Effects of Emotion and Interoception on Memory

Thesis submitted for the degree of Doctor of Philosophy

School of Psychology and Clinical Language Sciences

University of Reading

Dona Kandaleft

May 2022

Declaration: I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Dona Kandaleft

29th May 2022

Acknowledgments

This work would not have been possible without the guidance and support of my supervisors. First, I would like to thank my primary supervisor, Dr Michiko Sakaki, for her extensive work with me throughout my PhD. I learned countless skills from Dr Sakaki. I am very grateful for her continuous support and invaluable feedback and our lively conversations and meetings, all of which have made this journey enjoyable. I would like to thank my co-supervisors, Dr Kou Murayama, and Dr Etienne Roesch for their support, for always offering insightful feedback and recommendations, and for their help in planning the research. Their expertise in research and particularly in statistics has deeply impacted this work.

This work would also not have been possible without the love and support of my family. I would like to thank my mother, father and brother for their unwavering support throughout my PhD journey. I would also like to thank my friends for their encouragement and support. I would also like to thank the Memo lab members for their thoughtful notes and input.

Abstract

Emotional events are usually remembered better than neutral events. For example, people usually remember instances of own success or failure better than mundane events. Despite the abundant literature on the interaction between emotion and memory, there are still some unanswered questions with regards to the effects of emotion on memory and moderators of emotional memory. One of these questions concerns whether and how emotion affects memory for neutral information encountered later. The second question concerns the sources of individual differences in emotional memory. There are individual differences in emotional memory; such that some individuals may be predisposed to remember negative information more than positive or vice versa. Such differences in emotional memory may be rooted in individual differences in the bodily responses (interoception) as well as brain's functional organisation. In the present thesis, each of these questions was addressed across three studies. The first study examined how experiencing emotional arousal affects memory of neutral information encountered minutes later; and whether the goal-relevance of the information modulates the effects of emotional arousal. Using a public speech task combined with false heart rate feedback, the study found that emotional arousal does not affect memory of neutral items viewed minutes later, irrespective of their goal-relevance. The second study examined the effects of interoception on emotional memory by presenting heartbeat biofeedback while presenting emotional images. The study revealed that attending to heartbeat biofeedback leads to increased negativity bias in memory, suggesting that interoception may play key roles in individual differences in memory for emotional items concurrently presented. The third study investigated the association between resting-state functional connectivity and emotional memory in a large dataset, utilising machine learning algorithms. Yet resting-state functional connectivity was not associated with individual differences in emotional memory. In sum, the studies reported in the thesis cast doubts on some of the previous literature’s claims that a) emotional arousal affects memory for other information individuals encounter subsequently and b) resting-state connectivity is useful to predict individual differences in emotional memory or cognitive processing in general. The findings also showed the effect of attention to heartbeats on emotional memory, suggesting that interoception may be associated with individual differences in emotional memory. The research has practical implications and theoretical implications leading to better understanding of the effects and moderators of emotional memory.

Table of Contents

Chapter 3: Heart Rate Biofeedback Amplifies a Negativity Memory Bias....76

Chapter 1: General Introduction

1.1 Introduction

Emotionally laden events are often recalled more vividly and forgotten more slowly than neutral events (LaBar & Cabeza, 2006). Emotional events are also more likely to become intrusive (Ferree & Cahill, 2009). Recent research has also shown that emotions have prolonged effects leading to enhanced memory for neutral items encountered minutes after the emotional experiences (Tambini, Rimmele, Phelps, & Davachi, 2017). However, emotion does not always enhance memory (Mather & Sutherland, 2011). Three factors have shown to be relevant to the effects of emotions on memory: a) priority, b) interoception, and c) the brain's functional connectivity (Critchley & Garfinkel, 2016). Priority concerns stimuli's goal relevance and perceptual saliency (Mather & Sutherland, 2011); accumulative research has shown that emotion impacts memory differently depending on priority (Sakaki et al., 2014). With regards to the interception, bodily signals and the resulting detection of those signals—interoception—have been strongly associated with the emotional experience (Barrett, Bliss-Moreau, Quigley, & Aronson, 2004; Craig, 2002; Critchley & Garfinkel, 2017; Seth, 2013). Emerging evidence has associated interoception with emotional memory (Pollatos & Schandry, 2008; Werner, Peres, Duschek, & Schandry, 2010). In addition, the brain's functional connectivity pattern has been associated with interoception, emotional responses (Jackson et al., 2003; Tobia, Hayashi, Ballard, Gotlib, & Waugh, 2017), and memory of neutral material (Salami, Pudas, & Nyberg, 2014; Staffaroni et al., 2018). The present thesis therefore examines the prolonged effects of emotion on stimuli of varying priority, and how interoception and the brain's functional connectivity modulate the effects of emotion on memory.

The first section defines emotion and explains how emotions are triggered. In the next section, I describe evidence on the effect of emotion on memory, including which aspects of memory emotion enhances and the existing theories about the mechanisms behind the emotional enhancement effect in memory. I then identify several gaps/unanswered questions in the research on emotion and memory: a) the prolonged effects of emotion, b) the association of interoception, and c) the role of functional connectivity during rest. Understanding the effects of those factors on memory may help resolve the mixed findings on emotional memory (Bennion, Ford, Murray, & Kensinger, 2013). For each factor, I describe relevant prior studies.

1.2 Emotions

This thesis defines emotions as affective states of feeling pleasure or displeasure, energised or deactivated (Russell, 2003). Although some accounts have proposed that affective states are comprised only of valence and not arousal aspects (Barrett, Mesquita, Ochsner, & Gross, 2007), and others have also included a goal relevance component (Kaplan, Van Damme, & Levine, 2012), this thesis uses the two-dimensional model of valence and arousal (Russell, 1980). Arousal is a state of heightened physiological activity, leading to feelings of being energised. Physiological arousal and subjective ratings of arousal may not be the same, especially across valences (Bradley, Miccoli, Escrig, & Lang, 2008). Physiological arousal refers to the bodily arousal, often indexed by skin conductance, heart rate, or pupil dilation. More information about the physiological basis of arousal is in Section 1.3.3.2. On the other hand subjective arousal is often measured by rating the experienced arousal on a scale, often on a 9-point scale Self-Assessment Manikin (SAM; Bradley & Lang, 1994). Memory research has found generally that physiological arousal is what brings about the enhancement in emotional memory (Mather, 2007; Mather, Clewett, Sakaki, & Harley, 2016; Mather & Sutherland, 2011). For example, a neurobiological model of the emotional enhancement of memory defined arousal through the activation of the noradrenergic system, and specifically release of norepinephrine from the locus coeruleus (Mather et al., 2016). In this thesis in Study 1 we recorded physiological measurements of arousal, and in Study 2 we recorded physiological measurements and measured the self-reported arousal ratings to images. We acknowledge that self-report measurements may not accurately reflect physiological reactions.

Emotions are usually experienced in response to environmental events and signal the favourability of this event to one's wellbeing, goals, and expectations. They are also often accompanied by behavioural and cognitive changes (e.g., Moors, Ellsworth, Scherer, & Frijda, 2013; Scherer, Schorr, & Johnstone, 2001). Emotions may also stem from internal causes (Russel, 2003) and are influenced by a myriad of individual-specific effects such as past experiences (Damasio, 1994), interoceptive awareness (Barrett et al., 2004), psychological disorders (Etkin & Wager, 2007), age (Reed, Chan, & Mikels, 2014), and gender (J. S. Stevens & Hamann, 2012). The next section reviews theories on how emotion is elicited.

1.3 How Emotions Are Elicited

1.3.1 Jamesian theory of emotion

In a seminal study, William James (1884) proposed that emotions stem from the perception of changes in body signals through a three-step process: bodily reaction, detection of the bodily reaction, and the resulting experience of emotion. The theory posits that bodily reactions give rise to emotions; for example, shaking after a threatening event generates the feeling of fear rather than the event itself. The theory also suggests that encountering emotional stimuli automatically triggers physiological reactions. Furthermore, different emotions are proposed to have different physiological bases. For example, shaking would result in the emotion of fear. Therefore, according to James (1884), the ability to sense physiological signals would be crucial to the experiencing of emotion and to the intensity of the emotions experienced. Other support for the impact that physical reactions have on emotions has been uncovered by studies examining how facial expressions alter emotions.

For example smiling was often found to make people happier (Davis, Senghas, & Ochsner, 2009). The Jamesian theory of emotion remains influential today, with the established role of the physiological signals in experiencing emotion (Barrett et al., 2004; Friedman, 2010; Seth, 2013).

1.3.2 Beyond William James

However, there are limitations to the Jamesian model of emotion. Cannon (1927) argued that physiological signals are not distinguishable enough to account for distinct emotions. Cannon (1927) also argued that one could have an elevated heart rate, such as when exercising, without experiencing emotions. Relatedly, Schachter and Singer (1962) proposed the two-factor theory of emotion, with the first step being arousal sensation followed by social construction. The theory is similar to James (1884) in its proposal that physiological reactions trigger emotions. However, Schachter and Singer (1962) posited that the cognitive interpretation (i.e. the appraisal) of bodily reactions is critical in eliciting emotions. For example, according to the two-factor theory of emotion, one could interpret the same physiological reaction as fear or as excitement, depending on own cognitive evaluation of the situation. To support this, Schachter and Singer (1962) injected participants with epinephrine and found that it led participants to feel more elated when a confederate was happy or to feel angrier when the confederate was angry. Therefore, the same physiological reactions were met with different interpretations depending on the situational evaluation. The role the interpretations of the event played in the emotional response is detailed in the appraisal model, which is discussed in the next section.

1.3.3 Appraisal theories of emotions

Many diverse situations lead to experiencing the same emotion. For example, events such as viewing nice scenery, passing a test, or spending time with loved ones may all lead to feelings of happiness, which supports the notion that emotions are not solely based on automatic responses to stimuli. On the other hand, the same events may trigger a different emotional response in different people. For instance, changes in heart rates when attending a social gathering could be appraised as excitement in one person or as apprehension in a socially anxious person. Furthermore, emotions may be triggered by mental rather than external causes such as the anticipation of an event or through thoughts. The anticipation of a public speech, for example, may induce increased emotional arousal (Lorberbaum et al., 2004).

Appraisal theories posit that perceptions of changes in the environment are what trigger emotions (Ellsworth, 2013). There are several appraisal theories (e.g., Frijda, 1986; Lazarus, 1991; Roseman, 1984; Scherer, 2009). Most appraisal theories share the common belief that emotions are the response to appraisal of changes in the environment judged likely to affect well-being (Moors et al., 2013). Scherer, Schorr, and Johnstone (2001) summarised the assumptions of appraisal theories by stating that appraisals drive emotions, emotions are adaptive, and different appraisals of the same event explain the differing emotional responses to the same event.

Appraisal theories propose that emotions are multi-componential. Moors et al. (2013) stated that modern theories often include appraisal, feelings, somatic, action tendencies, expressive behaviour, and motor components. Changes in one component are often thought to lead to changes in others. Emotions would therefore encompass not only feelings but also physiological and behavioural changes, all of which inform and change one another. Below, I describe the appraisal, physiological, and feeling components.

1.3.3.1 Appraisal. The appraisal component refers to the assessment of the importance of an event on one’s wellbeing, goals, needs, and beliefs. The first theory of appraisal posited that appraisals are nonconscious or rational (Arnold, 1960). Further theories, though, proposed that appraisals include both conscious and unconscious processing (e.g., Lazarus, 1991; Leventhal & Scherer, 1987; Roseman & Smith, 2001). Ellsworth (2013) noted that, over time, associations become learned, and appraisal may become automatic to certain situations or bodily responses. Appraisal is often thought to be the central component of emotion, and that other components are synchronised with the appraisal. Appraisal has been hypothesised to depend on the significance of the event to one's goals (impeding or goal-congruent), needs, and attachments, in addition to the agency, certainty, and ability to control the event. Appraisal theories view emotions as adaptive responses to the environment. For example, Ellsworth (2013) posited that appraisals typically precede emotions, and that the first appraisal, which often leads to a change in emotion, is a perception of novelty in the environment. In turn, this may lead to physiological and behavioural changes such as widened pupils and movement toward the novelty.

Differences in appraisals may explain how the different emotional responses from the same valence can be induced. For example, fear differs from distress in that appraisals include an element of uncertainty in the former (Scherer et al., 2001). Another example is that sadness can be differentiated from anger by a sense of passivity in the former and a sense of protest in the latter. Ellsworth (2013) noted that appraisals are continuous and that emotions may consequently be complex and may not easily fit into categorical emotions. Indeed, the combination of appraisal variables may trigger emotions that do not belong to the basic emotion categories and may even defy description by any known language term for emotion.

1.3.3.2 Physiological changes. The somatic component includes bodily (peripheral and central physiological) responses. Those bodily responses are hypothesised to be affected by appraisal and, as other components do, to affect appraisals as well. Emotions are indeed often closely associated with the physiological state. For example, arousal has a well-established physiological basis (James A. Russel, 1980; Posner, Russell, & Peterson, 2005).

Sweat gland secretion is controlled by the sympathetic nervous system, and increased levels in skin conductance are often used as an index of sympathetic arousal (Lang, Greenwald, Bradley, & Hamm, 1993; Palomba, Sarlo, Angrilli, Mini, & Stegagno, 2000). Heart rate and pupil size are controlled by both the parasympathetic and sympathetic nervous system, and are usually increased during emotional arousal (Mendelowitz, 1999; C.A. Wang et al., 2018). Therefore, cardiac, electrodermal, and respiratory signals relay complementary information on autonomic nervous system activation (Kreibig, 2010). Several studies have successfully predicted the experienced emotions from participants' physiological states with high accuracy (Gouizi, Bereksi Reguig, & Maaoui, 2011; Kim, Bang, & Kim, 2004; Lisetti & Nasoz, 2004; Yin et al., 2017).

1.3.3.3 Feeling. The feelings component, emotional experience, includes subjective feelings and is often thought to be the conscious reflection of the other components (Moors et al., 2013). Many theories have equated the feeling component with emotion despite evidence that several components are implicated in emotion (Sander, Grandjean, & Scherer, 2018). While appraisal theories often use discrete emotions to describe the feeling component, a common explanation is using a dimensional approach to describe emotions on two dimensions: valence and arousal (Russell, 1980). The appraisal theory of emotion is an influential account for explaining emotion that considers the different emotional reactions to situations and emotions' varying effects on behaviours.

1.3.4 Circumplex model of emotion

While the appraisal theory has been influential, many studies on emotion and memory have relied on a two-dimensional model (i.e., the circumplex mode) for emotions. Emotional memory research has generally explained the enhancement in emotional memory on the effects of arousal and, to a lesser extent, valence (Bowen, Kark, & Kensinger, 2018; Hamann, 2001; Mather, 2007; Mather & Sutherland, 2009; Phelps, 2004). Therefore, regarding the effects of emotion on memory, valence and arousal may have more important effects than discrete emotions. In this thesis, then, I adhere to the circumplex model. By following emotional memory research, the present thesis utilises the circumplex model of emotion. The next section explores this account.

The circumplex model of affect largely concerns the experience of emotion—similar to the feelings component of the appraisal theory. The circumplex model posits that emotions can be understood by two dimensions: a) valence ranging from displeasure to pleasure, and b) arousal ranging from sleepy to excited (Russell, 1980). Other views hold that there is a need to categorise emotions (Ekman & Keltner, 1997; Remington, Fabrigar, & Visser, 2000). An influential traditional theory is the distinct basic emotions, usually attributed as happiness, sadness, anger, fear, surprise, and disgust, which are posited to have distinct neural and physiological bases (Ekman & Keltner, 1997). Typically, basic emotions theories are supported by evidence of the universal recognition of basic emotions in faces and by distinct neural bases for each of the basic emotions (Kragel, Knodt, Hariri, & LaBar, 2016; Saarimäki et al., 2016). Recent views, though, have prescribed to the circumplex model. For example, a recent meta-analysis found that the distinct neural bases of basic emotions were not consistent among studies (Siegel et al., 2018). Furthermore, many studies found no support for the universality of basic emotion recognition from facial expressions (e.g. Gendron, Crivelli, & Barrett, 2018; Gendron, Roberson, van der Vyver, & Barrett, 2014; Nelson & Russell, 2013).

The circumplex model has received ample support in behavioural and neural studies (Posner et al., 2005) and remains the most widely accepted theory for explaining emotion’s effects on memory (LeBlanc, McConnell, & Monteiro, 2015). Self-reports of experienced emotions typically support the circumplex theory, yielding two dimensions of valence and arousal (Feldman Barrett & Russell, 1998; Russell, 1980; Russell & Barrett, 1999). The subjective rating of emotional words also supports the circumplex effect. For example, a recent study asked participants to rate pairs of words on similarity, and found that they tended to choose similarity according to arousal and valence (Bliss-Moreau, Williams, & Santistevan, 2020). Neural evidence has shown that the circumplex model fits the observed brain mechanisms during emotional experiences (Colibazzi et al., 2010; Posner et al., 2009). Magnetoencephalography (MEG) brain also supports that arousal and valence have a dissociable and reliable neural basis (Grootswagers, Kennedy, Most, & Carlson, 2020). Arousal is most widely associated with the activation of the amygdala (Wilson-Mendenhall, Barrett, & Barsalou, 2013). For example, amygdala activation is associated with stimuli intensity across valences (H. Lin et al., 2020). Valence, however, is associated with the activation of the orbitofrontal cortex (Wilson-Mendenhall et al., 2013). Although a recent meta-analysis found that the valence network is located in the limbic and paralimbic regions (Lindquist, Satpute, Wager, Weber, & Barrett, 2016), the study did not account for the role of arousal and included valence with low and high arousal.

It is notable that, although widely used, the circumplex model has nuances and caveats. The discreet emotions have valid points and have received support for their specificity in physiological responses (Friedman, 2010). For example, in one analysis, mutilation disgust showed evidence of decreased sympathetic response, while fear and anger led to increased sympathetic responses despite being on similar valence and arousal levels (Kreibig, 2010). Another example is that anger and fear share similar valence and arousal levels. However, the two emotions are experienced substantially differently and have differing behavioural consequences. Anger includes a motivation to move toward the external input, whereas fear involves a motivation to avoid (Roseman, 2001). Therefore, motivational tendencies are important. Anger may be triggered by appraisals of obstacles to well-being or goals (Lang, 1995), where fear may stem from appraisals of imminent danger or harm. The appraisal of situations is crucial and includes factors such as agency, control, and novelty (Moors et al., 2013). Nevertheless, memory for anger and fear both rely on a similar set of brain regions, including the amygdala (Fabiansson, Denson, Moulds, Grisham, & Schira, 2012). As a result, this thesis incorporates the circumplex model of emotion because it has often been used to explain the effects of emotion on memory, which is the purpose of this thesis. Emotional enhancement in memory has been largely attributed to emotional arousal (LaBar & Cabeza, 2006; Mather & Sutherland, 2011). The improvement of emotional memory has been found across valences and has often been associated with emotional arousal levels. Research supporting the roles of arousal and valence in memory is discussed in the following sections.

1.4 Emotional Memory

1.4.1 Behavioural evidence

The memory of autobiographical events is enhanced for emotional compared to neutral events. For example, Talarico and Rubin (2007) found that memories of 11 September, 2001 were stronger, recalled with increased confidence, and rehearsed more than neutral events. Similarly, when participants were asked to recall personal events, they recalled emotional events with greater details than neutral events (St. Jacques & Levine, 2007). Many studies have also found that people rate their memory of emotional events as more vivid (Comblain, D’Argembeau, & Van der Linden, 2005; D’Argembeau, Comblain, & van der Linden, 2003; Schaefer & Philippot, 2005; Talarico, Labar, & Rubin, 2004).

Lab-based research has similarly shown that emotional words are better recalled than neutral words (reviewed in Hamann, 2001; LaBar & Cabeza, 2006; Mather, 2007; Talmi, 2013; Yonelinas & Ritchey, 2015). In a seminal study, Kensinger and Corkin (2003) across six studies found that negative and taboo words were generally better recalled than neutral words. The enhancing effects of emotional arousal remained even after controlling for the relatedness of emotional words. The enhancing effect of emotional arousal was stronger than the effect of valence. Taboo words, highly arousing with low valence loads, were better recalled than low-arousal negative words. Similarly, high arousing images were better recalled than low arousing images, regardless of valence, when tested 1 year later (Bradley, Greenwald, Petry, & Lang, 1992).

However, task-specific factors, such as the relatedness of emotional stimuli and the distinctiveness of emotional stimuli compared to neutral, may contribute to the emotional enhancement effect (Bennion et al., 2013; Talmi, 2013). One study found that reducing the distinctiveness of emotional stimuli by showing neutral and emotional items in separate blocks led to no emotional enhancement effect (Talmi, Luk, McGarry, & Moscovitch, 2007). This may suggest that lab-based studies inflate the emotional enhancement effect due to the nature of the stimuli. However, a recent study found that, although increasing the relatedness of neutral items enhanced memory, negative memory was still better than neutral regardless of its level of relatedness (Zarubin et al., 2020).

In this thesis, the terms ‘better’ or ‘enhanced’ memory refer to increased recall or recognition (both familiarity or recollection) of items, usually tested on free recall or recognition tests. Enhanced emotional memory refers enhanced memory of emotional items (positive, negative or both) compared to neutral stimuli. The memory tests could be done immediate to encoding or delayed. Immediate tests usually reflect the enhancement in encoding, while delayed tests reflect both enhanced encoding and consolidation (Talmi, 2013). However, in reviewing the evidence I do not always specify whether the enhancement in cited studies is caused by the effects of encoding, consolidation, or retrieval. Furthermore, while enhanced memory may refer to self-reported enhancement memory, this thesis is concerned with objective measurements of memory. Self-reports of enhanced memory do not always reflect enhanced memory when tested using objective measurements (Talarico &

Rubin, 2003). As reviewed in following sections, emotion alters the memory of associated information, sometimes enhancing and sometimes impairing associated information (Mather & Sutherland, 2011). Unless stated otherwise, the enhanced memory refers to the memory of emotional items themselves, or their integral intrinsic details. If I refer to peripheral or other associated information, this would also be specified.

1.4.2 The Role of Arousal in Emotional Memory

Research has mostly shown that arousal is the main factor in enhancing emotional memory (Hamann, 2001; Mather, 2007; Mather & Sutherland, 2009; Phelps, 2004). Across three studies, memory accuracy was correlated with both arousal and valence ratings, although more reliably for arousal (Mather & Nesmith, 2008; Mather & Sutherland, 2009). Arousal and valence ratings were also highly correlated. After controlling for the effects of valence, arousal retained a significant effect. When controlling for arousal, though, the effect of valence was not significant. Another study associated the physiological arousal experienced during a video game with the memory of items viewed during the game (Jeong & Biocca, 2012). Mather and Sutherland (2009) argued that the low association between physiological arousal and positive valence often observed in females may underlie a reduced memory enhancement of positive items compared to negative (e.g., Kensinger, 2007). Notably, fewer studies have investigated the effects of valence on memory. A recent meta-analysis did not find a sufficient number of studies comparing the neural correlates of negative and positive memory to obtain high power (Dahlgren, Ferris, & Hamann, 2020).

Pharmacological studies have also supported the notion that arousal is crucial for the emotional enhancement effect in memory. Impairing the b-adrenergic response by propranolol hydrochloride, for example, led to an impairment in memory of emotional but not neutral stimuli (Cahill, Prinst, Webertt, & McGaugh, 2013). In a review, Roozendaal and Hermans (2017) found that using pharmacological manipulations that increase norepinephrine levels either during consolidation or encoding leads to enhanced memory of emotional items. Those results also alluded to the selective aspect of emotional memory, with the b-adrenergic response selectively enhancing emotional responses. The selective enhancement in memory is addressed in a future section.

However, many studies posited that valence has important effects. Indeed, several studies have found negative memory to be better recalled than positive (reviewed in Kensinger, 2007; but see Juvina et al., 2018). This has led to the development of the negative emotional valence enhances recapitulation (NEVER) model (Bowen et al., 2018). The model proposes that negative items receive better encoding than positive and neutral items due to capturing more attention. This increased attention is hypothesised to result in better negative memory than neutral, which shows even minutes after encoding. On the other hand, the enhancement in positive memory may only show after long delays. Better memory of negative stimuli is likely triggered by high similarity in brain activation during retrieval and encoding. The model also posits than negative items receive better consolidation during sleep. However, experimentally inducing negative emotions, including through image presentation or films, is more successful than positive emotion induction (Uhrig et al., 2016; for a meta-analysis see Westermann, Spies, Stahl, & Hesse, 1996). Therefore, existing evidence may be biased toward a selective enhancement in negative memory. In sum, most research has indicated that emotional arousal leads to the enhancement in emotional memory, although interactions with valence are likely.

1.5 Theories of the Emotional Enhancement Effect

1.5.1 The Modulation Model

A common explanation of the enhancing role of emotion is that emotions lead to an increase in hormones such as epinephrine and corticosterone. The release of stress hormones leads to increased activation in the amygdala. This enhanced activation then influences activity in other regions such as the hippocampus, enhancing consolidation (McGaugh, 2004). The modulation model highlights the effects of consolidation and proposes consolidation as the major process responsible for the emotional enhancement effect rather than encoding. The model is supported by studies that have administered epinephrine after presenting emotional stimuli and shown that epinephrine enhanced memory (e.g., Cahill & Alkire, 2003; Cahill, Gorski, & Le, 2003). The modulation model is also supported by studies that have shown increased amygdala activation during the successful encoding of emotional items (e.g., Dahlgren et al., 2020; Murty, Ritchey, Adcock, & LaBar, 2010).

In line with the modulation model, studies have often found that lesions in the amygdala led no emotional enhancement effect in memory, which supports that the amygdala is the neural substrate for emotional memory. For example, in two patients with bilateral amygdala damage, emotional memory was impaired (Adolphs, Cahill, Schul, & Babinsky, 1997). Similarly, ten patients with Urbach-Wiethe disease, with degeneration of the amygdala, showed impaired emotional memory in comparison to healthy controls (Siebert, Markowitsch, & Bartel, 2003).

Functional neuroimaging studies have also found strong support for the role of the amygdala in the emotional enhancement effect. The amygdala is activated in response to emotionally arousing information, both positive and negative (Mather et al., 2004; for a meta-analysis see Phan, Wager, Taylor, & Liberzon, 2002; Rasch et al., 2009). The degree of activation in the amygdala may correlate with the arousal intensity rating (Phan et al., 2004; Touroutoglou, Bickart, Barrett, & Dickerson, 2014). Enhanced memory of emotional items has also been associated with increased amygdala activation during encoding (Ritchey, Dolcos, & Cabeza, 2008; Sakaki, Nga, & Mather, 2013; St. Jacques, Dolcos, & Cabeza, 2009), consolidation (Kark & Kensinger, 2019; McGaugh, 2004), and retrieval of emotional items (Bowen et al., 2018; Dolcos, Labar, & Cabeza, 2005). For example, the memory of emotional items was correlated with the activation of the amygdala during encoding (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Hamann, Ely, Grafton, & Kilts, 1999; Murty et al., 2009; Ritchey et al., 2008). In addition, recent meta-analyses have found that the amygdala was significantly activated during the encoding of subsequently remembered (i.e. successful encoding) emotional items (Dahlgren et al., 2020; Murty et al., 2010).

Furthermore, research has supported the role of the amygdala in projecting to the hippocampus during the encoding of emotional stimuli. A large study with over 500 individuals found that the encoding of positive and negative stimuli consistently leads to a rapid increase in the functional connectivity between the amygdala and the hippocampus (Fastenrath et al., 2014). Similarly, many studies have associated functional connectivity between the amygdala and the hippocampus during encoding with emotional memory (e.g., Dolcos, LaBar, & Cabeza, 2004; Murty et al., 2009; Ritchey et al., 2008). The functional connectivity between the amygdala with the prefrontal cortex has also been associated with emotional memory (Sakaki et al., 2013; St. Jacques et al., 2009).

1.5.2 Shortcomings in the Modulation Model

The modulation model does not, however, account for all the effects of emotional memory. For instance, it does not consider that emotional items are remembered better than neutral items even without any delay to allow consolidation. Emotionally arousing items often capture more attention than neutral ones (Pourtois, Schettino, & Vuilleumier, 2013). The effects of encoding are observed when memory tests are taken minutes after encoding. Such tests often show enhanced memory of emotional compared to neutral items (Hamann et al., 1999; Talmi, 2013). The effects of consolidation, by contrast, should show only when the delay between encoding and testing spans hours. Notably, the effects of emotional enhancement are often stronger when the delay between encoding and testing is longer (Sharot, Verfaelli, & Yonelinas, 2007; Yonelinas & Ritchey, 2015). However, that numerous studies have found enhanced emotional enhancement effects in *early* long-term memory suggest that consolidation cannot completely account for the emotional enhancement effect.

Furthermore, emotion often affects the memory of neutral information associated with the emotion-eliciting event. Emotion may enhance or impair the memory of temporally or spatially close information (Mather & Sutherland, 2011). Enhancement in memory is often selective to central events (Kensinger, 2009; Mather, 2007). The model does not specify the types of memory influenced by emotion (Yonelinas & Ritchey, 2015). For example, a past study administered epinephrine after viewing emotional and neutral items and found enhanced memory of emotional but not neutral items (Cahill et al., 2003). If epinephrine enhances memory consolidation, the memory of both neutral and emotional items should be enhanced due to the enhancement in consolidation. Therefore, the study suggests that norepinephrine does not generally improve all encountered information but rather specific aspects of that information. Similarly, presenting emotionally arousing stimuli after the encoding of emotional stimuli generally impairs memory of neutral items rather than enhances them (Schlüter et al., 2018). The modulation model does not explain the impairing effects of emotion. The next section details the focal enhancement in emotional memory in more detail.

1.5.3 Focal Enhancement in Emotional Memory

The emotional enhancing effects of emotion are often observed in the central—but not all—aspects of events. In a study on autobiographical memories, participants described the most traumatic memories of their lives (Christianson & Loftus, 1990). Participants indicated remembering a higher number of central than peripheral details. The number of central details recalled was associated with the subjective intensity rating of the event. Another study asked participants to recall traumatic memories and had independent judges rate the memory descriptions (Berntsen, 2002). Traumatic memories had a significantly higher number of central details than peripheral ones.

Laboratory studies have also shown an effect of the enhancement of central details compared to peripheral (Kensinger, 2009; Mather, 2007). One study presented negative or neutral objects superimposed on neutral backgrounds (Kensinger, Garoff-Eaton, & Schacter, 2007). The memory of emotional items was better than that of neutral objects. However, the memory of the background was impaired when the object was negative compared to when it was neutral. While the memory of central aspects—in this case the emotional item itself—is typically enhanced, the contextual details may not be improved by memory.

Other studies have investigated the effects of emotional stimuli presented temporally close to the emotional stimuli. Such studies have presented emotional or neutral “deviant” items followed or preceded by neutral items. The studies often result in impaired memory for neutral items preceding or followed by negative compared to neutral deviant items (e.g., Hurlemann et al., 2005; Knight & Mather, 2009; Miu, Heilman, Opre, & Miclea, 2005; Strange, Hurlemann, & Dolan, 2003). Therefore, evidence supports that, although the memory of emotionally arousing stimuli improves, the memory of items spatially or temporally surrounding the stimuli may be impaired.

1.5.4 The Emotional Binding Model

One method for explaining the enhancement of the central but not peripheral features of emotional stimuli is the emotional binding model. The model posits that experiencing emotion leads to enhanced item–emotion bindings (Yonelinas & Ritchey, 2015). Those bindings are supported by the amygdala, which has a slow forgetting time due to the low cell renewal rate and low interference that occurs because emotional events are typically encountered less than neutral events. The item–emotion binding refers to the emotional objects themselves, and does not include peripheral, extrinsic, or contextual details. Extrinsic details (“item–context bindings”), by contrast, are bound in the hippocampus. Specifically, the parahippocampal cortex is hypothesized to be responsible for context such as the location of emotional material. The perirhinal cortex is hypothesized to bind both neutral and emotional objects. The model suggests that, due to the high cell renewal rate in the hippocampus, memory of neutral information and associates of emotional information are more quickly forgotten than emotional information, which is bound in the amygdala. The model concerns the delayed enhancing effects of emotion occurring due to slow forgetting. Yonelinas and Ritchey (2015) argue that the memory of the central details of emotional material—though not extrinsic or peripheral information—is enhanced, especially when tested after a delay due to the varying forgetting rate.

The model supports abundant research showing that emotion has enhancing effects on central aspects of memory compared to contextual or peripheral information (reviewed in, Kensinger, 2009; Mather, 2007). However, importantly, the definitions of central and peripheral are not detailed. For example, contextual details that are goal-relevant often receive enhanced memory (Levine & Edelstein, 2010). The next section reviews the role of goal relevance in emotional memory.

1.5.5 Emotion Enhances the Memory of Goal-Relevant Information

The impairing effects of emotion on the memory of temporally or spatially close neutral items appear to cease when those neutral items are goal-relevant. For example, Lee et al. (2015) presented pairs of adjacent neutral images followed by fear-conditioning or neutral sounds. The study manipulated goal relevance by asking participants to remember or ignore an image based on its frame colour. Goal-relevant images were better recalled when followed by a fear conditioning than a neutral sound. Similarly, Ponzio and Mather (2014) presented images of neutral scenes with superimposed neutral objects and asked participants to focus on the object. The images were followed by a neutral or negative sound. The memory of the scenes (goal-irrelevant information) was impaired when those images preceded a negative compared to a neutral sound. However, there was no difference in the memory of objects (goal-relevant information) preceding negative or neutral sounds. Therefore, the emotion-induced memory impairment did not occur when the objects were prioritised. Another study found that neutral items that the memory of neutral items that received high attention —such as items in an intentional encoding task— and were preceding emotional oddballs was enhanced up to a week later (Knight & Mather, 2009).

The memory of peripheral information is also impacted by goal relevance. When Kensinger et al. (2007) changed the task to intentional encoding, asking participants to recall the details, the memory of neutral backgrounds was not impaired when the superimposed objects were negative compared to neutral (Study 4). This was opposed to the impairment in memory of background when no such instructions were made (Studies 1,2,3).

Levine and Edelstein (2009) reviewed evidence that the memory of central aspects is enhanced while that of peripheral information is impaired. The authors proposed that emotional arousal, particularly during negative valence, generally narrows attention. However, the authors also found studies that countered this evidence. The authors argued that a modulatory role of goal relevance could explain the mixed evidence. Specifically, the authors posited that highly goal-relevant items receive greater attention, which is reflected in enhanced memory when emotions are present. Goal-relevant material would receive more attention and processing, leaving fewer resources for goal-irrelevant material. Goal-irrelevant items, by contrast, receive low attention and possibly reduced deep processing and therefore are less likely to be stored in the long-term memory.

Notably, Levine and Edelstein (2009) argued that emotional valence may play a role in attention and emotional memory. For example, positive valence may lead to broadening rather than narrowing of attention. In addition, the authors noted that discrete emotions may have distinct effects due to the inherent differences in goal relevance in different emotions. Thus, the goal relevance account considers the appraisal model of emotion.

1.5.6 Arousal-Biased Competition

Mather and Sutherland (2011) further formalised the goal relevance effect and highlighted the crucial role of consolidation in the effect. The arousal-biased competition (ABC) theory posits that emotional arousal biases attention, enhancing the processing of high-priority items and impairing the processing of low-priority items (Mather & Sutherland, 2011). High-priority material could be due to bottom-up sensory or top-down cognitive causes. Bottom-up influences include high salience objects such as those with differences in contrast, colour, or object movement. Top-down influences include objects that are goal-relevant or expected to occur. Importantly, emotionally arousing objects are of high priority themselves. The enhanced processing of high arousal information is theorised to impact both the perception and consolidation of information. The theory proposes that arousal enhances the encoding of high-priority material, details, or even associations, and impairs the encoding of low-priority material. In addition, high-priority information receives enhanced consolidation through amygdala activation. The theory also proposes that the effects hold for both negative and positive material. The theory has been supported by short-term memory studies showing enhanced memory of high-salience objects and impaired memory of low-salience objects (e.g., Sutherland & Mather, 2012, 2015, 2018). The theory has also been supported by long-term memory research, including goal relevance studies reviewed in the previous section. Chapter 2 summarises the studies that have investigated the arousal-biased competition for anterograde effects.

The glutamate amplifies noradrenergic effects (GANE) model explains the neural mechanisms of the arousal-biased competition by proposing how arousal modulates the effects of priority in the brain (Mather et al., 2016). The model proposes that arousal increases interactions between the glutamate and norepinephrine around neurons processing high-priority items. The norepinephrine released under arousal interacts with glutamate, increasing release of glutamate, which in turn also increases norepinephrine near neurons that process high-priority information (i.e., hot spots). The GANE model also proposes that the increase in glutamate and norepinephrine in these local hotspots simultaneously increases the inhibitory transmitter GABA activity, which may inhibit activation in neighbouring regions and thereby inhibit competing representations.

The GANE model states that the amygdala mediates the effects of priority on memory. The activation of the locus coeruleus (LC) modulates the amygdala, leading to enhanced processing of salient information. This modulation of the amygdala is proposed to enhance the processing of that high-priority information in the medial temporal lobe (MTL) and the hippocampus. The model also suggests that the LC may enhance activity in the insula, which is thought to integrate external and internal bodily information (Craig, 2009). The role of the insula in mediating emotional arousal is well-supported (Critchley & Garfinkel, 2017; Pollatos, Schandry, Auer, & Kaufmann, 2007). Specifically, the insula is the main region for interoception, which refers to the processing of bodily signals (Craig, 2002, 2009; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004). Therefore, the GANE model may be also relevant in explaining the effects of interoception described later in this chapter (Critchley & Garfinkel, 2015).

