directed to an object, but not attentional capture or shifting (Zivony et al., 2018; Kiss et al., 2008; Theeuwes, 2010). The non-lateralized EPN and the lateralized N2pc have similar scalp topographies and latencies but whether these two are the same component still need investigation.

We found the Negative-Neutral difference P3b difference wave was reduced in DUAL condition and was not statistically significant in the MOT condition. Hoffman et al (2020) reported similar effects for the attentional manipulation, although they found a small but significant P3b(N-N) in the MOT condition. Both sets of results add to the evidence that the emotional attention capture can be suppressed by secondary inhibition that controlled by target facilitation (Noonan et al., 2018).

In sum, our ERP results show greater N2 and P3b amplitudes for negative pictures than neutral pictures and the amplitude of the N2 and P3b components was strongly reduced in the DUAL and MOT tasks, replicating the main results of Hoffman et al.'s (2020) Experiment 1. These results support the contention that attention is captured more readily by emotional than neutral stimuli, but that this capture is susceptible to

secondary inhibition that controlled by target facilitation (Noonan et al., 2018). Finally, in line with Hoffman et al. (2020), we found that the EPN component was not affected by the attentional manipulation.

Timing of attention capture and the suppression of attention capture

Our behavioural results support the contention that attentional capture by emotional salient stimuli is not fully automatic (Hoffman et al., 2020). We found that recognition accuracy of negative pictures was better than neutral pictures when they were task-relevant. The superiority of negative pictures was reduced when attention was shared between PIC task and MOT task; and further reduced when attention was fully engaged to the MOT task.

Consistent with the behavioural results, our ERP results show greater N2 and P3b amplitude for negative pictures than neutral pictures and the amplitude of the N2 and P3b components was strongly reduced in the DUAL and MOT tasks. The N2 is regarded as an index of selective attention, reflecting the evaluation of features of images according to their perceptual qualities and emotional salience (Dolcos and Cabeza, 2002; Schupp et al., 2004a, b). The P3b is a robust brain response that reflects the allocation of limited attention resources toward stimuli of motivational salience (Hajcak, MacNamara, & Olvet, 2010).

Taken together, the behaviours of the EPN, N2 and P3b ERPs provides powerful neurophysiological clues to the timing and nature of the brain mechanisms of emotional capture and attentional control, that are not available from the behavioural data alone. The presence of an EPN in all three tasks indicates that attention to

emotionally salient stimuli is not *proactively* suppressed when allocating attention to a competing task. Rather, the behaviour of this ERP component indicates that emotional stimuli do automatically engage attention at this early stage of processing.

The strongly reduced P3b in DUAL and MOT conditions indicates that individuals have effectively suppressed processing of the emotional distractor and have allocated attention to the competing motion task. The attenuation of the subsequent P3 component indicates that participants suppressed the distractor *reactively*, after emotional attention has been captured as indexed by the EPN.

4.5 Conclusion

This experiment replicated the results of Hoffman et al.'s (2020) Experiment 1, with addition of concurrent MEG measurements. ERP results showed that attention capture of emotional pictures is more effective for negative pictures, as reflected by greater N2 and P3b amplitudes. However, attentional capture of emotional salient stimuli can be suppressed, and this suppression happens close to the time of attention capture, which was reflected by equivalent P3b amplitude for negative and neutral pictures in MOT condition. Taken together, the behavioural and ERP results show that emotional capture of attention can be effectively suppressed by occupying attention resources in a limited capacity system (Lavie, 2005). However, this suppression occurs after an early initial stage of processing in which neural resources are more automatically allocated to emotional pictures. As noted in the introduction, the neural sources of these important ERP signposts are currently highly underspecified. We address this gap our knowledge in the following chapter, with source analyses of the MEG responses measured concurrently with the ERPs.

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Chapter 5:
Source analysis of neuromagnetic EPNm and P3bm components elicited in an emotional capture RSVP paradigm

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Xiaofei Dong and Blake W. Johnson conceived the experiment and prepared the stimuli. Xiaofei Dong conducted the experiment. Xiaofei Dong and Blake W. Johnson analysed the data and wrote the manuscript. All authors participated in discussion.

Abstract

Our behavioural and ERP results (N2 and P3b) have shown that negative pictures are more easily capture attention than neutral pictures when they are task relevant. However, the superiority of negative picture over neutral pictures on attention capture can be suppressed and the suppression of attention capture happens downstream of (subsequent to) emotional attention capture. Even though the ERP results have provided valuable information about the timing of emotional capture, our current knowledge of the anatomical generators of these components remains rudimentary and imprecise. In this chapter, we examined the MEG results recorded concurrently with EEG while participants performed an emotion-induced blindness task. Distributed source imaging was applied to MEG data during EPN and P3b(N-N) time window. We first found significantly greater anterior cingulate activation in motion tracking condition (MOT) compared to picture detection (PIC) and dual task (DUAL) conditions for negative pictures during EPN time window. The subsequent activity is distributed in AI and ACC during P3b time window for negative pictures, which showed significantly reduced left insula activation and greater anterior cingulate activation in MOT condition compared to PIC and DUAL conditions. The present results show with source-localized MEG that the “salience network”, composed of AI and ACC, sequentially detects salient stimuli and maintains a task set. These neuroanatomical processes ultimately account for participants’ task performance and electrophysiological responses during performance of an emotional capture RSVP task.

5.1 Introduction

In Chapter 4, we described the EPN and P3b ERP components measured with EEG recordings and elicited in an emotional capture RSVP experiment. Taken together, the behavioural and ERP results indicate that two temporally- and functionally-distinct stages of neural processing are operative in this experimental setup: An earlier stage, indexed by the EPN component at latency of about 276-390 ms, in which emotional stimuli automatically engage attentive processing; and a subsequent stage indexed by the P3b component at latency of about 440-596 ms, in which emotional processing can be suppressed while engaging attention with another attention-demanding task. In the present chapter, we proceed to investigate the relationship between the EEG and concurrent MEG measurements from that experiment; and to analyse and characterise the brain sources of the neuromagnetic versions of the EPN and P3b components.

The early posterior negativity (EPN) measured over temporo-occipital sites (Schupp et al., 2006) has been extensively studied (Schupp, Stockburger, Bublatzky et al., 2007; Schupp, Stockburger, Codispoti et al., 2007) and has been found to be larger for emotional than neutral images (Schupp et al., 2003; Codispoti et al., 2007), especially in the right hemisphere (Schupp et al., 2006). The EPN is regarded as an index of selective attention, reflecting the evaluation of features of images according to their perceptual qualities and emotional salience (Dolcos and Cabeza, 2002; Schupp et al., 2004a, b).

The neuroanatomical generators of the EPN remain unclear. Consistent with its temporo-occipital scalp distribution, a number of ERP source localization, and EEG-fMRI correlational analyses studies (Sabatinelli et al., 2007, 2013) have reported that the EPN elicited by emotion perception is associated with activity in extrastriate visual areas (Frühholz et al., 2011; Schönwald & Müller, 2014; Schettino et al., 2016; Schindler & Kissler, 2016), and the fusiform gyri (Schindler et al., 2015). In contrast, several other studies using tasks that involve attentional control have reported that the anterior cingulate cortex is involved in the attentional modulation of EPN (Schindler & Kissler, 2016; Crottaz-Herbette & Menon, 2006).

The P3b component is a positive ERP deflection located at central and parietal electrodes normally peaking around 250-500 ms after the presentation of stimuli (Duncan et al., 2009; Johnson & Donchin, 1980; Polich, 2007). P3b normally is evoked by task relevant stimuli (for a review, see Hajcak, MacNamara, & Olvet, 2010) or task irrelevant emotional stimuli processing (Conroy & Polich, 2007a; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). P3b is a robust index reflecting the allocation of limited attention resources toward stimuli of motivational salience. For example, several studies have reported that target stimuli fail to elicit a P3b when the attention is allocated to another task or the targets are ignored (Duncan-Johnson & Donchin, 1977; Hillyard, Hink, Schwent, & Picton, 1973). Similar results have been reported in attentional blink studies (AB): the P3b amplitude evoked by first target is greater when the second target was missed (Kranczioch, Debener, Maye, & Engel, 2007; Shapiro, Schmitz, Martens, Hommel, & Schnitzler, 2006; Sergent et

al., 2005). Attentional blink studies using fMRI (Marois et al., 2004; Kranczioch et al., 2005; Feinstein et al., 2004) and magnetoencephalography (MEG) (Gross et al., 2004) have concluded that anterior cingulate, lateral prefrontal and parietal regions are associated with the inhibition of irrelevant information so that the second target can be seen.

After decades of study, the generators of P3b also remain unsettled and are clearly complex. Studies have estimated the source of P3b to be located between frontal and hippocampal/temporal parietal brain areas (Polich, 2003; Soltani & Knight, 2000; Knight, 1997; Kirino et al., 2000).

EEG (electroencephalogram) and MEG (magnetoencephalogram) are records of brain electrical (Niedermeyer, 2004) and magnetic fields (Cohen, 1972), respectively. EEG and MEG are highly complementary methodologies since the source of brain signals that they record are essentially the same, i.e., synchronized postsynaptic currents within and between pyramidal cells (Hamalainen et al., 1993). However, distinct physical properties of the electric and magnetic fields distinguish them in several important respects (Dassios et al., 2007). MEG is sensitive to brain signals in sulcal walls (tangential current flow) (Srinivasan et al., 2007), while EEG captures brain signals in gyral crowns (radial current flow) more precisely (Nunez and Cutillo, 1995). In addition, the signal-to-noise ratio (SNR) of MEG decreases more rapidly with source depth than that of EEG (Cuffin and Cohen, 1979).