1.5.7 Drawbacks of the ABC Model

According to the ABC model, emotional arousal leads to amplification in the bias regardless of valence. However, there may be important valence effects. The broaden-and-build theory of positive emotions posits that positive emotions broaden the attention relative to negative and neutral states (Fredrickson, 2001, 2004). For example, compared to neutral states, participants in a positive emotion induction condition had enhanced attention to global configuration rather than detailed elements, therefore illustrating evidence of broadening of attention in positive emotion (Fredrickson & Branigan, 2005, Study 1). Some studies have shown that associative memory is enhanced by positive emotions (e.g., Madan, Scott, & Kensinger, 2019; Zimmerman & Kelley, 2010). The ABC theory would instead expect a decrease in memory due to the low priority of the associative details.

The influence of emotional valence on memory is in line with the appraisal theory of emotion. Emotions serve an adaptive purpose. Appraisal theories posit that appraisal has a bidirectional association with cognition (Scherer, 2009a). Appraisals often lead to motivational changes. Attention during emotional states may be directed to information that is typically useful when encountering such emotions (Levine & Pizarro, 2004). For example, Levine and Edelstein (2010) mention that positive emotions stem from appraisals of goal attainment, which in turn could lead to flexible, top-down processing, which includes drawing information from relational knowledge. On the other hand, negative emotions stem from the goal obstruction or threat of such obstruction, which leads to analytic, bottom-up processing. This is in line with Fredrickson (2004) and Kensinger (2009) findings of attention narrowing in negative emotion and attention broadening in positive emotion.

Furthermore, discrete emotions may alter motivation differently. Levine and Pizarro (2004) argued that the relevance of items may be different depending on the specific discrete emotion. For example, anger stems from appraisals of goal obstruction, which may trigger a motivation to remove the obstacle to the goal, therefore making goal-related information, such as the goals themselves or agents obstructing goals goal-relevant (high priority). Levine and Pizzaro (2004) also give an example on sadness, which although similar to anger is of negative valence and is caused by goal failure, leads to motivation of adjusting to the failure, which makes goal-relevant information the failure itself and its consequences. Fear may lead to increasing the goal-relevance of threat-related information including sources of threats and ways to avoid it. On the other hand, happiness may increase the priority of general knowledge and heuristics. The authors argue that those motivational changes caused by different discrete emotions are reflected in changes in memory. For example, depression was found to increase the memory of past failures while PTSD increased the memory of past threats to safety (Levine & Edelstein 2010).

Similarly, Kaplan et al. (2012) noted that the changes to motivation do not only depend on valence (failure or success), but also on whether the emotions were elicited pre-goal or post-goal. For example, experiencing a pre-goal emotion, when one anticipates a failure or attainment of a goal, may constrict attention to goal-relevant information and consequently lead enhanced memory of such information. Whereas post-goal emotions, when one has judged the attainment or failure of a goal, may lead to the broadening of attention to peripheral information. For example, the induction of happiness may lead to broader attention than induction of desire, as the first is usually elicited post-goal while the latter is pre-goal (Gable & Harmon-Jones, 2008). Another example of similar emotions that may lead to different goals, Kaplan et al. (2012) differentiates seeking (a pre-goal emotion) from playing (post-goal) in that seeking narrows attention to central information that is goal relevant, whereas playing shifts attention to new environments and communication with others.

Therefore, the appraisals themselves may alter motivation and attention. This in turn means that what counts as high-priority information is influenced by the appraisals. Furthermore, appraisal theories include a physiological component, which is triggered by appraisals, and physiological rather than self-reported arousal has been more strongly associated with the emotional enhancement effect on memory (Mather, 2007; Mather & Sutherland, 2009). Relatedly, the processing of physiological reactions has also recently been found to impact emotional memory (Critchley & Garfinkel, 2016; Pollatos & Schandry, 2008).

Finally, arousal may have inverted u-shape effects, whereby high levels of emotion may impair memory (Baldi & Bucherelli, 2005). In one study, the memory of associative items was shown to be impaired by moderate negative arousal and unaffected by highly arousing taboo words (Madan, Caplan, Lau, & Fujiwara, 2012). Other studies have reached similar results (Madan et al., 2019).

1.6 Unanswered Questions about Emotional Memory

As described above, many theories have explained the effects of emotion on memory. Nevertheless, none have been able to explain the entire set of empirical results I described. In addition, several important questions regarding the mechanisms of emotion and memory remain unanswered. The present thesis is interested in three questions about emotional memory. The first concerns the sustained effects of emotional arousal. Specifically, it remains unclear if emotional arousal has prolonged effects, leading to enhanced memory of prospective unrelated stimuli. It is also unclear if those effects interact with the items' priority. The next questions address factors that may impact emotional memory. Interoception, the detection, processing, and interpretation of physiological signals, has been closely associated with emotional responses (Barrett et al., 2004; Herbert, Pollatos, Flor, Enck, & Schandry, 2010; Pollatos, Herbert, Matthias, & Schandry, 2007). The effects of interoception on emotional memory have not yet been investigated outside of correlational approaches. Moreover, the effects of the brain's structure and function have been associated with emotional memory. However, the association between resting-state functional connectivity patterns and emotional memory remains unclear. The importance of interoception and functional connectivity was highlighted by Critchley and Garfinkel (2016). Examining those factors would lead to better understanding of the emotional memory and the processes that modulate it.

Emotional arousal was recently found to have enduring neural and memory effects, enhancing the memory of items viewed up to 30 minutes after emotional induction (Tambini et al., 2017). In general, few studies examined the prolonged effects of arousal on memory, and most focused on the effects of stimuli occurring immediately or seconds after emotionally arousing stimuli (e.g., Jia et al., 2020; Sakaki, Fryer, & Mather, 2014; Sutherland, McQuiggan, Ryan, & Mather, 2017). This is the case despite animal research showing prolonged activation in the amygdala after encountering emotionally arousing events (e.g., Galvez, Mesches, & Mcgaugh, 1996; McIntyre, Hatfield, & McGaugh, 2002; Young & Williams, 2010). Importantly, Tambini et al. (2017) found that the memory of items encountered minutes after emotionally arousing stimuli is enhanced. However, it is unknown if priority moderates the prolonged effects of arousal on memory. The thesis begins by investigating the memory of neutral items of varying priority, which are encountered minutes after an emotionally arousing event.

Interoception has been hypothesised to underlie the emotional response. Since Williams James (1884), research on emotion has considered it a key element in the experience of emotion (Bennett & Hacker, 2005; Damasio, 1994; Khalsa, Adolphs, Cameron, Critchley, Davenport, Feinstein, Feusner, Zucker, et al., 2018). Appraisal models also often include a physiological component (e.g., Ellsworth, 2013; Moors et al., 2013). Due to the interdependence of components, this likely impacts emotional appraisals. Recent models have posited that interoception is closely associated with emotions (Barrett, 2017; Critchley & Garfinkel, 2017; Seth, 2013). The thesis next examines the effects of interoception on emotional memory.

The functional connectivity in the brain is another likely factor that may moderate emotional memory. The functional organisation of the brain is associated with emotional processing (Y. Y. Lee & Hsieh, 2014; W. F. Z. Yang et al., 2021). Emotional memory is associated with amygdala activation in addition to its connectivity with the MTL and prefrontal cortex (Dahlgren et al., 2020; McGaugh, 2002; Murty et al., 2010). The functional connectivity has also been closely associated with the emotional response (Li et al., 2020; R. Smith, Allen, Thayer, & Lane, 2015; W. F. Z. Yang et al., 2021) and interoception (Chong, Ng, Lee, & Zhou, 2017; Kuehn, Mueller, Lohmann, & Schuetz-Bosbach, 2016; Ueno et al., 2020). It is therefore likely that the brain's functional connectivity is relevant to the emotional enhancement effect. In future sections, the thesis explores the association between individual differences in functional connectivity at rest and emotional memory measures. Below, I describe prior studies on each of the three issues in emotional memory in greater detail.

1.7 Prolonged Effects of Arousal

Despite that many studies have investigated the effects of emotion on the memory of temporally nearby items, few have investigated more prolonged effects (i.e., the effects on items encountered minutes later). However, as reviewed below, past evidence has suggested that emotional arousal may enhance the memory of subsequent items encountered minutes later (e.g., Tambini et al., 2017; van Marle, Hermans, Qin, & Fernández, 2009).

There is strong evidence that amygdala activation and connectivity during encoding is associated with future memory. For example, higher levels of amygdala activation have been associated with increased emotional arousal ratings (Phan et al., 2004; Touroutoglou et al., 2014), and improved emotional memory (Canli et al., 2000; Hamann et al., 1999; Murty et al., 2009; Ritchey et al., 2008). Furthermore, the functional connectivity between the amygdala and the hippocampus has been associated with subsequent memory (Dolcos et al., 2004; Murty et al., 2009; Sakaki et al., 2013). It is unclear, however, for how long the emotional stimuli encoding activation patterns are sustained and if they affect the memory of subsequent neutral items.

Existing evidence suggests that emotional arousal's hormonal and neural effects are prolonged, resulting in their effects on the memory of subsequently encountered information. For example, one study found increased levels of norepinephrine in the amygdala of rodents up to 30 minutes after footshock manipulations (Galvez et al., 1996; Hatfield, Spanis, & McGaugh, 1999; Young & Williams, 2010). Another study uncovered that increased norepinephrine levels in amygdala were sustained for up to two hours after footshock (McIntyre et al., 2002).

The prolonged presence of norepinephrine in the amygdala may contribute to the prolonged effects of emotional arousal. Increases in norepinephrine in the amygdala are associated with increased coupling of the amygdala with the hippocampus, thus enhancing memory (McGaugh, 2004). Past studies have found that impairing the b-adrenergic response by administering propranolol during encoding impairs the enhancement in memory of negative (Cahill et al., 2013; Rimmele, Lackovic, Tobe, Leventhal, & Phelps, 2012) and sometimes neutral stimuli (Rimmele et al., 2012). Taken together, the findings suggest that experiencing an emotionally arousing event leads to prolonged enhancement in the amygdala's norepinephrine levels, which in turn may contribute to enhanced emotional response and enhanced emotional memory.

Human studies have also supported the notion that emotional arousal has prolonged neural effects. One study found a higher increase in amygdala activation in response to emotional items when those clips were shown after a block of emotional, compared to neutral, clips (van Marle et al., 2009). The results suggest a prolonged increase in vigilance and reactivity after encountering emotionally arousing stimuli. Therefore, it is reasonable to assume that the increased amygdala activation enhanced the encoding of neutral items.

Another study found that the amygdala's connectivity with the hippocampus and medial ventral prefrontal cortex (PFC) increased after fear blocks (Hermans et al., 2017). The study also found that the multivoxel pairwise correlation structures (MVCS) exhibited during fear blocks in the amygdala and hippocampus were spontaneously reactivated during the subsequent resting blocks. However, the authors argued that explaining the results solely as persistent arousal was unlikely because the strengths of MVCS reinstatements were not correlated with the physiological measures of arousal (skin conductance, pupil dilation, and heart rate). Therefore, the results suggested increased consolidation rather than persistent arousal.

The behavioural evidence of the prolonged effects of emotion has been limited. Most of the research has instead investigated the effects of emotional memory of items encoded immediately or seconds after emotional stimuli using intermixed lists of neutral and emotional items. The research usually did not control for arousal-biased competition effects. Neutral items shown after emotional stimuli have often shown impaired memory (Schlüter, Hackländer, & Bermeitinger, 2019). The impairments likely occur due to the neutral and emotional items' competition for resources (Mather & Sutherland, 2011). Enhancing the priority of the subsequent neutral items led such impairment to cease (Sakaki et al., 2014).

However, a recent study presented emotional stimuli for 20 minutes followed by a 10-minute break, before presenting neutral stimuli for another 20 minutes (Tambini et al., 2017). The study found that the memory of neutral items improved significantly when preceded by a block of emotional stimuli compared to a block of neutral stimuli.

Taken together, the findings suggest that experiencing emotion may lead to prolonged increases in amygdala activation and norepinephrine levels. Both effects are expected to lead to enhanced emotional memory. It is unclear, however, how priority impacts the prolonged effects of emotional arousal on memory. It is likely that arousal enhances memory of high-priority items and impairs memory of low-priority items encountered minutes later. The present thesis begins by investigating the prolonged effects of emotional arousal and their interaction with the stimuli's priority. The second question, which has not been answered, concerns the effects of interoception on emotional memory.

1.8 Interoception

1.8.1 Definition of Interoception

Interoception is the ability to sense and interpret bodily signals (Craig, 2003). Bodily signals include cardiovascular, respiratory, electrodermal, and gastric signals; hunger and fullness signals; and muscular and visceral and pain signals (Craig, 2003; Khalsa, Adolphs, Cameron, Critchley, Davenport, Feinstein, Feusner, Garfinkel, et al., 2018). Interoceptive signals relay the organs' functional state and health. Consequently, interoception is essential for maintaining homeostasis (Tsakiris & Critchley, 2016). Interoceptive signals lead to changes in behaviour and cognition. For example, signals from gastric organs that lead to feelings of hunger can alter behaviour. Although older definitions of interoception included only visceral sensations and therefore excluded sensations such as pain and itching (Sherrington, 1952), evidence has supported a more inclusive definition (Craig, 2003) that has recently become widely used and accepted (Ceunen, Van Diest, & Vlaeyen, 2013). Most research investigating the association between interoception and emotions has focused on cardiac signals (Critchley & Garfinkel, 2017). This thesis is therefore concerned with the cardiac signals that specifically detect and interpret heartbeats.

1.8.2 Neural Models of Interoception

Several models have attempted to explain the neural basis of interoception (e.g., Barrett & Simmons, 2015; Craig, 2009; Seth, 2013). The models often posit that interoception has a major role in emotional responses. Craig (2009) proposed that the integration of interoceptive and exteroceptive signals in the anterior insular cortex gives rise to experiencing emotions. Craig (2009) postulates that the posterior insula receives interoceptive input from the body, which then transmits the signals to the mid-insula. In the mid-insula, the input is integrated with emotional stimuli and environmental conditions sent from the amygdala and the temporal lobe (hypothalamus). Those representations are then integrated with motivational conditions, including goal relevance, from the ventromedial PFC, the anterior cingulate cortex (ACC), and dorsolateral PFC, as well as with hedonic and social conditions. This integration of interoception and environmental and motivational conditions is not only relevant to emotions but to a sense of self, suggesting that awareness is built on homeostasis. Craig (2009) suggested that the anterior insular cortex is the substrate for the awareness of oneself, others, and the environment, and that it is consequently the main region involved in consciousness.

Seth (2013) also postulated that interoception is brought upon by predictive coding, whereby the brain creates top-down models with predictions about incoming interoceptive signals and receives bottom-up interoceptive signals. Seth (2013) argued that emotions arise from the active inference on the causes of physiological changes in the body. According to this theory, emotions arise from the predicted causes of changes in the body’s physiological condition. The model incorporates a desired state, and internal models that predict the incoming bodily (interoceptive) and exteroceptive signals. When interoceptive signals (bottom-up) input mismatches the interoceptive predictions, a prediction error occurs. The predictions are then updated to accommodate the interoceptive signals, which are in turn relayed to change autonomic reflexes such as breathing or heart rate. The theory, then, posits that predictive models are generated, compared with bottom-up input, and updated within the salience network— specifically the anterior insular cortex and the ACC. Similarly, past studies have shown that anticipation of emotions (Nitschke, Sarinopoulos, Mackiewicz, Schaefer, & Davidson, 2006) and empathy happen in the anterior insular cortex (Singer, Critchley, & Preuschoff, 2009). Seth (2013), similar to Craig (2009), linked interoception to emotions and the sense of selfhood.

Barrett (2017) proposed that the brain's function is to maintain allostasis—the maintenance of resources for physiological systems to support growth, survival, and reproduction. The brain maintains allostasis by creating an "internal model of the body in the world," which is predictive and anticipates the body's needs. Importantly, Barrett (2017) postulated that interoception is integral to the brain's internal model, and results from allostasis. Furthermore, Barrett (2017) posited that interoceptive signals are experienced as affect and that limbic regions, usually attributed to emotions, are the main regions involved in maintaining allostasis. Additionally, according to Barrett (2017), different emotions do not have distinct neural networks, and the same emotion experience could be generated by multiple brain activation patterns (degeneracy).

In the theory of constructed emotions, Barrett and Simmons (2015) argued in greater detail that the interoceptive inference occurs beyond the anterior insular cortex, extending across the cortical interoceptive network and somatosensory pathways. Barrett and Simmons (2015) posited that the agranular visceromotor cortices generate the allostatic predictions, which are relayed to the hypothalamus, brainstem, and spinal cord nuclei. The theory further suggests the allostatic predictions are accompanied by interoceptive predictions. The visceromotor cortices, including the cingulate cortex, medial PFC, orbitofrontal cortex, and ventral anterior insular cortex generate interoceptive predictions. In turn, those predictions are relayed to the posterior insula. Consequently, the theory proposes that interoception is not limited to the insula but rather is the result of a widespread brain network that supports allostasis. The interoceptive sensations were theorised to be experienced as sensations of affect.

1.8.3 Neural Evidence on Interoception and Emotion.

Studies investigating the neural basis of interoception showed a crucial role of the insula and the ACC. In a seminal study, Critchley et al. (2004) investigated the neural correlates of interoception. Participants heard tones and were asked to judge whether they were synchronous to their own heartbeats. The study found that, in comparison to the control (judging the quality of tones), the interoceptive task activated the insula, the ACC, and the somatomotor and parietal cortices. Performance on the interoception task—the accuracy in judging tones synchronous with own heartbeats—was correlated with activation in both the right anterior insular cortex and the grey matter volume in the right anterior insular cortex. Activation in the right anterior insular cortex also correlated with negative affect.

The integral role of the insula in interoception was supported in a recent meta-analysis (S. M. Schulz, 2016) that included nine studies investigating attention to heartbeats (cardiac interoceptive attention). The study found that cardiac interoceptive attention activated the insula, specifically the posterior insula. Activation in the anterior insula did not reach significance. The authors suggested that the anterior insula may be implicated in interoceptive tasks with accuracy judgment (e.g., judging tones as synchronous to own heartbeats), while the posterior insula was involved in attention to interoceptive signals. The meta-analysis also found increased activation in the medial frontal gyrus, which may reflect the task demand as well as process the interoceptive signals. The claustrum was also activated. This may suggest that attention is needed for the task, and that, due to the claustrum's widespread connectivity, interoceptive information is sent to widespread areas in the brain.

The ACC was also shown to be integral to interoception. Another meta-analysis investigated the neural basis of interoception (Adolfi et al., 2017). Rather than examining only cardiac interoceptive attention, it included neuroimaging studies of interoception from different visceral sources, including soft touch, gastric sensations, thirst, and breathlessness. The study found activation in the insula, particularly the right anterior insular cortex, in addition to the ACC and the thalamus. The ACC is likely implicated in interoception from visceral organs other than the heart. The roles of the insula and the ACC have been highlighted in prominent interoception theories (Craig, 2002, 2009; Critchley et al., 2004). The thalamus is likely implicated in the sending of bottom-up interoceptive signals to the interoceptive network.

Neuroimaging research has also supported an association between interoception and emotion. For example, evaluating the current bodily state and the emotional state activates similar brain regions, including the right anterior insula and the ventromedial prefrontal cortex (Terasawa, Fukushima, & Umeda, 2013). An overlap in brain regions implicated in interoception and emotions was also observed in other studies (Pollatos, Schandry, et al., 2007; Zaki, Davis, & Ochsner, 2012). The results suggested that emotional processing shares neural correlates with interoception.

A meta-analysis supported this overlap (Adolfi et al., 2017). Adolfi et al (2017) performed a meta-analysis on emotional studies—specifically, emotion recognition and emotional perception tasks. Emotion tasks activated the amygdala, inferior frontal gyrus, anterior insular cortex, ACC, left claustrum, and the thalamus. Therefore, emotion and interoception both activated the insular cortex, the ACC, and the PFC. Consequently, the meta-analysis supported the association between interoception and emotions.

Other meta-analyses investigating the neural basis of emotion have also shown activation of the insula and the ACC. Phan et al. (2002) performed a meta-analysis on the regions implicated in experiencing emotion. The authors found that the insula and the ACC were activated when emotion was induced through autobiographical recall or imagery. The insula and the ACC were also activated when the emotional tasks included cognitive demands such as rating of valence or arousal, recognition of emotion, or intentional encoding. The regions were elicited across all emotions. The authors argued that activation of the insula and ACC suggests that the regions are implicated in emotion processing elicited “internally”. Other meta-analyses also supported the role of the insula in emotions. A meta-analysis found that the anterior insular cortex was activated during empathy, referring to the understanding of others’ emotional states (Gu, Hof, Friston, & Fan, 2013). The meta-analysis also found that emotions of pain, negative emotions, and positive emotions activated the anterior insular cortex and the ACC. Other regions activated included the amygdala, prefrontal cortex, and thalamus. In a meta-analysis covering emotional recognition tasks, the insula was activated in response to angry and disgusted faces (Fusar-Poli et al., 2009), which may suggests that interoception is only crucial to certain emotions. The next section discusses the behavioural evidence of the association between interoception and emotion.

1.8.4 Behavioural Evidence on Interoception and Emotion

Behavioural studies examining the role of interoception and emotion have primarily used one or both of the following two tasks: a) heartbeat detection or b) heartbeat counting. The heartbeat counting task asks participants to count every time they feel a heartbeat to measure the accuracy of heartbeat detection (Schandry, 1981; Werner et al., 2013; Zamariola et al., 2018). In the heartbeat detection task, participants are presented with tones and asked to judge if they are synchronous or asynchronous with their own heartbeats (Blackwell, 1977). Using these tasks, research has found that individuals with higher interoceptive ability are more likely to report higher subjective arousal ratings for emotional stimuli (Pollatos, Gramann, & Schandry, 2007; Pollatos, Herbert, et al., 2007; Pollatos, Kirsch, & Schandry, 2005) and demonstrate enhanced heart rate responses to emotional stimuli (Pollatos, Herbert, et al., 2007).

Higher interoception has also been associated with increased negative emotional response to a stress task (Kindermann & Werner, 2014b, 2014a). Herbert et al. (2010) showed that participants with higher interoceptive awareness show increased arousal ratings to pleasant and unpleasant images relative to low interoceptive awareness. In line with these findings, Schulz and Vogele (2015) proposed a positive feedback loop between stress and interoception. According to the model, stress alters interoception, leading to heightened attention to and sensation of physical stress symptoms, which in turn increases stress (A. Schulz & Vögele, 2015).

Findings on the association between interoception and emotion suggest an association with emotional memory. Two studies found associations between interoception and emotional memory (Pollatos & Schandry, 2008; Werner et al., 2010). The studies found that individuals with better performance on tasks relating to accuracy in perceiving interoceptive signals had enhanced performance on emotional memory than those with lower interoceptive accuracy. However, the interoceptive task used in both studies received recent criticism, undermining its validity (Desmedt, Luminet, & Corneille, 2018; Murphy et al., 2018; Ring, Brener, Knapp, & Mailloux, 2015). The evidence is provided in greater detail in Chapter 3. The present thesis aims to test the association between interoception and emotional memory through manipulating interoception via true biofeedback.

1.9 Functional Connectivity and Emotion

Another question which has not been answered concerns the role of functional connectivity during rest. Evidence suggests that the brain's functional and anatomical structure influences the emotional experience (Hamann & Canli, 2004). Functional connectivity is also associated with interoception (Chong et al., 2017; Kuehn et al., 2016). It is therefore likely that functional connectivity is associated with emotional memory if interception is associated with emotional memory, as discussed above. Supporting this notion, in a commentary on the role of emotion and memory, Critchley and Garfinkel (2016) suggested including both interoception and the functional organisation of regions implicated in emotion in the GANE model. Indeed, the structure and activation of the amygdala, hippocampus, insula, hypothalamus, and prefrontal cortex have been associated with individual differences in emotional processing (Hamann & Canli, 2004). In particular, amygdala activation was found to be correlated with the memory of emotional items (Cahill et al., 1996; Canli et al., 2000; Hamann et al., 1999; Murty et al., 2009; Ritchey et al., 2008) in addition to emotional intensity and valence ratings (Phan et al., 2004). The degree of personal association with emotional stimuli was also correlated with the medial PFC and insula activation (Phan et al., 2004).

The present thesis is interested in the effect of the brain's functional connectivity during rest on emotional memory. During rest, the brain exhibits meaningful activity that is similar to task-evoked activity (S. M. Smith et al., 2009). Networks activated at rest have been implicated in cognition, language, perception, and motor movement (Damoiseaux et al., 2006; S. M. Smith et al., 2009). Functional connectivity refers to the temporal correlation in activity between separate regions. Functional connectivity at rest also reflects the brain's structural connectivity (Sarwar, Tian, Yeo, Ramamohanarao, & Zalesky, 2021; Suárez, Markello, Betzel, & Misic, 2020). Individual differences in functional connectivity during rest are likely stable across sessions (Finn et al., 2015; Gratton et al., 2018; W. D. Stevens & Spreng, 2014) and are often indicative of differences in task-evoked functional connectivity (Cole, Bassett, Power, Braver, & Petersen, 2014; Laird et al., 2011). Indeed, functional connectivity at rest has been associated with behavioural and cognitive measures (e.g. Barnes, Anderson, Plitt, & Martin, 2014; Dubois, Galdi, Han, Paul, & Adolphs, 2018; Finn et al., 2015; Q. Lin et al., 2018) and has shown strong evidence of age and sex differences (Biswal et al., 2010). Existing research examining the association between emotions and resting-state functional connectivity is limited. Because of the limited number of studies and the association between individual differences in task-evoked and resting-state functional connectivity, I review studies that included both task-evoked and resting-state functional connectivity.

Resting-state and task-evoked functional connectivity patterns have been associated with interoceptive abilities. Both during performing an interoceptive task (Kuehn et al., 2016) and during rest (Chong et al., 2017; Ueno et al., 2020), functional connectivity in the insula has been associated with individual differences in interoceptive accuracy. Similarly, resting-state functional connectivity has predicted the level of attention to interoceptive signals (S. D. Smith, Nadeau, Sorokopud-Jones, & Kornelsen, 2021). In a large-scale study including over 400 participants, resting-state functional connectivity was found to be different for individuals with high interoceptive attention (X. Wang, Tan, Van den Bergh, von Leupoldt, & Qiu, 2020). Specifically, the functional connectivity of the amygdala and the insula differed in these individuals. Furthermore, the authors found that the association between interoceptive attention and the level of self-reported bodily symptoms was partly explained by differences in resting-state functional connectivity. Evidence, then, suggests that differences in interoceptive abilities are associated with functional connectivity differences not only during related tasks but also during rest. Evidence of an association between functional connectivity patterns and interoception indicates that functional connectivity may also be associated with emotional memory. As shown in previous sections, the insula and the ACC are associated with emotional processing. Yet, most research on emotion has focused on the amygdala, as described below.

Individual differences in factors closely associated with the emotional experience are often reflected in the brain’s functional and anatomical structure. Regions implicated in emotional processing are modulated by personality traits, stress, gender, genetics, and psychological disorders. For example, early life stress may lead to a reduction in the volumes of the amygdala and hippocampus (Hanson et al., 2015). Amygdala activation in response to negative material has shown elevated levels in individuals with mood disorders (Phillips, Drevets, Rauch, & Lane, 2003) and anxiety (Stein, Simmons, Feinstein, & Paulus, 2007; Thomas et al., 2001). Bipolar depression has been associated with increased amygdala and insula activation as well (Marchand & Yurgelun-Todd, 2010). Alexithymia has been associated with decreased amygdala and insula reactivity during emotional processing (Moriguchi & Komaki, 2013; van der Velde et al., 2013). Chronic stress has shown to modulate the functional connectivity of the amygdala (Roozendaal, McEwen, & Chattarji, 2009; Zhang et al., 2018).

Consequently, the research also suggests an association between functional connectivity and the emotional response. For example, when viewing and evaluating emotional items, functional connectivity pattern in the ACC predicted depressive symptoms (R. Smith et al., 2015). Furthermore, task-evoked functional connectivity between the amygdala and the prefrontal cortex was associated with emotion regulation ability (H. Lee, Heller, van Reekum, Nelson, & Davidson, 2012). Task-evoked functional connectivity measured by EEG predicted the self-reported emotional response to positive, negative, and neutral films (Y.Y. Lee & Hsieh, 2014). Studies investigating resting-state functional connectivity also found an association between functional connectivity patterns and the emotional response. A past study predicted trait negative affect from fluctuations in whole-brain functional connectivity during rest (Li et al., 2020). Furthermore, resting-state functional connectivity within limbic regions predicted emotion recognition performance (W. F. Z. Yang et al., 2021).

Although the research on the resting-state functional connectivity and emotional processing is limited, existing evidence suggests that the brain’s resting-state functional connectivity patterns influence emotional processing and by consequence emotional memory. As reviewed below, although a limited number of studies investigated the association between resting-state functional connectivity and emotional memory, many studies investigated and found an association between *task-evoked* functional connectivity and emotional memory (e.g., Dolcos et al., 2004; Ritchey et al., 2008; St. Jacques et al., 2009).

Task-evoked (usually encoding-evoked) functional connectivity patterns have often been linked with emotional memory. For example, the positivity bias in aging is associated with differences in functional connectivity. Compared to younger adults, older adults exhibit increased functional connectivity between the amygdala and frontal cortical regions, including the ACC, posterior regions including the parahippocampal cortex, and visual cortices, when viewing negative material (St. Jacques, Dolcos, & Cabeza, 2010). These results indicate that the positivity bias is caused by increased emotion regulation and decreased visual processing of negative items, supporting the notion that ageing is accompanied by a motivation to regulate emotion (Carstensen, Fung, & Charles, 2003). Similarly, the functional connectivity between the amygdala and hippocampus is reduced in older age (St. Jacques et al., 2009). Task-induced functional connectivity in the amygdala, hippocampus and the PFC was associated with enhanced memory of emotional items (Dolcos et al., 2004; Murty et al., 2009; Ritchey et al., 2008; Sakaki et al., 2013; St. Jacques et al., 2009). The effects of functional connectivity and emotional memory were also evident in a study investigating the positivity effect in younger and older adults (Sakaki et al., 2013). During encoding, functional connectivity between the amygdala and the medial prefrontal cortex predicted positivity bias in memory in older adults.

Most of the research investigating the association between emotional memory and functional connectivity concerned connectivity during encoding. However, research suggests that resting-state functional connectivity is also associated with emotional memory. Resting-state functional connectivity between the amygdala and the prefrontal cortex in addition to the frontal middle gyrus were associated with positivity effect in older adults (Sakaki et al., 2013). Another study found that the resting-state functional connectivity between the anterior insula and the ACC was associated with the memory of neutral items shown after negative mood induction (Andreano, Touroutoglou, Dickerson, & Barrett, 2017).

Other support for the association between emotional memory and resting-state functional connectivity is the research investigating neutral memory. Neutral memory is strongly associated with resting-state functional connectivity of the medial temporal lobe (Fjell et al., 2016; Salami et al., 2014; Salami, Wahlin, Kaboodvand, Lundquist, & Nyberg, 2016). A study was able to find good retest reliability (1 week) for hippocampus and cingulate cortex functional connectivity association with individual differences in memory (Touroutoglou, Andreano, Barrett, & Dickerson, 2015). On the other hand, the association between the default mode network connectivity and neutral memory received mixed evidence (Salami et al., 2014; Staffaroni et al., 2018; Tambini, Ketz, & Davachi, 2010). The present thesis investigates the association between whole-brain functional connectivity and emotional memory in a large database including adults of all ages.

Therefore, most of the research investigating the association between emotional memory and functional connectivity was task-evoked and concerned the amygdala. Due to the association between interoception and emotion, it is also likely that the insula has an important role as well. Rather than investigating regions of interest, this thesis attempted to investigate the association of whole-brain functional connectivity with emotional memory using a machine learning algorithm that automatically selects the relevant connections.

1.10 Present Studies

The enhancing effects of emotion on memory are likely driven by increases in arousal. Arousal's effects have been hypothesised as selective, enhancing the memory of the emotional stimuli and central or goal-relevant neutral information and impairing peripheral or goal-incongruent information. Recently, emotional arousal was found to have prolonged effects, altering the memory of items encountered tens of minutes after the emotional episode (Tambini et al., 2017). However, the association between the prolonged effects of arousal and priority remains unknown. The present thesis begins by investigating the prolonged effects of emotional arousal on memory according to items' priority. The next two chapters investigate possible moderators of emotional memory, namely interoception and functional connectivity during rest. As described above, emotional processing has been closely associated with interoceptive ability and the brain's functional connectivity. For example, a recent commentary recommended incorporating interoception and functional connectivity in the GANE model of emotional memory (Critchley & Garfinkel, 2016). Evidence indicates that interoceptive abilities play an integral role in memory and the emotional experience (e.g., Barrett et al., 2004; Pollatos & Schandry, 2008). Neural differences have also been linked to individual differences in emotion (Hamann & Canli, 2004), interoception (Chong et al., 2017; Ueno et al., 2020), and memory (Sakaki et al., 2013). Chapters 3 and 4 examine the effects of interoception and the brain's functional connectivity memory of emotional items.

In the first empirical study (Chapter 2), emotional arousal was induced through a speech task paired with false increasing cardiac biofeedback. The study investigated the prolonged effects of arousal on memory of goal-congruent and goal-incongruent neutral stimuli. The next chapter investigated the effects of interoception on the memory of emotional stimuli themselves. Unlike in Chapter 2, in Chapter 3, we introduced true cardiac biofeedback while presenting emotional items. We then investigated how the memory is modulated by cardiac feedback. In the final empirical study (Chapter 4), we investigated if the brain's functional connectivity at rest predicts emotional memory. Specifically, we attempted to predict individuals’ emotional memory scores from resting-state functional connectivity in a large database using machine learning analyses.

Chapter 2: Does Arousal Have Long-Lasting Effects on Memory for Subsequent Neutral Information?

2.1 Abstract

Emotionally arousing events are usually recalled better than neutral. However, it is unclear whether emotional arousal has a ‘spill-over’ effect to enhance memory of subsequent unrelated information. There is mixed evidence regarding the prolonged effects of arousal, with some studies suggesting an enhancement, while some showing an impairment or no effect on the memory of subsequent items. The prolonged effects of emotional arousal on neutral memory remain unclear. Furthermore, it remains unclear whether the prolonged effects of arousal differ depending on item’s priority (i.e., goal-relevance). The present study investigates the effects of emotional arousal on the memory of goal-relevant and goal-irrelevant neutral items presented minutes after an emotionally arousing task. Emotional arousal was induced by a public speaking task paired with false biofeedback of an increasing heart rate. The control task consisted of a reading task paired with false biofeedback a decreasing heart rate. The study found that high priority items were recalled better than low priority items in both conditions. However, such priority effect did not significantly interact with emotional arousal. Arousal did not have a significant main effect either. The findings suggest that emotional arousal does not always have prolonged effects on the memory of neutral items encountered minutes later.

2.2 Introduction

Whereas the effects of emotion on the memory of neutral items encountered during an emotional event is well-researched, there is mixed evidence on the effect of emotion on the memory of subsequent neutral information (Schlüter et al., 2019). Recent evidence has shown that emotion enhances the memory of neutral unrelated items encountered minutes later (Tambini et al., 2017). However, past evidence also shows that when emotional stimuli precede neutral stimuli by seconds, they often impair or have no effect on the memory of those neutral items (Schlüter et al., 2019). According to the ABC theory, the prolonged effects of arousal may be modulated by the priority of neutral information (Mather & Sutherland, 2011). In the present study we investigate the prolonged effects of emotional arousal on the memory of neutral items of varying priority.

Most of such research concerned the prospective effects of emotions on neutral stimuli presented a few seconds later. The timing effects of emotional arousal are often studied in oddball paradigms. For example, Hurleman et al. (2005) presented neutral and "oddball" images. Neutral images were in the form of black and white line-drawing images. Oddball images were photographs which could be of negative, positive, or neutral valence. The study found that the memory of images presented after emotional, compared to neutral, oddballs was poorer. Further studies also investigated the memory of neutral items presented after emotional oddballs. The memory of neutral items presented immediately after emotionally-arousing items is usually impaired — termed emotion-induced anterograde amnesia (e.g., Hurlemann et al., 2005; Knight & Mather, 2009; Sakaki, Fryer, & Mather, 2014). Other studies, however, found no effect of emotion on the memory of neutral items presented after negative stimuli (Miu et al., 2005; Strange, Kroes, Fan, & Dolan, 2010).

Emotion-induced anterograde amnesia may be explained by the varying effects of arousal depending on priority, which is proposed in the arousal-biased competition theory

(Mather & Sutherland, 2011). Neutral items may compete with emotional items for processing resources, leading to impaired neutral memory. The arousal-biased competition (ABC) theory posits that arousal induces a winner-takes-all effect, enhancing the processing and memory of high priority information and impairing that of low priority information (Mather & Sutherland, 2011). The ABC theory has been influential in understanding the mixed effects of emotion on the memory of neighbouring neutral information. Information may be regarded to have a high priority due to bottom-up sensory or top-down cognitive factors. The enhancing effect of emotion on goal-relevant material has been previously documented (reviewed in Levine & Edelstein, 2009). The ABC theory proposes that arousal enhances the encoding of high priority material, details, or even associations, and impairs the encoding of that of low priority. The enhanced processing of highly-arousing information is theorised to impact both the short-term and the long-term memory of the information (e.g. Lee, Greening, & Mather, 2015; Sakaki et al., 2014; Sutherland & Mather, 2012). A likely explanation for emotion-induced anterograde amnesia is that neutral items compete with emotionally-arousing items in processing and memory. High arousal items are themselves high priority (Mather & Sutherland, 2011). Therefore, neutral items compete in processing with high priority items for attentional and processing resources, leading to impaired processing.

Studies investigating the short-term memory support the ABC effect. For example, in one study, participants heard a negative sound, such as a scream, or a neutral sound, before viewing letters with high salience (dark-shaded) and ones with low salience (lighter-shaded; Sutherland & Mather, 2012). Participants were then asked to recall the presented letters immediately after presentation. Emotional arousal enhanced the short-term memory of salient letters. Other studies have similarly found that arousal enhances the short-term memory of high priority items (Sutherland & Mather, 2015; Sutherland & Mather, 2018; but see Ásgeirsson & Nieuwenhuis, 2019).

Few studies have manipulated priority when investigating the anterograde effects of emotion on long-term memory. However, existing evidence suggests that when the neutral stimuli were prioritised, emotion-induced anterograde amnesia ceased (Sakaki et al., 2014). Sakaki et al. (2014) utilised a top-down approach and asked participants to prioritise images based on their temporal position relative to "oddball" images. The oddball pictures could be negative, positive or neutral. When neutral images presented subsequent to emotional oddballs were prioritised, there was no emotion-induced anterograde amnesia (Studies 2, 3). On the other hand, when neutral images presented subsequent to emotional oddballs were not prioritised, there was anterograde amnesia.

However, recent evidence suggests prolonged effects of emotions on memory (Tambini et al., 2017; Vaisvaser et al., 2013). A recent study showed that inducing arousal by presenting emotional pictures leads to an enhancement of the memory of neutral objects encountered tens of minutes later (Tambini et al., 2017). The study presented a 23-minute block of either negative or neutral items, followed by a 9-minute rest period, and a second 23-minute block of either negative or neutral items. fMRI scans were taken during the image presentation blocks. Six hours after encoding, a surprise memory test was administered. The memory of neutral items was significantly better when presented after a block of negative items than after a block of neutral items. Skin conductance also showed prolonged increase after negative blocks that was sustained until the neutral blocks. Notably, the functional connectivity patterns between the amygdala and the whole brain, the increased connectivity between the amygdala and the anterior hippocampus, and the increased connectivity within the anterior insula were also carried over from negative blocks to neutral blocks. On the other hand, connectivity patterns were not carried over from neutral to negative blocks. Therefore, the study showed that emotional arousal induction led to sustained neural and physiological effects for tens of minutes, and led to enhanced memory of unrelated subsequent neutral items.

Several studies show that arousal triggers prolonged functional connectivity patterns in the brain. Van Marle et al. (2010) found increased functional connectivity of the amygdala with the dorsal anterior cingulate cortex (ACC) and the anterior insula in a resting-state scan following the presentation of negative emotional clips. These regions are implicated in emotional awareness and bodily arousal (Craig, 2003; Critchley et al., 2004). The prolonged connectivity patterns of the amygdala suggest extended hypervigilance to emotional stimuli. Similarly, Eryilmaz et al. (2011) found that immediately after inducing emotions through clips, there was increased functional connectivity between the insula and the ACC, which suggests increased integration of interoceptive signals of bodily arousal. Other studies investigated the amygdala after stress manipulations using mental arithmetic and social judgement. Those studies found prolonged changes in functional connectivity, hours after stress. Veer et al. (2011) found that one hour after stress induction, the amygdala had increased functional connectivity with the posterior cingulate cortex and the medial prefrontal cortex, suggesting enhanced emotion regulation and enhanced memory. Similarly, Vaisvaser et al. (2013) found increased amygdala and hippocampus functional connectivity two hours after stress induction. Functional connectivity between the amygdala and hippocampus has been associated with enhanced emotional memory (Dolcos et al., 2004; St. Jacques et al., 2009).

On the other hand, behavioural studies suggest that the prolonged effects of emotions are weak. Sutherland and Mather (2012) found no anterograde effects of arousal on the short-term memory of neutral stimuli (of any priority) that were presented 4 – 6 seconds after emotional stimuli. This is in contrast to the enhanced short-term memory of high priority neutral stimuli, and the impaired short-term memory of low priority neutral stimuli presented .75 – 3 seconds after emotional stimuli. The study suggests that the anterograde effects of arousal are not likely to be prolonged. However, the study investigated only the short-term memory. The effects of arousal on memory is often shown hours after encoding, due to the enhancing effects of arousal on consolidation (Talmi, 2013) or the slower forgetting of emotional items (Yonelinas & Ritchey, 2015). The findings are coupled with evidence of the *immediate* anterograde effects of emotional arousal on the memory of neutral items. Emotion-induced anterograde amnesia does not always reach significance (Schlüter et al., 2019). Even increasing the priority of the neutral items subsequent to emotional item exposure does not always lead to an emotion-led enhancement in memory when compared to presentation after neutral (Jia et al., 2020; Sakaki et al., 2014; Sutherland et al., 2017).

It remains unclear how prolonged arousal affects the memory of neutral information of varying priority. In the present study, we administered a control task or induced emotional arousal through the use of public speech task. The tasks were followed by presenting neutral images of high and low goal-relevance. In order to make the speech task more emotionally arousing, a false biofeedback was administered showing increasing heart rate during the speech (Makkar & Grisham, 2013). A decreasing heart rate biofeedback was utilized for the control task — a silent reading task. False feedback manipulations presenting a slowing heart rate have often shown a reduction in apprehension and anxiety in comparison to an increasing heart rate (Costa, Adams, Jung, Guimbretière, & Choudhury, 2016; Makkar & Grisham, 2013; Wild, Clark, Ehlers, & McManus, 2008). We then investigated the memory of the items on the following day. We expected that emotional arousal would magnify the effects of goal-relevance, leading to better memory of goal-relevant items and more impaired memory of low-goal relevant items compared to the control condition.

2.3 Methods

2.3.1 Participants

A total of 80 participants (68 females), aged 18 – 44 years were recruited from the University of Reading. The study was approved by the University Research Ethics Committee at the University of Reading. An a-priori power analysis showed that a sample of 80 participants is needed to detect a small-medium effect size of $f = .16$ with a statistical power of 80% (G*Power 3.1 Software; Faul, Erdfelder, Buchner, & Lang, 2009).

2.3.2 Physiological Measurement

Skin conductance data were obtained by galvanic skin response electrodes placed on the third and fourth fingers. Heart rate was obtained with the use of a finger pulse transducer placed on the first finger. Physiological measurements were obtained by ADInstrument PowerLab 26T (ADInstruments, Oxford, UK) and GSR amplifier (ADInstruments), and analysed by LabChart version 7.3 (ADInstruments).

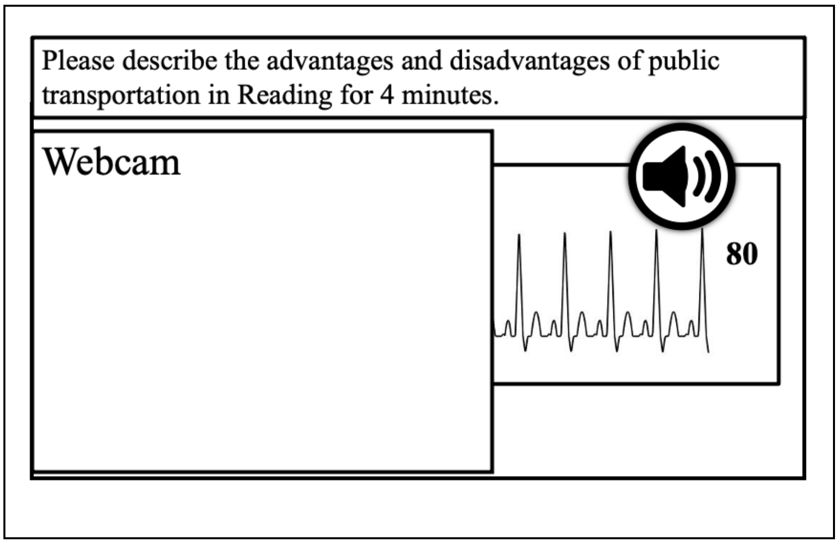
2.3.3 Stimuli

Sixty images of tools (e.g., comb, scissors, wheel) and sixty images of animals were selected from a public clipart repository. Images were in the form of black and white drawings and were displayed against a white background (see Appendix A). All images were 281 x 197 pixels in size. The images were split into two lists, each of which contained 30 tool and 30 animal images. One list was presented in the picture task while the other was used for the “new” images in the subsequent memory test. The allocation of the 2 image lists as “new” or “old” images was counterbalanced across participants.

2.3.4 Procedures

After obtaining consent, participants filled in a demographics questionnaire, The Social Phobia Inventory questionnaire (SPIN; Connor et al., 2000), Brief Fear of Negative Evaluation Scale (BFNE; Leary, 1983), Center for Epidemiologic Studies Depression (CES-

D; Radloff, 1977), and the Positive and Negative Affect Schedule questionnaire (PANAS; Watson, Clark, & Tellegen, 1988). The questionnaires were followed by a 3-minute baseline measurement of heart rate and skin conductance. Participants were asked to sit in a comfortable position with minimal movement. Next, participants were randomly assigned to a reading or speech task. The number of participants was counter-balanced across the two conditions. Participants were told of the nature of the task and were informed that they had one minute to prepare for the task — either prepare for reading or for making a speech about public transportation in Reading.



Please describe the advantages and disadvantages of public transportation in Reading for 4 minutes.

Figure 2.1. During the speech task, participants were asked to prepare and make a speech about public transportation in the town. During the speech performance participants viewed themselves on one side of the screen, and a false ECG simulation of an increasing heart rate on the other side. The ECG simulation included playing tones indicating the heartbeats.

Both the reading and speech task incorporated a false feedback manipulation consisting of (1) playing tones indicating the participants' heartbeat on speakers and (2) simultaneously presenting an electrocardiogram (ECG) simulation on the screen. The tones were adjusted to be audible but not distracting. Participants were asked if they could hear the sound during the training phase of the task, and the volume was adjusted if needed. The ECG simulation presented the current (false) heart rate and an online ECG graph. This false feedback manipulation was adapted from Makkar and Grisham (2013). The feedback was introduced to make the speech task more emotionally arousing, while the reading task was made more relaxing. The reading task was accompanied by a slowing heart rate presentation, going slowly from 105 to 72 beats per minute (bpm) and plateauing on the values 67 - 70 bpm. The speech task was accompanied by an increasing heart rate going from 72 bpm to 101 bpm and plateauing on the values 101 - 104 bpm.

In the reading task, participants were asked to silently read a two-page excerpt about public transportation in Reading (Reading Borough Council, 2011). The speech task was adapted from the simulated public speaking task (McNair et al., 1982). Participants were asked to make a speech about the advantages and disadvantages of public transport in Reading. Participants were falsely told that the speech will be recorded to be later analysed for presentation and critical thinking skills. Participants were placed in front of a computer screen, viewing themselves on the left side of the screen and viewing the ECG on the right side (Figure 2.1). The researcher was present during the speech performance. Participants were given 4 minutes to complete the speech and were reminded to end the speech soon if not finished within 4 minutes. If the participants finished before 4 minutes were up, they were encouraged to come up with more arguments.

Next, participants completed a second PANAS questionnaire to measure mood after the task. The picture task then started. A total of 60 images were displayed across 3 blocks separated by 1-minute breaks. Participants were instructed at the beginning of the task to focus particularly on one image type (e.g., “Please focus only on animal pictures”). In order to make sure that participants were following instructions and focusing on task, they were asked to press a key whenever a high-priority (goal-relevant) image was presented. Every image was presented for 3 seconds followed by a 1-second fixation cross (Figure 2.2). The task began with a training phase.

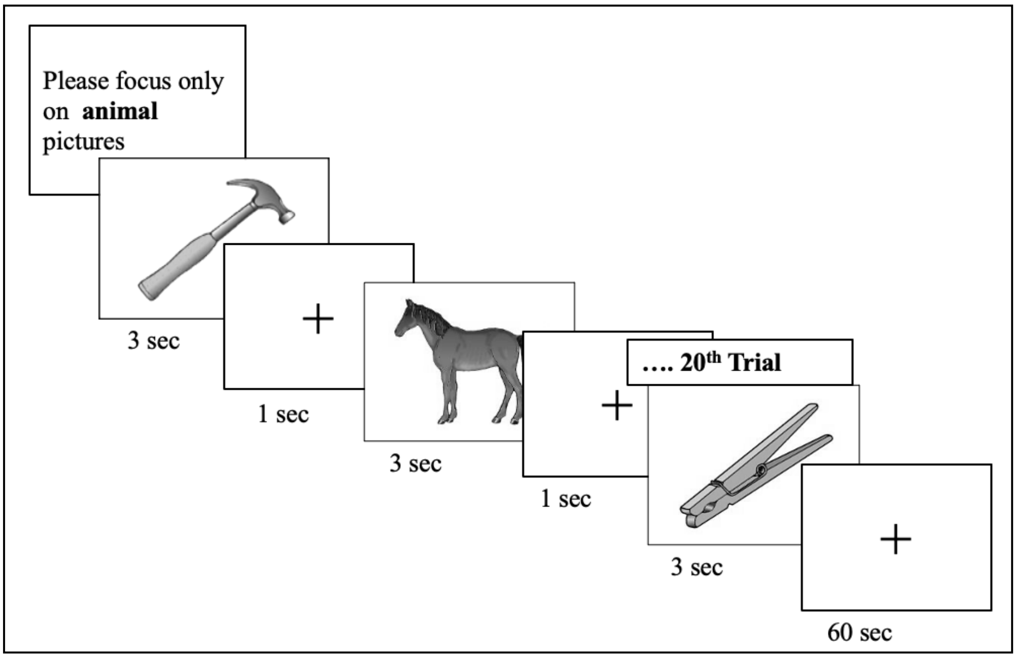


*Figure 2.2***.** The picture task presented images of animals and tools — one of which participants were asked to prioritise. A total of 60 images were shown across 3 blocks separated by 1-min breaks.

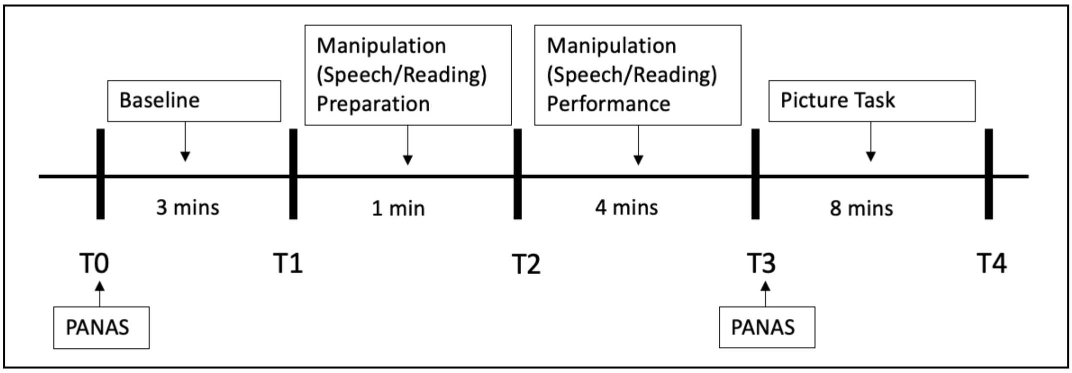


Figure 2.3. A timeline of the first session. After obtaining consent, a 3-min baseline measurement was taken, followed by preparation for the speech or reading task (1-min), performance of the speech or reading task (4-min), and the picture task (8-min). Positive and negative affect (PANAS; Watson, Clark, & Tellegen, 1988) were measured at baseline (T0) and prior to the picture task (T3).

A memory task was conducted online on the second day. After 24 hours had passed since the first session, participants were sent an invitation to complete an online memory test. Participants were instructed to have minimal distraction while completing the test and to complete the test on a personal computer or laptop. Participants had a 24-hour window in which to complete the test. The memory test was a recognition test consisting of 60 new and 60 old images. The corrected recognition rate was obtained for the memory by subtracting the false alarm rate from the hit rate.

2.4 Results

We first performed manipulation checks about the effects of the speech on the heart rate and skin conductance during the preparation phase, performance phase, and the picture viewing task. We also examined the effects of the manipulation on the self-reported negative affect. We then examined whether the manipulation led to changes in the memory and whether this effect interacted with items' priority.

2.4.1 Heart Rate

To examine the effects of the speech task on the heart rate, a 4 x 2 mixed ANOVA was conducted with time as a within-participant factor and condition as a between-participant factor. Timepoints were baseline, manipulation (speech or reading) preparation, manipulation performance, and picture task (Figure 2.3). There were no outliers, as no datapoints had a studentized residual values of over 3 standard deviations from the mean. There was a significant effect of time, $F(3, 77) = 7.12$, $p < .001$, partial η2 = .085, but no main effect of condition, $F(1, 77) = 1.99$, $p = .162$. Pairwise comparisons showed that the mean heart rate was significantly lower during the picture viewing task than baseline ($M_{picture\ task}$= 74.7, SD = 9.69; $M_{baseline}$= 77.3, SD = 10.5), and the manipulation preparation ($M_{preparation}$= 78.7, SD =

11.3), *ps* < .001 with Bonferroni's correction. There was a significant interaction between condition and time, *F*(3, 77) = 6.23, *p* < .001.

Post hoc simple main effects showed that during task preparation, the heart rate of participants in the speech group (*M* = 825, *SD* = 11.6) was significantly higher than the control (*M* = 74.9, *SD* = 9.78), *F*(1, 77) = 9.98, *p* = .002, partial η2 = .115.

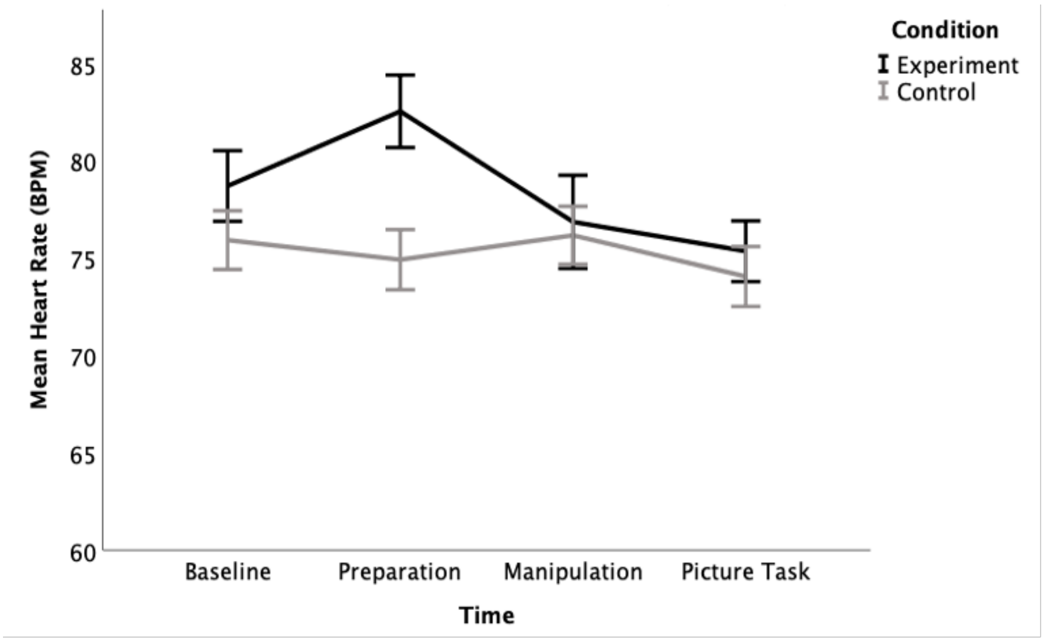


Figure 2.4. Mean heart rate during baseline, preparation for the manipulation task (speech/reading), performance of the manipulation task, and the picture viewing task. Error bars represent the standard error.

2.4.2 Skin Conductance

To examine the effects of the manipulation on skin conductance, a 4 x 2 mixed ANOVA was conducted with time as a within-participant factor and condition as a between-participant factor. There were 2 outliers with studentised residuals of 5.77 and -4.35 standard deviations from the mean. We excluded those participants from the skin conductance analyses. There was a significant main effect of time *F*(3, 75) = 67.9, *p* <.001, partial η2 = .475. Pairwise comparisons with Bonferroni's correction showed that, relative to baseline (*M*

$= .12$, $SD = 3.56$), skin conductance was significantly elevated throughout the preparation phase ($M = 5.56$, $SD = 5.49$, $p < .001$), the manipulation (speech or reading) performance ($M = 7.00$, $SD = 6.33$, $p < .001$), and the picture viewing task ($M = 6.64$, $SD = 7.62$, $p < .001$). Skin conductance during performance for the manipulation was also significantly higher than during manipulation preparation, $p = .001$. There was a main effect of condition $F(1, 75) = 9.16$, $p = .003$, partial η2 = .109. There was a significant interaction between time and condition, $F(3, 75) = 6.61$, $p < .001$, partial η2 = .081.

Simple main analyses showed that the skin conductance of participants in the experimental group was higher than that in the control group during manipulation preparation ($M_{experiment} = 6.93$, $SD = 4.83$; $M_{control} = 4.29$, $SD = 5.82$), $F(1, 75) = 4.65$, $p = .034$, partial η2 = .058, in addition to during performing the manipulation ($M_{experiment} = 10.05$, $SD = 5.95$; $M_{control} = 4.18$, $SD = 5.33$), $F(1, 75) = 20.85$, $p < .001$, partial η2 = .217, and during the picture task ($M_{experiment} = 8.57$, $SD = 6.36$; $M_{control} = 4.84$, $SD = 8.31$), $F(1, 75) = 4.84$, $p = .031$, partial η2 = .061.

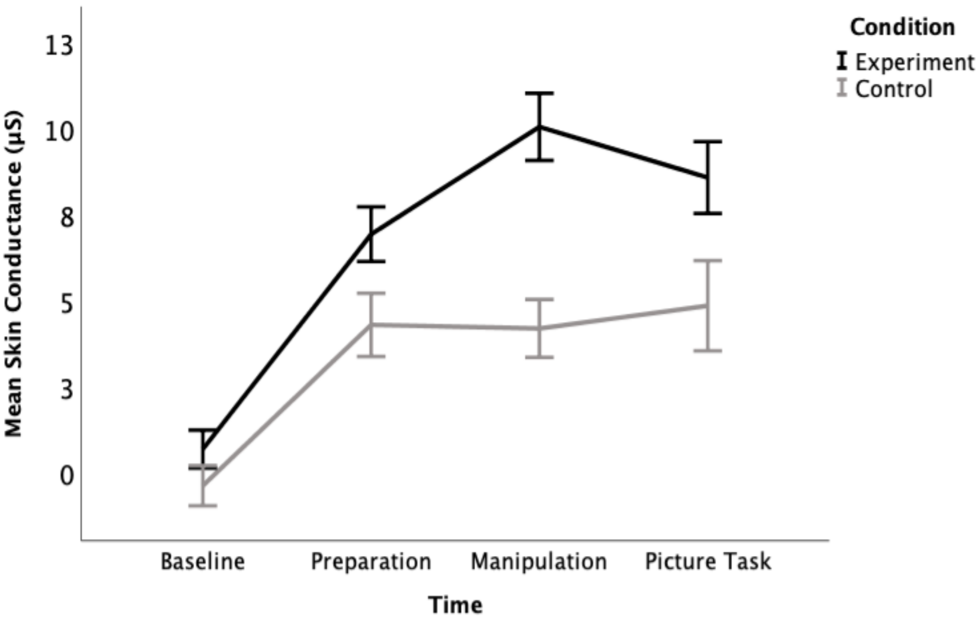


Figure 2.5. Mean skin conductance during baseline, preparation for the manipulation task (speech for the experimental group/reading for the control group), performance of the manipulation task, and the picture viewing task. Error bars represent the standard error.

2.4.3 Negative Affect

A mixed ANOVA was conducted for the negative affect before the reading (control) or speech (experiment) task allocation (Time 0; Figure 2.3) and after the manipulation (Time 3). There was no significant main effect of time, *F*(1, 78) = 3.47, *p* = .066, but there was a significant main effect of condition, *F*(1, 78) = 11.2, *p* = .001, partial η2 = .126, and a significant time and condition interaction, *F*(1, 78) = 14.7, *p* < .001, partial η2 = .159. Simple main effects analysis showed that at Time 3, negative affect was significantly higher for the experimental group (*M* = 17.8, *SD* = 6.77) than for the control group (*M* = 12.6, *SD* = 2.66), *F*(1, 78) = 21.1, *p* < .001, partial η2 = .213.

Table 2.1.

Negative affect before and after the speech (experimental) or reading (control) task

	Experimental *M* (*SD*)	Control *M* (*SD*)
Negative affect at baseline (T0)	14.7 (5.37)	13.6 (3.81)
Negative affect after manipulation (T3)	17.8 (6.77)	12.6 (2.66)

2.4.4 Memory

A mixed ANOVA was conducted on the corrected recognition rate with condition as a between-participant effect, and priority as a within-participant effect. There were no outliers with studentized residuals of 3 standard deviations or over. There was a main effect of priority, *F*(1, 78) = 33.2, *p* < .001, partial η2 = .298, but no main effect of condition *F*(1, 78) = 2.12, *p* = .149, and no interaction between priority and condition *F*(1, 78) = 1.54, *p* = .219.

A follow-up analysis was undertaken to investigate the effect of the image focus type (animals or objects) and image list allocation. The analysis showed no *Focus Type* x *Condition* x *Priority* interaction, *F*(1, 72) = .00, *p* = .995, nor an *Image List* x *Condition* x *Priority* interaction , *F*(1, 72) = .001, *p* = .834.

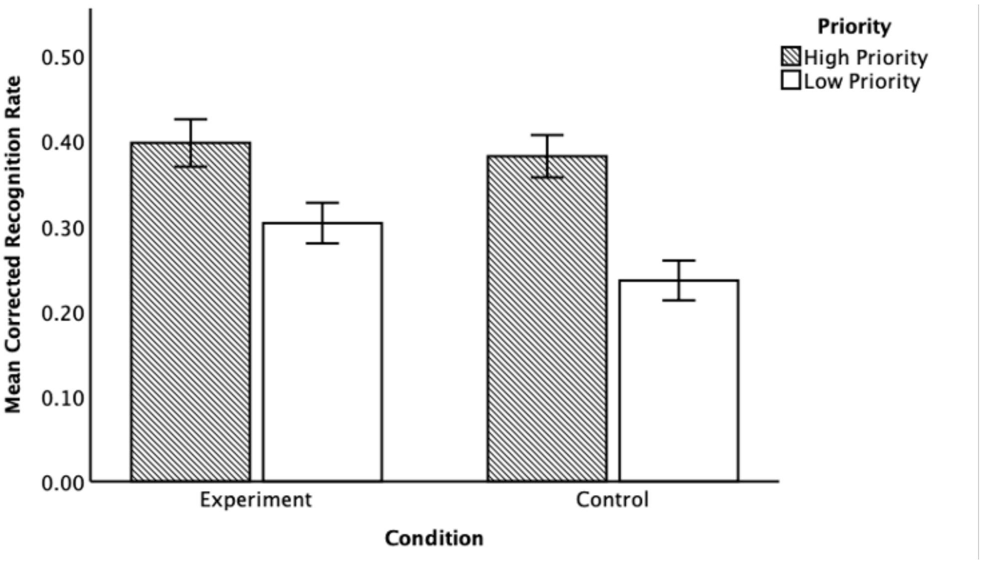


*Figure 2.6***.** Mean memory scores — calculated as the corrected recognition rate — of high priority and low priority images according to group condition. Error bars represent the standard error.

2.5 Discussion

Performing an emotionally-arousing task with an increasing heart rate biofeedback did not affect the memory for subsequent high or low priority items. The speech task increased the heart rate, skin conductance, and negative affect. The enhanced skin conductance response after the speech persisted even during the subsequent picture viewing task, which suggests that the emotional arousal from the speech was prolonged. The results did not replicate a previous finding of prolonged enhancement effect of experiencing emotional arousal (Tambini et al., 2017), but are in line with many past studies showing no effect of arousal on the memory of subsequent items (Miu et al., 2005; Strange et al., 2010; Sutherland et al., 2017).

One possible reason for not observing the prolonged effects of arousal in the present study is that the picture viewing task was significantly different in nature, and therefore unrelated, to the arousal induction. The speech task pertained to analysing public transportation, while the picture task showed clipart images of objects and animals. This is in contrast to Tambini et al. (2017) where the neutral images and emotional images (arousal induction) were simply two blocks of a picture viewing task. The inherent context-congruency (a form of priority) of the emotional induction and neutral images in Tambini et al. (2017) may explain their finding of prolonged enhancement in memory, while the context-incongruence in the present study and studies with similar methods, may explain the null effects (Shields, Sazma, McCullough, & Yonelinas, 2017). Similarly, a change of context, such as a change in rooms or odour between the stress induction and the stimuli encoding may lead to a ceasing of the enhancing effect of post-encoding stress on memory (Shields et al., 2017).

Although we attempted to manipulate priority, past evidence suggests that not all priority manipulations may trigger a winner-takes-all effect. In a past study, participants were presented with personality-related speech, memory-related speech, or a control task, before viewing. personality and memory-related word lists (Smeets, Giesbrecht, Jelicic, & Merckelbach, 2007). Participants assigned to the personality speech condition recalled significantly more personality-related words than did participants in the memory speech group or in the control group. Yet, the memory of memory-related words was not selectively enhanced for the memory-related speech group. Therefore, high relevance, hence priority, may not always lead to enhanced memory. The present findings suggest that manipulating priority through an active instruction to focus on one image type does not modulate the prolonged effects of arousal on memory.

There is evidence that manipulating priority may generally have small effects when the emotional arousal is induced prior to encoding the neutral stimuli. In a past study, participants were presented with two images sequentially (either one neutral and one negative, or two neutral) in each trial (Jia et al., 2020). Goal-relevance was manipulated by asking participants to attend to images with a coloured frame. Neutral images were remembered equally, whether preceded by a negative image or a neutral image, regardless of goal-relevance. Similarly, Sutherland et al. (2017) examined the effects of bottom-up and top-down salience on the memory of items encountered after emotional stimuli. Participants were presented with a neutral, positive or negative image for 1 second before viewing two neutral images simultaneously. The two neutral images differed in terms of level of salience and goal-relevance. The memory test showed no effect of pre-encoding emotional arousal on the memory of neutral items, regardless of goal-relevance or salience.

The small effects of priority when the emotion induction is pre-encoding are further highlighted in studies comparing pre-encoding to post-encoding effects. The small effects of priority on the memory of neutral items were also supported in further studies. Sakaki et al. (2014) found that the memory of high priority neutral items was not different when presented after emotional compared to neutral items. On the other hand, when emotional items *followed* neutral items, increasing priority led to emotion-induced enhancement in memory. Similarly, Knight and Mather (2009) found that the memory of neutral high priority items (e.g., items that received high attention, and items in an intentional learning task) did not differ, whether the items were preceded by emotional or neutral items. In contrast, high priority neutral items that were *followed* by emotional stimuli received enhanced memory. Therefore, the results are in line with the present study, suggesting that the biasing effects of emotional arousal may not be particularly strong when the arousal is pre-encoding. The results may be in line with modulation theories proposing stronger effects of consolidation than encoding in the emotional enhancement effect (e.g. McGaugh, 2004; Yonelinas et al., 2015).

The failure to find anterograde effects of arousal on memory is also similar to what was found in several previous studies. In a recent review of the immediate effects of emotional arousal on the memory of items preceding or following emotional items (Schlüter et al., 2019), it was found that while emotion-induced anterograde amnesia usually takes place, the anterograde amnesia does not always reach significance. The present study used a longer delay between emotional and neutral stimuli than the studies reviewed by Schlüter et al. (2019). However, past evidence suggests that increased delay may in fact further decrease the biasing effect of emotion on memory. Sutherland et al. (2012) found that a delay of over 4 seconds between emotional arousal and neutral stimuli led no effects of arousal on the short-term memory. Taken together, the findings suggest that the anterograde effects of emotional arousal may be of a small effect size, or may depend on the presence of certain conditions such as sustained context-congruence.

Furthermore, a similar line of research investigated memory after inducing stress conditions (e.g., Cornelisse, van Stegeren, & Joëls, 2011; Smeets, Jelicic, & Merckelbach, 2006; Weymar, Schwabe, Löw, & Hamm, 2012; Wirkner, Weymar, Löw, & Hamm, 2013). The studies usually induced stress using public speaking and mental arithmetic tasks, using the Trier Social Stress Task (TSST; Kirschbaum, Pirke, & Hellhammer, 1993), or submerging the participant's hand in ice water – a cold-pressor task – which could be also accompanied by social evaluation, or a combination of both tasks. These methods are well-supported in terms of increasing the sympathetic nervous system reaction (SNS) and the hypothalamic-pituitary-adrenal axis (HPA) response (Skoluda et al., 2015). A recent meta-analysis found no effect of stress experienced prior to encoding items on the memory of those items (Shields et al., 2017). The meta-analysis of 33 studies investigated stress, either during or prior to encoding. There was no effect of pre-encoding stress on memory, when the delay between the stress and encoding was less than 10 minutes. The present study's finding of no effect of pre-encoding emotional arousal on memory is in line with the meta-analysis. Notably, though, the manipulation in the present study may differ significantly from stress-inducing tasks. The simulated speaking task usually increases emotional arousal, but does not elicit an HPA response (For a meta-analysis see, Garcia-Leal, Graeff, & Del-Ben, 2014).

The present study suggests that top-down goal relevance does not affect the memory of items encountered subsequent to the induction of emotional arousal. Emotional arousal did not affect the memory of subsequent unrelated items, regardless of priority. The study adds to the previous literature finding no or only a small effects of pre-encoding arousal on memory (Schlüter et al., 2019; Shields et al., 2017). It is likely that the change in context between the speech task and the encoding task contributed to the null effects. Future studies should investigate the effects of introducing top-down prioritisation when emotion induction is context-congruent to the encoding task. For example, participants could be asked to prioritise one type of the neutral stimuli introduced after inducing emotional arousal through presenting images (Tambini et al., 2017), or after presenting a speech that is topic related to the subsequent stimuli (Smeets et al., 2007).

This study has several limitations. The study included both males and females, and there are gender differences in the effects of emotion on memory. For example, the increase in alpha amylase, an index of noradrenergic activity, was associated with greater arousal-biased competition effects in females but not males (Clewett, Sakaki, Huang, Nielsen, & Mather, 2017). Furthermore, ovarian hormones may interact with noradrenergic activity, moderating the effects of goal-relevance on memory (Clewett et al., 2017). Second, the study introduced emotional arousal immediately before the picture viewing task. The delay between stress induction and encoding may moderates memory. Small delays may not cause a significant effect of arousal on memory, while longer delays may lead to an impairment in memory (Shields et al., 2017). Therefore, the current findings likely relate to no or short delays between emotional arousal and encoding, and do not generalize to instances with longer delays. Third, the test was conducted online, which could have been a context change which impaired the effect of arousal. Participants may not have focused during the online test. However, the test detected a main effect of priority in memory, suggesting that participants had a satisfactory engagement with the test. Furthermore, participants could complete the online test anytime on the day following the memory test, meaning 16-hours to 24-hours after the first session. Therefore, the duration between encoding and the memory test varied among participants. This variation may have affected the results. However, evidence suggests that memory consolidation predominantly takes place during sleep rather than during wakefulness (Nishida, Pearsall, Buckner, & Walker, 2009; Björn Rasch & Born, 2013; Tempesta, Socci, De Gennaro, & Ferrara, 2018). Therefore, we do not expect the variation in waking hours between encoding and the memory test to confound the findings. Finally, the attention to images of animals, but not objects, has been found in a past study to be affected by priority (Sutherland et al., 2017). In the present study however, we found no difference between the memory of the animal and the object pictures. Future studies should investigate what type of stimuli are affected by arousal, and what types of prioritisation or relevance interact with arousal.

Due to the low effects of prolonged emotional arousal, the next chapter will investigate the memory of emotional items themselves. While in the present study, the heart rate biofeedback manipulations did not affect the memory of neutral items viewed after the emotionally-arousing task, it is still likely that biofeedback would affect the memory of emotionally-arousing stimuli. Past studies have found that heart rate biofeedback modulated the emotional response to emotional events (Makkar & Grisham, 2013; Wild et al., 2008). The effects of biofeedback on emotional memory remain unknown. The next study investigates the effects of true biofeedback on the memory of emotional items.

Chapter 3: Heart Rate Biofeedback Amplifies a Negativity Memory Bias

3.1 Abstract

Interoception refers to the detection and perception of physiological signals. Deficits in interoception have been associated with altered emotional experiences, emotional processing, and psychopathological conditions. However, most studies on interoception and emotion have relied on a correlational approach based on individual differences in interoceptive ability (i.e., the ability to detect body sensations); thus, there has been a limited understanding of the causal role of interoception in emotional processing. To address this issue, this study focused on emotional memory and investigated the effects of heartbeat biofeedback on emotional memory. The participants (n = 34) heard tones synchronized with their heartbeats or tones irrelevant to their heartbeats while viewing emotionally positive, negative, and neutral images. The results indicated that listening to one's own heartbeats resulted in an increased negativity bias in memory (i.e., enhanced memory for negative rather than positive images) compared to listening to tones irrelevant to their heartbeats. Listening to one's own heartbeat also enhanced the arousal ratings of negative images compared to positive images. Our results suggest that interoception may play a critical role in the negativity bias in memory.

3.2 Introduction

Interoception refers to the process of sensing the body’s physiological state through the detection, processing, and interpretation of signals from organ systems involved in homeostasis (Cameron, 2001; Craig, 2002; Khalsa, Adolphs, Cameron, Critchley, Davenport, Feinstein, Feusner, Zucker, et al., 2018). While it covers a range of signals, including cardiovascular, hunger, pain, temperature, visceral, and skeletal signals (Khalsa et al., 2018), research on emotion and interoception has primarily focused on one’s ability to detect own heartbeats. These studies generally suggest that interoception is essential for emotional processing (Bonaz et al., 2021; Craig, 2003; Weng et al., 2021; Wiens, 2005). In fact, deficits in interoceptive ability have been associated with altered emotional experiences (Pollatos, Gramann, et al., 2007; Pollatos et al., 2005; Wiens, Mezzacappa, & Katkin, 2000), emotional memory (Pollatos & Schandry, 2008; Werner et al., 2010), and decision-making (Dunn, Galton, et al., 2010; Lenggenhager, Azevedo, Mancini, & Aglioti, 2013). Dysfunctions in interceptions have also been associated with psychopathological conditions such as depression (Dunne, Flores, Gawande, & Schuman-Olivier, 2021; Furman, Waugh, Bhattacharjee, Thompson, & Gotlib, 2013) and anxiety (Trevisan, Mehling, & McPartland, 2021; Yoris et al., 2015). However, previous research on interoception predominantly relies on the correlational approach based on individual differences in interoceptive ability (Chong et al., 2017; Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). To address the causal effects of interoception on emotional memory, in the present study, we used concurrent biofeedback of participants’ own heartbeats and investigated how listening to their own heartbeats modulates emotional memory.