As an imaging method, MEG has several potential advantages relative to EEG. First, EEG signals are more likely to be distorted by electrical conductivity

differences between the scalp, skull and other biological tissues that intervene between the brain sources and recording electrodes (Winter et al., 2007; Baillet, 2017). EEG source localization is thus highly dependent upon a precise characterisation of the conductive properties of the volume conductor (brain and cranium) and therefore prone to uncontrolled biases resulting from model errors (Vorwerk et al., 2014). Approximations in modelling the head shape (Lanfer et al., 2012; Fiederer et al., 2016), electrode size and drifts in skin-contact impedances (Pursiainen et al., 2012) impose a localization and amplitude error on estimated EEG sources. In contrast, magnetic fields are in principle unaffected by electrically conductive inhomogeneities, making MEG source localisation highly robust to errors in modelling of the volume conductor. Sources of bias are well identified and controlled by, for example, using individual anatomy from magnetic resonance images to define the forward model (Lopes da Silva, 2013; Baillet, 2017). Second, measurement of EEG signals requires a reference site, as EEG measures the voltage potential differences between electrodes attached to the scalp. There is no perfectly electrically neutral locus on the scalp and consequently the shape of voltage time series and their spatial topographies can vary significantly as a function of the selected reference location (Biasiucci et al., 2019). In contrast MEG measures of magnetic induction are absolute and therefore reference-free measures (Baillet, 2017).

Studies have found that the signal topographies of EEG and MEG are partially independent (Malmivuo, 2012) and almost orthogonal to each other, which means that signals recorded by these two methods are complementary (Dassios et al., 2007).

Therefore, the simultaneous acquisition of EEG and MEG are non-redundant and in principle use of both measures can improve the precision of source localization over that obtained using either modality alone (Cohen and Cuffin, 1983; Cuffin and Cohen, 1979). Simulation (Fuchs et al., 1998; Liu et al., 2002) and experimental (Sharon et al., 2007) studies have shown better localization accuracy of the combined solution than either measurement alone. However relatively few studies employ concurrent EEG/MEG. This is primarily for practical reasons. There are relatively few MEG facilities in comparison to EEG labs; and concurrent EEG adds considerably to the setup times and analytic requirements of a MEG experiment.

In summary, the ERP evidence points to two functionally important and temporally distinct stages of neural processing, reflected by the EPN and P3b components, in the emotional capture RSVP paradigm. However, the anatomical sources of these ERP components remain highly underspecified, for several reasons: the underlying generator configurations for both components are likely to be spatially extensive and anatomically complex; and the precise configuration of generators for each component seems to be highly task-dependent. These problems are strongly compounded by the biophysical properties of surface-recorded electrical potentials, which are intrinsically difficult to unmix and invert into source space.

By their nature, MEG signals are more readily assigned to anatomical generators within the brain. In the present analyses we leverage this capability to provide a more detailed specification of brain regions involved in attentional capture and suppression,

with analyses of MEG data collected concurrently with the EPN and P3b ERPs measured in an emotional capture RSVP experiment.

5.2 Method

5.2.1 Pre-processing

Off-line data were analysed using BESA Research Version 7.0 (BESA Research GmbH: Grafelfing, Germany). The MEG data were digitally filtered using .1 Hz low cut-off filter (forward, 6 dB/oct) and 40 Hz high cut-off filter (zero phase, 24 dB/oct). Epochs were time-locked to target picture onset (from 200 ms prior to and 1,000 ms after) and baseline-corrected to the pre-stimulus interval based on the timing of photodetector triggers.

5.2.2 Head models

EEG source analyses used a 4 shell ellipsoidal head model (Head, scalp, bone, CSF) with radii 85 mm, 6 mm, 7 mm, 1 mm) and relative conductivities 0.33, 0.0042, 1). A single-shell sphere head model was used (Sarvas, 1987) for MEG source analysis with radius 92.2 mm.

5.2.3 Source probe analysis

As an initial step we wished to compare MEG recordings to the grand average ERP waveforms described in Chapter 4, in order to assess if the MEG responses showed comparable changes as a function of the experimental variables Attention (PIC, DUAL and MOT) and Valence (NEG and NEU). Since MEG measurements cannot be grand averaged in sensor space, we first transformed averaged MEG data into a standard brain source montage, reducing each set of 160 sensor waveforms to 15 regional sources, including left and right frontal (FL; FR), midline frontal (FM), central cortex (CM), parietal cortex (PM), midline fronto-polar (FpM), midline

occipito-polar (OpM) cortex, left and right anterior temporal lobes (TAL; TAR) and left and right posterior temporal lobes (TPL; TPR). In each participant, a common spatial montage was used as a spatial filter to derive source waveforms for both negative and neutral Valence conditions. For comparison, the same source montage procedure was applied to the ERP data described in Chapter 4.

Statistical analyses were computed using BESA Statistics (v2.0; BESA GmBH: Grafelfing, Germany; Maris and Oostenveld, 2007). Comparisons were made between task conditions (PIC, DUAL and MOT), separately for both negative and neutral pictures. A two-stage cluster-based permutation test was applied to the source waveforms (Maris & Oostenveld, 2007) between all task conditions at every time point and at each source, using a critical alpha value of .05 and 10,000 random permutations. Finally, followed a significant ANOVA effect, a post-hoc Scheffe's test was computed for pairwise comparisons.

5.2.3.1 Source Probe Waveforms: MEG

Univariate ANOVAs were conducted for NEG and NEU valences, with the null hypothesis that the MEG source waveforms of PIC, DUAL and MOT task were equal. The multiple comparisons problem is addressed with a cluster-level permutation test across time. Significant effects are summarised in Table 1.

Table 1 Permutation test results: MEG source probe waveforms.

	Cluster	*p*	Start time (ms)	End time (ms)	Brain source
negative					
	1	.000	22	643	TAR

	2	.002	24	650	FR
	3	.002	36	616	FpM
	4	.006	342	760	CR
	5	.013	251	530	TAL
neutral					
	1	.005	100	539	FR
	2	.006	93	536	FpM
	3	.014	235	545	TAL
	4	.036	232	449	FL
	5	.052	32	299	PL

Significant clusters are shown in Figures 1 and 2. The results showed that clusters in the left temporal anterior (TAL) region for negative (Figure 1, E) and neutral pictures (Figure 2, C) resemble the N2 morphologies and time windows from the ERPs (in Figure 3, Chapter 4). Similarly, clusters in midline fronto-polar (FpM) region for negative (Figure 1, C) and neutral pictures (Figure 2, B) corresponded to P3b EEG components in morphology and time window (in Figure 5, Chapter 4). The ERF amplitudes of these significant clusters modulated by the task effects showed two patterns: (1) clusters in TAR, FR and FL regions have the same pattern as ERP amplitudes e.g. MOT>DUAL>PIC; (2) clusters in FpM, CR and TAL regions have the opposite pattern as ERP amplitudes e.g. PIC>DUAL>MOT. This indicates that MEG data may contain at least two functionally distinct sources.

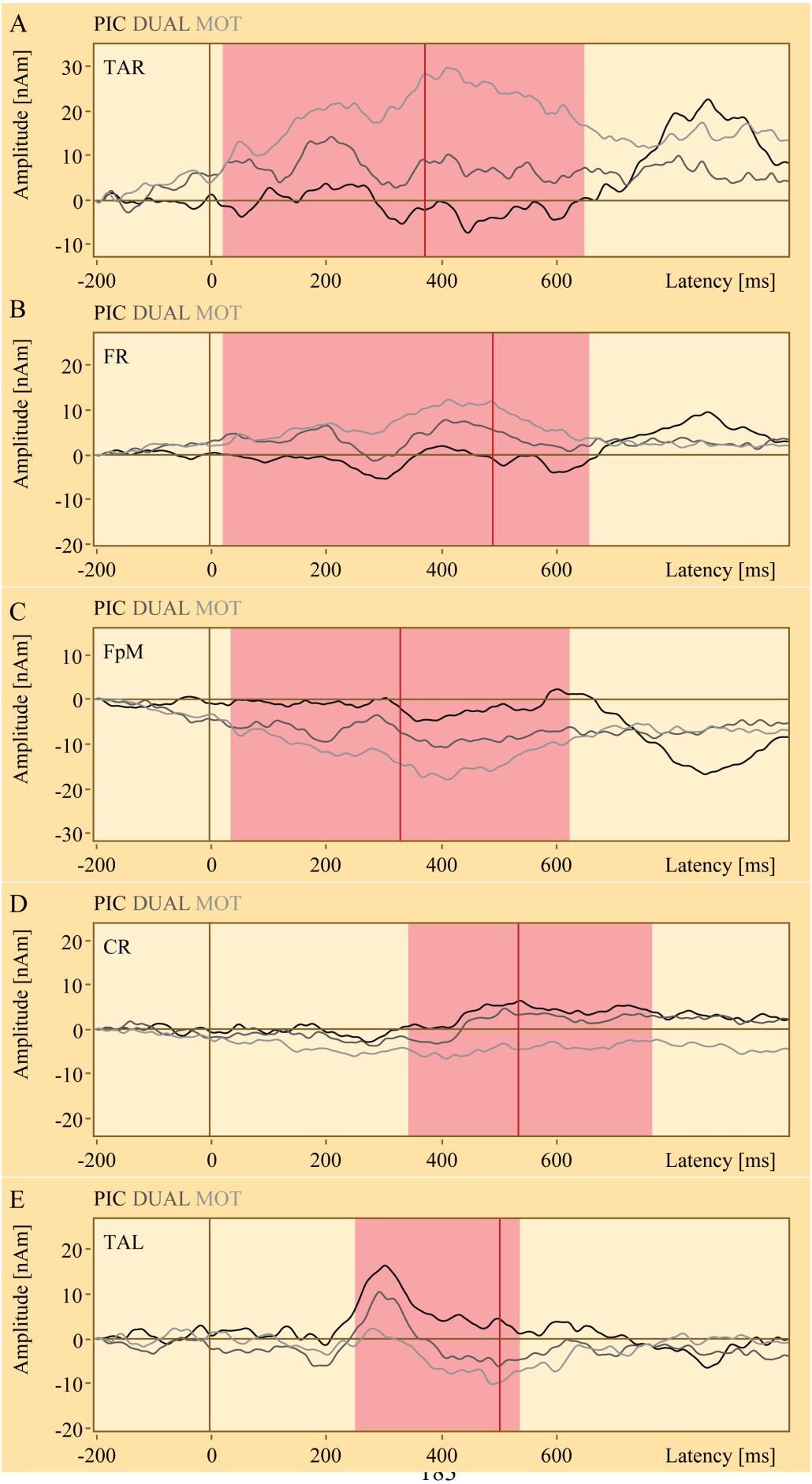
A
PIC DUAL MOT
TAR
Amplitude [nAm]
30
20
10
0
-10
-200
0
200
400
600
Latency [ms]
B
PIC DUAL MOT
FR
Amplitude [nAm]
20
10
0
-10
-20
-200
0
200
400
600
Latency [ms]
C
PIC DUAL MOT
FpM
Amplitude [nAm]
10
0
-10
-20
-30
-200
0
200
400
600
Latency [ms]
D
PIC DUAL MOT
CR
Amplitude [nAm]
20
10
0
-10
-20
-200
0
200
400
600
Latency [ms]
E
PIC DUAL MOT
TAL
Amplitude [nAm]
20
10
0
-10
-20
-200
0
200
400
600
Latency [ms]

Figure 1: ANOVA results for negative pictures. Significant clusters were obtained for five regional sources. Red shading indicates time windows of significant effects. Note oppositely-directed experimental effects in different clusters, e.g. TAR versus TAL.

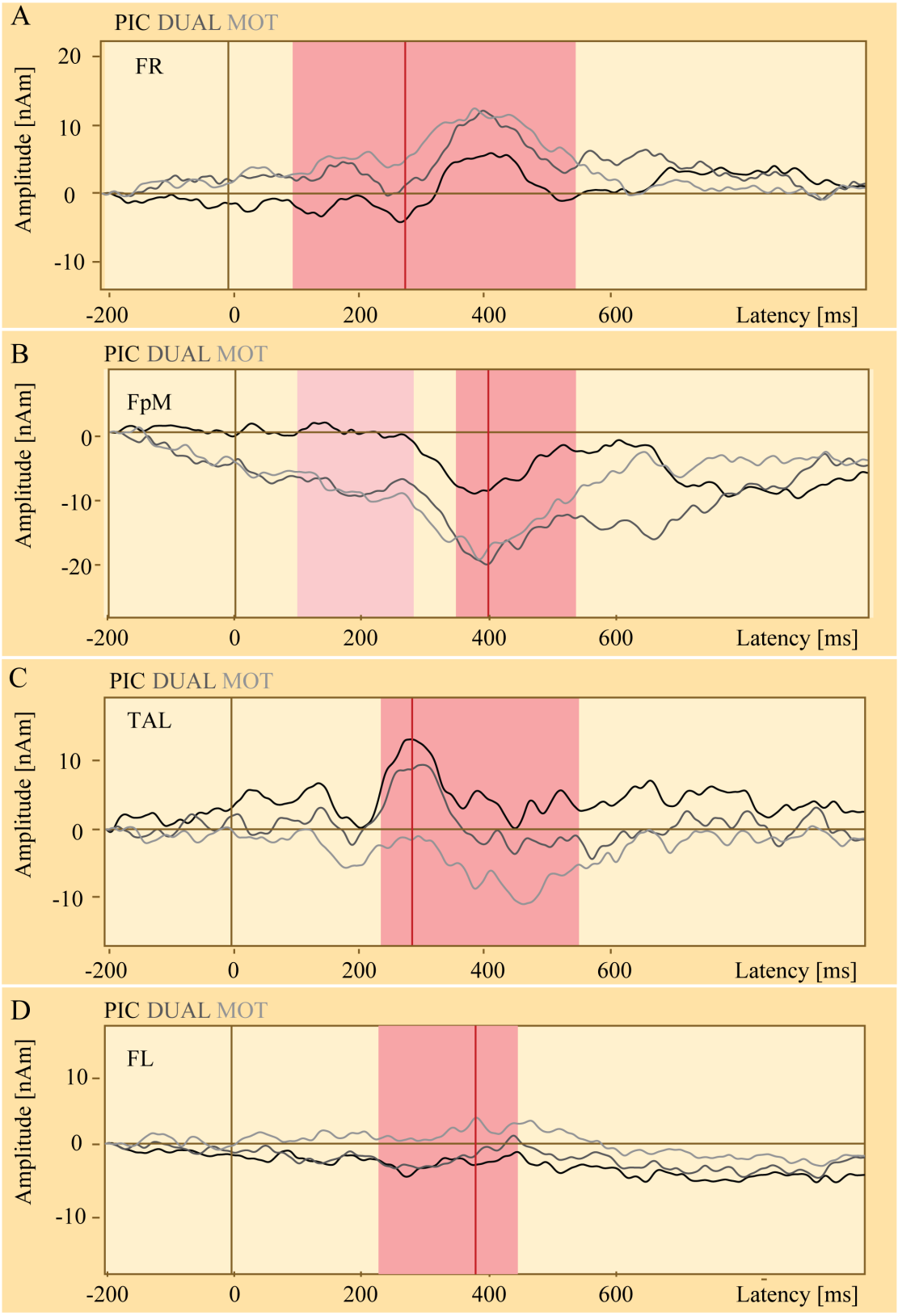

Figure 2: ANOVA results for neutral pictures. Significant clusters were obtained for four regional sources. Red shading indicates time windows of significant effects. Note oppositely-directed experimental effects in different clusters, e.g. FR versus TAL.

5.2.3.2 Source Probe Waveforms: EEG

Univariate ANOVAs were conducted for NEG and NEU valences, with the null hypothesis that the EEG source waveforms elicited in PIC, DUAL and MOT tasks were equal amplitude. The multiple comparisons problem is addressed with a cluster-level permutation test across time. There was no significant effect of task for either negatively ($p > .05$) or neutrally ($p > .05$) valanced pictures. Results are summarised in Table 2.

Table 2 Permutation test results: EEG source probe waveforms

	Cluster ID	*p*	Start time (ms)	End time (ms)	Brain source
negative					
	1	.066	401	586	PL
	2	.138	413	545	CL
	3	.204	372	460	TAR
	4	.514	303	346	TAL
	5	.517	141	177	TPR
neutral					
	1	.092	390	482	TAR
	2	.101	364	477	TPR
	3	.125	416	503	PL
	4	.237	235	293	PR
	5	.273	432	493	TAL

In sum, the source probe analysis did not find significant effects in EEG. However, significant effects were found in MEG source waveforms. Especially, clusters in TAL

and FpM source regions are correspond to N2 and P3b components in morphology and time window. Hence, we can conclude that source modeling is not likely to be effective for EEG in the current study and move on to the MEG source analysis.

5.2.4 Distributed source imaging

Having demonstrated that MEG shows comparable experimental responses to the ERP grand average responses, we proceeded to a more detailed analysis of the anatomical locations of these responses. We applied Classical Low-Resolution Electromagnetic Tomography Analysis Recursively Applied (CLARA; Iordanov et al., 2014, 2016) as implemented in BESA Research (v7.0). According to this distributed source imaging technique, the inverse solution is defined as a collection of elementary dipoles distributed over nodes on a mesh of the cortical volume. CLARA reduces the source space during repeated estimations to render more focal source images. Each step starts with the computation of a spatially smoothed LORETA solution (Pascual-Marqui et al., 2002) and removing voxels that are below 1% max amplitude threshold. Then a spatial weighting term for each voxel is defined for the LORETA image in the next step. CLARA is roughly 2-3x more precise than the well-known LORETA method (Pascual-Marqui et al., 2002) and the accuracy is quite good (about 72%-86%) (Beniczky et al., 2016). The BESA adult MRI template was used to visualize functional CLARA maps with respect to brain anatomy (Richards et al., 2016). We computed CLARA maps from averaged data for different conditions using the EPN (276-390 ms) and P3b (440-596 ms) time windows derived from the ERP results of Chapter 4.

Combined EEG and MEG analysis is technically complex, was not available in the BESA Research (Version 7.0) used in the present thesis, and was not feasible within the time constraints of the present thesis. We plan to carry out the combined analysis after completion of the thesis and publish the results as a separate publication.

5.2.5 Statistical Analysis

Cluster-based permutation tests were applied to CLARA distributed source images using BESA Statistics 2.0 (Maris & Oostenveld, 2007; Maris, 2012). Comparisons were made between tasks and between negative and neutral pictures using parameter-free permutation testing on the basis of ANOVA and t-tests. The analysis occurred in two (for ANOVA three) stages. First, a parametric test was computed to retrieve a preliminary statistical comparison between conditions at every time point and at each source. The preliminary results are used for cluster-building by identifying clusters that differed between the conditions. The identified clusters were obtained based on data and are used for subsequent permutation testing. Then, the permutation tests used a bootstrapping procedure to determine the probability values for differences between conditions in these clusters. The final probability value was based on the percentage of permutations in which the identified cluster remained significant. In the current analysis, a critical alpha value of 0.05 and 10,000 random permutations were used. Finally, followed a significant ANOVA effect, a post-hoc Scheffe's test was computed for pairwise comparisons.