Neural evidence shows an association between interoceptive awareness and experiencing emotion. Evaluating the current emotional state and the bodily state (e.g. “is your current heart rate fast?") activate overlapping regions including the right anterior insula, ventromedial prefrontal cortex, and bilateral lingual gyrus (Terasawa et al., 2013). Furthermore, performing an heartbeat detection task —judging presented tones as synchronous or asynchronous with own heartbeats— and evaluating own emotional state both activated the anterior insula and the inferior frontal gyrus (Zaki et al., 2012). Similarly, evaluating emotional arousal and performing the heartbeat counting task — estimating the number of heartbeats one experienced in certain time— activated the insula, medial frontal gyrus and dorsal cingulate (Pollatos, Gramann, et al., 2007).

Furthermore, higher scores on interoceptive accuracy tasks (e.g., heartbeat detection and heartbeat counting task) were associated with higher subjective arousal ratings for emotional stimuli (Pollatos, Gramann, et al., 2007; Pollatos, Herbert, et al., 2007; Pollatos et al., 2005). For example, in a seminal study conducted by Wiens et al. (2000), participants who were able to detect their own heartbeats with higher accuracy in the heartbeat detection task reported higher arousal ratings for fear, anger, and amusement-inducing clips than those who showed lower accuracy in the heartbeat detection task.

In addition to emotional experiences, previous research has suggested that interoception may affect emotional memory (Pollatos & Schandry, 2008). Emotional events, pictures, and words are usually better recalled than neutral events (LaBar & Cabeza, 2006), which is mostly attributed to the effects of emotional arousal on memory (Mather, 2007). If interoception affects emotional arousal as documented above, it is likely that it also modulates emotional memory. In line with this idea, a study found that higher interoceptive ability (measured by the heartbeat counting task) was associated with enhanced memories of emotional pictures but not neutral ones (Pollatos & Schandry, 2008). Similarly, in a fear-conditioning paradigm, Katkin et al. (2001) found that participants with higher interoceptive ability (measured by the heartbeat detection task) acquired stronger conditioned responses than those with lower interoceptive ability. In another study, higher interoceptive ability was associated with enhanced implicit memory of emotional words (Werner et al., 2010).

In summation, research has largely confirmed the role of interoception in emotional experiences and memory. However, because most studies are based on individual differences in interoceptive ability, they do not necessarily indicate the causal role of interoception. In fact, the heartbeat counting task has come under increasing criticism for its validity. One main criticism is that the heartbeat counting task pertains to one's general knowledge of own heart rate rather than the detection of one's own heartbeat (Murphy et al., 2018; Ring et al., 2015). In fact, Desmedt, Luminet, and Corneille (2018) found that over 90% of the participants used knowledge about their average heart rates to estimate their heartbeats in the task. The heartbeat detection task has been considered more reliable but has also received some questions about its utility for research given the difficulty of the task (for a review, see Brewer, Murphy, & Bird, 2021); only a third or fewer participants were able to detect their heartbeats in some studies (Brener & Ring, 2016; Brener, Xiaoqing, & Ring, 1993). In addition, while both tasks aim to test one's interoceptive ability, a recent study found no correlation between their performance (Ring & Brener, 2018).

Given these limitations and the recent developments in biofeedback intervention (e.g. Farb et al., 2013; Meyerholz et al., 2019; Weng et al., 2021), other studies have used biofeedback to directly manipulate interoception and examine its effect on cognitive processing. For example, Peira et al. (2014) examined the effects of heartbeat biofeedback on emotion regulation and found that receiving feedback on one's own heart rate led to higher success in implementing emotion regulation while viewing negative images. In another study, participants listened to their heartbeats while playing an ultimatum game (Lenggenhager et al., 2013). In the ultimatum game, a proposer offers a split of the initial endowment between himself/herself and a responder; the responder observes the split and can reject the offer, which results in no monetary gain for both the proposer and the responder. When participants were provided with feedback about their heartbeats when they played the game as responders, they rated offers from the proposer as unfair. Heartbeat feedback also enhanced participants' tendency to make unfair offers when they were assigned as proposers. These results suggest that heart rate biofeedback may be effective in altering interoception and affecting emotions and cognitive processes (see also Iodice, Porciello, Bufalari, Barca, & Pezzulo, 2019).

In the current study, we aimed to extend these studies by investigating the effects of heartbeat biofeedback on emotional memory. More specifically, we presented participants with tones signalling their own heartbeats or tones irrelevant to their heartbeats while showing emotional and neutral images. We then examined how our biofeedback manipulation affected the participants' memory performance for emotional images. We also examined the effects of manipulation on the subjective arousal ratings for these images. Previous correlational studies suggest that interoceptive ability is associated with increased arousal ratings for emotional stimuli as well as enhanced emotional memory (Pollatos et al., 2005; Pollatos & Schandry, 2008; Werner et al., 2010). Based on these studies, we expected that increasing interoception by giving feedback on one's own heartbeats would increase self-reported arousal ratings for emotional images as well as memory of the emotional images.

3.3 Methods

3.3.1 Design

This study used a 2 (feedback: heartbeats vs. control) × 3 (valence: positive, negative, or neutral) design; both factors were manipulated in a within-participant manner.

3.3.2 Participants

Thirty-six participants were recruited for this study. Data from two participants were excluded because the electrodes failed to pick up heartbeat signals, resulting in a total of 34 participants (27 women). None of the included participants had a history of psychiatric or psychopathological disorders such as major depression, bipolar disorder, panic disorder, phobias, PTSD, schizophrenia, anxiety disorder, autism, eating disorders, obsessive-compulsive disorders, or personality disorders (see Appendix B). We recruited the maximum number of participants possible in February and March 2020, prior to the national lockdown in the UK due to the COVID-19 pandemic. Sensitivity analysis showed that a sample of 34 participants was sufficient to detect a medium-sized effect of $f = .28$ with 80% statistical power (G*Power 3.1 Software; Faul, Erdfelder, Buchner, & Lang, 2009). This study was approved by the University Research Ethics Committee at the University of Reading.

3.3.3 ECG Measurement

Electrocardiogram (ECG) measurements were performed using a PowerLab 26T (ADInstruments, Oxford, UK). In the heartbeat feedback condition, LabChart version 7.3 (ADInstruments, Oxford, UK) was used to detect R-peaks and play synchronous beeps. Participants were asked to attach electrodes below the right and left clavicle and on the lower left abdomen (e.g. Hakimi & Setarehdan, 2018; Reimer, Mehler, Coughlin, Godfrey, & Tan, 2009). They were shown an illustration of the location of the electrodes, and were asked to attach the electrodes by themselves based on the figure, with the presence of a researcher who made sure that the positions of the electrodes were appropriate. Participants were then asked to sit in a comfortable position and refrain from moving for the rest of the session.

3.3.4 Stimuli

Sixty pictures (24 negative, 24 positive, and 12 neutral) were selected from the International Affective Picture System (IAPS; Lang et al., 1998). The IAPS has normative ratings of valence and arousal, and the average valence and arousal ratings of the chosen images are displayed in Table 3.1. Eight additional neutral pictures were used as filler pictures. These filler pictures were shown at the beginning of each block to account for the primary effect and were discarded from the analysis. All the images were 600 × 429 pixels.

The picture-viewing task included four blocks (two for the heartbeat feedback condition and two for the control condition). The selected 68 images were therefore split into four sets (each of which included six negative, six positive, and three neutral images, as well as two additional filler images). The allocation of sets to the condition and the order of the four sets were fully counterbalanced across participants.

Table 3.1.

Average normative valence and arousal ratings of pictures used in the present study from the normative data from the IAPS (Bradley & Lang, 2007)

	Valence		Arousal	
	M	*SD*	*M*	*SD*
Negative	3.17	.82	4.87	.49
Neutral	5.09	.20	3.28	.24
Positive	6.85	.99	4.89	.56

3.3.5 Procedures

After obtaining consent, participants completed the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988)[1], followed by a picture-viewing task. The picture viewing task consisted of a) two blocks for the heartbeat feedback condition,

---

[1] The results for the PANAS are reported in Appendix C as they are not relevant to the main focus of the manuscript.

during which participants were given feedback about their heartbeats, and b) two blocks for the control condition, during which they were not given feedback about their heartbeats. Participants alternated between heartbeat feedback blocks and control blocks; the first block was counterbalanced across participants, so that half of the participants completed the heartbeat feedback condition first, while the other half completed the control condition first. In the heartbeat feedback condition, the participants were presented with tones synchronized with their heartbeats. In the control condition, they were presented with equally spaced tones at 40 tones per minutes (tones were 1.5 sec apart with a .05 sec duration) that were irrelevant to their heartbeats. The tones for the two conditions differed in their frequency (500 Hz or 1000 Hz), and the assignment of the tone frequency to the condition was counterbalanced across participants.

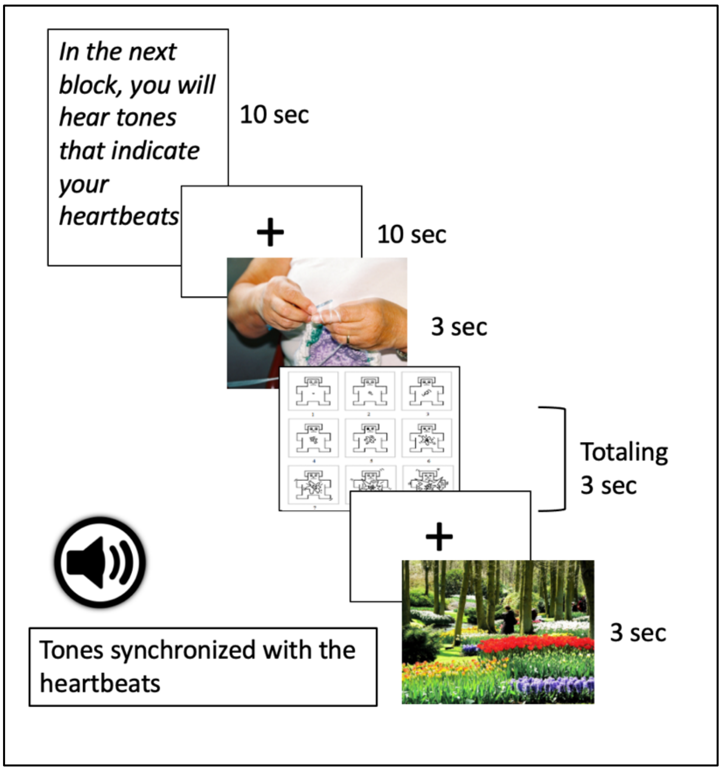


Figure 3.1. A schematic illustration of each task in the heartbeat feedback condition. Participants first saw an instruction about the sound, followed by a 10-sec fixation period and

a sequence of images. They then rated arousal level based on a 9-point scale Self-Assessment Manikin (SAM; Bradley & Lang, 1994).

Prior to each block, the participants were given instructions about the nature of the next block. Prior to the control blocks, the participants were told: "*In the coming block, you will hear tones that are irrelevant to your heartbeats.*" In contrast, prior to the heartbeat feedback blocks, the participants were told: "*In the next block, you will hear tones that indicate your heartbeats.*" The message was followed by a 10-second fixation cross, during which the participants started hearing the corresponding tones, which then continued playing throughout the block. After this 10-sec fixation, participants saw 17 pictures; they were first presented with two neutral filler pictures, followed by 15 pictures (six negative, six positive, and three neutral images) in a random order. Each picture (including filler images) was displayed for 3 seconds (Figure 3.1), followed by a question about the arousal level on a 9-point Likert scale Self-Assessment Manikin (SAM; Bradley & Lang, 1994), ranging from "*completely relaxed*" to "*very excited*" with a 3-sec time limit. If the participants pressed the key to indicate their arousal rating earlier than 3 s, a fixation cross was displayed for the remaining duration before the next picture was shown. When no response was made within 3 s, the trial automatically proceeded (the average number of these trials was 0.53).

A surprise free-recall memory task was then administered after a 5-minute break, during which participants completed a demographic questionnaire and two additional questionnaires unrelated to the present study (PANAS and CES-D; Radloff, 1977; Appendix C), in order to ensure that all participants had a similar time interval between the picture viewing task and the memory test. Participants were told to wait silently if they completed all the questionnaires before 5 min. Participants were then told to remember and describe as many pictures as possible from the picture-viewing task. When participants stopped writing their responses, the researcher waited for 30 seconds and then asked participants if they could remember any more pictures. After the memory task, participants completed post-task questionnaires, which included manipulation checks on the trust in the heart rate feedback condition and expecting a memory test (Appendix C).

3.3.6 Picture Coding

The memory test data were coded by two coders, each of whom independently matched all free recall responses to the images of the study. The coders were blind to the block condition of the recalled items. The coders had an agreement rate of 93.8%. The coders then resolved the disagreements through discussion. Sixty-four entries could not be matched to the image. Most of those entries were too general (e.g., “flowers,” which could be referring to a picture of flower bouquets or a garden with flowers).

3.3.7 ECG Analysis

To examine the effects of biofeedback on heart rates, we analysed participants’ heart rates in every block of the picture-viewing task (duration = 112 s). The analysis was performed using LabChart version 7.3 (ADInstruments, Oxford, UK).

3.4 Results

We first examined the effects of heartbeat feedback on emotional memory. Next, we addressed the effect of heartrate feedback on the arousal ratings for emotional and neutral images. Finally, we examined whether providing feedback on heartbeats has a systematic impact on heart rates.

3.4.1 Emotional Memory

To examine the effects of heartbeat feedback on memory performance, a 2 (feedback) × 3 (valence) repeated measures ANOVA was conducted on the proportion of items recalled.

The analysis showed a statistically significant effect of valence, *F* (2, 66) = 27.5, *p* < .001, partial η2 = .455, reflecting that both negative items (*M* = .207, *SD* = .104) and positive items (*M* = .168, SD = .082) were better recalled than neutral items (*M* = .069, *SD* = .075, *ps* < .001 with Bonferroni's correction); the difference between positive and negative items was not statistically significant (*p* = .058). The ANOVA did not show statistically significant main effects of feedback condition, *F* (1, 33) = 1.01, *p* = .322. However, there was a statistically significant interaction between feedback condition and valence, *F* (2, 66) = 3.69, *p* = .030, partial η2 = .10.

In order to investigate the significant interaction between valence and condition, simple main effect analyses were conducted. These analyses revealed that, in the heartbeat feedback condition, participants remembered negative items (*M* = .225, *SD* = .127) significantly more than positive items (*M* = .142, *SD* = .115), *F* (1, 33) = 10.79, *p* = .002, partial η2 = .246. In contrast, in the control condition, there were no statistically significant differences between the negative (*M* = .189, *SD* = .132) and positive items (*M* = .194, SD = .130), *F* (1, 33) = .04, *p* = .835. Contrary to the hypotheses, there was no significant difference in memory between the heart rate feedback and control for negative or positive items, *F* (1, 33) = 1.91, *p* = .176 *and F* (1, 33) = 2.68, *p* = .111, respectively. There was also no significant difference between the memory of neutral items shown during the heart rate condition (*M* = .05, SD = .096) and the control condition (*M* = .088, SD = .102), *F* (1, 33) = 3.09, *p* = .088. These results showed that the heart rate feedback increased the negativity bias in memory.

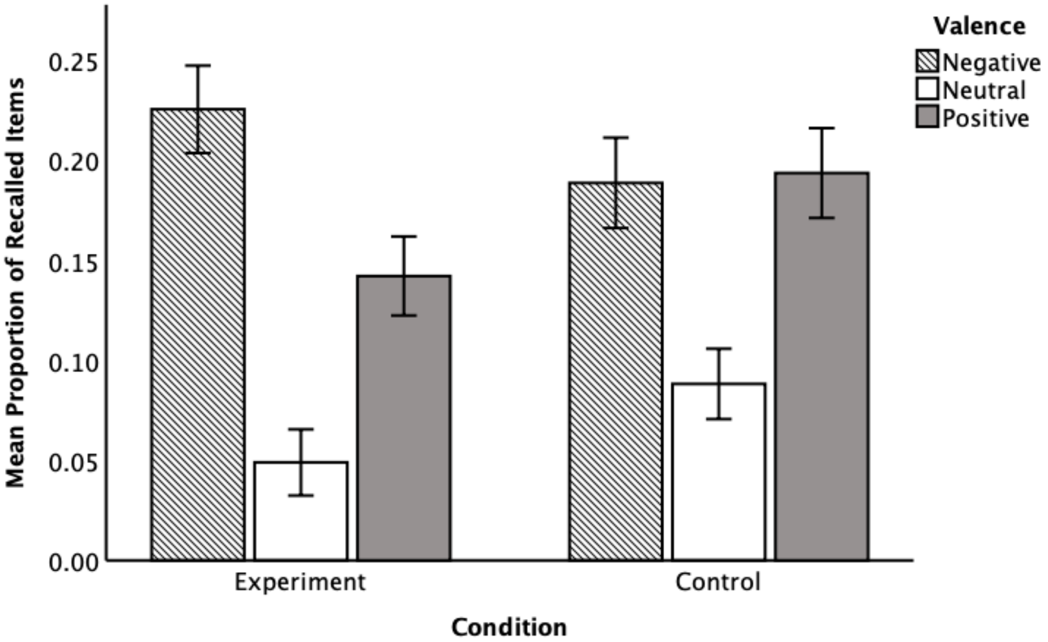


Figure 3.2. Mean proportions of recalled items according to their valence and feedback condition. Error bars represent the standard error.

3.4.2 Arousal Responses

A similar two-way repeated ANOVA on mean arousal ratings during the picture-viewing task showed statistically significant main effects of valence, *F* (2, 66) = 92.5, *p* < .001, partial η2 = .737. This significant effect of valence reflects that negative items were rated as more arousing (*M* = 5.33, *SD* = 1.71) than positive (*M* = 3.56, *SD* = 1.51, *p* < .001) and neutral items (*M* = 2.18, *SD* = .85, *p* < .001), whereas positive items were rated as more arousing than neutral items (*p* < .001; Bonferroni's correction). The ANOVA did not show statistically significant main effects of feedback condition, *F* (1,33) = 1.34, p =.256. In addition, there was a statistically significant interaction between the valence and feedback conditions, *F* (2, 66) = 3.23, *p* = .046, partial η2 = .089.

To identify the interaction pattern, simple main effects analyses were run. The analyses showed that in both conditions, negative items received higher arousal ratings than positive items, *F* (1, 33) = 56.6, *p* < .001, partial η2 = .632 *and F* (1, 33) = 43.3, *p* < .001, partial η2 = .567 for the heartbeat feedback control and control conditions, respectively. However, the difference in arousal ratings between the negative and positive images was statistically significantly larger in the heartbeat feedback condition (*M* = 1.95, *SD* = 1.51) than in the control condition (*M* = 1.58, *SD* = 1.40), *t*(33) = 2.41, *p* = .022, Cohen's *d* = .25. Thus, as in the memory results, providing heartrate feedback had different effects on arousal ratings for negative and positive images.

Contrary to the hypotheses, there was no statistically significant difference in the arousal rating of negative items between the heart rate feedback condition (*M* = 5.37, *SD* = 1.77) and the control condition (*M* = 5.28, *SD* = 1.72), *F* (1, 33) = .438, *p* = .513. Furthermore, the arousal rating of positive items in the heart rate feedback (*M* = 3.42, *SD* = 1.50) was significantly lower than the control condition (*M* = 3.70, *SD* = 1.57), *F* (1, 33) = 7.81, *p* = .009, partial η2 = .191. There was no significant difference in the arousal rating of neutral items between the heart rate feedback condition (*M* = 2.16, *SD* = .91) and the control condition (*M* = 2.21, *SD* = .89), *F* (1, 33) = .234, *p* = .632. Therefore, in contrast to the hypothesis, we found significant change in the heart rate condition only for positive but not negative items, and this change was in the opposite direction than expected.

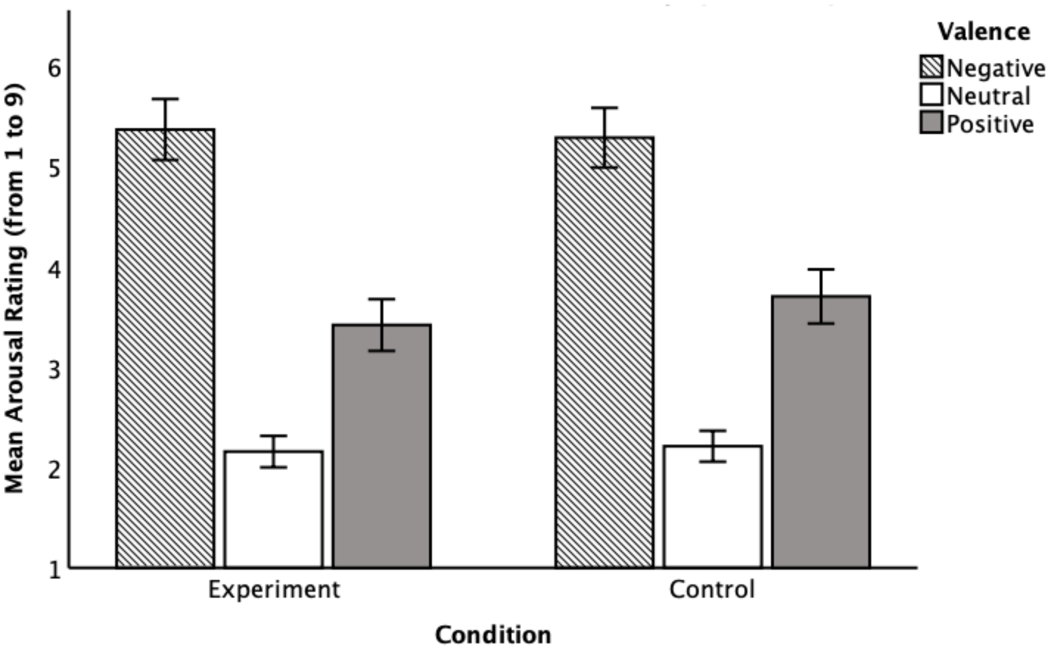


Figure 3.3. Mean arousal rating of images in the experiment and control blocks. Error bars represent the standard error.

3.4.3 Heart Rates

The average heart rate during the control blocks (*M* = 83.9, *SD* = 11.9) was not significantly different from that during the experimental blocks (*M* = 83.7, *SD* = 12.4), *t*(33) = .41, *p* = .681. These results suggest that participants' heart rates were not systematically altered by our manipulation.

3.5 Discussion

Influential theories of emotion focus on interoception as a key element of emotion (Barrett, 2017; Damasio, 1994; James, 1884; Seth, 2013). While there has been a significant increase in research on interoception and emotion (e.g., Füstös, Gramann, Herbert, & Pollatos, 2013; Pollatos et al., 2005; Werner et al., 2010), these studies are predominantly based on individual differences in interoceptive ability. As a result, the causal role of interoception in emotional experiences and memory has not been clearly understood. In the present study, we provided participants with feedback about their heart rates while viewing emotional and neutral images and examined how this manipulation altered subjective arousal evaluations of the images and their memory of them. We found that our heartbeat feedback did not systematically change heart rates but led to a stronger negativity bias in memory (i.e., better memory for negative than positive items). The heartbeat feedback condition also led to higher arousal ratings for negative items compared to positive items than for the control condition.

The negativity bias in memory and arousal ratings elicited under the heartbeat feedback condition is in line with the previous literature, which suggests that interoception is more important in processing negative stimuli than positive stimuli. For example, Motomura et al. (2019) found that stimulating the anterior insular cortex, a brain region implicated in interoception and heart rate monitoring (Critchley et al., 2004; Zaki et al., 2012), led to enhanced recognition of anger but not other basic emotions. Furthermore, the authors found that surgical removal of the insula led to reduced recognition of anger but not of other emotions in faces (Motomura et al., 2019). A meta-analysis also found that the right anterior insula was associated with empathy for negative but not positive emotions (Gu et al., 2013). Additionally, anxiety has been associated with increased activation of the insula in response to emotional material (Shah, Klumpp, Angstadt, Nathan, & Phan, 2009; Stein et al., 2007).

Another method used to examine the effects of cardiac interoceptive signals is to present stimuli at systole, when the arterial baroreceptor discharge, which provides information about cardiac signals, or at diastole, when baroreceptors are silent (Critchley & Garfinkel, 2017; Garfinkel & Critchley, 2016). These studies have shown that the presence of interoceptive signals specifically enhances the processing of threat and fearful stimuli but not positive stimuli (Critchley & Garfinkel, 2017; Garfinkel & Critchley, 2016). For example, Garfinkel et al. (2014) found that fearful, but not happy, disgusted, or neutral, faces were more successfully detected and received higher intensity ratings at systole than at diastole (Study 1). The authors also found that fearful faces induced higher amygdala activation at systole than at diastole (Study 2). Another study found that faces with an expression of disgust, but not happy, sad, or neutral, were rated as more emotionally intense during systole than diastole (Gray et al., 2012).

Our results are consistent with those of previous studies that used heart rate biofeedback. For example, a previous study found that hearing one's own heartbeats led to rating unfavourable offers as more unfair (Lenggenhager et al., 2013). Makkar and Grisham (2013) also revealed that presenting false increasing heart rate feedback while performing a stressful task led to higher rumination and negative emotions, which were mediated by increased self-focus, focusing on bodily reactions, level of anxiety, and mulling on past failures (Focus of Attention Questionnaire; Woody, 1996). In addition, a recent neuroimaging study demonstrated an overlap in brain connectivity patterns during performing an interoception task vs. processing negative information (i.e., thinking about worries) (X. Wu, Shi, Wei, & Qiu, 2019). Increased focus on internal body sensations, feelings, and thoughts has also been associated with negative emotions in a meta-analysis (Mor & Winquist, 2002). In summary, our results are in line with the growing body of literature, which suggests that interoception is particularly relevant to the processing of negative rather than positive information.

It should be noted that our results are not necessarily consistent with studies that relied on individual differences in interoceptive ability; these studies (as reviewed in the Introduction) typically show that those with higher interoceptive abilities tend to show increased arousal ratings and memory performance for both positive and negative items than those with lower interoceptive abilities (e.g., Pollatos et al., 2005; Pollatos & Schandry, 2008;

Werner et al., 2010; Wiens et al., 2000). This discrepancy in results may be due to differences between the facet of interoception of our manipulation targets and the facet of interoception assessed in previous studies. In a recent model, Murphy et al. (2019) proposed that interoceptive attention, the propensity to focus on interoceptive signals, should be distinguished from interoceptive accuracy, the accuracy in perceiving interoceptive signals. As described earlier, prior studies on interoception and emotional memory primarily assessed interoception using a heartbeat counting task or heartbeat detection task. While these tasks concern the accuracy facet of interoception, in our study, we presented participants with heartbeat feedback, which is likely to increase the accuracy of perceiving heartbeats and facilitate general attention to heartbeats. While previous research on interoceptive attention is limited, it has been shown to be positively correlated with individual differences in negative emotions such as anxiety (Palser et al., 2018) and neuroticism (Pearson & Pfeifer, 2020). Thus, our manipulation may have affected interoceptive attention, which may have been more relevant to negative than positive emotions.

However, studies have shown that interoceptive accuracy measured by the heartbeat detection task or the heartbeat counting task is particularly relevant to negative emotions. For example, higher levels of interoceptive accuracy are typically associated with individual differences in negative emotions, such as trait anxiety, anxiety sensitivity, and panic disorder (Domschke, Stevens, Pfleiderer, & Gerlach, 2010). A large-scale study also showed that interoceptive abilities assessed by the heartbeat counting task were positively associated with experiencing anxiety symptoms such as trembling and shaking (Dunn, Stefanovitch, et al., 2010). Further research is needed to clearly understand the role of interoceptive attention and accuracy in the processing of emotional stimuli.

Our study has several limitations that raise important questions for future research. First, although we selected picture stimuli so that arousal levels for the positive and negative images were similar based on normative data (Bradley & Lang, 2007), the participants in this study rated negative pictures as more arousing than positive pictures (see Figure 3.3). Therefore, it remains unclear whether the observed negativity bias stems from the arousal mismatch of negative and positive images or the valence-specific effects of interoception. This is especially relevant given that previous studies suggest that interoception is mostly concerned with processing information with high arousal negative valence (Garfinkel et al., 2014; Motomura et al., 2019). Second, we did not obtain valence ratings of images from our participants; therefore, it is unclear how interoception affected valence ratings. Interoception is often considered to be associated with arousal but not valence ratings (e.g., Barrett, Quigley, Bliss-Moreau, & Aronson, 2004; Pollatos et al., 2005; Pollatos & Schandry, 2008). However, one study found that valence but not arousal ratings were more affected following the inhibition of the interoceptive network (Mai, Braun, Probst, Kammer, & Pollatos, 2019). Future studies should control for arousal levels and address how interoception interacts with the valence and arousal dimensions of emotional experiences. Third, in the present study, the sample size was modest and consisted mostly of females. Gender differences may exist in emotional memory and interoception (Canli, Desmond, Zhao, & Gabrieli, 2002; Grabauskaitė, Baranauskas, & Griškova-Bulanova, 2017); thus future research needs to test the effects of heartrate feedback in males and females. Fourthly, a notable limitation in the study is that tones played in the control condition were played at a slower rate than the heart rate biofeedback condition (40 bpm and an average of 85 bpm, respectively). The slower rate, in addition to the steady pace, of tones in the control condition may have been more relaxing and less arousing than the faster rate of tones in the heartrate feedback condition. The increased arousal in the heartbeat feedback blocks may explain the negativity bias observed in this condition. However, participants’ heart rates (which is considered to be one of the key measures of arousal) remained equivalent across the conditions, suggesting that they had experienced similar arousal levels across blocks. Nevertheless, the steady presentation of tones during the control condition may pose a low cognitive load and increase boredom, which are associated with lower arousal (Danckert, Hammerschmidt, Marty-Dugas, & Smilek, 2018; Pattyn, Neyt, Henderickx, & Soetens, 2008). Thus, future studies should use equivalent rate of tones across conditions. Finally, the memory test in the present study was conducted a few minutes after the encoding task. Thus, our memory measures are unlikely to reflect the effects of emotions on consolidation. The effects of emotional arousal on memory often occur during consolidation and are therefore evident when memory tests are taken hours after encoding (Talmi, 2013). Future studies are needed to investigate the effects of interoception on long-term memory.

In summary, the present study showed that online heart rate feedback led to negative effects on emotional reactions and a negativity bias in memory. Our results suggest that concurrent heartrate feedback increases interoceptive accuracy and attention, which amplifies negative emotions and leads to memory negativity bias. These results are largely consistent with previous evidence that interoception is more implicated in processing negative information than positive information (e.g., Garfinkel & Critchley, 2016; Motomura et al., 2019). By showing the possible negative effects of heartrate feedback, our results also suggest that caution should be exercised before manipulating interoceptive abilities (e.g., Leganes-Fonteneau et al., 2021; Melloni et al., 2013).

The present study suggests that interoception is associated in emotion, and emotional memory. The insula is often thought to be the neural correlate for interoception (Craig, 2009; Seth, 2013). The functional connectivity of the insula was found to reflect interoceptive ability (S. D. Smith et al., 2021; X. Wang et al., 2020). The functional connectivity has been recently found to predict cognitive factors such as intelligence (e.g., Dubois, Galdi, Han, Paul, & Adolphs, 2018; Finn et al., 2015) and neutral memory (e.g., Fjell et al., 2016; Salami, Wahlin, Kaboodvand, Lundquist, & Nyberg, 2016), and to reflect even emotional processing (Y.Y. Lee & Hsieh, 2014). Therefore, it is likely that functional connectivity reflects individual differences in emotional memory. The next study will investigate how functional connectivity is associated with emotional memory. Rather than constrict the search to select regions of interest, such as the insula or the amygdala, the study will investigate the whole-brain functional connectivity and utilise a machine learning algorithm to automatically select the relevant connections.

Chapter 4: Resting-State Functional Connectivity Does Not Predict Individual Differences in the Effects of Emotion on Memory[1]

---

[1] This manuscript is under revision in Scientific Reports

4.1 Abstract

Emotion-laden events and objects are typically better remembered than neutral ones. This is usually explained by stronger functional coupling in the brain evoked by emotional content. However, most research on this issue has focused on functional connectivity evoked during or after acquisition. The effect of an individual's functional connectivity at rest is unknown. Our pre-registered study addresses this issue by analysing a large database, the Cambridge Centre for Ageing and Neuroscience, which includes resting-state data and emotional memory scores from 303 participants aged 18-87 years. We applied regularised regression to select the relevant connections and replicated previous findings that whole-brain resting-state functional connectivity can predict age and intelligence in younger adults. However, whole-brain functional connectivity predicted neither an emotional enhancement effect (i.e., the degree to which emotionally positive or negative events are remembered better than neutral events) nor a positivity bias effect (i.e., the degree to which emotionally positive events are remembered better than negative events), failing to support our pre-registered hypotheses. These results imply a small or no association between individual differences in functional connectivity at rest and emotional memory, and support recent notions that resting-state functional connectivity is not always useful in predicting individual differences in behavioural measures.

4.2 Introduction

Emotional events are typically remembered better and more vividly relative to neutral ones (Schaefer & Philippot, 2005; St. Jacques & Levine, 2007; Talarico & Rubin, 2007). This emotional enhancement effect has been found in laboratory studies (Kensinger, 2009; Kensinger & Corkin, 2003; LaBar & Cabeza, 2006; Mather, 2007; Yonelinas & Ritchey, 2015) as well as autobiographical memory (Talarico et al., 2004). Previous research has also suggested that individual differences in this emotional memory enhancement effect may have important consequences on wellbeing and psychopathology. For example, the enhancement effects of emotion on memory are considered to result in spontaneous and intrusive recollection of traumatic memories (Ferree & Cahill, 2009). Likewise, one's tendency to preferentially remember negative information is frequently present in psychopathological conditions, including depression and anxiety, and is associated with symptom severity (Duyser et al., 2020). This negative memory bias has also been associated with smaller hippocampal grey and white matter volume (Gerritsen et al., 2012), which is in turn associated with major depression (MacQueen & Frodl, 2011). In contrast, one's tendency to preferentially remember positive over negative information is referred to as "positivity bias", and is often associated with better emotional wellbeing in old age (Brassen, Gamer, & Bchel, 2011; Mather & Carstensen, 2005). In the current study, we tested whether such individual differences in the emotional enhancement effects of memory can be predicted by resting-state functional connectivity in the brain. Functional connectivity (FC) refers to the strength of connections between brain areas that share functional properties. We distinguish task-induced FC in response to a stimulus, from resting-state FC, which reflects the connectivity of an individual at rest.

The brain mechanisms behind the emotion-induced enhancement effects in memory have been intensively studied in task-fMRI studies, where researchers examined blood oxygen level dependent (BOLD) signals obtained while participants encoded emotional vs. non-emotional information. Meta-analyses based on these studies reported that the enhancement of emotional memory is associated with increased activation in the amygdala, hippocampus, and regions in the ventral visual stream during the encoding of emotional items (Dahlgren et al., 2020; Murty et al., 2010). In addition to the activation level, increased task-induced FC across the amygdala, hippocampus and the prefrontal cortex (PFC) during encoding of emotional items is associated with enhanced memory for emotional compared with neutral items (Dolcos et al., 2004; Murty et al., 2009; Ritchey et al., 2008; Sakaki et al., 2013; St. Jacques et al., 2009). Previous studies also extended their focus to FC after learning (i.e., during consolidation) (de Voogd, Klumpers, Fernández, & Hermans, 2017; Kark & Kensinger, 2019). Stronger FC between the amygdala and visuosensory areas after learning was associated with the negative memory bias in memory, whereas stronger FC between the amygdala and anterior cingulate after learning was associated with the positivity bias in memory (Kark & Kensinger, 2019).

In contrast, it has been less clear whether resting-state FC *before* learning predicts individual differences in emotional memory. Resting-state FC refers to the temporal correlation in activity between regions that are not actively engaged in any task, and is considered to reflect the brain's functional and structural connectivity (Suárez et al., 2020). Individual differences in resting-state FC have also been used to predict individual differences in brain activation during various tasks, including working memory, language tasks, emotion recognition, and interpreting social interactions (Tavor et al., 2016). Research on memory has further demonstrated an association between memory performance for neutral items and resting-state FC of the MTL (Salami et al., 2014, 2016) and the default mode network (DMN) which has been implicated in age-related cognitive decline (Fjell et al., 2016; Staffaroni et al., 2018).

In addition, recent advances in machine learning have allowed researchers to identify and study complex data models, that can be used to predict individual differences from a wide range of behavioural and cognitive measures (Bleidorn & Hopwood, 2019). Studies implementing such analyses found that resting-state FC predicts behavioural measures including attention span (Fong et al., 2019; Rosenberg et al., 2015), decision-making strategies (Barnes et al., 2014), intelligence (Dubois et al., 2018; Finn et al., 2015), motor skills learning (J. Wu, Srinivasan, Kaur, & Cramer, 2014) and personality (Dubois et al., 2018), acting as a behavioural "fingerprint" (Finn et al., 2015).

In contrast, few studies have investigated whether resting-state FC predicts individual differences in emotional memory. On the one hand, FC during rest resembles the FC observed during a task (Laird et al., 2011; S. M. Smith et al., 2009) and previous findings support an association between emotional memory enhancement effects and FC during rest before (Andreano et al., 2017; Sakaki et al., 2013) or after encoding (de Voogd et al., 2017; Kark & Kensinger, 2019). Therefore, it is reasonable to hypothesise that whole-brain resting-state FC is predictive of individual differences in emotional memory. On the other hand, recent evidence emphasised that robust cognitive tasks may not always yield reliable inter-individual measures (Hedge, Powell, & Sumner, 2018). Similar low reliability was also reported for the emotional enhancement effect in memory, despite robust and strong group-wise effects for better memory for emotional rather than neutral items (Schümann, Joue, Jordan, Bayer, & Sommer, 2020). Therefore, even though resting-state FC has a relatively high temporal reliability (Finn et al., 2015; Gratton et al., 2018), resting-state FC may not be able to reliably predict emotional memory enhancement effects.

We investigated whether resting-state FC predicts emotional memory using a large database — the Cambridge Centre for Ageing and Neuroscience (Cam-CAN) — that includes emotional memory scores, structural and functional MRI (fMRI) scans of 303 individuals of ages 18-87 years (Shafto et al., 2014; Taylor et al., 2017). In the Cam-CAN project, participants completed an emotional memory task (in a different session from the MRI session), where they learned neutral objects superimposed onto emotionally positive, neutral, and negative backgrounds (Henson et al., 2016). Consistent with the emotion induced enhancement effect observed in the literature, participants had a better memory for objects learned with positive or negative backgrounds than objects learned with neutral backgrounds (Table 4.2). Based on this task, we created two continuous measures of emotional memory: a) better memory for positive and negative information than neutral information (emotional enhancement effects) and b) preferential memory for positive rather than negative information (the positivity bias). Our study also attempts to predict age and intelligence from resting-state FC; these latter analyses served as control checks to ensure that our method and data can replicate previous findings (Dubois et al., 2018; Finn et al., 2015; Vergun et al., 2013).

We preregistered the above hypotheses and analysis pipelines, which are accessible at https://osf.io/untzm. Following an analysis pipeline previously used to predict individual differences in personality and intelligence from resting-state FC (Dubois et al., 2018), we used regularised linear regression to predict the emotional enhancement effect and the positivity bias in memory from whole-brain resting-state FC. The brain was parcellated into 268 nodes obtained from Shen et al. (2013). Seven nodes were excluded from the analysis due to missing data, therefore comprising a total number of predictors of 33,930 connections. Due to the expected collinearity and large number of predictors, we used common parameter regularization techniques to avoid over-fitting of the data models. Specifically, we used Elastic Net penalization, which combines ridge (L1) and lasso (L2) penalization schemes. Ridge regularization adds a Gaussian prior to the parameters of the model. Lasso penalization provides an upper bound to the parameter, while creating opportunities to reduce the number of predictors altogether. Additionally, we used leave-one-out cross-validation to train and test the models, and permutation testing to compute a p-value when R^2 showed a positive relationship (permutation analyses were not run when R^2 was negative because negative R^2 means that the models performed poorly).

4.3 Methods

4.3.1 Cam-CAN Database

Data used in the preparation of this work were obtained from the Cam-CAN repository (available at http://www.mrc-cbu.cam.ac.uk/datasets/camcan/) (Shafto et al., 2014; Taylor et al., 2017). A total of 306 participants, aged 18-87, have completed the structural MRI brain scans, resting-state fMRI scans, the emotional memory test and the intelligence test in the Cam-CAN dataset. Two participants were completely missing signal in significant portions of the cerebellum and the brain stem leading to errors in preprocessing. One participant had an incomplete resting-state fMRI scan lasting less than the database's acquisition time of 8 minutes and 40 seconds. Therefore, the final sample size included 303 participants (N = 155 females; 18-87 years, *M*age = 54.3, *SD* = 18.1) who had structural and functional resting-state brain scans, behavioural measures on emotional memory, and intelligence scores. The data analysed in this study was the Cam-CAN consortium which has gained ethical approval from the Cambridgeshire 2 (now East of England-Cambridge Central) Ethics Committee.

4.3.2 Emotional Memory Task

The memory task in the Cam-CAN database consisted of 120 trials, presented in two blocks (Henson et al., 2016). In brief, every trial started with presentation of a background image for 2.5 seconds; the background was either positive, negative or neutral. Participants then saw a neutral object superimposed on the background for 7.5 seconds, during which they were asked to link the item and background by mentally creating a story that combines them. Participants performed a surprise memory test 10 minutes later.

During the memory test, participants were shown an object and asked to indicate whether or not it had been shown during the study phase (i.e., object memory). For objects indicated as ‘shown’, participants were asked to identify the valence of the background on which the object was superimposed (i.e., associative valence memory), then describe the background scene (i.e., background memory). Participants’ responses to the background memory test were coded to reflect whether participants described correct details, correct gist, incorrect information or no responses were given. The test had 160 trials (120 trials with old stimuli and 40 trials with new stimuli).

The current study used the d’ measure of discriminability (Green & Swets, 1966) for the object and the associative valence memory. For the background memory, we computed the proportion of trials where participants could correctly recalled gist. For all memory scores, two memory variables were created: the emotional enhancement effect and the positivity bias. The emotional enhancement effect was obtained by subtracting performance in the neutral condition from the average performance in the positive and negative conditions. The positivity bias measure was computed by subtracting performance in the negative condition from performance in the positive condition.

4.3.3 Intelligence

The Cam-CAN database included a fluid intelligence test, the Cattell Culture Fair Scale 2 Form A (Cattell, 1971). The test has four subsets of nonverbal intelligence tests. A principal component analysis was performed on the scores of the four subsets to get one composite score of intelligence.

4.3.4 MRI data acquisition

MRI scans were acquired using 3 T Siemens TIM Trio scanner (Shafto et al., 2014). Structural T1-weighted images were acquire using the 3D MPRAGE sequence: repetition time (TR) = 2250 ms, echo time (TE) = 2.99 ms, Inversion Time (TI) = 900 ms, flip angle = 9 degrees, GRAPPA acceleration factor = 2, resolution 1.0 mm isotropic. Every participant had one resting-state fMRI scan with an acquisition time of 8 minutes and 40 seconds, and a total of 261 volumes. Resting-state BOLD fMRI scans had the following parameters: TR = 1970 ms; TE = 30 ms; flip angle = 78 degrees; slices = 32 of thickness = 23.7 mm; field of view (FOV) = 192 mmx 192mm; voxel size = 3 mm x 3 mm x 4.44 mm.

4.3.5 fMRI Preprocessing

We initially processed the raw functional MRI (fMRI) data obtained from the Cam-CAN database using FMRIB Software Library (FSL; Smith et al., 2004). Preprocessing included deleting the first two volumes in every scan, applying motion correction to the raw resting-state images using FSL MCFLIRT (Glasser et al., 2013), applying field map distortion correction, setting high pass filtering cut-off to 100 seconds, and performing nonlinear registration of brain-extracted T1 images to Montreal Neurological Institute (MNI) space using FSL FNIRT (12 degrees of freedom). Each participant's T1 structural image was skull/neck stripped using the FSL's brain extraction tool (BET) and then used to create participant's specific masks for the white matter, grey matter and cerebrospinal fluid (CSF) using FSL FAST. Although Dubois et al. (2018) found stronger prediction results when using multimodal surface-based alignment and registration (MSM) compared with MNI, we refrained from using MSM as it excludes subcortical regions, which are relevant for emotional memory (Murty et al., 2010)

We next applied the same denoising steps as included in 'Pipeline A' from Dubois et al. (2018) given that this pipeline had the best prediction performance in predicting personality traits in this study. The pipeline started by z-score normalization of each voxel's signals. Voxels in the white matter and CSF were then detrended by regressing out the temporal drifts. Next, the mean signals of CSF and white matter voxels were computed and regressed out from grey matter voxels. Motion regression was then performed using translational and rotational and temporal parameters as covariates in linear regression. Low-pass filtering was performed using a Gaussian kernel with standard deviation of 1 TR. Finally, grey matter voxels were detrended for temporal drifts, followed by a global signal regression. The preprocessing and denoising pipeline scripts used are publicly available (https://github.com/donakand/EmotionalMemory).

The denoised resting-state images were then segmented into 268 nodes (Shen et al., 2013); for each node, we averaged signals in all included voxels for each timepoint to create timeseries for each parcel. A total of 46 participants had missing data in one or more brain nodes; these missing data were restricted to seven nodes: 51, 58, 60, 185, 189, 194 and 202, corresponded to the left and right temporal lobes, located close to the surfaces of the brain (Shen et al., 2013). To keep as many participants as possible, these seven nodes were excluded from the analysis. A connectivity matrix was created by correlating parcels' time-series using Pearson's correlation. The connectivity matrix consisted of 33,930 edges (connections) per participant.

4.3.6 Machine Learning Analyses

Our main machine learning analyses used methods described in Dubois et al. (2018) Four separate analyses were carried out for different outcome variables: a) the emotional enhancement effect, b) the positivity bias, c) intelligence and d) age (as exploratory analysis that we did not pre-register). In all models, we included the connectivity from 33,930 edges as predictors. In addition, age, gender, handedness, and intelligence were used as control variables in the emotional enhancement effect and positivity bias analyses. Age, gender and handedness were controlled in the analysis of intelligence. Gender, handedness and intelligence were controlled for in the analysis of age. Similar to Dubois et al. (2018), the effects of these control variables were regressed out from the outcome measure using multiple linear regression before running a subsequent machine learning analysis. One participant was missing handedness information. The handedness for this participant was replaced by the median handedness value.

For each machine learning analysis, we generated an Elastic Net model, implemented with Scikit Learn in python version 0.19.2 (Pedregosa et al., 2011). Similar to Dubois et al. (2018) to choose optimal parameters, the model's alpha value was tuned using a grid search of the parameter space, and a three-fold nested cross-validation. The Elastic Net mixing parameter L1 was set as 0.01. However, we also performed exploratory analyses where L1 was chosen through three-fold nested cross-validation. The model was trained and tested using a leave-one-out cross-validation. The model was evaluated using R^2. As in Dubois et al. (2018), in the current study R^2 was not the square of the correlation coefficient, but rather determined using equation (1). Therefore, R^2 could take negative values in case of squared sum of errors larger than that of the null model — a horizontal line through the mean. As in Dubois et al. (2018), models were also evaluated on the normalized root mean squared deviation (nRMDS), which is the square root of the ratio of the standard deviation of residuals divided by the standard deviation of the observed values, and can be obtained directly from the R^2, as in equation (2).

$$R^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y})^2} \tag{1}$$

$$\text{nRMSD} = \sqrt{1 - R^2} \tag{2}$$

To evaluate these results against a null hypothesis, under which the data is not predictive of our variables, and obtain a *p*-value, we generated a null distribution by generating 1000 shuffled permutations of the memory scores in the dataset. We ran our models on every shuffled dataset. The one-tailed *p*-value of the (actual) dataset model was then calculated by computing the number of permutations for which R^2 was larger than the dataset's model, divided by 1000.

To assert the specificity of the results obtained from our preregistered methodology, we conducted further analyses using alternative methods. The exploratory analyses retained the same control variables as our main analyses and were also evaluated using R^2. The main analyses were run again while only changing the cross-validation from leave-one-out to 10-Fold cross-validation. This is due to a recent argument suggesting more robustness with k-Fold cross-validation in neuroimaging (Poldrack, Huckins, & Varoquaux, 2020). In keeping with the original methodology by Dubois et al. (2018), we set up the Elastic Net model using a proportion of L1 regularization of 0.01. However, other studies have obtained good prediction using larger L1 ratios (Liu, Chokka, Cao, & Chokka, 2021; Veretennikova, Sikorskii, & Boivin, 2018), or pure Lasso (L1 = 1; Fishburn et al., 2019; Shimizu et al., 2015; Toiviainen, Alluri, Brattico, Wallentin, & Vuust, 2014). Therefore, we ran the main analyses again, tuning the L1 parameter in a nested 3-Fold cross-validation from values: .1, .5, .7, .9, .99, 1. Finally, the main analyses were replicated using a different learning algorithm, Random Forest, rather than regularized linear regression. Random Forest is one of the most robust algorithms and has been used in psychology (Haque, Kabir, & Khanam, 2021; Parikh, Li, & He, 2019; Priya, Garg, & Tigga, 2020). The algorithm does not require assumptions of linearity or collinearity of variables, and has shown good reliability (Dimitriadis & Liparas, 2018; Geurts, Irrthum, & Wehenkel, 2009; Golino & Gomes, 2016). The maximum depth parameter was chosen from values: 5, 10, 20, 40, 50 using a nested 3-Fold cross-validation .

Several past studies have successfully used similar parameters to implement Random Forest models in psychological and neuroimaging studies (Dadi et al., 2020; Han & Adolphs, 2020; J. Kim, Zhou, Schiavon, Raftery, & Brager, 2018; Pereira, Tavares, Mihaylova, Mladenov, & Georgieva, 2018).

4.4 Results

The analysis procedure for the main analyses (where we predicted the emotional enhancement effects, the positivity bias and intelligence from resting-state FC across all participants) was preregistered, and the scripts used are publicly available (https://osf.io/bm98y).

4.4.1 Behavioural Results

A composite score for intelligence was computed from the four subsets of Cattell through principal component analysis. The derived factor explained 67.8% of the total variance, and had loadings ranging from .81 to .84 with the four Cattell subsets. As reported in the original paper about the dataset (Henson et al., 2016), participants showed better object memory for positive and negative backgrounds than neutral backgrounds (Table 4.2). We further computed a measure of the emotional enhancement effect variable by subtracting object memory performance in the neutral condition from the average memory performance in the positive and negative conditions. We also created another measure of positivity bias by subtracting object memory performance in the negative condition from memory performance in the positive condition.

From the original dataset, we used 303 participants (Table 4.1) — all the participants in the database who completed the resting-state fMRI, emotional memory task, and the intelligence test. We computed the following exploratory correlations as quality checks. Older individuals performed more poorly on the intelligence score than younger individuals, $r(301) = -.63$, $p < .001$. In contrast, age was not significantly correlated with the positivity bias, *r*(301) = .11, *p* = .06, nor with the emotional enhancement effect of memory, *r*(301) = .01, *p* = .89. There were no significant gender differences in intelligence, *t*(301) = 1.77, *p* = .08, the positivity bias, *t*(301) = -1.40, *p* = .17, or in the emotional enhancement effect, *t*(301) = .27, *p* =.79.

Table 4.1

Characteristics of participants across ages (18-87 years), younger adults (18-40 years), middle-aged (41-60 years), and older adults (61-87 years).

	All	Younger Adults	Middle-Aged	Older Adults
N	303	85	98	120
Age	54.3 (18.1)	31.8 (5.8)	50.7 (5.8)	73.3 (7.0)
Gender (Males:Females)	155:148	44:41	48:50	63:57
Intelligence	.00 (1.00)	.73 (.66)	.23 (.73)	-.71 (.93)
Education Level (N)				
Degree	191	68	65	58
A-Levels	55	9	19	27
GCSE/O-Level	36	8	12	16
None	20	0	2	18

Note: Intelligence refers to the composite score of intelligence on the fluid intelligence test. Information about education level was missing for one participant in the older adults age group. All data are specified as mean (sd) unless otherwise specified

Table 4.2

The mean and standard deviation of memory scores for participants across all ages (18-87 years old)

Memory Type	Negative		Positive		Neutral		*F(2, 604)*	Partial η^2	*p*
	M	*SD*	*M*	*SD*	*M*	*SD*			
Object memory	2.64_a	.79	2.70_b	.74	2.58_c	.76	18.6	.058	<.001
Associative valence memory	1.59_a	.75	1.19_b	.63	$.90_c$	.62	424.1	.584	<.001
Background memory	$.16_a$	.09	$.14_b$	.08	$.08_c$	.06	114.2	.274	<.001

Note: The object memory refers to participants' memory performance for neutral objects learned with positive, negative or neutral backgrounds. The associative valence refers to memory for whether each neutral object was associated with a positive, negative or neutral background. The background memory concerns memory performance for the details of the background image associated with each neutral object (Henson et al., 2016). The d' scores are used for the object and associative valence memory. The proportion of correct gist memories is used for the background memory measure. Means with different subscript letters were statistically different ($p < .05$) according to pairwise comparisons with Bonferroni correction.

4.4.2 Preregistered Predictive Modelling

We followed a strategy first described by Dubois et al. (2018). We used Elastic Net models with a high ratio of ridge (.9) and tuned the models' alpha parameter through a grid search. Analyses were run to predict the emotional enhancement effect in memory, the positivity bias in memory, age, and intelligence from the connectivity matrix. The control variables were age, gender, handedness and intelligence (unless they are the predicted variable). We ran one thousand permutations of the data, which allowed us to calculate one-tailed *p*-values for each model that returned positive R^2. Results are shown in Figure 4.1. The models predicting the emotional enhancement effect and the positivity bias performed poorly, demonstrating negative correlations between the predicted and observed values (Table 4.3; Figure 4.1). The model predicting intelligence also performed poorly and did not achieve a significant correlation between predicted and observed values (Table 4.3; Figure 4.1).

Table 4.3

Model prediction results when including participants across all age groups (18-87 years old)

Dependent Variable	r	R^2	nRMSD	p
	Main Analyses			
Emotion enhancement effect	-.09	-.31	1.14	.88
Positivity bias	.03	-.19	1.09	.53
Intelligence	.09	-.09	1.05	.21
	Exploratory Analysis			
Age	.44	.19	.90	.001

Note: For all variables, we used Elastic Net, with ridge-lasso ratio =.01. The models were trained using leave-one-out cross-validation. *P*-values were calculated as the number of permutations with lower R^2 divided by 1,000. The emotion enhancement effect refers to the degree to which neutral objects were learned better when they were paired with emotional rather than neutral background images. The positivity bias represents the degree to which objects paired with positive backgrounds were remembered better than those paired with negative backgrounds.

4.4.3 Exploratory Analyses

As described in the previous section, our pre-registered analyses failed to predict our two emotional memory measures from resting-state FC. We also failed to replicate previous findings showing that resting-state FC can predict intelligence. We therefore ran a series of unplanned exploratory analyses to identify when resting-state FC predicts behavioural measures. First, we ran an exploratory analysis to test if we can replicate previous findings that one's chronological age is predicted by resting-state FC (Tsvetanov et al., 2016; Vergun et al., 2013). The model obtained good prediction, achieving strong correlation between predicted and observed values, *r*(301) = .44 (Table 4.3; Figure 4.1), suggesting that resting-state FC is predictive of an individual's age.

4.4.3.1 Analysis for Each Age Group. Next, we performed an exploratory analysis after splitting the sample into three age groups: younger (aged 18-40 years; N = 85), middle-aged (aged 41-60 years; N = 98) and older adults (aged 61 years and over; N = 120) given that previous studies on intelligence and resting-state FC primarily focused on younger adults (Dubois et al., 2018; Finn et al., 2015), whereas our participants included those aged between 18 and 87 years. Note that past studies also showed the non-linear effects of age; suggesting that older adults may rely on a different set of regions (relative to younger adults) to perform the same task (Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, 2012). To test the possibility that the emotional enhancement effect, the positivity bias and intelligence are successfully predicted after splitting participants into separate age groups, the analyses were repeated separately for each age group, with the same methodology as the whole-sample analyses described above. The model successfully predicted intelligence in younger adults, but not for middle-aged or older adults (Table 4.4; Appendix D). However, the model still failed to predict the emotional memory enhancement effect and the positivity bias across all groups (Table 4.4).

Table 4.4

Model prediction results of participants for each age group

Dependent Variable	Group	*R*	R^2	nRMSD	*p*
Emotion enhancement effect					
	Younger adults	-.13	-.33	1.15	.92
	Middle-aged	-.08	-.24	1.11	.77
	Older adults	-.17	-.31	1.15	.87
Positivity Bias					
	Younger adults	-.23	-.49	1.22	.94
	Middle-aged	-.15	-.41	1.19	.75
	Older adults	.16	-.06	1.03	.14
Intelligence					
	Younger adults	.38	.14	.93	.02
	Middle-aged	.17	-.05	1.03	.14
	Older adults	.00	-.17	1.08	.38

Note: For all analyses, we used Elastic Net, with ridge-lasso ratio =.01. The models were trained using leave-one-out cross-validation. *P*-values were calculated as the number of permutations with lower R^2 divided by 1,000.

4.4.3.2 Other Emotional Memory Measures. Results presented so far concerned memory accuracy for neutral objects that were superimposed on negative, neutral or positive images (so called 'object memory'). Yet the Cam-CAN study tested three types of memory: object, associative valence and background memory (Shafto et al., 2014). While the effects of valence on this object memory measure were significant, they were relatively small (Henson et al., 2016); which may have resulted in our failure to predict the emotional memory enhancement effects using resting-state FC. To address this issue, we applied the same analysis method again to the two other types of memory in the Cam-CAN dataset: associative valence memory and background memory. The associative valence memory measure concerns whether each correctly-recalled neutral object was associated with a positive, negative or neutral background and showed stronger effects of valence compared with object memory (Henson et al., 2016; see Table 4.2). In contrast, the background memory concerns participants' gist memory for contents of the positive, negative and neutral background images. This gist background memory also showed significant effects of valence, such that participants had a better background memory for the negative than the positive condition, which was better than the neutral condition (see Table 4.2).

As done in the object memory, we obtained the emotional enhancement effect and the positivity bias for both the associative and background memory measures and ran the same set of analyses. But the models derived from resting-state FC could not significantly predict either the emotional enhancement effect or the positivity bias even in these measures (Table 4.5; Appendices E, F). We also ran the same analysis after splitting participants into three age groups, but the models could not predict the emotional enhancement effect or positivity bias in any group.

Table 4.5

Model prediction results for other memory measures

Dependent Variable	Ages	*r*	R^2	nRMSD
Emotional enhancement effect – Associative Valence Memory				
	All ages	-.01	-.14	1.07
	Younger adults	.10	-.14	1.07
	Middle-aged	-.27	-.47	1.21
	Older adults	.05	-.17	1.08
Positivity bias – Associative Valence Memory				
	All ages	.20	.00	1.00
	Younger adults	.20	-.03	1.02
	Middle-aged	-.12	-.22	1.10
	Older adults	.05	-.17	1.08
Emotional enhancement effect – Background Memory				
	All ages	-.15	-.33	1.15
	Younger adults	-.15	-.43	1.20
	Middle-aged	-.05	-.35	1.16
	Older adults	-.06	-.27	1.13
Positivity bias – Background Memory				
	All ages	-.19	-.39	1.18
	Younger adults	-.11	-.27	1.13
	Middle-aged	-.18	-.41	1.19
	Older adults	.15	-.11	1.05

4.4.4 Robustness Check

To check that the results were not specific to the analysis method we used, we ran a series of analyses with other methods and parameters. First, we ran the same set of analyses while changing the lasso-to-ridge ratio from .01 to an automatic selection in 3-fold nested cross-validation among 6 ratios (.1, .5, .7, .9, .99, 1), to check whether the quality of parameter regularization would impact the results (Fishburn et al., 2019; Liu et al., 2021; Shimizu et al., 2015; Toiviainen et al., 2014; Veretennikova et al., 2018). The results showed similar patterns; resting-state FC successfully predicted age and intelligence in younger adults but none of the other variables (Table 4.6).

The same set of analyses were also run again but using 10-fold cross-validation instead of leave-one-out cross-validation, as k-fold cross-validation may show higher robustness than leave-one-out cross-validation (Poldrack et al., 2020). Once again, age was successfully predicted. Likewise, intelligence in younger adults was predicted by resting-state FC. Nevertheless, none of the rest of variables were predicted by resting-state FC (Table 4.6).

Thirdly, the analyses were run using a Random Forest Regressor instead of a linear regression. Leave-one-out cross-validation was used, allowing for a maximum depth among 5 values (5, 10, 20, 40, 50), similar to parameters used in previous studies (Dadi et al., 2020; Han & Adolphs, 2020; J. Kim et al., 2018; Pereira et al., 2018). The results were again similar, showing good prediction for age and intelligence in younger adults, but not the other variables (Table 4.6).

Table 4.6

Prediction results of alternative models

Dependent Variable	Ages	Model	*r*	R^2	nRMSD
Object emotion enhancement effect					
	All Ages	Elastic Net, fixed L1, LOOCV	-.09	-.31	1.14
	All Ages	Elastic Net, fixed L1, 10-Fold CV	.03	-.15	1.07
	All Ages	Elastic Net, tuned L1, LOOCV	-.09	-.33	1.15
	All Ages	Random Forest, LOOCV	.04	-.10	1.05
Object positivity bias					
	All Ages	Elastic Net, fixed L1, LOOCV	.03	-.19	1.09
	All Ages	Elastic Net, fixed L1, 10-Fold CV	.02	-.25	1.12
	All Ages	Elastic Net, tuned L1, LOOCV	.03	-.22	1.10
	All Ages	Random Forest, LOOCV	.01	-.13	1.07
Intelligence					
	All Ages	Elastic Net, fixed L1, LOOCV	.09	-.09	1.05
	All Ages	Elastic Net, fixed L1, 10-Fold CV	.06	-.14	1.07
	All Ages	Elastic Net, tuned L1, LOOCV	.14	-.07	1.04
	All Ages	Random Forest, LOOCV	.14	-.04	1.02
Age					
	All Ages	Elastic Net, fixed L1, LOOCV	.44	.19	.90
	All Ages	Elastic Net, fixed L1, 10-Fold CV	.43	.18	.91
	All Ages	Elastic Net, tuned L1, LOOCV	.41	.15	.92
	All Ages	Random Forest, LOOCV	.32	.10	.95

Note: Fixed L1 is ridge-lasso ratio =.01. Tuned L1 refers to the procedures where L1 was chosen using a 3-fold nested cross-validation from the values :.1, .5, .7, .9, .99, 1. LOOCV refers to leave one-out cross validation. Random forest models tune the maximum depth parameter from the 5 values: 5, 10, 20, 40, 50, using a nested 3-fold nested cross-validation.

Figure 4.1.

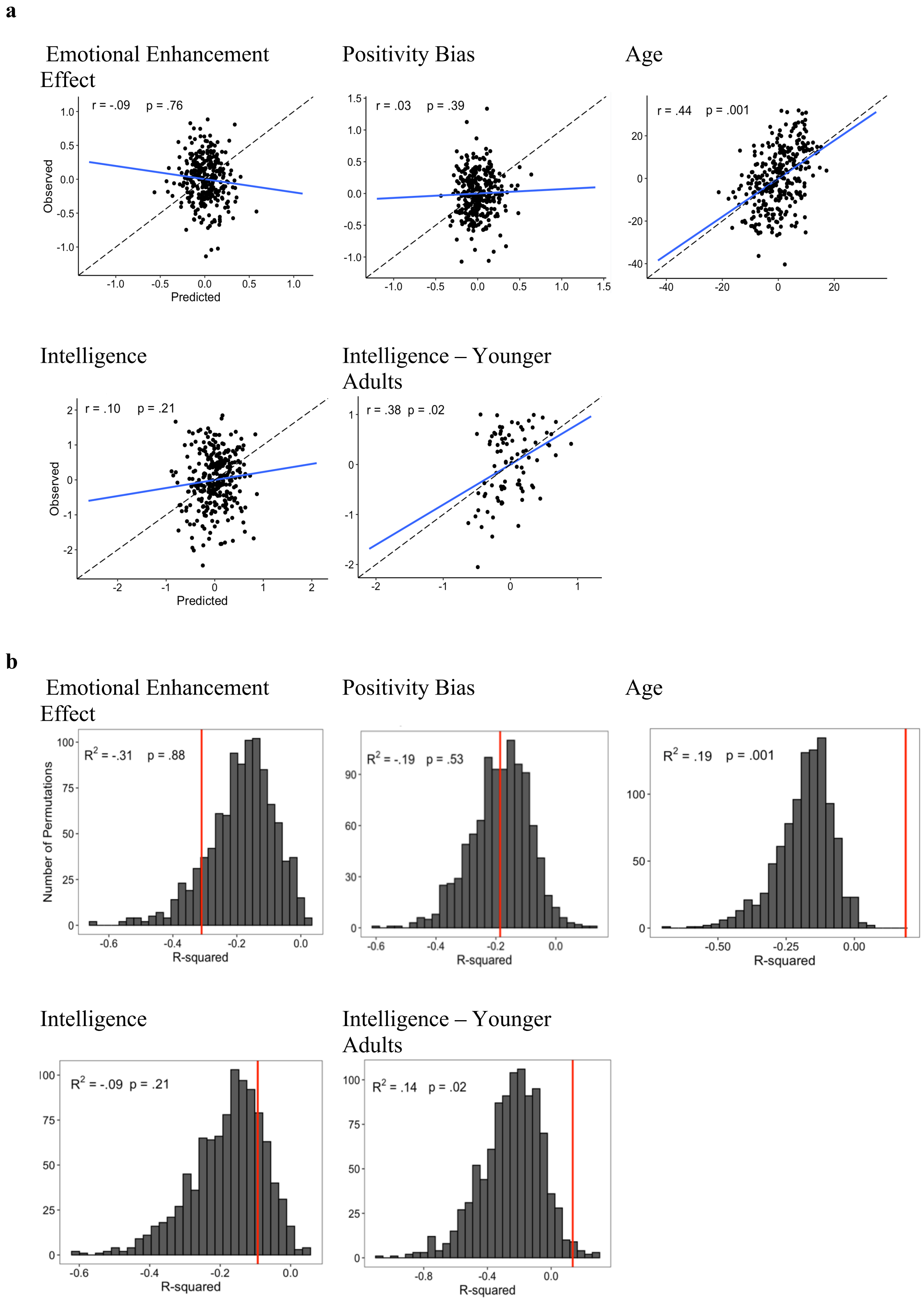

a
Emotional Enhancement Effect
r = -.09 p = .76
Positivity Bias
r = .03 p = .39
Age
r = .44 p = .001
Intelligence
r = .10 p = .21
Intelligence – Younger Adults
r = .38 p = .02
Observed
Predicted
b
Emotional Enhancement Effect
R^2 = -.31 p = .88
Positivity Bias
R^2 = -.19 p = .53
Age
R^2 = .19 p = .001
Intelligence
R^2 = -.09 p = .21
Intelligence – Younger Adults
R^2 = .14 p = .02
Number of Permutations
R-squared

Figure 4.1. The prediction performance of the models for emotional enhancement effect, positivity bias, age, intelligence, and intelligence for younger adults only. (a) Scatter plots showing demeaned and deconfounded observed values versus those predicted by the models. Pearson's correlation and the one tailed *p*-value of the correlation obtained from permutation are shown on the graph. The best fitting line is displayed in blue. Slopes closer to 1 (dotted line) show good prediction (Dubois et al., 2018). (b) The distribution of the permutation models' R^2 (in grey), which is the null distribution. The model's R^2 are shown in red. The models' R^2 and one-tailed *p*-value obtained from permutation are displayed on the figures.

4.5 Discussion

In this study, we examined whether resting-state FC predicts individual differences in the emotional enhancement effect in memory, the positivity bias in memory, intelligence and age. Neither the emotional memory enhancement effect, nor the positivity bias was significantly predicted by resting-state FC. In contrast to these measures of emotional memory, models derived from resting-state FC successfully predicted chronologic age, replicating previous findings (Tsvetanov et al., 2016; Vergun et al., 2013). These results suggest that the methods used in this study were able to predict behavioural phenotypes based on resting-state FC. Yet, contrary to our prediction (preregistered), intelligence was not predicted from resting-state FC when participants of all ages were included.

To check whether the failure to predict intelligence or emotional memory measures using resting-state FC was due to the wide age range of participants, we split participants into three groups: younger (18-40 years), middle-aged (41-60 years), and older adults (61-87 years). Previous studies suggest that resting-state FC patterns undergo a nonlinear trajectory with age, such as increasing FC within DMN during late adulthood before its rapid decline after age 74 (Staffaroni et al., 2018). In addition, age-related compensatory recruitment of the prefrontal cortex can result in age-related shifts in brain regions responsible for tasks relevant to intelligence (Grady, 2012). However, neither the emotional memory enhancement effect nor the positivity bias was predicted by the models in any age groups. The only exception was intelligence in younger adults; when including only younger adults as done in past studies (Dubois et al., 2018; Finn et al., 2015), resting-state FC successfully predicted individual differences in intelligence.

Importantly, even after splitting participants into three age groups, resting-state FC did not predict the two emotional memory measures in any age groups. These results suggest that the predictive power of resting-state FC is lower for emotional memory measures than for intelligence. The results could also suggest that the utilized emotional memory measures are not appropriate or reflective of a reliable effect. These results are in line with those from past studies on resting-state FC. For example, a recent study failed to replicate past findings in predicting habitual use of emotion regulation strategies from resting-state FC (Dörfel, Gärtner, & Scheffel, 2020). Another study showed that resting-state FC predicts working memory, but not executive control, language, or verbal memory performance in older adults (Jockwitz et al., 2017). Similarly, in Dubois et al. (2018), resting-state FC predicted intelligence in younger adults, but not personality traits of neuroticism, consciousness, extraversion, and agreeableness. There are several possible reasons behind the weaker predictive power of resting-state FC for our emotional memory measures.

The first possibility might be a low reliability of emotional memory measures. A recent study reported that the emotional memory enhancement effect had a very low test-retest reliability when the same participants were tested twice over a delay of 10 weeks (Schümann et al., 2020) presumably due to the correlation between emotional and neutral memory measures and low between-subject variability in these subtraction scores (Hedge et al., 2018). In the Cam-CAN data, there were strong correlations between emotional and neutral memory measures; positive and negative object memory scores were highly correlated, $r(301) = .90, p < .011$; and neutral object memory performance was also highly correlated with both positive, $r(301) = .89, p < .001$, and negative memory performance, $r(301) = .88, p < .001$. The associative valence memory performance also showed high correlations between positive and negative conditions, $r(301) = .77, p < .001$, between neutral and negative conditions, $r(301) = .85, p < .001$, and between positive and neutral conditions, $r(301) = .84, p < .001$; although the magnitudes of correlation were weaker for the background memory, it still showed moderate correlations between negative and positive $r(301) = .41, p < .001$, between negative and neutral $r(301) = .35, p < .001$, and between positive and neutral conditions $r(301) = .39, p < .001$. Such strong correlations could have resulted in low reliability for our dependent variables (i.e., the emotional memory enhancement effect and the positivity bias score) that were derived by subtracting one from another highly correlated variable (Infantolino, Luking, Sauder, Curtin, & Hajcak, 2018). Thus, our failure to predict emotional memory measures may have been driven by the limited reliability of the measures.

The second possibility concerns our dependent measures. In our main analysis, we used memory performance for neutral objects learned with emotional backgrounds as the key dependent variable. Thus, the dependent measures were not about emotional items themselves but more about the effects of emotion (induced by the background images) on memory for nearby neutral information (i.e., neutral objects presented with the background images). Previous research has repeatedly shown that while emotional items are preferentially remembered better than neutral items in many situations, the effects of emotional items on nearby neutral information are more complex (Chiu, Dolcos, Gonsalves, & Cohen, 2013; Mather, 2007; Mather & Sutherland, 2011); such that emotion sometimes enhances memory for nearby neutral information but sometimes impairs memory for nearby neutral information (Mather & Sutherland, 2011; Murray & Kensinger, 2013; Sakaki et al., 2014; Waring & Kensinger, 2009). These findings point to the likelihood that resting-state FC has low prediction power for individual differences in memory for neutral items nearby emotional items (arguably due to the complex nature of the effects) but may be able to predict individual differences in memory for emotional items themselves. To address this possibility, we performed exploratory analyses on two additional memory measures that are more about emotional background images (i.e., valence and the content of a background image associated with each neutral object). However, once again, resting-state FC failed to predict individual differences in these two measures. Thus, resting-state FC does not seem to reliability predict individual differences in the effects of emotion on memory, irrespective of whether memory concerns emotional items per se or nearby neutral information. Nevertheless, it is important to note that in the Cam-CAN project, the two measures of the emotional background images were not independent from the object memory measure; participants were given a chance to answer the valence and the content of a background image associated with each neutral object only when they recognized the neutral object as studied (see Methods). Thus, it is possible that resting-state FC can predict individual differences in emotional memory in other tasks (e.g., a simple recognition test; a free recall without constraints of associated object memory). Future research needs to address this issue.

Third and relatedly, the current study used performance in the memory test performed 10 minutes after the encoding session. However, previous research has suggested that the effects of emotion on memory are due to long-term consolidation effects (Ritchey et al., 2008); thus future studies with long-term memory measures obtained after consolidation may obtain a different result. Furthermore, in the Cam-CAN project, the resting-state BOLD signals were obtained on a different day from the emotional memory task. Thus, the design could be particularly vulnerable to the low reliability of our emotional memory measures. It is therefore possible that resting-state BOLD signals have stronger predictive power for emotional memory measures when they are obtained on the same day.

Fourth, our sample size was modest especially after splitting participants into three age groups (Poldrack et al., 2020; Yarkoni & Westfall, 2017), which could have resulted in the failure to predict emotional memory measures by resting-state FC. On the one hand, even with this same sample size, intelligence in younger adults was still predicted by resting-state FC as observed in previous studies (Basten, Hilger, & Fiebach, 2015; Dubois et al., 2018; Hearne, Mattingley, & Cocchi, 2016; Jiang et al., 2020; Tsvetanov et al., 2016). Yet, our sample size may not have been large enough to address the heterogeneity within older adults (Eavani et al., 2018). In addition, participants only had one resting-state session, which may have resulted in higher noise and lower prediction power than combining two or more sessions (Dubois et al., 2018). Future research needs to use a larger sample combined with multiple resting-state sessions and address the effects of resting-state FC.