5.3 Results

5.3.1 Distributed source imaging (CLARA)

5.3.3.1 ANOVA results

EPN time window. Table 3 shows univariate ANOVA results comparing the functional source activation images of PIC, DUAL and MOT task for negative pictures during the EPN time window. The overall ANOVA showed one significant cluster encompassing the entire time window, with a peak in anterior cingulate cortex, BA 32. Mean cluster amplitudes for negative pictures were: PIC = 10.14 nAm, DUAL = 8.95 nAm, MOT = 17.24 nAm (see Figure 3). Post hoc comparisons confirmed that MOT had significantly greater magnitude of activation than PIC and DUAL conditions (PIC vs. DUAL: ns; PIC vs. MOT: p = .015; DUAL vs. MOT: p = .005).

The ANOVA for neutral pictures showed no significant clusters during the EPN time window.

Table 3: Task effects for negatively-valanced pictures.

Time window (ms)	*p*	Talairach coordinates (mm)			Brain source
		x	y	z	
276-390	.007	-3.5	32.1	2.7	cingulate gyrus, BA 32

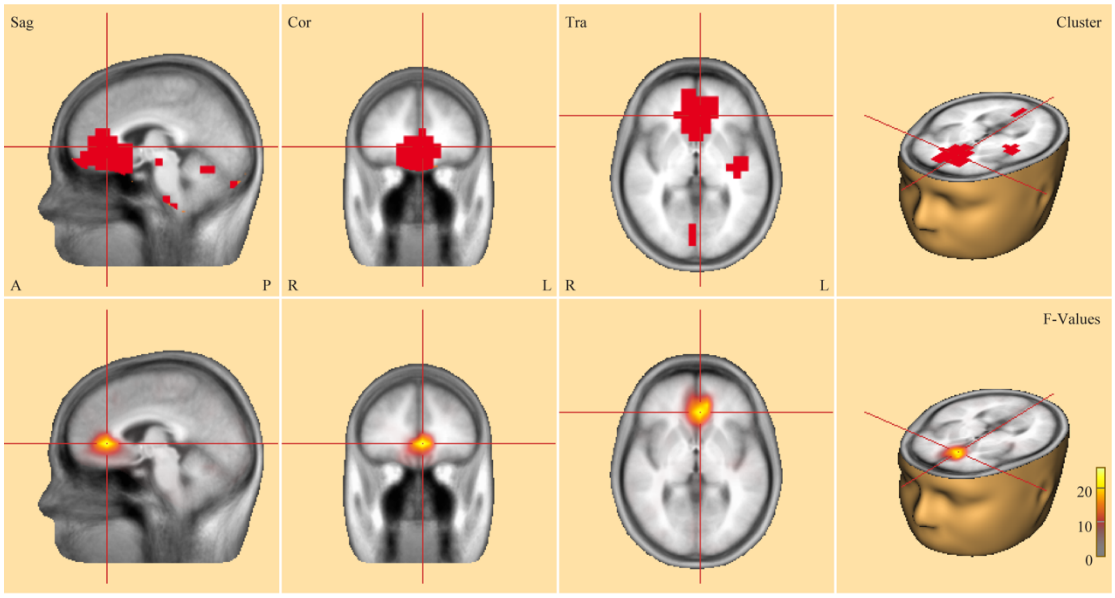

Figure 3: Significant clusters for task effects during EPN time window (276-390 ms) for negative pictures. Top panels show significant clusters, bottom panel shows F-values. Cluster peak is centred in anterior cingulate cortex, BA32.

P3b time window. Table 4 shows ANOVA results comparing the functional source activation images of PIC, DUAL and MOT task for negative and neutral pictures during P3b time window.

For negative pictures, ANOVA showed two significant clusters. The first cluster occurred in a time window of 440-469 ms and with peak magnitude centred in the left insula (BA 41, 22; see Figure 4), with relative activation magnitudes DUAL > PIC > MOT (PIC = 6.31 nAm, DUAL = 7.19 nAm, MOT = 2.24 nAm). The second cluster occurred in a time window of 470-490 ms, centred in anterior cingulate cortex (BA 24; see Figure 5), with relative activation magnitudes MOT > DUAL > PIC (PIC = 9.46 nAm; DUAL = 13.21; nAm; MOT = 19.65 nAm). Although the overall ANOVA was statistically significant, post-hoc comparisons did not show any significant contrasts for either time window.

For neutral pictures, ANOVA showed a single significant cluster within a time window of 548-566 ms, centred in right parahippocampal gyrus (BA 35,36; see Figure 6) with relative activation magnitudes of DUAL > PIC > MOT (PIC = 4.70 nAm, DUAL = 9.74 nAm, MOT = 2.02 nAm). Although the overall ANOVAs was statistically significant, post-hoc comparisons did not show any significant contrasts.

Table 4: Summary of ANOVA results for task effects during P3b time window.

Conditions	Time window (ms)	*p*	Talairach coordinates (mm)			Brain source
			x	y	z	
negative	440-469	.039	-38.5	-23.9	9.7	left insula, BA 41,22
	470-490	.016	-10.5	32.1	2.7	anterior cingulate, BA 24
neutral	548-566	.03	31.5	-30.9	-25.3	right parahippocampal gyrus, BA 35,36

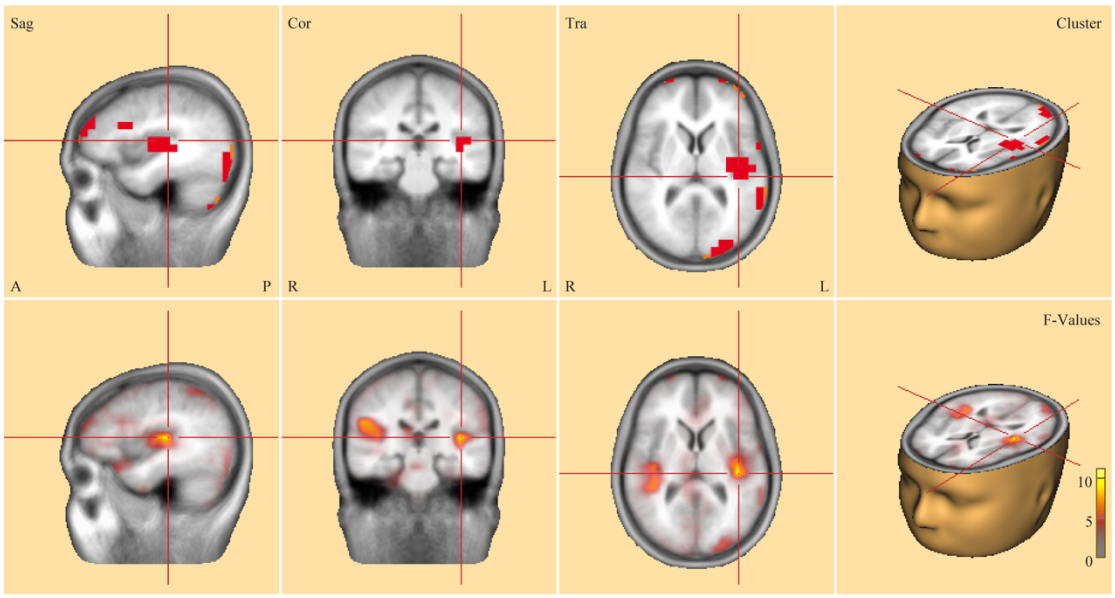

Figure 4: Significant clusters for task effects during P3b time window (440-469 ms) for negative pictures. Top panels show significant clusters, bottom panel shows F-values. Cluster peak is centred in left insula cortex, BA41, 22.

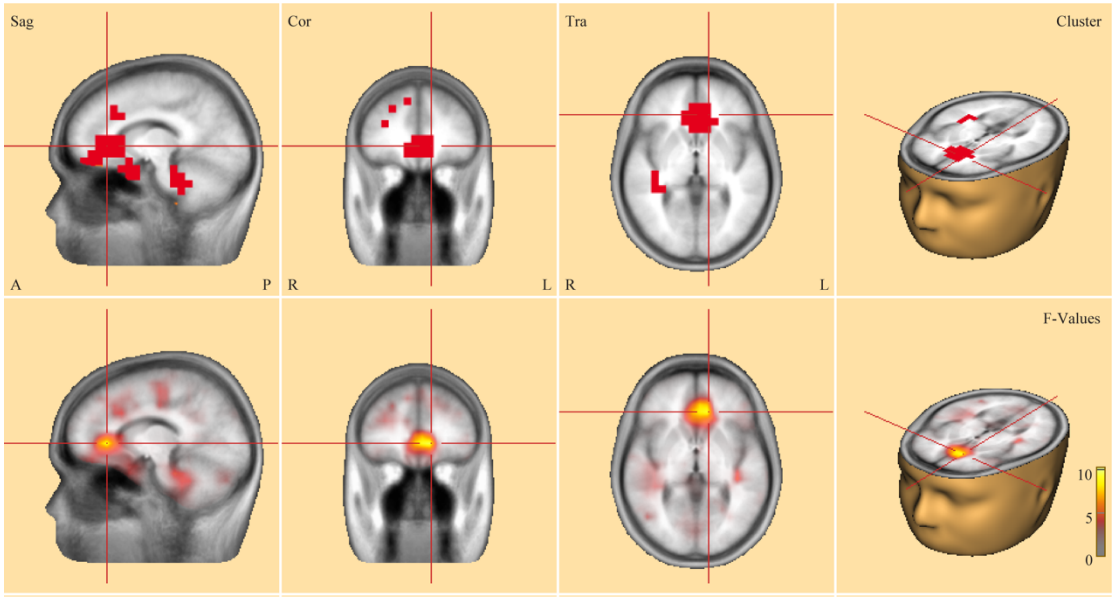

Figure 5: Significant clusters for task effects during P3b time window (470-490 ms) for negative pictures. Top panels show significant clusters, bottom panel shows F-values. Cluster peak is centred in anterior cingulate cortex, BA 24.