Finally, although the main analyses investigated the effect across ages, it is notable that the preprocessing methods and predictive models used may be most appropriate for younger adults as the methods were developed and used primarily for a younger adult sample (Dubois et al., 2018). Unplanned exploratory analyses showed that intelligence was successfully predicted from resting-state FC in younger adults but not in middle-aged or older adults. Yet, as described earlier, age was predicted by resting-state FC successfully for participants from different age groups in this study. Such results for age were consistent with other findings (Tsvetanov et al., 2016), suggesting that our analysis and denoising method was appropriate. The alternative reason behind the failure of predictions for middle-aged and older adults concerns the effects of age on individual differences. Previous longitudinal studies have suggested heterogeneity within older adults in their cognitive performance, brain structure and its functioning (Eavani et al., 2018; Olaya, Bobak, Haro, & Demakakos, 2017).

Thus, the age-related increases in the heterogeneity may have made it difficult for us to predict cognitive measures in middle-aged or older adults relative to younger adults. In line with this idea, a recent large-scale study including 711 older adults also found no association between cognitive performance and resting-state FC (Jockwitz et al., 2017, but see Greene, Gao, Scheinost, & Constable, 2018). Future research needs to take into account the effects of age on heterogeneity within participants.

In summary, the present study used a machine learning approach (which allowed us to select the most informative connections across the whole brain rather than relying on a priori selected regions) in predicting individual differences in emotional memory measures. While models derived from resting-state FC predicted age (for all participants) and intelligence for younger adults, they did not reliably predict the emotional memory enhancement effect and the positivity bias in memory for any age group. The results suggest the neural basis of individual differences in the emotional memory enhancement effect and positivity bias may not be meaningful or large enough to be predicted from resting-state FC. The results are in line with recent findings on low-reliability of the emotional enhancement effects in memory (Schümann et al., 2020), suggesting that more research should be done on the viability of the emotional enhancement effect and positivity bias as stable traits. Our results also support the use of an existing pipeline (Dubois et al., 2018) to denoise and predict traits at least for adult participants. Future research would be able to use this pipeline to minimise bias in choosing methods based on the results obtained (p-hacking; Yarkoni & Westfall, 2017).

4.6 Data Availability

Data used in the preparation of this work were obtained from the Cam-CAN repository (available at http://www.mrc-cbu.cam.ac.uk/datasets/camcan/). Users must agree to the terms and conditions and submit an application to access the Cam-CAN database. The dataset generated and analysed during the current study is available on https://osf.io/bm98y.

Chapter 5: General Discussion

5.1 Summary

The thesis looked at three factors that may influence emotional memory: prolonged effects of arousal, interoception, and functional connectivity during rest. In sum, the research did not find any significant prolonged effects of arousal on memory, but found that interoception is associated with negative more than positive emotional processing and memory, and that resting-state connectivity is not associated with individual differences in emotional memory.

Study 1 found that emotional arousal did not exhibit prolonged effects on the memory of neutral items, regardless of the items' goal-relevance status. The study induced emotional arousal through the use of a speech task paired with a false biofeedback manipulation of an increasing heart rate. The results suggest that arousal may not exhibit prolonged effects on the memory of unrelated information, even if they are relevant to actively-held goals. The study shows the temporal limitations of the ABC theory.

Study 2 found that attending to interoceptive signals leads to increased negativity bias in memory and arousal ratings. During the study, participants heard what they thought was their own heartbeats on speaker while viewing emotional and neutral images. During control blocks, participants heard steady tones that were unrelated to heartbeats. The study found that, compared to control blocks, participants remembered more negative items than positive during heart rate feedback blocks, and rated negative items as being more emotionally arousing than were positive ones. The study suggests that cardiac interoception is implicated more in negative emotions than in positive emotions.

Study 3 found that resting-state functional connectivity did not predict any of the emotional memory measures. Intelligence was predicted by resting-state functional connectivity for younger adults. The study investigated a database of 303 individuals aged between 18 and 87 years. The study suggests that functional connectivity may not have a strong association with emotional memory. The study might indicate that individual differences in emotional memory may not be stable.

5.2 Strengths

This thesis aimed to study aspects of memory that are currently under-investigated, but which could lead to a better understanding of mixed findings on emotional memory (Bennion et al., 2013). The thesis looks at three aspects. The first aspect is the prolonged effects of arousal. Previous studies have often looked at the memory of emotional items themselves, but the prolonged effects remain mostly overlooked. Second, the appraisal of emotional arousal itself is associated with individual factors. One important factor relating to the experience of emotion is interoception (Craig, 2009; Critchley & Garfinkel, 2017). However, it has not been widely investigated in memory. The second study investigated the association between interoception and emotional memory. The third study took a broader approach, investigating whether or not resting-state functional connectivity, which is associated with both emotion and interoception, is associated with emotional memory.

5.2.1 Study 1

One strength of the study is that it investigated the effects of arousal on the memory of prospective information that did not relate to the source of arousal. Neutral items were presented minutes after the induction of emotional arousal through a speech task paired with false biofeedback. Examining the effects of emotional arousal on the memory of neutral rather than emotional items could clarify the role of arousal in emotional memory while averting the possible confounds arising from the distinctiveness or interrelatedness of emotional items (Bennion et al., 2013; Talmi, 2013).

A second strength is that the prospective effects of arousal have been mostly investigated with regard to stimuli viewed seconds rather than minutes after emotional stimuli (Jia et al., 2020; Knight & Mather, 2009; Sakaki et al., 2014; Sutherland et al., 2017).

The prolonged effects of emotional arousal on neutral items of varying goal-relevance remain unknown. However, in the present study, the memory of neutral items was shown not to differ when presented after the emotionally-arousing task or the control task. The effects of emotion on memory may be stronger for emotional items than for neutral items learned later. This is why, the following chapters examined the memory of emotional items, rather than neutral items associated with emotion.

Another strength of Study 1 is that it included subjective and physiological measurements to test whether the manipulation elicited arousal, and whether this arousal persisted. As expected, the results showed that negative mood was higher after performing the speech task than the control task. In addition, skin conductance levels showed that emotional arousal was increased by the speech task compared to the control. The increase seen in skin conductance persisted during the picture task. On the other hand, heart rates were increased by the preparation of the speech task, but this increase was not prolonged. Skin conductance is usually an index of sympathetic activity (Lang et al., 1993; Palomba et al., 2000). On the other hand, the heart rate is controlled by both sympathetic and parasympathetic systems (Mendelowitz, 1999; C.-A. Wang et al., 2018). Therefore, the findings may indicate that parasympathetic activity increased after emotional arousal, indicating the beginning of recovery. Future studies could investigate the effects of sympathetic and parasympathetic activation in detail. The studies could use additional indices such as T-wave for sympathetic activity (Palomba et al., 2000), heart rate variability (Kreibig, 2010), and respiratory sinus arrhythmia (Palomba et al., 2000) for parasympathetic activity. Taken together, the physiological measures and mood manipulation checks increase the confidence in that the emotional arousal task succeeded in increasing emotional arousal and negative affect.

Finally, the memory test was taken one day after encoding which could be important given that consolidation largely takes place during sleep (Nishida et al., 2009; Björn Rasch & Born, 2013; Tempesta et al., 2018). Emotional memory effects are largely due to consolidation (McGaugh, 2004). Immediate effects of emotional memory are often thought to be due to encoding effects, including more attention to emotional items (Talmi, 2013). Therefore, the study includes the effects of both encoding and consolidation and concerns the long-term memory.

5.2.2 Study 2

Research that has investigated the association between interoception and emotional response usually uses a correlational approach (Herbert et al., 2010; Pollatos et al., 2005; Pollatos & Schandry, 2008). Furthermore, previous studies have often used the heartbeat counting task which has been criticised (e.g., Ring et al., 2015). Study 2 used a true biofeedback manipulation to investigate interoception. Specifically, participants were presented with blocks of audible heartbeats.

The research into true biofeedback has been limited, and none to our knowledge investigated how it affects emotional memory. The salience of heartbeats likely increases both attention and accuracy in detecting heartbeats. Biofeedback manipulations have been largely in the form of false biofeedback, usually of falsely increasing or decreasing heart rate (Makkar & Grisham, 2013; Wild et al., 2008). The usual aim of false biofeedback manipulations is to alter the emotional response to match the presented biofeedback. Study 2 found that presenting true biofeedback leads to enhanced memory and emotional arousal rating of negative compared to positive items, which suggests that interoception is implicated in negative emotional processing. The present study offers support for using true biofeedback in studies investigating interoception, and joins nascent studies attempting to manipulate interoception rather than relying on interceptive accuracy tasks (Iodice et al., 2019; Lenggenhager et al., 2013).

The design of the study was such as to account for possible confounds. The arousal level of images, the free recall test, and the screening for psychopathological disorders were carefully chosen to avoid possible confounds. The study included both positive and negative images. Positive and negative images were chosen to be of equal arousal and valence intensity, based on previous normative ratings (Bradley & Lang, 2007). Furthermore, participants were screened for current and history diagnoses of psychiatric or psychopathological disorders. Anxiety has been associated with abnormal insular activity (Shah et al., 2009; Stein et al., 2007) and behavioural differences in interoceptive attention tasks (Palser et al., 2018). Depression was also associated with dysfunctions in interoception (Dunne et al., 2021; Furman et al., 2013).

The memory test used in this study was a free recall test. The test was scored independently by two scorers. The emotional enhancement effect shows more reliably in free recall tests than recognition tests (Baraly, Hot, Davidson, & Talmi, 2016), especially when tested after a delay (Lipinska, Stuart, Thomas, Baldwin, & Bolinger, 2019; Yonelinas & Ritchey, 2015). Many explanations have been proposed for the advantage of free recall test in research on emotion and memory. For example, the free recall test may utilise intentional controlled processing more than recognition tests (Craik & McDowd, 1987). Therefore, free recall tests may more strongly reflect the enhancing effects of encoding, consolidation and retrieval of emotion on memory on recall tests (Baraly et al., 2016). Whereas, on the other hand, Baraly et al. (2016) argue that simply superficial encoding should lead to successful recognition in a recognition test. The controlled processing nature of the free recall tests may also lead to reflecting of emotion-related goals (L. Yang & Ornstein, 2011). A second explanation has been proposed by Yonelinas et al. (2015) in a review that found that recollection (which plays a larger role in recall than recognition) of emotional items is enhanced more than familiarity (which plays a large role in recognition). The enhancement of recollection compared to familiarity has been also previously supported (LaBar & Cabeza, 2006). Yonelinas et al. (2015) argue that recollection is associated with the activation of the amygdala more than the hippocampus, which may explain the reduced forgetting rate of recollection of emotional items. However, the free recall tests may be particularly susceptible to effects of not controlling the inherently increased distinctiveness and cohesiveness of emotional stimuli, compared to neutral (Baraly et al., 2016).

5.2.3 Study 3

One important strength for Study 3 is that it was pre-registered. The main analyses methods, including the scripts, were publicly uploaded before analysis. Furthermore, the pre-processing, denoising and machine learning analysis pipelines were previously used in a study (Dubois et al., 2018). Those methods were shown to be suitable for predicting psychological measures from resting-state functional connectivity.

Second, after completing the pre-registered analyses, a large number of exploratory analyses were performed in order to check the veracity of the findings. The exploratory analyses were clearly labelled in order to be differentiated from the pre-registered main analyses. The analyses included using different machine learning algorithms and cross-validation methods, splitting up participants according to age, and investigating various emotional memory measures. The negative findings of exploratory analyses bolstered the confidence that resting-state functional connectivity may not predict emotional memory. Furthermore, the exploratory analyses predicting age and intelligence in younger adults also bolstered confidence in the suitability of the methods used, because they replicated the findings of past studies (Dubois et al., 2018; Tsvetanov et al., 2016).

Furthermore, the study did not include pre-defined regions of interest, but rather investigated whole-brain functional connectivity. The algorithms chose the relevant connections automatically. Different tuning parameters of those regularisation settings were also explored. Choosing small regions of interest based on past evidence, instead of the machine learning approach, may have led to missing important but overlooked regions.

The study assessed different memory types: the memory of neutral items superimposed on emotional backgrounds, the memory of the valence of backgrounds associated with those neutral items, and the gist memory of emotional backgrounds. Therefore, the study included object and associative memory. The memory of associative items could differ significantly from the emotional objects themselves (Kensinger, 2009; Mather, 2007). Furthermore, scores of emotional enhancement and of positivity bias were calculated for each memory type and were investigated. Positivity bias was previously found to be associated with resting-state functional connectivity (Sakaki et al., 2013). Therefore, the inclusion of different types of memory increased the confidence in the negative findings obtained, and are in line with recent research questioning the utility of functional connectivity in predicting behavioural and cognitive factors (Marek et al., 2022).

5.3 Limitations

The present thesis relied on the circumflex model of emotion. However, there are many limitations to the model. Using an appraisal account may have been a more nuanced approach. The appraisal model, due to the componential take, would acknowledge that the processing of interoceptive signals may affect emotional response (Ellsworth, 2013; Moors et al., 2013). Appraisal models propose the interdependence of emotional components, including the somatic component on feelings and vice versa.

Second, the appraisal model would explain goal-congruence effects that are inherent to emotions. Different discrete emotions may impact memory differently (as reviewed in

Levine & Pizarro, 2004). For example, experiencing emotion such as anger may lead to increased focus on goal-related information, whereas fear may increase focus on threats. Therefore, different emotions may modulate goals differently, despite having similar valence and arousal levels. Such differences in goals could be reflected in differences in memory. Study 1 manipulated the goal-relevance of the neutral stimuli, but did not take into account the discrete emotions elicited, and how they inherently impact the goal-relevance of items.

Investigating the distinct emotions elicited by the speech in Study 1 may have led to better and more nuanced findings. Furthermore, participants may have varied in their appraisal of the speech task. Second, in Studies 2 and 3, no account was taken of discrete emotions depicted or elicited by the individual images. It is likely that different discrete emotions were depicted. Everyday emotions are usually not triggered by mixtures of unrelated emotional stimuli, but more likely by singular coherent events. Future studies could investigate emotional memory while accounting for discrete emotions. For example, anger or fear could be manipulated through tasks involving false feedback about performance (e.g., Kligyte, Connelly, Thiel, & Devenport, 2013). Studies 1 and 2 could be replicated while using such emotional tasks to investigate the effects of distinct emotions. Such studies would bridge the current gap in appraisal-based studies in emotional memory, and would illuminate the varying roles of distinct emotions on memory and attention.

Another limitation of the studies is that, in Studies 1 and 2, the sample comprised mostly of females. There are gender differences in emotional memory, and even the neural basis of neural memory (Canli et al., 2002; Glaser, Mendrek, Germain, Lakis, & Lavoie, 2012). Females may even have a different relationship compared with males between noradrenergic activity and selective memory (Clewett et al., 2017). Furthermore, there may be gender differences in interoception (Grabauskaitė et al., 2017). Therefore, it is possible that the present studies did not detect gender differences.

Other than general limitations, each of the studies has its several limitations. One limitation of Study 1 is that it included the use of false biofeedback in the speech and control tasks. This may have resulted in prediction errors between predicted or incoming interoceptive signals (Seth, 2013). Prediction errors are usually resolved by changing predictions to match the biofeedback, paying less attention to own interoceptive input, or changing behaviour to make the predicted and incoming signals match (Barrett & Simmons, 2015). The mismatch between actual and biofeedback interoceptive signals may have confounded the effects of arousal. For example, one study found that presenting false (incongruent) biofeedback led to a decrease in heart rate variability compared to true biofeedback (Hodossy & Tsakiris, 2020). Therefore, the effects of using false biofeedback with the emotionally-eliciting task may have caused confounding effects rather than simply making the task more arousing. However, importantly, the control task also included false biofeedback.

Furthermore, Study 1 induced negatively-valenced emotional arousal. The findings of the study may not generalise to positively-valenced or neutral (e.g., exercise-induced) emotional arousal. Valence may have important effects on attention and memory (Kensinger, 2007). Positive emotion may lead to broadening of attention (Fredrickson, 2004). This may be reflected in enhanced associative memory when positive valence is elicited (Madan et al., 2019). This may suggest that positive valence may be more successful than negative in having prolonged effects on memory. Future studies should investigate the prolonged effects of positive and neutral emotional arousal.

Relatedly, the valence-specific findings in Study 2 should be interpreted carefully. The study found lower arousal ratings of positive compared to negative items across conditions. Previous research similarly suggests that positive stimuli is not as successful in eliciting an emotional response as is negative stimuli (Westermann et al., 1996). Therefore, rather than creating negativity bias, interoceptive signals may have highlighted a discrepant physiological response to negative compared to positive items. Future studies could place neutral, negative and positive in separate blocks (e.g., Talmi et al., 2007).

In Studies 2 and 3, the memory test was taken only minutes after encoding. Emotional memories often show increased enhancement in memory over neutral after longer delays (Sharot et al., 2007; Yonelinas & Ritchey, 2015). Therefore, the findings concern the effects of interoception on encoding. The effects of consolidation were not shown.

Furthermore, in Study 3, the scanning sessions were taken on different days from the memory task. This may have amplified the effects of the possible low reliability of both emotional memory (Schümann et al., 2020) and functional connectivity (Noble, Scheinost, & Constable, 2019). It is possible that if the scans and memory task had been taken during the same session, different results would have been obtained. However, the use of different sessions may be a more stringent test of the utility of functional connectivity in predicting traits. Another limitation of Study 3 is that the denoising pipeline was developed for a sample of younger adults (Dubois et al., 2018). However, this was used for adults of all ages. Although exploratory analyses split participants according to age, the results of middle-aged and particularly older adults should be viewed cautiously, because the pipeline may have been unsuitable.

5.4 Implications

The studies support the enhancing role of emotion on memory. Across Studies 2 and 3, emotionally-arousing items were better recalled than neutral. The findings support a large body of literature showing that emotional arousal enhances memory (Bowen et al., 2018; Hamann, 2001; Mather, 2007; Mather & Sutherland, 2009; Phelps, 2004). Although Study 1 did not find an enhancement in memory, it concerned the prolonged effects of arousal.

An important implication of the studies is the clarification of the temporal effects of arousal. While the memory of emotionally-arousing items was enhanced (Studies 2 and 3), there was no effect of pre-encoding emotional arousal on the memory of prospective neutral items (Study 1). Therefore, the results suggest a temporal limit to the effects of emotional arousal. Previous studies suggest that arousal affects the memory of items encountered seconds later (Hurlemann et al., 2005; Knight & Mather, 2009; Sakaki et al., 2014). Future studies should investigate the timing of when emotional arousal ceases to affect memory. For example, Sutherland and Mather (2012) examined the durations at which arousal affected working memory. The study found that 4 to 6 seconds after arousal induction, arousal exhibited no effect on working memory. Studies using a similar design, e.g. introducing neutral items at varying time delays from emotional arousal, could find the timing at which emotion ceases to affect memory.

The findings of Study 1 prompt the investigation of context-congruence as a factor in emotional memory. In contrast to Study 1, Tambini et al. (2017) found prolonged effects of arousal on memory. One major difference between the studies is the extent of context-congruence between emotional arousal and encoding tasks. Although the goal-relevance of the items was manipulated, this type of prioritisation did not interact with arousal. The ABC theory does not make distinctions among different types of priority. However, there are likely differences between various types of priority (Sutherland et al., 2017). Future research should investigate the effects of change in context-congruence after emotional arousal. Such findings may have wider implications with regard to emotional recovery, which are explored later in this section.

Study 2 supports the view that interoception is implicated in negative emotions. The findings are in line with lesion and electrocortical stimulation (e.g., Motomura et al., 2019). However, the findings are different from correlational studies showing a positive association between interoceptive ability and emotional intensity ratings to positive and negative stimuli (e.g., Herbert, Pollatos, Flor, Enck, & Schandry, 2010; Pollatos, Kirsch, & Schandry, 2005; Pollatos & Schandry, 2008). Future studies should replicate the study, including using a larger sample, and incorporating positive images that are as equally arousing to participants as negative images. A replication of the findings would lead to an important revision of theoretical models, and would show the limitations of past evidence conflating interoceptive awareness with performance on interoceptive accuracy tasks.

The study supports the use of interoceptive signals in investigating the effects of interoception. However, the present manipulation makes it unclear whether the findings are due to an enhancement in attention, accuracy, or both. Future research should investigate methods in eliciting interoceptive accuracy and attention separately, as evidence suggests that they are not correlated (Garfinkel et al., 2015). Interoceptive accuracy could be manipulated by presenting heartbeats that are congruent to own heartbeats or incongruent but falsely presented as true feedback (e.g., Hodossy & Tsakiris, 2020). Interoceptive attention could be introduced through active instructions to focus on heartbeat versus exteroceptive attention. Other interoception modalities such as respiratory signals, should also be explored.

Third, in Study 3, machine learning models were unable to predict emotional memory from whole-brain functional connectivity. The results suggest that resting-state databases may not be helpful when it comes to studying individual differences in emotional memory. The results are in line with broader evidence showing no effect with regard to predicting behavioural or cognitive measures from resting-state scans (Marek et al., 2022). Specifically, Marek and colleagues found that to have replicable effects, a very large sample size of tens of thousands of individuals should be used. This recent study calls into question the use of resting-state scans to predict individual differences. Our findings are also in line with these recent findings, and call into question the utility of large resting-state data, which are both time consuming and expensive, in predicting individual difference measures.

Another explanation is that emotional memory has a low degree of reliability (Schümann et al., 2020). In the Cam-CAN database, brain scans were taken on a different day from the emotional memory tasks (Shafto et al., 2014). Research suggests that mood affects emotional memory (Dolcos et al., 2017; Gaddy & Ingram, 2014). Investigating mood effects, and finding other factors that influence emotional memory, are of interest and could contribute to emotional memory research. Research on moderators could illuminate the mixed findings and could inform control measures for future studies.

The studies infer information about the effects of emotional arousal on memory. In Study 1 there was no enhancement in the memory of neutral items viewed after a manipulation that increased emotional arousal. This is in line with pharmacological studies showing that inhibiting the arousal response by administering propranolol usually impairs the memory of emotional but not neutral items (Cahill et al., 2013). Therefore, the findings Study1 support that physiological arousal does not impact the memory of neutral items or items unrelated to the arousal, even if we attempt to increase priority.

In Study 2, arousal rating of images shown during both the control and heart rate biofeedback condition were collected. Physiological arousal measurements were also collected. However, technical issues prevent the measurement of physiological arousal response to individual images. Emotional items were recalled better than neutral across conditions. The heart rate biofeedback led to increased negativity bias in memory and arousal rating (higher arousal rating of negative items compared to positive). Therefore, the changes in subjective arousal were in line with changes in memory. However, items rated as more highly arousing were not necessarily better recalled. For example, during the control blocks there was no difference in arousal rating for positive and negative items shown, yet there was a negativity bias in the memory of those items. On one hand, the results suggest that valence plays a role in emotional memory and may interact with arousal (Steinmetz, Addis, & Kensinger, 2010). On the other hand, the results may be also in line with previous research showing only a moderate correlation between the amygdala activation and arousal rating of stimuli (Touroutoglou et al., 2014), and an association between memory and physiological rather than subjective arousal (Mather, 2007; Mather et al., 2016; Mather & Sutherland, 2011). Yet, the physiological arousal response to images of different valences in this study was not available. Finally, the results also suggest that interoception may be implicated in the experience and memory of negative emotions more than positive.

In Study 3, the memory of emotionally arousing items was better than neutral across all memory measures. The normative arousal ratings were higher for negative items than positive (5.03 and 5.99 respectively on 9-point scale; Henson et al., 2016). Yet, there was not a clear enhancement in the memory of negative compared to positive stimuli. The memory of neutral items presented on negative backgrounds was enhanced compared to those presented on positive backgrounds. However, there was an opposite pattern of enhanced memory of valence associations, showing better memory of the valence of positive backgrounds compared to negative. The findings support that positive valence may enhance associative memory more than negative valence (Kensinger, 2009). In sum, the studies in this thesis support that arousal enhances memory, but only of emotional items themselves or those closely associated with it, such as neutral items *unitised* with emotional items in Study 3. The results support a valence-arousal interaction (Steinmetz et al., 2010), and an interaction between interoception and both memory and subjective arousal (Critchley & Garfinkel, 2016; Pollatos & Schandry, 2008).

Other than theoretical implications, the findings have practical implications. They may offer practical knowledge for use in the educational field, and offers practical knowledge on the effects of daily occurrences such as watching the news, and the effects of smart wearable devices on emotion and memory. Each of those implications will be discussed below.

First, the effects of low arousal on memory have been documented in educational settings. Boredom is associated with lower arousal (Danckert et al., 2018; Pattyn et al., 2008). For example, boredom in the classroom has been associated with negative performance, even after controlling for appropriate factors (Pekrun, Hall, Goetz, & Perry, 2014). Low arousal levels have also been shown to lead to an increase in overgeneral memories (McBride & Cappeliez, 2004). Low levels of arousal may explain the low levels of memory of lecture and class material. Increasing arousal levels, such as through activities might enhance learning. Given, in Study 1, the effects of pre-learning activities that elicit negatively-valenced high arousal, which is likely equivalent to tests, may have little or no impact on enhancing learning. However, other high arousing but not negatively-valenced method is physical exercise, may lead to enhanced academic achievement when incorporated into academic lessons (Watson, Timperio, Brown, Best, & Hesketh, 2017), which may be explained by that post-encoding emotional arousal may enhance memory (Shields et all., 2016).

Second, the effects of negatively-valenced emotional arousal on memory were not prolonged when the modality changed. The results indicate that emotionally-arousing experiences such as watching the news or getting into a minor accident, could have little impact on the memory of later events — even if they are of high goal-relevance. Future studies should investigate the prolonged effects of emotional arousal when the context is not changed.

Furthermore, research on the congruence of context to emotional events could lead to practical implications on recovery from emotional episodes. For example, a change in context such as a change in physical location, may lead to no effects of emotion on memory (Shields et al., 2017). The present study supports this finding, and suggests that intentional change in context may be helpful in mitigating the effects of emotions in memory, including the winner takes all effect.

Third, attending to an online presentation of one's own heartbeats was shown to amplify the negativity bias in memory, and make negative items appear to be more arousing. With the availability of smart watches, online access to heart rate is becoming more easily available. The present research shows that online presentation of heart rate may lead to increased bias, amplifying the intensity of negative experiences compared to positive. More research should investigate this effect. For example, smart watches display the heart rate, but usually do not play audible beeps synchronised with heartbeats. Future studies could investigate the effects of presenting the heart rate on the screen, without the auditory beeps.

5.5 Conclusion

The present thesis contributes to a more nuanced understanding of the effects and moderators of emotion on memory. The results confirm recent findings relating to the low reliability of functional connectivity associations (Marek et al., 2022) and of emotional memory (Schümann et al., 2020). The thesis confirms lesion-based studies on the role of interoception in negative emotion (Motomura et al., 2019), and offers novel findings on the role of interoception on emotional memory. The thesis provides novel findings about the prolonged effects of emotional arousal, and suggests temporal limits to the ABC theory (Mather & Sutherland, 2011). The findings help in furthering the field of emotional memory, and have wider implications on emotional recovery, interoception and functional connectivity.

References

Adolfi, F., Couto, B., Richter, F., Decety, J., Lopez, J., Sigman, M., … Ibáñez, A. (2017). Convergence of interoception, emotion, and social cognition: A twofold fMRI meta-analysis and lesion approach. *Cortex*, *88*, 124–142. https://doi.org/https://doi.org/10.1016/j.cortex.2016.12.019

Adolphs, R., Cahill, L., Schul, R., & Babinsky, R. (1997). Impaired declarative memory for emotional material following bilateral amygdala damage in humans. *Learning and Memory*, *4*(3), 291–300. https://doi.org/10.1101/lm.4.3.291

Anderson, J. S., Ferguson, M. A., Lopez-Larson, M., & Yurgelun-Todd, D. (2011). Reproducibility of single-subject functional connectivity measurements. *American Journal of Neuroradiology*, *32*(3), 548–555.

Andreano, J. M., Touroutoglou, A., Dickerson, B. C., & Barrett, L. F. (2017). Resting connectivity between salience nodes predicts recognition memory. *Social Cognitive and Affective Neuroscience*, *12*(6), 948–955. https://doi.org/10.1093/scan/nsx026

Arnold, M. B. (1960). Emotion and personality.

Ásgeirsson, Á. G., & Nieuwenhuis, S. (2019). Effects of arousal on biased competition in attention and short-term memory. *Attention, Perception, and Psychophysics*, *81*(6), 1901–1912. https://doi.org/10.3758/s13414-019-01756-x

Baldi, E., & Bucherelli, C. (2005). The Inverted "U-Shaped" Dose-Effect Relationships in Learning and Memory: Modulation of Arousal and Consolidation. *Nonlinearity in Biology, Toxicology, Medicine*, *3*(1), nonlin.003.01.0. https://doi.org/10.2201/nonlin.003.01.002

Baraly, K. A., Hot, P., Davidson, P., & Talmi, D. (2016). How emotional arousal enhances episodic memory. *Learning and Memory: A Comprehensive Reference*.

Barnes, K. A., Anderson, K. M., Plitt, M., & Martin, A. (2014). Individual differences in intrinsic brain connectivity predict decision strategy. *Journal of Neurophysiology*, *112*(8), 1838–1848. https://doi.org/10.1152/jn.00909.2013

Barrett, L. F. (2017). The theory of constructed emotion: an active inference account of interoception and categorization. *Social Cognitive and Affective Neuroscience*, *12*(1), 1–23. https://doi.org/10.1093/scan/nsw154

Barrett, L. F., Bliss-Moreau, E., Quigley, K. S., & Aronson, K. R. (2004). Interoceptive sensitivity and self-reports of emotional experience. *Journal of Personality and Social Psychology*, *87*(5), 684–697. https://doi.org/10.1037/0022-3514.87.5.684

Barrett, L. F., Mesquita, B., Ochsner, K. N., & Gross, J. J. (2007). The experience of emotion. *Annu. Rev. Psychol.*, *58*, 373–403. https://doi.org/10.1146/annurev.psych.58.110405.085709

Barrett, L. F., & Simmons, W. K. (2015). Interoceptive predictions in the brain. *Nature Reviews Neuroscience*, *16*(7), 419–429. https://doi.org/10.1038/nrn3950

Basten, U., Hilger, K., & Fiebach, C. J. (2015). Where smart brains are different: A quantitative meta-analysis of functional and structural brain imaging studies on intelligence. *Intelligence*, *51*, 10–27.

Bennett, M. R., & Hacker, P. M. S. (2005). Emotion and cortical-subcortical function: Conceptual developments. *Progress in Neurobiology*, *75*(1), 29–52. https://doi.org/10.1016/j.pneurobio.2004.11.002

Bennion, K. A., Ford, J. H., Murray, B. D., & Kensinger, E. A. (2013). Oversimplification in the study of emotional memory. *Journal of the International Neuropsychological Society*, *19*(9), 953–961. https://doi.org/10.1017/S1355617713000945.Oversimplification

Berntsen, D. (2002). Tunnel memories for autobiographical events: Central details are remembered more frequently from shocking than from happy experiences. *Memory & Cognition*, *30*(7), 1010–1020. https://doi.org/10.3758/BF03194319

Biswal, B. B., Mennes, M., Zuo, X.-N., Gohel, S., Kelly, C., Smith, S. M., … Colcombe, S. (2010). Toward discovery science of human brain function. *Proceedings of the National Academy of Sciences*, *107*(10), 4734–4739. https://doi.org/10.1073/pnas.091185510

Blackwell, B. (1977). Realtion of heart rate control to heartbeat perception. *Biofeedback and Self-Regulation*, *2*(4), 317–392. https://doi.org/10.1007/BF00998623

Bleidorn, W., & Hopwood, C. J. (2019). Using Machine Learning to Advance Personality Assessment and Theory. *Personality and Social Psychology Review*, *23*(2), 190–203. https://doi.org/10.1177/1088868318772990

Bliss-Moreau, E., Williams, L. A., & Santistevan, A. C. (2020). The immutability of valence and arousal in the foundation of emotion. *Emotion*, *20*(6), 993–1004. https://doi.org/10.1037/emo0000606

Bonaz, B., Lane, R. D., Oshinsky, M. L., Kenny, P. J., Sinha, R., Mayer, E. A., & Critchley, H. D. (2021). Diseases, Disorders, and Comorbidities of Interoception. *Trends in Neurosciences*, *44*(1), 39–51. https://doi.org/10.1016/j.tins.2020.09.009

Bowen, H. J., Kark, S. M., & Kensinger, E. A. (2018). NEVER forget: negative emotional valence enhances recapitulation. *Psychonomic Bulletin and Review*, *25*(3), 870–891. https://doi.org/10.3758/s13423-017-1313-9

Bradley, M. M., Greenwald, M. K., Petry, M. C., & Lang, P. J. (1992). Remembering Pictures: Pleasure and Arousal in Memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *18*(2), 379–390. https://doi.org/10.1037/0278-7393.18.2.379

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, *25*(1), 49–59. https://doi.org/10.1016/0005-7916(94)90063-9

Bradley, M. M., & Lang, P. J. (2007). The International Affective Picture System (IAPS) in the study of emotion and attention. *Handbook of Emotion Elicitation and Assessement*, *29*, 29–46.

Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, *45*(4), 602–607.

Brassen, S., Gamer, M., & Bchel, C. (2011). Anterior cingulate activation is related to a positivity bias and emotional stability in successful aging. *Biological Psychiatry*, *70*(2), 131–137. https://doi.org/10.1016/j.biopsych.2010.10.013

Brener, J., & Ring, C. (2016). Towards a psychophysics of interoceptive processes: the measurement of heartbeat detection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1708), 20160015. https://doi.org/10.1098/rstb.2016.0015

Brener, J., Xiaoqing, L., & Ring, C. (1993). A method of constant stimuli for examining heartbeat detection: Comparison with the Brener-Kluvitse and Whitehead methods. *Psychophysiology*, *30*(6), 657–665. https://doi.org/10.1111/j.1469-8986.1993.tb02091.x

Brewer, R., Murphy, J., & Bird, G. (2021). Atypical interoception as a common risk factor for psychopathology: A review. *Neuroscience & Biobehavioral Reviews*, *130*, 470–508. https://doi.org/10.1016/j.neubiorev.2021.07.036

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

Cahill, L., & Alkire, M. T. (2003). Epinephrine enhancement of human memory consolidation: interaction with arousal at encoding. *Neurobiology of Learning and Memory*, *79*(2), 194–198.

Cahill, L., Gorski, L., & Le, K. (2003). Enhanced human memory consolidation with post-learning stress: Interaction with the degree of arousal at encoding. *Learning and Memory*, *10*(4), 270–274. https://doi.org/10.1101/lm.62403

Cahill, L., Haier, R. J., Fallon, J., Alkire, M. T., Tang, C., Keator, D., … McGaugh, J. L. (1996). Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(15), 8016–8021. https://doi.org/10.1073/pnas.93.15.8016

Cahill, L., Prinst, B., Webertt, M., & McGaugh, J. L. (2013). β Adrenergic activation and memory for emotional events. *The Science of Mental Health: Stress and the Brain*, *9*(6499), 98–100.

Cameron, O. G. (2001). *Visceral sensory neuroscience: Interoception*. Oxford University Press.

Canli, T., Desmond, J. E., Zhao, Z., & Gabrieli, J. D. E. (2002). Sex differences in the neural basis of emotional memories. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(16), 10789–10794. https://doi.org/10.1073/pnas.162356599

Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *20*(19), RC99–RC99. https://doi.org/10.1523/jneurosci.20-19-j0004.2000

Cannon, W. B. (1927). The James-Lange theory of emotions: A critical examination and an alternative theory. *The American Journal of Psychology*, *39*(1/4), 106–124.

Carstensen, L. L., Fung, H. H., & Charles, S. T. (2003). Socioemotional selectivity theory and the regulation of emotion in the second half of life. *Motivation and Emotion*, *27*(2), 103–123. https://doi.org/10.1023/A:1024569803230

Cattell, R. B. (1971). Abilities: Their structure, growth, and action.

Ceunen, E., Van Diest, I., & Vlaeyen, J. W. S. (2013). Accuracy and awareness of perception: Related, yet distinct (commentary on Herbert et al., 2012). *Biological Psychology*, *92*(2), 426–427. https://doi.org/10.1016/j.biopsycho.2012.09.012

Chiu, Y. C., Dolcos, F., Gonsalves, B. D., & Cohen, N. J. (2013). On opposing effects of emotion on contextual or relational memory. *Frontiers in Psychology*, *4*(MAR), 103. https://doi.org/10.3389/fpsyg.2013.00103

Chong, J. S. X., Ng, G. J. P., Lee, S. C., & Zhou, J. (2017). Salience network connectivity in the insula is associated with individual differences in interoceptive accuracy. *Brain Structure and Function*, *222*(4), 1635–1644. https://doi.org/10.1007/s00429-016-1297-7

Christianson, S. Å., & Loftus, E. F. (1990). Some characteristics of people's traumatic memories. *Bulletin of the Psychonomic Society*, *28*(3), 195–198. https://doi.org/10.3758/BF03334001

Clewett, D., Sakaki, M., Huang, R., Nielsen, S. E., & Mather, M. (2017). Arousal amplifies biased competition between high and low priority memories more in women than in men: The role of elevated noradrenergic activity. *Psychoneuroendocrinology*, *80*, 80–91. https://doi.org/https://doi.org/10.1016/j.psyneuen.2017.02.022

Cole, M. W., Bassett, D. S., Power, J. D., Braver, T. S., & Petersen, S. E. (2014). Intrinsic and task-evoked network architectures of the human brain. *Neuron*, *83*(1), 238–251. https://doi.org/10.1016/j.neuron.2014.05.014

Colibazzi, T., Posner, J., Wang, Z., Gorman, D., Gerber, A., Yu, S., … Peterson, B. S. (2010). Neural Systems Subserving Valence and Arousal During the Experience of Induced Emotions. *Emotion*, *10*(3), 377–389. https://doi.org/10.1037/a0018484

Comblain, C., D'Argembeau, A., & Van der Linden, M. (2005). Phenomenal characteristics of autobiographical memories for emotional and neutral events in older and younger adults. *Experimental Aging Research*, *31*(2), 173–189. https://doi.org/10.1080/03610730590915010

Connor, K. M., Davidson, J. R. T., Erik Churchill, L., Sherwood, A., Foa, E., & Weisler, R. H. (2000). Psychometric properties of the social phobia inventory (SPIN). New self-rating scale. *British Journal of Psychiatry*, *176*(APR.), 379–386. https://doi.org/10.1192/bjp.176.4.379

Cornelisse, S., van Stegeren, A. H., & Joëls, M. (2011). Implications of psychosocial stress on memory formation in a typical male versus female student sample. *Psychoneuroendocrinology*, *36*(4), 569–578. https://doi.org/10.1016/j.psyneuen.2010.09.002

Costa, J., Adams, A. T., Jung, M. F., Guimbretière, F., & Choudhury, T. (2016). EmotionCheck: leveraging bodily signals and false feedback to regulate our emotions. In *Proceedings of the 2016 ACM International Joint Conference on Pervasive and Ubiquitous Computing* (pp. 758–769).

Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience*, *3*(8), 655–666. https://doi.org/10.1038/nrn894

Craig, A. D. (2003). Interoception: The sense of the physiological condition of the body. *Current Opinion in Neurobiology*, *13*(4), 500–505. https://doi.org/10.1016/S0959-4388(03)00090-4

Craig, A. D. (2009). How do you feel - now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*(1), 59–70. https://doi.org/10.1038/nrn2555

Craik, F. I. M., & McDowd, J. M. (1987). Age differences in recall and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *13*(3), 474.

Critchley, H. D., & Garfinkel, S. N. (2016). Bodily arousal differentially impacts stimulus processing and memory: Norepinephrine in interoception. *The Behavioral and Brain Sciences*, *39*, e205. https://doi.org/10.1017/S0140525X15001764

Critchley, H. D., & Garfinkel, S. N. (2017). Interoception and emotion. *Current Opinion in Psychology*, *17*, 7–14. https://doi.org/10.1016/j.copsyc.2017.04.020

Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, *7*(2), 189–195. https://doi.org/10.1038/nn1176

D'Argembeau, A., Comblain, C., & van der Linden, M. (2003). Phenomenal characteristics of autobiographical memories for positive, negative, and neutral events. *Applied Cognitive Psychology*, *17*(3), 281–294. https://doi.org/10.1002/acp.856

Dadi, K., Varoquaux, G., Houenou, J., Bzdok, D., Thirion, B., & Engemann, D. (2020). Beyond brain age: Empirically-derived proxy measures of mental health. *BioRxiv*, 1–34.

Dahlgren, K., Ferris, C., & Hamann, S. (2020). Neural correlates of successful emotional episodic encoding and retrieval: An SDM meta-analysis of neuroimaging studies. *Neuropsychologia*, *143*, 107495. https://doi.org/10.1016/j.neuropsychologia.2020.107495

Damasio, A. (1994). Descartes' error: Emotion, rationality and the human brain. *New York: Putnam*, 352.

Damoiseaux, J. S., Rombouts, S., Barkhof, F., Scheltens, P., Stam, C. J., Smith, S. M., & Beckmann, C. F. (2006). Consistent resting-state networks across healthy subjects. *Proceedings of the National Academy of Sciences*, *103*(37), 13848–13853. https://doi.org/10.1073/pnas.0601417103

Danckert, J., Hammerschmidt, T., Marty-Dugas, J., & Smilek, D. (2018). Boredom: Under-aroused and restless. *Consciousness and Cognition*, *61*, 24–37. https://doi.org/10.1016/j.concog.2018.03.014

Davis, J. I., Senghas, A., & Ochsner, K. N. (2009). How does facial feedback modulate emotional experience? *Journal of Research in Personality*, *43*(5), 822–829. https://doi.org/10.1016/j.jrp.2009.06.005

de Voogd, L. D., Klumpers, F., Fernández, G., & Hermans, E. J. (2017). Intrinsic functional connectivity between amygdala and hippocampus during rest predicts enhanced memory under stress. *Psychoneuroendocrinology*, *75*, 192–202. https://doi.org/10.1016/j.psyneuen.2016.11.002

Desmedt, O., Luminet, O., & Corneille, O. (2018). The heartbeat counting task largely involves non-interoceptive processes: Evidence from both the original and an adapted counting task. *Biological Psychology*, *138*, 185–188. https://doi.org/10.1016/j.biopsycho.2018.09.004

Dimitriadis, S. I., & Liparas, D. (2018). How random is the random forest? Random forest algorithm on the service of structural imaging biomarkers for Alzheimer's disease: From Alzheimer's disease neuroimaging initiative (ADNI) database. *Neural Regeneration Research*, *13*(6), 962–970. https://doi.org/10.4103/1673-5374.233433

Dolcos, F., Katsumi, Y., Weymar, M., Moore, M., Tsukiura, T., & Dolcos, S. (2017). Emerging directions in emotional episodic memory. *Frontiers in Psychology*, *8*(DEC), 1867. https://doi.org/10.3389/fpsyg.2017.01867

Dolcos, F., Labar, K. S., & Cabeza, R. (2005). Remembering one year later: Role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(7), 2626–2631. https://doi.org/10.1073/pnas.0409848102

Dolcos, F., LaBar, K. S., & Cabeza, R. (2004). Interaction between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron*, *42*(5), 855–863. https://doi.org/10.1016/S0896-6273(04)00289-2

Domschke, K., Stevens, S., Pfleiderer, B., & Gerlach, A. L. (2010). Interoceptive sensitivity in anxiety and anxiety disorders: An overview and integration of neurobiological findings. *Clinical Psychology Review*, *30*(1), 1–11. https://doi.org/10.1016/j.cpr.2009.08.008

Dörfel, D., Gärtner, A., & Scheffel, C. (2020). Resting state cortico-limbic functional connectivity and dispositional use of emotion regulation strategies: A replication and extension study. *Frontiers in Behavioral Neuroscience*, *14*, 128. https://doi.org/10.3389/fnbeh.2020.00128

Dubois, J., Galdi, P., Han, Y., Paul, L. K., & Adolphs, R. (2018). Resting-State Functional Brain Connectivity Best Predicts the Personality Dimension of Openness to Experience. *Personality Neuroscience*, *1*, 1–21. https://doi.org/10.1017/pen.2018.8

Dunn, B. D., Galton, H. C., Morgan, R., Evans, D., Oliver, C., Meyer, M., … Dalgleish, T. (2010). Listening to Your Heart: How Interoception Shapes Emotion Experience and Intuitive Decision Making. *Psychological Science*, *21*(12), 1835–1844. https://doi.org/10.1177/0956797610389191

Dunn, B. D., Stefanovitch, I., Evans, D., Oliver, C., Hawkins, A., & Dalgleish, T. (2010). Can you feel the beat? Interoceptive awareness is an interactive function of anxiety- and depression-specific symptom dimensions. *Behaviour Research and Therapy*, *48*(11), 1133–1138. https://doi.org/10.1016/j.brat.2010.07.006

Dunne, J., Flores, M., Gawande, R., & Schuman-Olivier, Z. (2021). Losing trust in body sensations: Interoceptive awareness and depression symptom severity among primary care patients. *Journal of Affective Disorders*, *282*, 1210–1219. https://doi.org/10.1016/j.jad.2020.12.092

Duyser, F. A., van Eijndhoven, P. F. P., Bergman, M. A., Collard, R. M., Schene, A. H., Tendolkar, I., & Vrijsen, J. N. (2020). Negative memory bias as a transdiagnostic cognitive marker for depression symptom severity. *Journal of Affective Disorders*, *274*, 1165–1172. https://doi.org/10.1016/j.jad.2020.05.156

Eavani, H., Habes, M., Satterthwaite, T. D., An, Y., Hsieh, M. K., Honnorat, N., … Davatzikos, C. (2018). Heterogeneity of structural and functional imaging patterns of advanced brain aging revealed via machine learning methods. *Neurobiology of Aging*, *71*, 41–50. https://doi.org/10.1016/j.neurobiolaging.2018.06.013

Ekman, P., & Keltner, D. (1997). Universal facial expressions of emotion. *Segerstrale U, P. Molnar P, Eds. Nonverbal Communication: Where Nature Meets Culture*, *27*, 46.

Ellsworth, P. C. (2013). Appraisal theory: Old and new questions. *Emotion Review*, *5*(2), 125–131. https://doi.org/10.1177/1754073912463617

Eryilmaz, H., Van De Ville, D., Schwartz, S., & Vuilleumier, P. (2011). Impact of transient emotions on functional connectivity during subsequent resting state: A wavelet correlation approach. *NeuroImage*, *54*(3), 2481–2491. https://doi.org/10.1016/j.neuroimage.2010.10.021

Etkin, A., & Wager, T. D. (2007). Functional neuroimaging of anxiety: A meta-ana lysis of emotional processing in PTSD, social anxiety disorder, and specific phobia. *American Journal of Psychiatry*, *164*(10), 1476–1488. https://doi.org/10.1176/appi.ajp.2007.07030504

Fabiansson, E. C., Denson, T. F., Moulds, M. L., Grisham, J. R., & Schira, M. M. (2012). Don’t look back in anger: Neural correlates of reappraisal, analytical rumination, and angry rumination during recall of an anger-inducing autobiographical memory. *NeuroImage*, *59*(3), 2974–2981. https://doi.org/10.1016/j.neuroimage.2011.09.078

Farb, N. A. S., Segal, Z. V., & Anderson, A. K. (2013). Mindfulness meditation training alters cortical representations of interoceptive attention. *Social Cognitive and Affective Neuroscience*, *8*(1), 15–26. https://doi.org/10.1093/scan/nss066

Fastenrath, M., Coynel, D., Spalek, K., Milnik, A., Gschwind, L., Roozendaal, B., … de Quervain, D. J. F. (2014). Dynamic modulation of amygdala-hippocampal connectivity by emotional arousal. *Journal of Neuroscience*, *34*(42), 13935–13947. https://doi.org/10.1523/JNEUROSCI.0786-14.2014

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Feldman Barrett, L., & Russell, J. A. (1998). Independence and bipolarity in the structure of current affect. *Journal of Personality and Social Psychology*, *74*(4), 967.

Ferree, N. K., & Cahill, L. (2009). Post-event spontaneous intrusive recollections and strength of memory for emotional events in men and women. *Consciousness and Cognition*, *18*(1), 126–134. https://doi.org/10.1016/j.concog.2008.11.008

Finn, E. S., Shen, X., Scheinost, D., Rosenberg, M. D., Huang, J., Chun, M. M., … Constable, R. T. (2015). Functional connectome fingerprinting: identifying individuals using patterns of brain connectivity. *Nature Neuroscience*, *18*(11), 1664.

Fishburn, F. A., Hlutkowsky, C. O., Bemis, L. M., Huppert, T. J., Wakschlag, L. S., & Perlman, S. B. (2019). Irritability uniquely predicts prefrontal cortex activation during preschool inhibitory control among all temperament domains: A LASSO approach. *NeuroImage*, *184*, 68–77. https://doi.org/10.1016/j.neuroimage.2018.09.023

Fjell, A. M., Sneve, M. H., Storsve, A. B., Grydeland, H., Yendiki, A., & Walhovd, K. B. (2016). Brain Events Underlying Episodic Memory Changes in Aging : A Longitudinal Investigation of Structural and Functional Connectivity. *Cerebral Cortex*, *26*(May 2015), 1272–1286. https://doi.org/10.1093/cercor/bhv102

Fong, A. H. C., Yoo, K., Rosenberg, M. D., Zhang, S., Li, C. S. R., Scheinost, D., … Chun, M. M. (2019). Dynamic functional connectivity during task performance and rest predicts individual differences in attention across studies. *NeuroImage*, *188*, 14–25. https://doi.org/10.1016/j.neuroimage.2018.11.057

Fredrickson, B. L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American Psychologist*, *56*(3), 218–226. https://doi.org/10.1037/0003-066X.56.3.218

Fredrickson, B. L. (2004). The broaden–and–build theory of positive emotions. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *359*(1449), 1367–1377.

Fredrickson, B. L., & Branigan, C. (2005). Positive emotions broaden the scope of attention and thought-action repertoires. *Cognition and Emotion*, *19*(3), 313–332. https://doi.org/10.1080/02699930441000238

Friedman, B. H. (2010). Feelings and the body: The Jamesian perspective on autonomic specificity of emotion. *Biological Psychology*, *84*(3), 383–393. https://doi.org/https://doi.org/10.1016/j.biopsycho.2009.10.006

Frijda, N. H. (1986). *The emotions*. Cambridge University Press.

Furman, D. J., Waugh, C. E., Bhattacharjee, K., Thompson, R. J., & Gotlib, I. H. (2013). Interoceptive awareness, positive affect, and decision making in Major Depressive Disorder. *Journal of Affective Disorders*, *151*(2), 780–785. https://doi.org/10.1016/j.jad.2013.06.044

Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., … Politi, P. (2009). Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *Journal of Psychiatry and Neuroscience*, *34*(6), 418 LP – 432. Retrieved from http://jpn.ca/content/34/6/418.abstract

Füstös, J., Gramann, K., Herbert, B. M., & Pollatos, O. (2013). On the embodiment of emotion regulation: interoceptive awareness facilitates reappraisal. *Social Cognitive and Affective Neuroscience*, *8*(8), 911–917. https://doi.org/10.1093/scan/nss089

Gable, P. A., & Harmon-Jones, E. (2008). Approach-motivated positive affect reduces breadth of attention. *Psychological Science*, *19*(5), 476–482.

Gaddy, M. A., & Ingram, R. E. (2014). A meta-analytic review of mood-congruent implicit memory in depressed mood. *Clinical Psychology Review*, *34*(5), 402–416. https://doi.org/10.1016/j.cpr.2014.06.001

Galvez, R., Mesches, M. H., & Mcgaugh, J. L. (1996). Norepinephrine release in the amygdala in response to footshock stimulation. *Neurobiology of Learning and Memory*, *66*(3), 253–257.

Gamst, G., Meyers, L. S., Burke, H. M., & Guarino, A. J. (2017). Scale Development and Validation. *Public Health Research Methods*, *54*(6), 379–409. https://doi.org/10.4135/9781483398839.n13

Garcia-Leal, C., Graeff, F. G., & Del-Ben, C. M. (2014). Experimental public speaking: Contributions to the understanding of the serotonergic modulation of fear. *Neuroscience and Biobehavioral Reviews*, *46*(P3), 407–417. https://doi.org/10.1016/j.neubiorev.2014.09.011

Garfinkel, S. N., & Critchley, H. D. (2016). Threat and the Body: How the Heart Supports Fear Processing. *Trends in Cognitive Sciences*, *20*(1), 34–46. https://doi.org/10.1016/j.tics.2015.10.005

Garfinkel, S. N., Minati, L., Gray, M. A., Seth, A. K., Dolan, R. J., & Critchley, H. D. (2014). Fear from the heart: Sensitivity to fear stimuli depends on individual heartbeats. *Journal of Neuroscience*, *34*(19), 6573–6582. https://doi.org/10.1523/JNEUROSCI.3507-13.2014

Garfinkel, S. N., Seth, A. K., Barrett, A. B., Suzuki, K., & Critchley, H. D. (2015). Knowing your own heart: Distinguishing interoceptive accuracy from interoceptive awareness. *Biological Psychology*, *104*, 65–74. https://doi.org/10.1016/j.biopsycho.2014.11.004

Gendron, M., Crivelli, C., & Barrett, L. F. (2018). Universality Reconsidered: Diversity in Making Meaning of Facial Expressions. *Current Directions in Psychological Science*, *27*(4), 211–219. https://doi.org/10.1177/0963721417746794

Gendron, M., Roberson, D., van der Vyver, J. M., & Barrett, L. F. (2014). Perceptions of emotion from facial expressions are not culturally universal: Evidence from a remote culture. *Emotion*, *14*(2), 251–262. https://doi.org/10.1037/a0036052

Gerritsen, L., Rijpkema, M., Van Oostrom, I., Buitelaar, J., Franke, B., Fernández, G., & Tendolkar, I. (2012). Amygdala to hippocampal volume ratio is associated with negative memory bias in healthy subjects. *Psychological Medicine*, *42*(2), 335–343. https://doi.org/10.1017/S003329171100122X

Geurts, P., Irrthum, A., & Wehenkel, L. (2009). Supervised learning with decision tree-based methods in computational and systems biology. *Molecular BioSystems*, *5*(12), 1593–1605. https://doi.org/10.1039/b907946g

Glaser, E., Mendrek, A., Germain, M., Lakis, N., & Lavoie, M. E. (2012). Sex differences in memory of emotional images: A behavioral and electrophysiological investigation. *International Journal of Psychophysiology*, *85*(1), 17–26. https://doi.org/10.1016/j.ijpsycho.2012.01.007

Glasser, M. F., Sotiropoulos, S. N., Wilson, J. A., Coalson, T. S., Fischl, B., Andersson, J. L., … Jenkinson, M. (2013). The minimal preprocessing pipelines for the Human Connectome Project. *NeuroImage*, *80*, 105–124. https://doi.org/10.1016/j.neuroimage.2013.04.127

Golino, H. F., & Gomes, C. M. A. (2016). Random forest as an imputation method for education and psychology research: its impact on item fit and difficulty of the Rasch model. *International Journal of Research and Method in Education*, *39*(4), 401–421. https://doi.org/10.1080/1743727X.2016.1168798

Gouizi, K., Bereksi Reguig, F., & Maaoui, C. (2011). Emotion recognition from physiological signals. *Journal of Medical Engineering and Technology*, *35*(6–7), 300–307. https://doi.org/10.3109/03091902.2011.601784

Grabauskaitė, A., Baranauskas, M., & Griškova-Bulanova, I. (2017). Interoception and gender: What aspects should we pay attention to? *Consciousness and Cognition*, *48*, 129–137. https://doi.org/10.1016/j.concog.2016.11.002

Grady, C. (2012). The cognitive neuroscience of ageing. *Nature Reviews Neuroscience*, *13*(7), 491–505. https://doi.org/10.1038/nrn3256

Gratton, C., Laumann, T. O., Nielsen, A. N., Greene, D. J., Gordon, E. M., Gilmore, A. W., … Petersen, S. E. (2018). Functional Brain Networks Are Dominated by Stable Group and Individual Factors, Not Cognitive or Daily Variation. *Neuron*, *98*(2), 439-452.e5. https://doi.org/10.1016/j.neuron.2018.03.035

Gray, M. A., Beacher, F. D., Minati, L., Nagai, Y., Kemp, A. H., Harrison, N. A., & Critchley, H. D. (2012). Emotional appraisal is influenced by cardiac afferent information. *Emotion*, *12*(1), 180–191. https://doi.org/10.1037/a0025083

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics* (Vol. 1). Wiley New York.

Greene, A. S., Gao, S., Scheinost, D., & Constable, R. T. (2018). Task-induced brain state manipulation improves prediction of individual traits. *Nature Communications*, *9*(1), 1–13. https://doi.org/10.1038/s41467-018-04920-3

Grootswagers, T., Kennedy, B. L., Most, S. B., & Carlson, T. A. (2020). Neural signatures of dynamic emotion constructs in the human brain. *Neuropsychologia*, *145*, 106535. https://doi.org/10.1016/j.neuropsychologia.2017.10.016

Gu, X., Hof, P. R., Friston, K. J., & Fan, J. (2013). Anterior insular cortex and emotional awareness. *Journal of Comparative Neurology*, *521*(15), 3371–3388. https://doi.org/10.1002/cne.23368

Hakimi, N., & Setarehdan, S. K. (2018). Stress assessment by means of heart rate derived from functional near-infrared spectroscopy. *Journal of Biomedical Optics*, *23*(11), 1. https://doi.org/10.1117/1.jbo.23.11.115001

Hamann, S. (2001). Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences*, *5*(9), 394–400. https://doi.org/10.1016/S1364-6613(00)01707-1

Hamann, S. B., Ely, T. D., Grafton, S. T., & Kilts, C. D. (1999). Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nature Neuroscience*, *2*(3), 289–293. https://doi.org/10.1038/6404

Hamann, S., & Canli, T. (2004). Individual differences in emotion processing. *Current Opinion in Neurobiology*, *14*(2), 233–238. https://doi.org/10.1016/j.conb.2004.03.010

Han, Y., & Adolphs, R. (2020). Estimating the heritability of psychological measures in the Human Connectome Project dataset. *PLoS ONE*, *15*(7 July), e0235860. https://doi.org/10.1371/journal.pone.0235860

Hanson, J. L., Nacewicz, B. M., Sutterer, M. J., Cayo, A. A., Schaefer, S. M., Rudolph, K. D., … Davidson, R. J. (2015). Behavioral Problems After Early Life Stress: Contributions of the Hippocampus and Amygdala. *Biological Psychiatry*, *77*(4), 314–323. https://doi.org/https://doi.org/10.1016/j.biopsych.2014.04.020

Haque, U. M., Kabir, E., & Khanam, R. (2021). Detection of child depression using machine learning methods. *PLoS ONE*, *16*(12 December 2021), e0261131. https://doi.org/10.1371/journal.pone.0261131

Hatfield, T., Spanis, C., & McGaugh, J. L. (1999). Response of amygdalar norepinephrine to footshock and GABAergic drugs using in vivo microdialysis and HPLC. *Brain*

Research, *835*(2), 340–345. https://doi.org/https://doi.org/10.1016/S0006-8993(99)01566-8

Hearne, L. J., Mattingley, J. B., & Cocchi, L. (2016). Functional brain networks related to individual differences in human intelligence at rest. *Scientific Reports*, *6*(1), 1–8. https://doi.org/10.1038/srep32328

Hedge, C., Powell, G., & Sumner, P. (2018). The reliability paradox: Why robust cognitive tasks do not produce reliable individual differences. *Behavior Research Methods*, *50*(3), 1166–1186. https://doi.org/10.3758/s13428-017-0935-1

Henson, R. N., Campbell, K. L., Davis, S. W., Taylor, J. R., Emery, T., Erzinclioglu, S., … Kievit, R. A. (2016). Multiple determinants of lifespan memory differences. *Scientific Reports*, *6*(1), 32527. https://doi.org/10.1038/srep32527

Herbert, B. M., Pollatos, O., Flor, H., Enck, P., & Schandry, R. (2010). Cardiac awareness and autonomic cardiac reactivity during emotional picture viewing and mental stress. *Psychophysiology*, *47*(2), 342–354. https://doi.org/10.1111/j.1469-8986.2009.00931.x

Hermans, E. J., Kanen, J. W., Tambini, A., Fernández, G., Davachi, L., & Phelps, E. A. (2017). Persistence of Amygdala–Hippocampal Connectivity and Multi-Voxel Correlation Structures During Awake Rest After Fear Learning Predicts Long-Term Expression of Fear. *Cerebral Cortex*, *27*(5), 3028–3041. https://doi.org/10.1093/cercor/bhw145

Hodossy, L., & Tsakiris, M. (2020). Wearing your heart on your screen: Investigating congruency-effects in autonomic responses and their role in interoceptive processing during biofeedback. *Cognition*, *194*, 104053. https://doi.org/https://doi.org/10.1016/j.cognition.2019.104053

Hurlemann, R., Hawellek, B., Matusch, A., Kolsch, H., Wollersen, H., Madea, B., … Dolan, R. J. (2005). Noradrenergic Modulation of Emotion-Induced Forgetting and

Remembering. *Journal of Neuroscience*, *25*(27), 6343–6349. https://doi.org/10.1523/JNEUROSCI.0228-05.2005

Infantolino, Z. P., Luking, K. R., Sauder, C. L., Curtin, J. J., & Hajcak, G. (2018). Robust is not necessarily reliable: From within-subjects fMRI contrasts to between-subjects comparisons. *NeuroImage*, *173*, 146–152. https://doi.org/10.1016/j.neuroimage.2018.02.024

Iodice, P., Porciello, G., Bufalari, I., Barca, L., & Pezzulo, G. (2019). An interoceptive illusion of effort induced by false heart-rate feedback. *Proceedings of the National Academy of Sciences*, *116*(28), 13897–13902. https://doi.org/10.1073/pnas.1821032116

Jackson, D. C., Mueller, C. J., Dolski, I., Dalton, K. M., Nitschke, J. B., Urry, H. L., … Davidson, R. J. (2003). Now You Feel It, Now You Don't: Frontal Brain Electrical Asymmetry and Individual Differences in Emotion Regulation. *Psychological Science*, *14*(6), 612–617. https://doi.org/10.1046/j.0956-7976.2003.psci_1473.x

James A. Russel. (1980). A Circumplex Model of Affect. *Journal of Personality and Social Psychology*, *39*(6), 1161–1178.

James, W. (1884). What is an emotion? *Mind*, *9*(34), 188–205. https://doi.org/10.1093/mind/os-IX.34.188

Jeong, E. J., & Biocca, F. A. (2012). Are there optimal levels of arousal to memory? Effects of arousal, centrality, and familiarity on brand memory in video games (Computers in Human Behavior (2012) 28 (285-291)). *Computers in Human Behavior*, *28*(4), 1533. https://doi.org/10.1016/j.chb.2012.02.018

Jia, X., Gao, C., Wang, Y., Han, M., Cui, L., & Guo, C. (2020). Emotional arousal influences remembrance of goal-relevant stimuli. *Emotion*, *20*(8), 1357–1368. https://doi.org/10.1037/emo0000657

Jiang, R., Zuo, N., Ford, J. M., Qi, S., Zhi, D., Zhuo, C., … Sui, J. (2020). Task-induced brain connectivity promotes the detection of individual differences in brain-behavior relationships. *NeuroImage*, *207*, 116370. https://doi.org/10.1016/j.neuroimage.2019.116370

Jockwitz, C., Caspers, S., Lux, S., Eickhoff, S. B., Jütten, K., Lenzen, S., … Amunts, K. (2017). Influence of age and cognitive performance on resting-state brain networks of older adults in a population-based cohort. *Cortex*, *89*, 28–44. https://doi.org/10.1016/j.cortex.2017.01.008

Juvina, I., Larue, O., & Hough, A. (2018). Modeling valuation and core affect in a cognitive architecture: The impact of valence and arousal on memory and decision-making. *Cognitive Systems Research*, *48*, 4–24. https://doi.org/10.1016/j.cogsys.2017.06.002

Kaplan, R. L., Van Damme, I., & Levine, L. J. (2012). Motivation matters: Differing effects of pre-goal and post-goal emotions on attention and memory. *Frontiers in Psychology*, *3*(OCT), 404. https://doi.org/10.3389/fpsyg.2012.00404

Kark, S. M., & Kensinger, E. A. (2019). Post-encoding amygdala-visuosensory coupling is associated with negative memory bias in healthy young adults. *Journal of Neuroscience*, *39*(16), 3130–3143. https://doi.org/10.1523/JNEUROSCI.2834-18.2019

Katkin, E. S., Wiens, S., & Öhman, A. (2001). Nonconscious fear conditioning, visceral perception, and the development of gut feelings. *Psychological Science*, *12*(5), 366–370. https://doi.org/10.1111/1467-9280.00368

Kensinger, E. A. (2007). Negative emotion enhances memory accuracy: Behavioral and neuroimaging evidence. *Current Directions in Psychological Science*, *16*(4), 213–218. https://doi.org/10.1111/j.1467-8721.2007.00506.x

Kensinger, E. A. (2009). Remembering the details: Effects of emotion. *Emotion Review*, *1*(2), 99–113. https://doi.org/10.1177/1754073908100432

Kensinger, E. A., & Corkin, S. (2003). Memory enhancement for emotional words: Are emotional words more vividly remembered than neutral words? *Memory and Cognition*, *31*(8), 1169–1180. https://doi.org/10.3758/BF03195800

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of Memory and Language*, *56*(4), 575–591. https://doi.org/10.1016/j.jml.2006.05.004

Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., … Participants, I. S. 2016. (2018). Interoception and Mental Health: A Roadmap HHS Public Access. *Biological Psychiatry: Cognitive Neuscience & Neuroimaging*, *3*(6), 501–513. Retrieved from https://doi.org/10.1016/j.bpsc.2017.12.004.

Khalsa, S. S., Adolphs, R., Cameron, O. G., Critchley, H. D., Davenport, P. W., Feinstein, J. S., … Zucker, N. (2018). Interoception and Mental Health: A Roadmap. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, *3*(6), 501–513. https://doi.org/10.1016/j.bpsc.2017.12.004

Kim, J., Zhou, Y., Schiavon, S., Raftery, P., & Brager, G. (2018). Personal comfort models: Predicting individuals' thermal preference using occupant heating and cooling behavior and machine learning. *Building and Environment*, *129*, 96–106. https://doi.org/10.1016/j.buildenv.2017.12.011

Kim, K. H., Bang, S. W., & Kim, S. R. (2004). Emotion recognition system using short-term monitoring of physiological signals. *Medical and Biological Engineering and Computing*, *42*(3), 419–427. https://doi.org/10.1007/BF02344719

Kindermann, N. K., & Werner, N. S. (2014a). Cardiac perception enhances stress experience. *Journal of Psychophysiology*, *28*(4), 225–232. https://doi.org/10.1027/0269-8803/a000114

Kindermann, N. K., & Werner, N. S. (2014b). The impact of cardiac perception on emotion experience and cognitive performance under mental stress. *Journal of Behavioral Medicine*, *37*(6), 1145–1154. https://doi.org/10.1007/s10865-014-9564-7

Kirschbaum, C., Pirke, K. M., & Hellhammer, D. H. (1993). The “Trier social stress test” - A tool for investigating psychobiological stress responses in a laboratory setting. *Neuropsychobiology*, *28*(1–2), 76–81. https://doi.org/10.1159/000119004

Kligyte, V., Connelly, S., Thiel, C., & Devenport, L. (2013). The influence of anger, fear, and emotion regulation on ethical decision making. *Human Performance*, *26*(4), 297–326.

Knight, M., & Mather, M. (2009). Reconciling findings of emotion-induced memory enhancement and impairment of preceding items. *Emotion (Washington, D.C.)*, *9*(6), 763–781. https://doi.org/10.1037/a0017281

Kragel, P. A., Knodt, A. R., Hariri, A. R., & LaBar, K. S. (2016). Decoding Spontaneous Emotional States in the Human Brain. *PLoS Biology*, *14*(9), e2000106. https://doi.org/10.1371/journal.pbio.2000106

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, *84*(3), 394–421. https://doi.org/10.1016/j.biopsycho.2010.03.010

Kuehn, E., Mueller, K., Lohmann, G., & Schuetz-Bosbach, S. (2016). Interoceptive awareness changes the posterior insula functional connectivity profile. *Brain Structure and Function*, *221*(3), 1555–1571. https://doi.org/10.1007/s00429-015-0989-8

LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*(1), 54–64. https://doi.org/10.1038/nrn1825

Laird, A. R., Fox, P. M., Eickhoff, S. B., Turner, J. A., Ray, K. L., Mckay, D. R., … Fox, P. T. (2011). Behavioral interpretations of intrinsic connectivity networks. *Journal of Cognitive Neuroscience*, *23*(12), 4022–4037. https://doi.org/10.1162/jocn_a_00077

Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology*, *30*(3), 261–273.

Lazarus, R. S. (1991). Cognition and motivation in emotion. *American Psychologist*, *46*(4), 352.

Leary, M. R. (1983). A brief version of the Fear of Negative Evaluation Scale. *Personality and Social Psychology Bulletin*, *9*(3), 371–375.

LeBlanc, V. R., McConnell, M. M., & Monteiro, S. D. (2015). Predictable chaos: a review of the effects of emotions on attention, memory and decision making. *Advances in Health Sciences Education*, *20*(1), 265–282. https://doi.org/10.1007/s10459-014-9516-6

Lee, H., Heller, A. S., van Reekum, C. M., Nelson, B., & Davidson, R. J. (2012). Amygdala–prefrontal coupling underlies individual differences in emotion regulation. *NeuroImage*, *62*(3), 1575–1581. https://doi.org/https://doi.org/10.1016/j.neuroimage.2012.05.044

Lee, T.-H., Greening, S. G., & Mather, M. (2015). Encoding of goal-relevant stimuli is strengthened by emotional arousal in memory. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01173

Lee, Y. Y., & Hsieh, S. (2014). Classifying different emotional states by means of eegbased functional connectivity patterns. *PLoS ONE*, *9*(4), e95415. https://doi.org/10.1371/journal.pone.0095415

Leganes-Fonteneau, M., Bates, M. E., Muzumdar, N., Pawlak, A., Islam, S., Vaschillo, E., & Buckman, J. F. (2021). The cardiovascular mechanisms of interoceptive awareness: Effects of resonance breathing. *International Journal of Psychophysiology*, *169*, 71–87. https://doi.org/10.1016/j.ijpsycho.2021.09.003

Lenggenhager, B., Azevedo, R. T., Mancini, A., & Aglioti, S. M. (2013). Listening to your heart and feeling yourself: Effects of exposure to interoceptive signals during the ultimatum game. *Experimental Brain Research*, *230*(2), 233–241. https://doi.org/10.1007/s00221-013-3647-5

Leventhal, H., & Scherer, K. (1987). The relationship of emotion to cognition: A functional approach to a semantic controversy. *Cognition and Emotion*, *1*(1), 3–28.

Levine, L. J., & Edelstein, R. S. (2010). Emotion and memory narrowing: A review and goal-relevance approach. *Cognition and Emotion: Reviews of Current Research and Theories*, *23*(5), 168–210.

Levine, L. J., & Pizarro, D. A. (2004). Emotion and memory research: A grumpy overview. *Social Cognition*, *22*(5), 530–554. https://doi.org/10.1521/soco.22.5.530.50767

Li, Y., Zhuang, K., Yi, Z., Wei, D., Sun, J., & Qiu, J. (2020). The trait and state negative affect can be separately predicted by stable and variable resting-state functional connectivity. *Psychological Medicine*, 1–11. https://doi.org/10.1017/S0033291720002391

Lin, H., Müller-Bardorff, M., Gathmann, B., Brieke, J., Mothes-Lasch, M., Bruchmann, M., … Straube, T. (2020). Stimulus arousal drives amygdalar responses to emotional expressions across sensory modalities. *Scientific Reports*, *10*(1), 1–12. https://doi.org/10.1038/s41598-020-58839-1

Lin, Q., Rosenberg, M. D., Yoo, K., Hsu, T. W., O'Connell, T. P., & Chun, M. M. (2018). Resting-state functional connectivity predicts cognitive impairment related to Alzheimer's disease. *Frontiers in Aging Neuroscience*, *10*(APR), 94. https://doi.org/10.3389/fnagi.2018.00094

Lindquist, K. A., Satpute, A. B., Wager, T. D., Weber, J., & Barrett, L. F. (2016). The Brain Basis of Positive and Negative Affect: Evidence from a Meta-Analysis of the Human Neuroimaging Literature. *Cerebral Cortex*, *26*(5), 1910–1922. https://doi.org/10.1093/cercor/bhv001

Lipinska, G., Stuart, B., Thomas, K. G. F., Baldwin, D. S., & Bolinger, E. (2019). Preferential Consolidation of Emotional Memory During Sleep: A Meta-Analysis. *Frontiers in Psychology*, *10*. https://doi.org/10.3389/fpsyg.2019.01014

Lisetti, C. L., & Nasoz, F. (2004). Using noninvasive wearable computers to recognize human emotions from physiological signals. *Eurasip Journal on Applied Signal Processing*, *2004*(11), 1672–1687. https://doi.org/10.1155/S1110865704406192

Liu, Y. S., Chokka, S., Cao, B., & Chokka, P. R. (2021). Screening for bipolar disorder in a tertiary mental health centre using EarlyDetect: A machine learning-based pilot study. *Journal of Affective Disorders Reports*, 100215.

Lorberbaum, J. P., Kose, S., Johnson, M. R., Arana, G. W., Sullivan, L. K., Hamner, M. B., … George, M. S. (2004). Neural correlates of speech anticipatory anxiety in generalized social phobia. *NeuroReport*, *15*(18), 2701–2705.