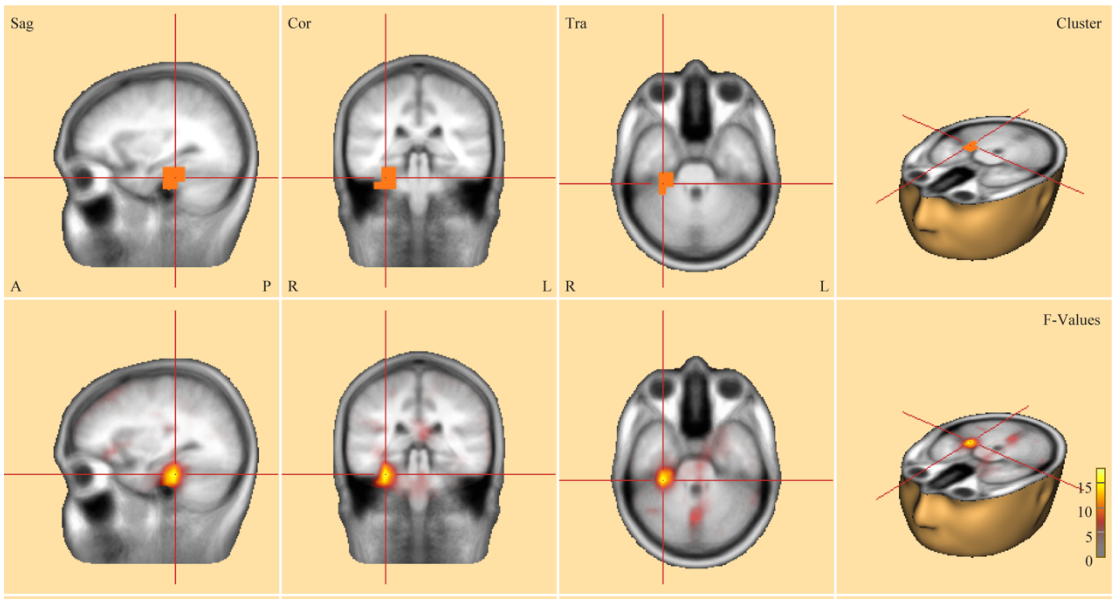

Figure 6: Significant clusters for task effects during P3b time window (548-566 ms) for neutral pictures. Top panels show significant clusters, bottom panel shows F-values. Cluster peak is centred in right parahippocampal gyrus, BA 35, 36.

5.3.3.2 Negative versus neutral contrasts

EPN time window. Table 5 shows the results of two-tailed t-tests comparing the

functional source activation images of negative and neutral pictures in each of PIC,

DUAL and MOT conditions during the EPN time window. In the PIC and MOT conditions, no significant clusters were obtained. In the DUAL condition, a single significant cluster was obtained within a time window of 333-390 ms and centred in left visual association cortex (BA 18; see Figure 7) and with relative activation magnitudes of NEU > NEG (neutral = 9.48 nAm, negative =3.10 nAm).

Table 5: Summary of t-test results for emotional valence contrasts in DUAL condition during EPN time window.

Time window (ms)	*p*	Talairach coordinates (mm)			Brain source
		x	y	Z	
333-390	.001	-10.5	-93.9	9.7	left visual association cortex, BA18

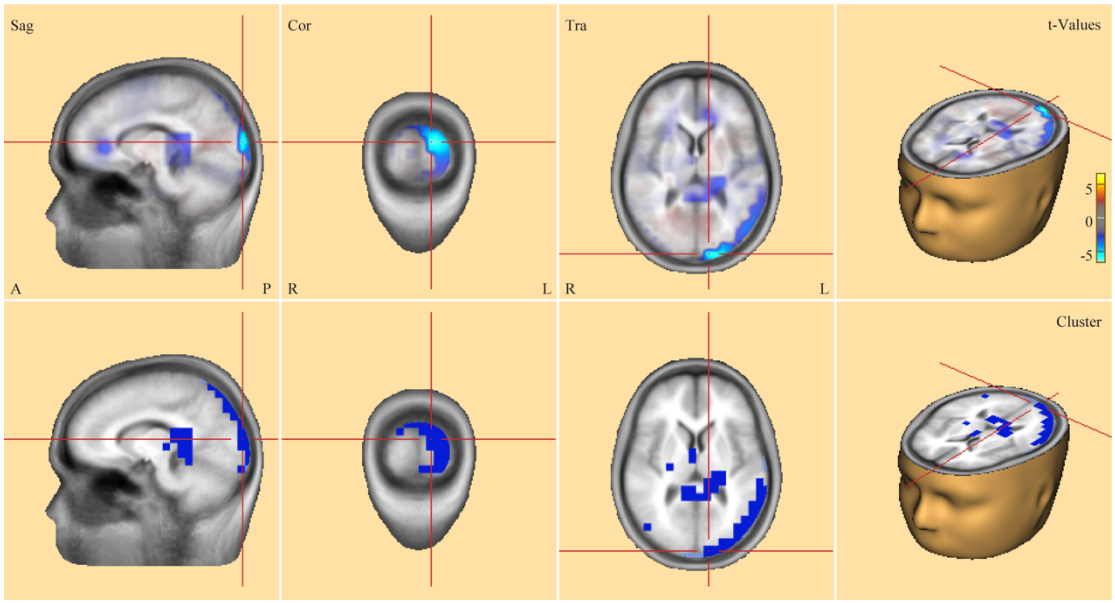

Figure 7: Significant clusters for valance effects during EPN time window (333-390 ms). Top panels show t-values, bottom panel shows significant clusters. Cluster peak is centred in left visual association cortex, BA 18.

P3b time window. Table 6 shows the results of two-tailed t-tests comparing the functional source activation images of negative and neutral pictures for PIC, DUAL and MOT conditions. In the PIC condition, a significant cluster was obtained in a time

window of 449-506 ms, centred in the left medial frontal gyrus (BA10; see Figure 8) and with relative activation magnitudes of NEG > NEU (neutral = 2.80 nAm, negative = 7.38 nAm).

In the MOT condition, two significant clusters were obtained: 440-480 ms, centred in right medial frontal gyrus (BA 18; see Figure 9) with relative activation magnitudes of NEU > NEG (neutral = 4.86 nAm, negative = 1.47 nAm); and 546-596 ms, in right cerebellum (see Figure 10) with relative activation magnitudes of NEG > NEU (neutral = 5.28 nAm, negative = 23.00 nAm).

Table 6: Summary of t-test results for emotional valence contrasts in PIC and MOT conditions during P3b time window.

Conditions	Time window (ms)	*p*	Talairach coordinates (mm)			Brain source
			x	y	z	
PIC	449-506	.035	-45.5	46.1	16.7	left medial frontal gyrus, BA 10
MOT	440-480	.003	3.5	-93.9	16.7	right medial frontal gyrus, BA 18
	546-596	.04	24.5	-37.9	-32.3	right cerebellum

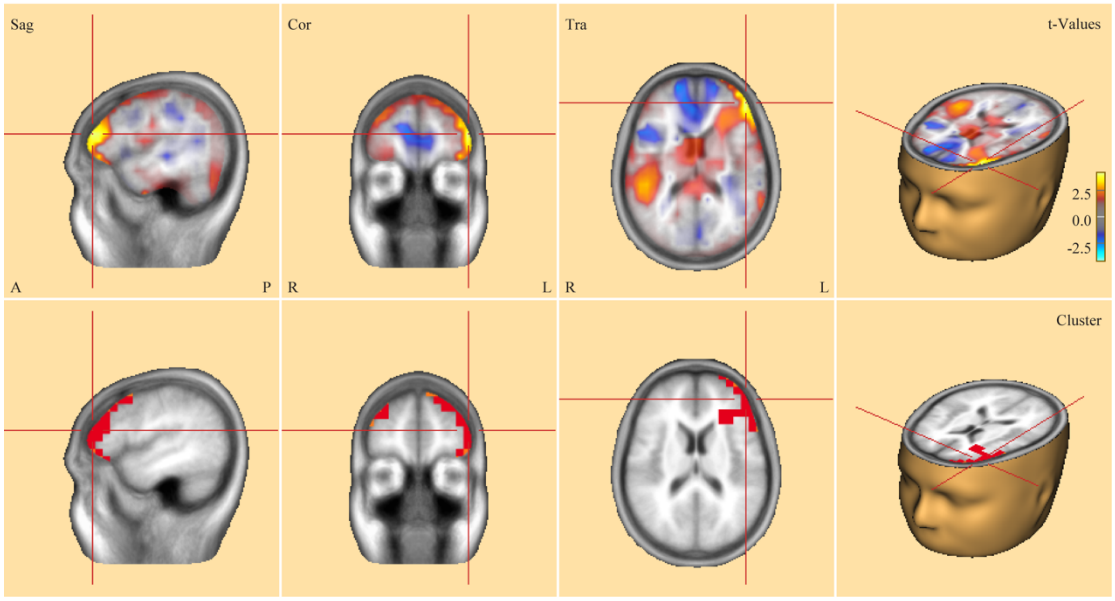

Figure 8: Significant clusters for valance effects during P3b time window (449-506 ms). Top panels show t-values, bottom panel shows significant clusters. Cluster peak is centred in left medial frontal gyrus, BA 10.

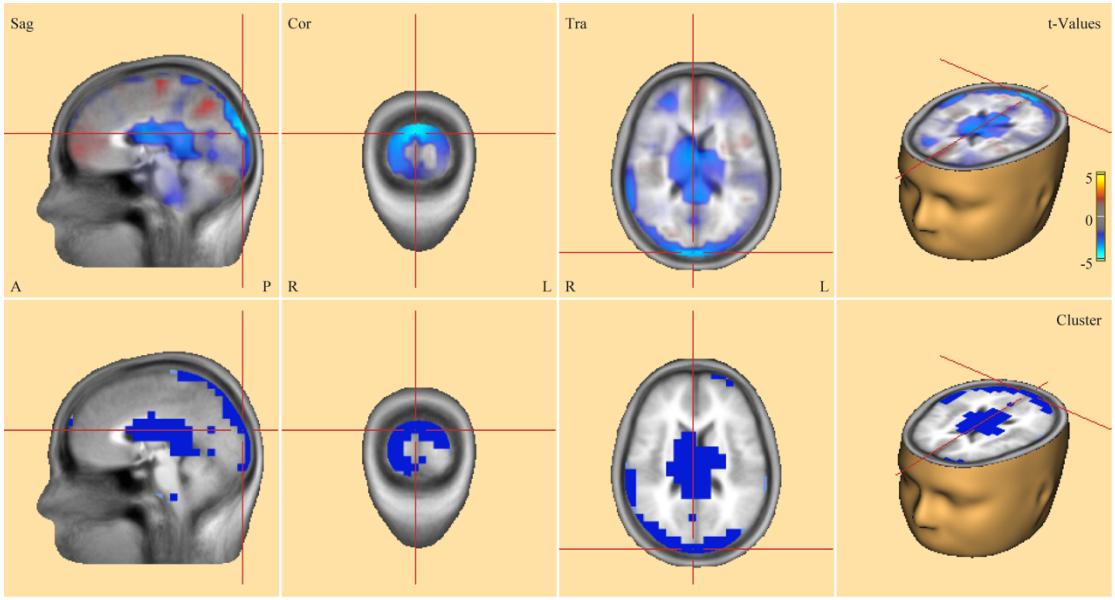

Figure 9: Significant clusters for valance effects during P3b time window (440-480 ms). Top panels show t-values, bottom panel shows significant clusters. Cluster peak is centred in left medial frontal gyrus, BA 18.

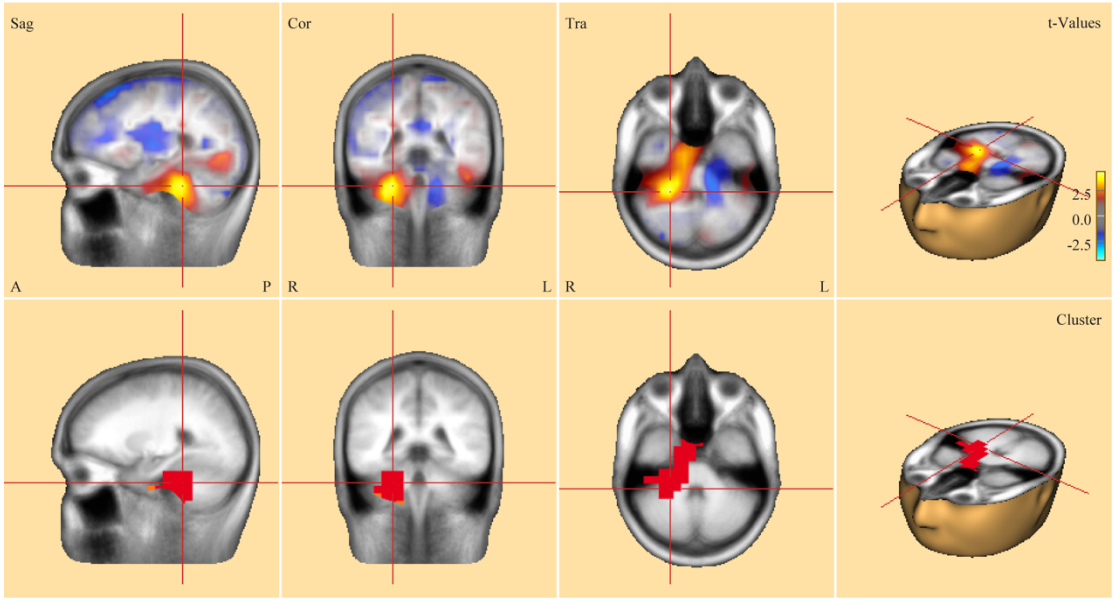

Figure 10: Significant clusters for valance effects during P3b time window (546-596 ms). Top panels show t-values, bottom panel shows significant clusters. Cluster peak is centred in right cerebellum.

Table 7: Overall summary of results.

Measure	Time window	Result	Brain region
ANOVA (negative)	EPN	MOT > DUAL, PIC	cingulate gyrus
ANOVA (negative)	P3b	DUAL, PIC > MOT	left insula
	P3b	MOT > DUAL, PIC	ACC
ANOVA (neutral)	P3b	DUAL > PIC, MOT	right parahippocampal gyrus
TTEST (DUAL)	EPN	NEU > NEG	left visual association cortex
TTEST (PIC)	P3b	NEU < NEG	left medial frontal
TTEST (MOT)	P3b	NEU > NEG	left medial frontal
	P3b	NEU < NEG	right cerebellum

5.4 Discussion

The aims of the present chapter were to achieve a more precise characterisation of the neuroanatomical generators of the EPN and P3b ERP components elicited in an emotional capture RSVP experiment. To achieve this, we leveraged the more tractable characteristics of the neuromagnetic inverse problem relative to those of the electrical inverse problem. ERP measurements described in Chapter 4 were used as a bridge to the extant literature, but source analyses were based on the concurrent MEG measurements. The results of these analyses contribute to the literature by defining the substrates of neural inhibition and the mechanisms by which they impact attention capture of emotional distractors.

The main findings of the current analyses are clear.

First, we found that, for negative pictures, the entire EPN time window is dominated by a robust activation of anterior cingulate cortex, with greater activation in MOT condition relative to PIC and DUAL conditions. In striking contrast, no significant anterior cingulate clusters were obtained for neutral pictures. Taken together, these findings indicate that ACC activation is linked to processing of negatively valanced pictures (To et al., 2017; Shackman et al., 2011; Etkin et al., 2011). In particular, Etkin et al., 2011 have shown that negative emotional images activate anterior cingulate cortices. Similar evidence showing that the ACC is involved in cognitive and emotional processes has been recently reported (To et al., 2017).

This result is also congruent with prior studies investigating the cognitive control functions of the ACC. Medalla and Barbas (2009) reported that ACC played a pivotal role in suppressing noise in dorsolateral areas during challenging cognitive tasks involving conflict. The ACC has also been implicated in maintaining task sets (Menon and Uddin, 2010; Shenhav et al., 2017) or switching attention according to control demand (Kolling et al., 2016; Jiang et al., 2015). Our findings are consistent with these results and further highlight that the implementation of attentional control during tasks involving conflict and the cognitive effort (Aben et al., 2020) are both important for the activation of ACC. In the PIC condition, participants were required to ignore moving circles. In the DUAL condition, high working memory load is required, but participants do not need to inhibit the distractor pictures. To perform the MOT task, participants had to focus attention on moving circles while inhibiting background distractors.

Previous functional magnetic resonance imaging (fMRI) studies have highlighted that insula (Han et al., 2010; Hart et al., 2010; Downar et al. 2000; Menon and Uddin 2010) is the key neural structure with respect to process of valence. Importantly, studies have a particular focus on the insula when participants need to decide the behaviourally significance of the emotional information (Han et al., 2019; Marxen et al., 2020). Similarly, our results show activation of the left insula, for negative pictures, during the initial phase of the P3b. Strikingly this functional activation pattern was distinct from and oppositely directly to that observed for the ACC activation described above, with greater relative activation magnitude for

DUAL and PIC conditions relative to the MOT condition. Since the post-hoc tests did not show significant contrasts between paired conditions (we note this is not a contradictory result, since the overall ANOVA and the post-hoc contrasts address different hypotheses and use different models of the data) we do not wish to overinterpret the relative activation magnitudes (i.e. the mean activation magnitude of PIC was slightly greater than for DUAL). However the results of the MEG source probe analysis (Fig 1) provides additional evidence to support the conclusion that the AI cluster shows a different - and probably oppositely directed: PIC > DUAL > MOT - activation pattern than observed the P3b ERP described in Chapter 4, the EPN ACC activation pattern described above, and the P3b ACC activation pattern described below. Hence, our MEG data reveal a new anatomico-functional pattern that was not predictable from the ERPs. Our results confirm the role of insula in salience detecting and alerting demonstrated in previous studies (Jiang et al., 2015; Han et al., 2019) and consistent with our ERP results showing that the emotional salience of stimuli is processed in later stage in an EIB paradigm.

Third, our results show a second and subsequent P3b time window for negative pictures, again characterised by ACC activation and with a MOT > DUAL > PIC pattern of relative magnitudes similar to that exhibited by the ACC during the EPN time window. Taken together then, the P3b results indicate two temporally, anatomically and functionally distinct stages of processing for negative pictures. A recent paper discussed about sensor-level analysis suggests that it is not possible to infer two distinct sources from cluster-based permutation tests (Sassenhagen and

Draschkow, 2019). However, the inferences of current thesis refer to the results of source-level cluster analysis where these spatial inferences remain valid.

A fourth result was that the ANOVA for neutral pictures showed a P3b time window cluster centred in the right parahippocampal gyrus, with relative activation magnitudes of DUAL > PIC > MOT. The parahippocampal gyrus has been implicated in many aspects of high-level cognitive processing, including memory access and visuospatial processing (Aminoff et al., 2013; Bohbot et al., 2015). Hence, the relative activation magnitudes shown here are readily interpretable in terms of the extra memorial and visual processing required in the divided attention DUAL task.

Significant clusters for the t-test contrasts for negative and neutral pictures were not consistent across task conditions, and accordingly perhaps less robust and more tentative than the ANOVA results described above. Nonetheless most of these results are readily interpretable in terms of the known functions of the neuroanatomical clusters and in the context of results from previous neuroimaging studies.

A fifth result was the finding of a significant NEU > NEG cluster in visual association cortex in DUAL condition during the EPN time window. This result is in accord with previous studies reporting that visual association cortex underlies our ability to process visual information and memory formation (Zeki, 1993; Rosen et al., 2017).

A sixth result was the finding of two significant t-contrast clusters in left medial frontal cortex in PIC and MOT conditions. These results are consistent with previous studies showing that medial frontal gyrus is involved in inhibiting ongoing

action (Sharp et al., 2010; Gavazzi et al., 2020), since in both the PIC and MOT conditions, participants are required to prioritize one task and inhibit another task.

Finally, a seventh result was the finding a significant t-contrast cluster in MOT condition during the P3b time window in the cerebellum, a structure that is known to function in a variety of motor and cognitive tasks (Schmahmann & Caplan, 2006; Strick et al., 2009).

The results of the present study make the following contributions to the emotional attentional capture literature (Schindler & Bublatzky, 2020; Keefe et al., 2019; Hoffman et al., 2020):

First, this line of research (e.g. Keefe et al., 2019) primarily aims to explore the role of cognitive control on emotional processing and but to date has failed to reach clear conclusions. Some recent studies suggest that emotional attentional capture is robust and is to a certain extent immune to attentional manipulations (Vuilleumier & Huang, 2009; Carretié, 2014; Keefe et al., 2019). Others propose that emotional attentional capture is not fully automatic (e.g., Hoffman et al., 2020). The present study replicates the results of Hoffman et al (2020) study showing that the emotional attentional capture can be suppressed and further highlight that the suppression of emotional attentional capture happens in a relative later stage of processing.

Second, previous studies aim to identify the anatomical generators of EPN and P3b components, but the results remain rudimentary and imprecise. The present study complements previous studies (Schindler & Kissler, 2016; Crottaz-Herbette & Menon, 2006) showing that the anterior cingulate cortex is involved in the attentional

modulation of EPN. Our results also concluded that two important generators of the P3b component elicited in an emotional capture RSVP tasks, are located in the insula and anterior cingulate cortex, structures that have been strongly implicated in the detection and inhibition of irrelevant information, (Marois et al., 2004; Kranczioch et al., 2005; Feinstein et al., 2004; Gross et al., 2004).

Third, our results constitute a confirmation of the 'salience network' model and further clarify the functional role of insula and anterior cingulate cortex. The anterior insula (AI), along with dorsal anterior cingulate cortex (dACC) and some other structures, has been suggested to form a cingulo-opercular "salience" network (Menon and Uddin, 2010; Uddin, 2015). Recent studies have found that the AI plays a role in identifying salient stimuli in the environment (Downar et al. 2000; Menon and Uddin 2010) and dACC plays a key role in switching or maintaining attention according to task demands (Menon and Uddin, 2010; Shenhav et al., 2017). However, other studies suggest that AI also involved in maintaining task sets (Sridharan et al. 2008; Nelson et al., 2010; Dosenbach et al. 2006; Dubis et al. 2016). Our results support the proposal that the AI and ACC are activated by emotionally salient stimuli and clarify the role of AI in salience detecting and alerting and the role of ACC in the implementation of proactive and reactive attentional control (Jiang et al., 2015; Han et al., 2019).

The relative activations and opposite activations that we find in ACC and insula corresponds well with the putative functional roles of these structures. AI activation by negative pictures was significantly greater for PIC and DUAL conditions than

MOT condition, a result that may be due to the fact that negative pictures were not behaviourally relevant event in the MOT condition. In contrast, ACC activation is significantly greater in MOT condition than PIC and DUAL conditions, showing that attentional control is associated with the activation of ACC.

Summary

Overall, our results provide a bridge between emotional capture in an RSVP paradigm, and separate lines of research on the neural bases of emotional attentional processing. The results of our EEG study (Chapter 4) showed that emotional attentional capture can be suppressed, and that that suppression happens downstream of (subsequent to) attentional capture. The source-localized MEG results first confirm that an attention control modulation of negative pictures activate the ACC during EPN time window. The subsequent activity is distributed in AI and ACC during P3b time window for negative pictures, which sequentially process emotionally salient stimuli and invoke attentional control according to task demand. Our MEG data analyses reveal that both the content and the timing of these brain responses are best explained by a "salience network" consist of AI and ACC (Menon and Uddin, 2010; Uddin, 2015), which both detect and alert the emotional salient stimuli and maintain the task set. Together, these results show how AI and ACC generate a cascade of responses that ultimately accounts for subjects' task performance and electrophysiological response.

5.5 References

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Chapter 6:
General Discussion

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CHAPTER 6 GENERAL DISCUSSION

With an estimated prevalence of around 7% (Kessler et al., 2005b), Social Anxiety Disorders have a significant impact on society. Along with having biased cognitive and attentional processing in social interaction, individuals with SAD have difficulties in understanding the social world. One such difficulty is that of suppressing emotional distractors in order to focus on a target, and that is the focus of the present thesis. An increased understanding of the differences between individuals with high levels of social anxiety and individuals with low levels of social anxiety should benefit our understanding of the clinical impairments in SAD. However, there is still a gap between our understanding and the neural mechanisms of emotional attentional capture and the suppression of emotional attentional capture.

To enhance our understanding of emotional attentional capture and the mechanisms underlying emotional attentional capture in individuals with social anxiety, a series of three studies was conducted, aiming to address following main questions: the effect of emotion salience on the attention processing of stimuli from multiple spatial frequencies (Chapter 3); the effect of voluntary control in mediating the emotional attentional capture in healthy samples (Chapter 4); and the neuroanatomical sources of emotional attentional capture (). The key points arising from the findings of these studies were as follows.

6.1 Summary of Findings

After reviewing existing research at both the behavioural and neural levels (Chapter 2), the following points emerged. First, the prior literature examining emotional attention processing of social anxiety has been limited by an over-focus on disengagement from emotional salient stimuli, and there is little research directly examining the attentional capture of emotional stimuli. Second, the findings from these studies are inconsistent, which could be due to different magnitudes of threat stimuli used, and the effect of physical characteristics of stimuli (e.g. spatial frequency). Third, despite increasing agreement of an attention control deficit in social anxiety, the effect of voluntary control in modulating emotional attentional capture remains largely unexplored. Given these, an ERP study (Chapter 3) was carried out to examine (1) the effects of individual threats and spatial frequency on attentional processing of a range of threatening faces; and (2) the characteristics of attentive processing in early and later stages of social anxiety. Taken together, the results provide good evidence that individuals with social anxiety show early vigilance and later avoidance for all faces; with preference for low spatial frequencies, and a specific attentional avoidance of fearful faces: (1) Regardless of emotional valence, individuals with high social anxiety showed pronounced P1 and reduced P250 to low spatial frequency (vs. high spatial frequency) faces, suggesting a general pattern of initial vigilance and later avoidance to LSF faces in social anxiety. (2) Individuals with low levels of social anxiety showed enhanced P250 to both fearful and disgusted (vs. neutral) faces, individuals with high level of social anxiety showed pronounced P250 to disgusted faces alone.

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Despite the decreased behavioural performance of individuals with high levels of social anxiety, this does not rule out the possibility that they could suppress the emotional attention processing in later stages to compensate for their attentional processing deficit. In addition, though emotional information is task irrelevant in many tasks, the primary task was not difficult enough to fully occupy attentional resources. There is still a gap between our understanding and the effect of secondary inhibition (via target facilitation) on emotional attentional in social anxiety. In addition, though behavioural evidence is of great importance, there is also a need to understand the underlying biological mechanisms utilized in suppression of emotional attention capture in social anxiety. Therefore, a concurrent EEG/MEG study (Chapter 4) using a modified emotion-induced blindness task was conducted to (1) replicate the behavioural results of Hoffman et al. (2020) to demonstrate that emotional capture of attention can be suppressed through target facilitation (Chapter 4); (2) replicate the ERP results of Hoffman et al. (2020) to determine the timing of neural processes associated with suppression of emotional capture (Chapter 4); (3) carry out concurrent MEG recordings to more clearly define the neuroanatomical substrates of emotional capture and suppression (Chapter 5). The behavioural results showed that negative pictures are more salient and capture attention more readily than neutral pictures, but the attentional capture by emotional salience can be suppressed through target facilitation. For the recognition of pictures, negative pictures have a greater probability of correct response than neutral pictures and the accuracy of recognition was reduced when attention was shared between picture recognition and motion tracking. The motion tracking accuracy for negative and neutral pictures were not significantly different in the DUAL and MOT conditions (Chapter 4). The

ERP results allocates the timing of this suppression to a relatively late stage of processing. The presence of an EPN in all three tasks indicates that emotional stimuli do automatically engage attention at this early stage of processing. The reduced N2 and P3b components in the DUAL and MOT tasks indicates that emotional attention capture can be suppressed, and the suppression of emotional attention capture happens shortly after the capture of emotional attention indexed by the EPN (Chapter 4).

Previous studies have aimed to identify the anatomical generators of EPN and P3b components, but the results remain rudimentary and imprecise. The MEG study of Chapters 5 was designed to examine the neuroanatomical generators of these ERP components during emotional attention capture and suppression.

The MEG analyses described in Chapter 5 showed (1) greater activation of anterior cingulate cortex in MOT condition compared to PIC and DUAL condition for negative pictures, peaking at EPN latency; (2) greater activation of the left insula when viewing negative animate pictures in PIC and DUAL conditions compared to MOT condition, during the P3b time window; (3) In contrast, greater activation of the ACC was found in the MOT condition compared to PIC and DUAL conditions in a subsequent portion of the P3b time window.

These results confirm that the activation of ACC during the EPN time window is related to processing of negative, not neutral pictures (Medalla and Barbas, 2009; Han et al., 2019). The activation in AI and ACC during the P3b time window for negative pictures is consistent with previous studies showing that AI plays a role in processing emotionally salient stimuli

(Downar et al. 2000; Menon and Uddin 2010); and the activation of anterior cingulate invokes attentional control according to task demand (Uddin, 2015).

Taken together these results point to the importance of a "salience network" which importantly includes functioning of the AI and ACC (Menon and Uddin, 2010; Uddin, 2015) for processing of emotionally salient stimuli and maintaining the task set, generating a cascade of responses that ultimately accounts for subjects' task performance and electrophysiological response.

6.2 Contributions to the literature

The results of this thesis make the following methodological and empirical contributions the attentional capture and social anxiety literature.

In recent years, researchers have explored the attentional bias of socially anxious individuals using socially threatening (anger, fear or disgust) faces (Langner et al., 2009, 2015). Considering whether individuals with high social anxiety have an attentional bias to threatening faces rather than neutral or positive pictures, mixed results have been reported (Wieser, Hambach, & Weymar, 2018; Eastwood & Smilek, 2005; Gilboa-Schechtman, Foa, & Amir, 1999). One possible explanation for these inconsistencies is that different types of threat faces might have different effects. Differences in neural responses to different types of emotions (e.g., fear, disgust, and anger) have been found in healthy individuals (You & Li, 2016; Zhang, Liu, Wang, Ai, & Luo, 2016). In addition, studies have reported that socially anxious individuals have a preference for low spatial frequencies in facial stimuli (Langner, Becker, Rinck, & Knippenberg, 2015; Langner, Becker, & Rinck, 2009). It is still an open question of whether SAD individuals have different neural responses to different types of threat emotions presented in different spatial frequency channels.

The results of our first experiment showed how the attention modulation of socially anxious individuals is affected by different types of threatening faces based on spatial frequency channels. Our results elucidate the temporal profile of early vigilance and later avoidance in social anxiety, highlighting its broad implication for all faces and predominance in the low spatial frequency. Furthermore, our results demonstrate specific attentional avoidance of fear faces in social anxiety.

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To date, limited tools exist for researchers to explore the automaticity and the neural mechanism of attentional bias in social anxiety. It remains strongly debated whether this bias derives from an impairment of the controlled (top-down) processing or a facilitation of automatic (bottom-up) processing (Cisler, & Koster, 2010). The most widely used paradigms, including emotional Stroop (Williams, Mathews, & MacLeod, 1996), dot probe task (Macleod et al., 1986), visual search task (Öhman, Flykt, & Esteves, 2001) and emotional spatial cues task (Fox, Russo, Bowles, & Dutton, 2001), do not directly examine the automaticity of emotional attention capture.

The modified emotion-induced blindness paradigm (Hoffman et al., 2020) used in our second study examines the automaticity of emotional capture by manipulating the degree of attention allocated to emotional distractors. The results of this thesis replicated the main results of Hoffman et al (2020; Experiment 1) in healthy adult participants, suggesting that modified EIB paradigm is an efficient measure of the automaticity of emotional capture. Future studies should aim to employ this task socially anxious participants. The ultimate goal is to establish the task as a simple, valid and robust tool for other researchers in the field to measure automaticity of emotional capture.

The primary aim of this thesis was to investigate the neural mechanisms of inhibition and the mechanisms by which they impact emotional attentional capture. Our ERP results in Chapter 4 showed that emotional capture of attention can be suppressed and that the suppression happens downstream of the emotional attentional capture. The MEG results discussed in Chapter 5 examined the brain function during suppression of emotional attentional capture. Results showed that anterior cingulate activation was associated with

inhibition of the processing of emotional distractors. Our results are largely congruent with prior studies showing that AI is important to identify salient stimuli in the environment and ACC plays a key role in maintaining task sets (Menon and Uddin, 2010; Shenhav et al., 2017). Our MEG data analyses reveal that both the brain function and the time course of the suppression of emotional attentional capture are best explained by a "salience network" consist of AI and ACC (Menon and Uddin, 2010; Uddin, 2015), which both detect the emotional salient stimuli and maintain the task set. Together, these results show how AI and ACC generate a cascade of responses that ultimately accounts for subjects' task performance and electrophysiological response.

6.3 Practical implications

Knowing the differences between individuals with high levels of social anxiety and individuals with low levels of social anxiety in emotional attentional capture can be useful for understanding and devising clinical interventions for social anxiety disorder.

Most importantly, these findings help inform evidence-based interventions in this population, especially for the development of training and development programmes which attempt to facilitate social and adaptive functions in individuals who are high in social anxiety. For example, being able to identify problems (e.g., initial hypervigilance and later avoidance toward LSFs or the abnormal processing of emotional faces) that individuals are experiencing can offer context-specific targets for individualized interventions.

The findings of this thesis can also apply to the diagnosis of social anxiety. Given that symptoms of social anxiety co-occur highly with other mood disorders, it is important to understand the trigger factors in this issue in order to help design a variable programme of management strategies and intervention to reduce social anxiety. The differences between individuals with high levels of social anxiety and individuals with low levels of social anxiety in emotional attentional capture, suppression and brain activities are good indexes for making a distinction between social anxiety and other mood disorders.

Our results confirm the role of insula in salience detecting and alerting demonstrated in previous studies (Jiang et al., 2015; Han et al., 2019) and further highlight that the implementation of attentional control during tasks involving conflict and the cognitive effort (Aben et al., 2020) are both important for the activation of ACC.

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Previous studies indicates that anxiety disorders are related to inappropriate insula activation when anticipating of negative stimuli (Sarinopoulos et al., 2010; Straube et al., 2007) and excessive activation of ACC during emotional conflict processing (Comte et al., 2015). Even through the 'fear network', consisting of amygdala, insula and anterior cingulate cortex (ACC) (Klucken et al., 2009; Hamm & Weike, 2005; Tabbert et al., 2006), is believed to be the core node of abnormal brain activations that related to anxiety disorders, the patterns of brain activation during attentional capture and suppression in individuals with high social anxiety as compared to low social anxiety is remain unclear. Future studies using EIB paradigm and MEG technique would allow us to explore the different activation patterns of insula and ACC during attentional capture and suppression in participants with high and low levels of social anxiety.

6.4 Limitations of the thesis

In this section, some ideas about the limitations and possible improvements of present studies are presented.

Due to time constraints and difficulties recruiting participants, the present thesis did not explore the brain mechanism of suppression among socially anxious individuals. This prevented us from comparing behavioural and neural differences that might relate to suppression in EIB paradigm. Given that the widely prevalence of social anxiety in the population, this may have limited the significance of current study. Using a large and well-distributed participant profile with high and low levels of social anxiety would enable the specific effects of the social anxiety to be measured and would allow us to draw further conclusions.

Due to the tight budget, the present study did not use individual anatomy from magnetic resonance images to define the forward model (Lopes da Silva, 2013; Baillet, 2017). This reduced the accuracy of the source localisation results and decreased the chance of statistically significant results being detected. The findings from the present work would benefit from well identified head models from individual anatomy in order to strengthen significant findings and explanations arising from the analysis.

6.5 Conclusions

One aim of this thesis was to explore how the attentional modulation of socially anxious individuals is affected by different types of threatening faces based on spatial frequency channels. The results support the following conclusions: individuals with high social anxiety have initial hypervigilance and later avoidance toward LSFs during visual search tasks; the HSA and LSA group have different attention modulation patterns in response to fearful faces.

The results of the thesis also replicate and validate a task used for measuring the automaticity of emotional attentional capture. Behavioural and ERP results found that negative pictures capture attention more readily, but the emotional attentional capture can be suppressed, and the suppression happens downstream of the emotional attentional capture. This task can also be used for clinical settings to compare the behavioural performance between individuals with high social anxiety and individuals with low social anxiety.

The results of the thesis also contribute to our understanding of the neurophysiological mechanisms that support the suppression of the emotional attentional capture. Taken together, the MEG results indicate that AI is important to identify salient stimuli in the environment and ACC plays a key role in inhibiting the processing of emotional distractors.

6.6 References

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