MacQueen, G., & Frodl, T. (2011). The hippocampus in major depression: Evidence for the convergence of the bench and bedside in psychiatric research. *Molecular Psychiatry*, *16*(3), 252–264. https://doi.org/10.1038/mp.2010.80

Madan, C. R., Caplan, J. B., Lau, C. S. M., & Fujiwara, E. (2012). Emotional arousal does not enhance association-memory. *Journal of Memory and Language*, *66*(4), 695–716. https://doi.org/10.1016/j.jml.2012.04.001

Madan, C. R., Scott, S. M. E., & Kensinger, E. A. (2019). Positive emotion enhances association-memory. *Emotion*, *19*(4), 733–740. https://doi.org/10.1037/emo0000465

Mai, S., Braun, J., Probst, V., Kammer, T., & Pollatos, O. (2019). Changes in emotional processing following interoceptive network stimulation with rTMS. *Neuroscience*, *406*, 405–419. https://doi.org/10.1016/j.neuroscience.2019.03.014

Makkar, S. R., & Grisham, J. R. (2013). Effects of False Feedback on Affect, Cognition, Behavior, and Postevent Processing: The Mediating Role of Self-Focused Attention. *Behavior Therapy*, *44*(1), 111–124. https://doi.org/10.1016/j.beth.2012.07.005

Marchand, W. R., & Yurgelun-Todd, D. (2010). Striatal structure and function in mood disorders: A comprehensive review. *Bipolar Disorders*, *12*(8), 764–785.

https://doi.org/10.1111/j.1399-5618.2010.00874.x

Marek, S., Tervo-Clemmens, B., Calabro, F. J., Montez, D. F., Kay, B. P., Hatoum, A. S., … Dosenbach, N. U. F. (2022). Reproducible brain-wide association studies require thousands of individuals. *Nature*, *603*(7902), 654–660. https://doi.org/10.1038/s41586-022-04492-9

Mather, M. (2007). Emotional Arousal and Memory Binding: An Object-Based Framework. *Perspectives on Psychological Science*, *2*(1), 33–52. https://doi.org/10.1111/j.1745-6916.2007.00028.x

Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K., … Carstensen, L. L. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, *15*(4), 259–263. https://doi.org/10.1111/j.0956-7976.2004.00662.x

Mather, M., & Carstensen, L. L. (2005). Aging and motivated cognition: The positivity effect in attention and memory. *Trends in Cognitive Sciences*, *9*(10), 496–502. https://doi.org/10.1016/j.tics.2005.08.005

Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2016). Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behavioral and Brain Sciences*, *39*. https://doi.org/10.1017/S0140525X15000667

Mather, M., & Nesmith, K. (2008). Arousal-enhanced location memory for pictures. *Journal of Memory and Language*, *58*(2), 449–464. https://doi.org/10.1016/j.jml.2007.01.004

Mather, M., & Sutherland, M. (2009). Disentangling the effects of arousal and valence on memory for intrinsic details. *Emotion Review*, *1*(2), 118–119. https://doi.org/10.1177/1754073908100435

Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspectives on Psychological Science*, *6*(2), 114–133. https://doi.org/10.1177/1745691611400234

McBride, C., & Cappeliez, P. (2004). Effects of manipulating valence and arousal components of mood on specificity of autobiographical memory. *Psychological Reports*, *95*(2), 615–630. https://doi.org/10.2466/pr0.95.2.615-630

McGaugh, J. L. (2002). Memory consolidation and the amygdala: A systems perspective. *Trends in Neurosciences*, *25*(9), 456–461. https://doi.org/10.1016/S0166-2236(02)02211-7

McGaugh, J. L. (2004). the Amygdala Modulates the Consolidation of Memories of Emotionally Arousing Experiences. *Annual Review of Neuroscience*, *27*(1), 1–28. https://doi.org/10.1146/annurev.neuro.27.070203.144157

McIntyre, C. K., Hatfield, T., & McGaugh, J. L. (2002). Amygdala norepinephrine levels after training predict inhibitory avoidance retention performance in rats. *European Journal of Neuroscience*, *16*(7), 1223–1226. https://doi.org/10.1046/j.1460-9568.2002.02188.x

McNair, D. M., Frankenthaler, L. M., Czerlinsky, T., White, T. W., Sasson, S., & Fisher, S. (1982). Simulated public speaking as a model of clinical anxiety. *Psychopharmacology*, *77*(1), 7–10.

Melloni, M., Sedeño, L., Couto, B., Reynoso, M., Gelormini, C., Favaloro, R., … Ibanez, A. (2013). Preliminary evidence about the effects of meditation on interoceptive sensitivity and social cognition. *Behavioral and Brain Functions*, *9*(1), 1–6. https://doi.org/10.1186/1744-9081-9-47

Mendelowitz, D. (1999). Advances in parasympathetic control of heart rate and cardiac function. *Physiology*, *14*(4), 155–161.

Meyerholz, L., Irzinger, J., Witthöft, M., Gerlach, A. L., & Pohl, A. (2019). Contingent biofeedback outperforms other methods to enhance the accuracy of cardiac interoception: A comparison of short interventions. *Journal of Behavior Therapy and Experimental Psychiatry*, *63*, 12–20. https://doi.org/10.1016/j.jbtep.2018.12.002

Miu, A. C., Heilman, R. M., Opre, A., & Miclea, M. (2005). Emotion-induced retrograde amnesia and trait anxiety. *Journal of Experimental Psychology: Learning Memory and Cognition*, *31*(6), 1250–1257. https://doi.org/10.1037/0278-7393.31.6.1250

Moors, A., Ellsworth, P. C., Scherer, K. R., & Frijda, N. H. (2013). Appraisal theories of emotion: State of the art and future development. *Emotion Review*, *5*(2), 119–124.

Mor, N., & Winquist, J. (2002). Self-focused attention and negative affect: A meta-analysis. *Psychological Bulletin*, *128*(4), 638–662. https://doi.org/10.1037/0033-2909.128.4.638

Moriguchi, Y., & Komaki, G. (2013). Neuroimaging studies of alexithymia: physical, affective, and social perspectives. *BioPsychoSocial Medicine*, *7*(1), 8. https://doi.org/10.1186/1751-0759-7-8

Motomura, K., Terasawa, Y., Natsume, A., Iijima, K., Chalise, L., Sugiura, J., … Umeda, S. (2019). Anterior insular cortex stimulation and its effects on emotion recognition. *Brain Structure and Function*, *224*(6), 2167–2181. https://doi.org/10.1007/s00429-019-01895-9

Murphy, J., Catmur, C., & Bird, G. (2019). Classifying individual differences in interoception: Implications for the measurement of interoceptive awareness. *Psychonomic Bulletin and Review*, *26*(5), 1467–1471. https://doi.org/10.3758/s13423-019-01632-7

Murphy, J., Millgate, E., Geary, H., Ichijo, E., Coll, M. P., Brewer, R., … Bird, G. (2018). Knowledge of resting heart rate mediates the relationship between intelligence and the heartbeat counting task. *Biological Psychology*, *133*, 1–3. https://doi.org/10.1016/j.biopsycho.2018.01.012

Murray, B. D., & Kensinger, E. A. (2013). A review of the neural and behavioral consequences for unitizing emotional and neutral information. *Frontiers in Behavioral Neuroscience*, *7*(APR 2013), 42. https://doi.org/10.3389/fnbeh.2013.00042

Murty, V. P., Ritchey, M., Adcock, R. A., & LaBar, K. S. (2010). FMRI studies of successful emotional memory encoding: A quantitative meta-analysis. *Neuropsychologia*, *48*(12), 3459–3469. https://doi.org/10.1016/j.neuropsychologia.2010.07.030

Murty, V. P., Sambataro, F., Das, S., Tan, H. Y., Callicott, J. H., Goldberg, T. E., … Mattay, V. S. (2009). Age-related alterations in simple declarative memory and the effect of negative stimulus valence. *Journal of Cognitive Neuroscience*, *21*(10), 1920–1933. https://doi.org/10.1162/jocn.2009.21130

Nelson, N. L., & Russell, J. A. (2013). Universality revisited. *Emotion Review*, *5*(1), 8–15. https://doi.org/10.1177/1754073912457227

Nishida, M., Pearsall, J., Buckner, R. L., & Walker, M. P. (2009). REM Sleep, Prefrontal Theta, and the Consolidation of Human Emotional Memory. *Cerebral Cortex*, *19*(5), 1158–1166. https://doi.org/10.1093/cercor/bhn155

Nitschke, J. B., Sarinopoulos, I., Mackiewicz, K. L., Schaefer, H. S., & Davidson, R. J. (2006). Functional neuroanatomy of aversion and its anticipation. *NeuroImage*, *29*(1), 106–116. https://doi.org/https://doi.org/10.1016/j.neuroimage.2005.06.068

Noble, S., Scheinost, D., & Constable, R. T. (2019). A decade of test-retest reliability of functional connectivity: A systematic review and meta-analysis. *NeuroImage*, *203*, 116157. https://doi.org/10.1016/j.neuroimage.2019.116157

Olaya, B., Bobak, M., Haro, J. M., & Demakakos, P. (2017). Trajectories of Verbal Episodic Memory in Middle-Aged and Older Adults: Evidence from the English Longitudinal Study of Ageing. *Journal of the American Geriatrics Society*, *65*(6), 1274–1281. https://doi.org/10.1111/jgs.14789

Palomba, D., Sarlo, M., Angrilli, A., Mini, A., & Stegagno, L. (2000). Cardiac responses associated with affective processing of unpleasant film stimuli. *International Journal of Psychophysiology*, *36*(1), 45–57. https://doi.org/10.1016/S0167-8760(99)00099-9

Palser, E. R., Palmer, C. E., Galvez-Pol, A., Hannah, R., Fotopoulou, A., & Kilner, J. M. (2018). Alexithymia mediates the relationship between interoceptive sensibility and anxiety. *PLOS ONE*, *13*(9), e0203212. Retrieved from https://doi.org/10.1371/journal.pone.0203212

Parikh, M. N., Li, H., & He, L. (2019). Enhancing diagnosis of autism with optimized machine learning models and personal characteristic data. *Frontiers in Computational Neuroscience*, *13*, 9. https://doi.org/10.3389/fncom.2019.00009

Pattyn, N., Neyt, X., Henderickx, D., & Soetens, E. (2008). Psychophysiological investigation of vigilance decrement: Boredom or cognitive fatigue? *Physiology and Behavior*, *93*(1–2), 369–378. https://doi.org/10.1016/j.physbeh.2007.09.016

Pearson, A., & Pfeifer, G. (2020). Two Measures of Interoceptive Sensibility and the Relationship With Introversion and Neuroticism in an Adult Population. *Psychological Reports*, 0033294120965461. https://doi.org/10.1177/0033294120965461

Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., … Duchesnay, É. (2011). Scikit-learn: Machine learning in Python. *Journal of Machine Learning Research*, *12*, 2825–2830. Retrieved from http://dl.acm.org/citation.cfm?id=2078195%5Cnhttp://arxiv.org/abs/1201.0490

Peira, N., Fredrikson, M., & Pourtois, G. (2014). Controlling the emotional heart: Heart rate biofeedback improves cardiac control during emotional reactions. *International Journal of Psychophysiology*, *91*(3), 225–231. https://doi.org/10.1016/j.ijpsycho.2013.12.008

Pekrun, R., Hall, N. C., Goetz, T., & Perry, R. P. (2014). Boredom and academic achievement: Testing a model of reciprocal causation. *Journal of Educational*

Psychology, *106*(3), 696–710. https://doi.org/10.1037/a0036006

Pereira, V., Tavares, F., Mihaylova, P., Mladenov, V., & Georgieva, P. (2018). Factor Analysis for Finding Invariant Neural Descriptors of Human Emotions. *Complexity*, *2018*. https://doi.org/10.1155/2018/6740846

Phan, K. L., Taylor, S. F., Welsh, R. C., Ho, S.-H., Britton, J. C., & Liberzon, I. (2004). Neural correlates of individual ratings of emotional salience: a trial-related fMRI study. *NeuroImage*, *21*(2), 768–780. https://doi.org/https://doi.org/10.1016/j.neuroimage.2003.09.072

Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage*, *16*(2), 331–348. https://doi.org/10.1006/nimg.2002.1087

Phelps, E. A. (2004). Human emotion and memory: Interactions of the amygdala and hippocampal complex. *Current Opinion in Neurobiology*, *14*(2), 198–202. https://doi.org/10.1016/j.conb.2004.03.015

Phillips, M. L., Drevets, W. C., Rauch, S. L., & Lane, R. (2003). Neurobiology of emotion perception II: Implications for major psychiatric disorders. *Biological Psychiatry*, *54*(5), 515–528. https://doi.org/10.1016/S0006-3223(03)00171-9

Poldrack, R. A., Huckins, G., & Varoquaux, G. (2020). Establishment of best practices for evidence for prediction: a review. *JAMA Psychiatry*, *77*(5), 534–540.

Pollatos, O., Gramann, K., & Schandry, R. (2007). Neural systems connecting interoceptive awareness and feelings. *Human Brain Mapping*, *28*(1), 9–18. https://doi.org/10.1002/hbm.20258

Pollatos, O., Herbert, B. M., Matthias, E., & Schandry, R. (2007). Heart rate response after emotional picture presentation is modulated by interoceptive awareness. *International Journal of Psychophysiology*, *63*(1), 117–124.

https://doi.org/10.1016/j.ijpsycho.2006.09.003

Pollatos, O., Kirsch, W., & Schandry, R. (2005). On the relationship between interoceptive awareness, emotional experience, and brain processes. *Cognitive Brain Research*, *25*(3), 948–962. https://doi.org/10.1016/j.cogbrainres.2005.09.019

Pollatos, O., & Schandry, R. (2008). Emotional processing and emotional memory are modulated by interoceptive awareness. *Cognition and Emotion*, *22*(2), 272–287. https://doi.org/10.1080/02699930701357535

Pollatos, O., Schandry, R., Auer, D. P., & Kaufmann, C. (2007). Brain structures mediating cardiovascular arousal and interoceptive awareness. *Brain Research*, *1141*(1), 178–187. https://doi.org/10.1016/j.brainres.2007.01.026

Ponzio, A., & Mather, M. (2014). Hearing something emotional influences memory for what was just seen: How arousal amplifies effects of competition in memory consolidation. *Emotion (Washington, D.C.)*, *14*(6), 1137–1142. https://doi.org/10.1037/a0037983

Posner, J., Russell, J. A., Gerber, A., Gorman, D., Colibazzi, T., Yu, S., … Peterson, B. S. (2009). The neurophysiological bases of emotion: An fMRI study of the affective circumplex using emotion-denoting words. *Human Brain Mapping*, *30*(3), 883–895. https://doi.org/10.1002/hbm.20553

Posner, J., Russell, J. A., & Peterson, B. S. (2005). The circumplex model of affect: An integrative approach to affective neuroscience, cognitive development, and psychopathology. *Development and Psychopathology*, *17*(3), 715–734. https://doi.org/10.1017/S0954579405050340

Pourtois, G., Schettino, A., & Vuilleumier, P. (2013). Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology*, *92*(3), 492–512. https://doi.org/10.1016/j.biopsycho.2012.02.007

Priya, A., Garg, S., & Tigga, N. P. (2020). Predicting Anxiety, Depression and Stress in

Modern Life using Machine Learning Algorithms. *Procedia Computer Science*, *167*, 1258–1267. https://doi.org/10.1016/j.procs.2020.03.442

Radloff, L. S. (1977). The CES-D scale: A self-report depression scale for research in the general population. *Applied Psychological Measurement*, *1*(3), 385–401. https://doi.org/10.1177/014662167700100306

Rasch, B., Spalek, K., Buholzer, S., Luechinger, R., Boesiger, P., Papassotiropoulos, A., & De Quervain, D. J. F. (2009). A genetic variation of the noradrenergic system is related to differential amygdala activation during encoding of emotional memories. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(45), 19191–19196. https://doi.org/10.1073/pnas.0907425106

Rasch, Björn, & Born, J. (2013). About sleep’s role in memory. *Physiological Reviews*, *93*(2), 681–766. https://doi.org/10.1152/physrev.00032.2012

Reed, A. E., Chan, L., & Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: Age differences in preferences for positive over negative information. *Psychology and Aging*, *29*(1), 1–15. https://doi.org/10.1037/a0035194

Reimer, B., Mehler, B., Coughlin, J. F., Godfrey, K. M., & Tan, C. (2009). An on-road assessment of the impact of cognitive workload on physiological arousal in young adult drivers. In *Proceedings of the 1st international conference on automotive user interfaces and interactive vehicular applications* (pp. 115–118). https://doi.org/10.1145/1620509.1620531

Remington, N. A., Fabrigar, L. R., & Visser, P. S. (2000). Reexamining the circumplex model of affect. *Journal of Personality and Social Psychology*, *79*(2), 286–300. https://doi.org/10.1037/0022-3514.79.2.286

Rimmele, U., Lackovic, S. F., Tobe, R. H., Leventhal, B. L., & Phelps, E. A. (2012). Beta-adrenergic blockade at memory encoding, but not retrieval, decreases the subjective sense of recollection. *Journal of Cognitive Neuroscience*, *10*(6), 895–907. https://doi.org/10.1162/jocn_a_00941

Ring, C., & Brener, J. (2018). Heartbeat counting is unrelated to heartbeat detection: A comparison of methods to quantify interoception. *Psychophysiology*, *55*(9), e13084. https://doi.org/10.1111/psyp.13084

Ring, C., Brener, J., Knapp, K., & Mailloux, J. (2015). Effects of heartbeat feedback on beliefs about heart rate and heartbeat counting: A cautionary tale about interoceptive awareness. *Biological Psychology*, *104*, 193–198. https://doi.org/10.1016/j.biopsycho.2014.12.010

Ritchey, M., Dolcos, F., & Cabeza, R. (2008). Role of amygdala connectivity in the persistence of emotional memories over time: An event-related fMRI investigation. *Cerebral Cortex*, *18*(11), 2494–2504. https://doi.org/10.1093/cercor/bhm262

Roozendaal, B., McEwen, B. S., & Chattarji, S. (2009). Stress, memory and the amygdala. *Nature Reviews Neuroscience*, *10*(6), 423–433. https://doi.org/10.1038/nrn2651

Roseman, I J. (1984). Review of personality and social psychology. Vol. 5. Emotions, relationships, and health.

Roseman, Ira J, & Smith, C. A. (2001). Appraisal theory. *Appraisal Processes in Emotion: Theory, Methods, Research*, 3–19.

Rosenberg, M. D., Finn, E. S., Scheinost, D., Papademetris, X., Shen, X., Constable, R. T., & Chun, M. M. (2015). A neuromarker of sustained attention from whole-brain functional connectivity. *Nature Neuroscience*, *19*(1), 165–171. https://doi.org/10.1038/nn.4179

Russell, J. A. (1980). A circumplex model of affect. *Journal of Personality and Social Psychology*, *39*(6), 1161–1178. https://doi.org/10.1037/h0077714

Russell, J. A. (2003). Core Affect and the Psychological Construction of Emotion. *Psychological Review*, *110*(1), 145–172. https://doi.org/10.1037/0033-295X.110.1.145

Russell, J. A., & Barrett, L. F. (1999). Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology*, *76*(5), 805–819. https://doi.org/10.1037/0022-3514.76.5.805

Saarimäki, H., Gotsopoulos, A., Jääskeläinen, I. P., Lampinen, J., Vuilleumier, P., Hari, R., … Nummenmaa, L. (2016). Discrete Neural Signatures of Basic Emotions. *Cerebral Cortex*, *26*(6), 2563–2573. https://doi.org/10.1093/cercor/bhv086

Sakaki, M., Fryer, K., & Mather, M. (2014). Emotion Strengthens High-Priority Memory Traces but Weakens Low-Priority Memory Traces. *Psychological Science*, *25*(2), 387–395. https://doi.org/10.1177/0956797613504784

Sakaki, M., Nga, L., & Mather, M. (2013). Amygdala functional connectivity with medial prefrontal cortex at rest predicts the positivity effect in older adults' memory. *Journal of Cognitive Neuroscience*, *25*(8), 1206–1224. https://doi.org/10.1162/jocn_a_00392

Salami, A., Pudas, S., & Nyberg, L. (2014). Elevated hippocampal resting-state connectivity underlies deficient neurocognitive function in aging. *Proceedings of the National Academy of Sciences*, *111*(49), 17654–17659. https://doi.org/10.1073/pnas.1410233111

Salami, A., Wahlin, A., Kaboodvand, N., Lundquist, A., & Nyberg, L. (2016). Longitudinal Evidence for Dissociation of Anterior and Posterior MTL Resting-State Connectivity in Aging: Links to Perfusion and Memory. *Cerebral Cortex*, *26*(10), 3953–3963. https://doi.org/10.1093/cercor/bhw233

Sander, D., Grandjean, D., & Scherer, K. R. (2018). An Appraisal-Driven Componential Approach to the Emotional Brain. *Emotion Review*, *10*(3), 219–231. https://doi.org/10.1177/1754073918765653

Sarwar, T., Tian, Y., Yeo, B. T. T., Ramamohanarao, K., & Zalesky, A. (2021). Structure-function coupling in the human connectome: A machine learning approach. *NeuroImage*, *226*, 117609. https://doi.org/10.1016/j.neuroimage.2020.117609

Schachter, S., & Singer, J. (1962). Cognitive, social, and physiological determinants of emotional state. *Psychological Review*, *69*(5), 379.

Schaefer, A., & Philippot, P. (2005). Selective effects of emotion on the phenomenal characteristics of autobiographical memories. *Memory*, *13*(2), 148–160. https://doi.org/10.1080/09658210344000648

Schandry, R. (1981). Heart Beat Perception and Emotional Experience. *Psychophysiology*, *18*(4), 483–488. https://doi.org/10.1111/j.1469-8986.1981.tb02486.x

Scherer, K. R. (2009a). Emotions are emergent processes: they require a dynamic computational architecture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1535), 3459–3474.

Scherer, K. R. (2009b). The dynamic architecture of emotion: Evidence for the component process model. *Cognition & Emotion*, *23*(7), 1307–1351. https://doi.org/10.1080/02699930902928969

Scherer, K. R., Schorr, A., & Johnstone, T. (2001). *Appraisal processes in emotion: Theory, methods, research*. Oxford University Press.

Schlüter, H., Hackländer, R. P., & Bermeitinger, C. (2019). Emotional oddball: A review on memory effects. *Psychonomic Bulletin & Review*, *26*(5), 1472–1502. https://doi.org/10.3758/s13423-019-01658-x

Schulz, A., & Vögele, C. (2015). Interoception and stress. *Frontiers in Psychology*, *6*, 993. https://doi.org/10.3389/fpsyg.2015.00993

Schulz, S. M. (2016). Neural correlates of heart-focused interoception: A functional magnetic resonance imaging meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1708), 20160018. https://doi.org/10.1098/rstb.2016.0018

Schümann, D., Joue, G., Jordan, P., Bayer, J., & Sommer, T. (2020). Test-retest reliability of the emotional enhancement of memory. *Memory*, *28*(1), 49–59.

https://doi.org/10.1080/09658211.2019.1679837

Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences*, *17*(11), 565–573. https://doi.org/10.1016/j.tics.2013.09.007

Shafto, M. A., Tyler, L. K., Dixon, M., Taylor, J. R., Rowe, J. B., Cusack, R., … Matthews, F. E. (2014). The Cambridge Centre for Ageing and Neuroscience (Cam-CAN) study protocol : a examination of healthy cognitive ageing, 1–25. https://doi.org/10.1186/s12883-014-0204-1

Shah, S. G., Klumpp, H., Angstadt, M., Nathan, P. J., & Phan, K. L. (2009). Amygdala and insula response to emotional images in patients with generalized social anxiety disorder. *Journal of Psychiatry and Neuroscience*, *34*(4), 296–302.

Sharot, T., Verfaelli, M., & Yonelinas, A. P. (2007). How emotion strengthens the recollective experience: A time-dependent hippocampal process. *PLoS ONE*, *2*(10), e1068. https://doi.org/10.1371/journal.pone.0001068

Shen, X., Tokoglu, F., Papademetris, X., & Constable, R. T. (2013). Groupwise whole-brain parcellation from resting-state fMRI data for network node identification. *NeuroImage*, *82*, 403–415. https://doi.org/10.1016/j.neuroimage.2013.05.081

Sherrington, C. (1952). *The integrative action of the nervous system*. CUP Archive.

Shields, G. S., Sazma, M. A., McCullough, A. M., & Yonelinas, A. P. (2017). The effects of acute stress on episodic memory: A meta-analysis and integrative review. *Psychological Bulletin*, *143*(6), 636–675. https://doi.org/10.1037/bul0000100

Shimizu, Y., Yoshimoto, J., Toki, S., Takamura, M., Yoshimura, S., Okamoto, Y., … Doya, K. (2015). Toward probabilistic diagnosis and understanding of depression based on functional MRI data analysis with logistic group LASSO. *PLoS ONE*, *10*(5), e0123524. https://doi.org/10.1371/journal.pone.0123524

Siebert, M., Markowitsch, H. J., & Bartel, P. (2003). Amygdala, affect and cognition:

Evidence from 10 patients with Urbach-Wiethe disease. *Brain*, *126*(12), 2627–2637. https://doi.org/10.1093/brain/awg271

Siegel, E. H., Sands, M. K., Van den Noortgate, W., Condon, P., Chang, Y., Dy, J., … Barrett, L. F. (2018). Emotion fingerprints or emotion populations? A meta-analytic investigation of autonomic features of emotion categories. *Psychological Bulletin*, *144*(4), 343–393. https://doi.org/10.1037/bul0000128

Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences*, *13*(8), 334–340. https://doi.org/https://doi.org/10.1016/j.tics.2009.05.001

Skoluda, N., Strahler, J., Schlotz, W., Niederberger, L., Marques, S., Fischer, S., … Nater, U. M. (2015). Intra-individual psychological and physiological responses to acute laboratory stressors of different intensity. *Psychoneuroendocrinology*, *51*, 227–236. https://doi.org/https://doi.org/10.1016/j.psyneuen.2014.10.002

Smeets, T., Giesbrecht, T., Jelicic, M., & Merckelbach, H. (2007). Context-dependent enhancement of declarative memory performance following acute psychosocial stress. *Biological Psychology*, *76*(1), 116–123. https://doi.org/https://doi.org/10.1016/j.biopsycho.2007.07.001

Smeets, T., Jelicic, M., & Merckelbach, H. (2006). Stress-induced cortisol responses, sex differences, and false recollections in a DRM paradigm. *Biological Psychology*, *72*(2), 164–172. https://doi.org/https://doi.org/10.1016/j.biopsycho.2005.09.004

Smith, R., Allen, J. J. B., Thayer, J. F., & Lane, R. D. (2015). Altered functional connectivity between medial prefrontal cortex and the inferior brainstem in major depression during appraisal of subjective emotional responses: A preliminary study. *Biological Psychology*, *108*, 13–24. https://doi.org/10.1016/j.biopsycho.2015.03.007

Smith, S. D., Nadeau, C., Sorokopud-Jones, M., & Kornelsen, J. (2021). The Relationship

Between Functional Connectivity and Interoceptive Sensibility. *Brain Connectivity*. https://doi.org/10.1089/brain.2020.0777

Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., … Beckmann, C. F. (2009). Correspondence of the brain's functional architecture during activation and rest. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(31), 13040–13045. https://doi.org/10.1073/pnas.0905267106

Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., … Matthews, P. M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage*, *23*(SUPPL. 1), S208–S219. https://doi.org/10.1016/j.neuroimage.2004.07.051

St. Jacques, P. L., Dolcos, F., & Cabeza, R. (2009). Effects of aging on functional connectivity of the amygdala for subsequent memory of negative pictures: A network analysis of functional magnetic resonance imaging data. *Psychological Science*, *20*(1), 74–84. https://doi.org/10.1111/j.1467-9280.2008.02258.x

St. Jacques, P. L., Dolcos, F., & Cabeza, R. (2010). Effects of aging on functional connectivity of the amygdala during negative evaluation: A network analysis of fMRI data. *Neurobiology of Aging*, *31*(2), 315–327. https://doi.org/10.1016/j.neurobiolaging.2008.03.012

St. Jacques, P. L., & Levine, B. (2007). Ageing and autobiographical memory for emotional and neutral events. *Memory*, *15*(2), 129–144. https://doi.org/10.1080/09658210601119762

Staffaroni, A. M., Brown, J. A., Casaletto, K. B., Elahi, F. M., Neuhaus, J., Cobigo, Y., … Kramer, J. H. (2018). The Longitudinal Trajectory of Default Mode Network Connectivity in Healthy Older Adults Varies As a Function of Processing Speed. *The Journal of Neuroscience*, *38*(11), 2809–2817.

https://doi.org/10.1523/JNEUROSCI.3067-17.2018

Stein, M. B., Simmons, A. N., Feinstein, J. S., & Paulus, M. P. (2007). Increased amygdala and insula activation during emotion processing in anxiety-prone subjects. *American Journal of Psychiatry*, *164*(2), 318–327. https://doi.org/10.1176/ajp.2007.164.2.318

Steinmetz, K. R. M., Addis, D. R., & Kensinger, E. A. (2010). The effect of arousal on the emotional memory network depends on valence. *Neuroimage*, *53*(1), 318–324.

Stevens, J. S., & Hamann, S. (2012). Sex differences in brain activation to emotional stimuli: A meta-analysis of neuroimaging studies. *Neuropsychologia*, *50*(7), 1578–1593. https://doi.org/10.1016/j.neuropsychologia.2012.03.011

Stevens, W. D., & Spreng, R. N. (2014). Resting-state functional connectivity MRI reveals active processes central to cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(2), 233–245. https://doi.org/10.1002/wcs.1275

Strange, B. A., Hurlemann, R., & Dolan, R. J. (2003). An emotion-induced retrograde amnesia in humans is amygdala- and β-adrenergic-dependent. *Proceedings of the National Academy of Sciences*, *100*(23), 13626–13631. https://doi.org/10.1073/pnas.1635116100

Strange, B., Kroes, M., Fan, J., & Dolan, R. (2010). Emotion Causes Targeted Forgetting of Established Memories. *Frontiers in Behavioral Neuroscience*, *4*. https://doi.org/10.3389/fnbeh.2010.00175

Suárez, L. E., Markello, R. D., Betzel, R. F., & Misic, B. (2020). Linking Structure and Function in Macroscale Brain Networks. *Trends in Cognitive Sciences*, *24*(4), 302–315. https://doi.org/10.1016/j.tics.2020.01.008

Sutherland, M. R., & Mather, M. (2012). Negative arousal amplifies the effects of saliency in short-term memory. *Emotion*, *12*(6), 1367–1372. https://doi.org/10.1037/a0027860

Sutherland, M. R., & Mather, M. (2015). Negative arousal increases the effects of stimulus salience in older adults. *Experimental Aging Research*, *41*(3), 259–271. https://doi.org/10.1080/0361073X.2015.1021644

Sutherland, M. R., & Mather, M. (2018). Arousal (but not valence) amplifies the impact of salience. *Cognition and Emotion*, *32*(3), 616–622. https://doi.org/10.1080/02699931.2017.1330189

Sutherland, M. R., McQuiggan, D. A., Ryan, J. D., & Mather, M. (2017). Perceptual salience does not influence emotional arousal's impairing effects on top-down attention. *Emotion (Washington, D.C.)*, *17*(4), 700–706. https://doi.org/10.1037/emo0000245

Talarico, J. M., Labar, K. S., & Rubin, D. C. (2004). Emotional intensity predicts autobiographical memory experience. *Memory and Cognition*, *32*(7), 1118–1132. https://doi.org/10.3758/BF03196886

Talarico, J. M., & Rubin, D. C. (2003). Confidence, not consistency, characterizes flashbulb memories. *Psychological Science*, *14*(5), 455–461.

Talarico, J. M., & Rubin, D. C. (2007). Flashbulb memories are special after all; in phenomenology, not accuracy. *Applied Cognitive Psychology: The Official Journal of the Society for Applied Research in Memory and Cognition*, *21*(5), 557–578.

Talmi, D. (2013). Enhanced Emotional Memory: Cognitive and Neural Mechanisms. *Current Directions in Psychological Science*, *22*(6), 430–436. https://doi.org/10.1177/0963721413498893

Talmi, D., Luk, B. T. C., McGarry, L. M., & Moscovitch, M. (2007). The contribution of relatedness and distinctiveness to emotionally-enhanced memory. *Journal of Memory and Language*, *56*(4), 555–574. https://doi.org/10.1016/j.jml.2007.01.002

Tambini, A., Ketz, N., & Davachi, L. (2010). Enhanced Brain Correlations during Rest Are Related to Memory for Recent Experiences. *Neuron*, *65*(2), 280–290. https://doi.org/10.1016/j.neuron.2010.01.001

Tambini, A., Rimmele, U., Phelps, E. A., & Davachi, L. (2017). Emotional brain states carry over and enhance future memory formation. *Nature Neuroscience*, *20*(2), 271–278. https://doi.org/10.1038/nn.4468

Tavor, I., Parker Jones, O., Mars, R. B., Smith, S. M., Behrens, T. E., & Jbabdi, S. (2016). Task-free MRI predicts individual differences in brain activity during task performance. *Science*, *352*(6282), 216–220. https://doi.org/10.1126/science.aad8127

Taylor, J. R., Williams, N., Cusack, R., Auer, T., Shafto, M. A., Dixon, M., … Henson, R. N. (2017). The Cambridge Centre for Ageing and Neuroscience (Cam-CAN) data repository: structural and functional MRI, MEG, and cognitive data from a cross-sectional adult lifespan sample. *Neuroimage*, *144*, 262–269.

Tempesta, D., Socci, V., De Gennaro, L., & Ferrara, M. (2018). Sleep and emotional processing. *Sleep Medicine Reviews*, *40*, 183–195. https://doi.org/https://doi.org/10.1016/j.smrv.2017.12.005

Terasawa, Y., Fukushima, H., & Umeda, S. (2013). How does interoceptive awareness interact with the subjective experience of emotion? An fMRI Study. *Human Brain Mapping*, *34*(3), 598–612. https://doi.org/10.1002/hbm.21458

Thomas, K. M., Drevets, W. C., Dahl, R. E., Ryan, N. D., Birmaher, B., Eccard, C. H., … Casey, B. J. (2001). Amygdala Response to Fearful Faces in Anxious and Depressed Children. *Archives of General Psychiatry*, *58*(11), 1057–1063. https://doi.org/10.1001/archpsyc.58.11.1057

Tobia, M. J., Hayashi, K., Ballard, G., Gotlib, I. H., & Waugh, C. E. (2017). Dynamic functional connectivity and individual differences in emotions during social stress. *Human Brain Mapping*, *38*(12), 6185–6205. https://doi.org/10.1002/hbm.23821

Toiviainen, P., Alluri, V., Brattico, E., Wallentin, M., & Vuust, P. (2014). Capturing the musical brain with Lasso: Dynamic decoding of musical features from fMRI data.

NeuroImage, *88*, 170–180. https://doi.org/10.1016/j.neuroimage.2013.11.017

Touroutoglou, A., Andreano, J. M., Barrett, L. F., & Dickerson, B. C. (2015). Brain network connectivity-behavioral relationships exhibit trait-like properties: Evidence from hippocampal connectivity and memory. *Hippocampus*, *25*(12), 1591–1598. https://doi.org/10.1002/hipo.22480

Touroutoglou, A., Bickart, K. C., Barrett, L. F., & Dickerson, B. C. (2014). Amygdala task-evoked activity and task-free connectivity independently contribute to feelings of arousal. *Human Brain Mapping*, *35*(10), 5316–5327. https://doi.org/10.1002/hbm.22552

Trevisan, D. A., Mehling, W. E., & McPartland, J. C. (2021). Adaptive and Maladaptive Bodily Awareness: Distinguishing Interoceptive Sensibility and Interoceptive Attention from Anxiety-Induced Somatization in Autism and Alexithymia. *Autism Research*, *14*(2), 240–247. https://doi.org/10.1002/aur.2458

Tsakiris, M., & Critchley, H. (2016). Interoception beyond homeostasis: Affect, cognition and mental health. *Philosophical Transactions of the Royal Society B: Biological Sciences*. The Royal Society. https://doi.org/10.1098/rstb.2016.0002

Tsvetanov, K. A., Henson, R. N. A., Tyler, L. K., Razi, A., Geerligs, L., Ham, T. E., & Rowe, J. B. (2016). Extrinsic and intrinsic brain network connectivity maintains cognition across the lifespan despite accelerated decay of regional brain activation. *Journal of Neuroscience*, *36*(11), 3115–3126. https://doi.org/10.1523/JNEUROSCI.2733-15.2016

Ueno, D., Matsuoka, T., Kato, Y., Ayani, N., Maeda, S., Takeda, M., & Narumoto, J. (2020). Individual Differences in Interoceptive Accuracy Are Correlated With Salience Network Connectivity in Older Adults. *Frontiers in Aging Neuroscience*, *12*, 407. https://doi.org/10.3389/fnagi.2020.592002

Uhrig, M. K., Trautmann, N., Baumgärtner, U., Treede, R.-D., Henrich, F., Hiller, W., &

Marschall, S. (2016). Emotion Elicitation: A Comparison of Pictures and Films. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.00180

Vaisvaser, S., Lin, T., Admon, R., Podlipsky, I., Greenman, Y., Stern, N., … Hendler, T. (2013). Neural traces of stress: Cortisol related sustained enhancement of amygdala-hippocampal functional connectivity. *Frontiers in Human Neuroscience*, *7*(JUN), 313. https://doi.org/10.3389/fnhum.2013.00313

van der Velde, J., Servaas, M. N., Goerlich, K. S., Bruggeman, R., Horton, P., Costafreda, S. G., & Aleman, A. (2013). Neural correlates of alexithymia: A meta-analysis of emotion processing studies. *Neuroscience & Biobehavioral Reviews*, *37*(8), 1774–1785. https://doi.org/https://doi.org/10.1016/j.neubiorev.2013.07.008

van Marle, H. J. F., Hermans, E. J., Qin, S., & Fernández, G. (2009). From Specificity to Sensitivity: How Acute Stress Affects Amygdala Processing of Biologically Salient Stimuli. *Biological Psychiatry*, *66*(7), 649–655. https://doi.org/https://doi.org/10.1016/j.biopsych.2009.05.014

van Marle, H. J. F., Hermans, E. J., Qin, S., & Fernández, G. (2010). Enhanced resting-state connectivity of amygdala in the immediate aftermath of acute psychological stress. *NeuroImage*, *53*(1), 348–354. https://doi.org/10.1016/j.neuroimage.2010.05.070

Veer, I. M., Oei, N. Y. L., Spinhoven, P., van Buchem, M. A., Elzinga, B. M., & Rombouts, S. A. R. B. (2011). Beyond acute social stress: Increased functional connectivity between amygdala and cortical midline structures. *NeuroImage*, *57*(4), 1534–1541. https://doi.org/10.1016/j.neuroimage.2011.05.074

Veretennikova, M. A., Sikorskii, A., & Boivin, M. J. (2018). Parameters of stochastic models for electroencephalogram data as biomarkers for child’s neurodevelopment after cerebral malaria. *Journal of Statistical Distributions and Applications*, *5*(1), 1–12. https://doi.org/10.1186/s40488-018-0086-7

Vergun, S., Deshpande, A., Meier, T. B., Song, J., Tudorascu, D. L., Nair, V. A., … Prabhakaran, V. (2013). Characterizing functional connectivity differences in aging adults using machine learning on resting state fMRI data. *Frontiers in Computational Neuroscience*, *7*(APR 2013), 38. https://doi.org/10.3389/fncom.2013.00038

Wang, C.-A., Baird, T., Huang, J., Coutinho, J. D., Brien, D. C., & Munoz, D. P. (2018). Arousal Effects on Pupil Size, Heart Rate, and Skin Conductance in an Emotional Face Task. *Frontiers in Neurology*, *9*. https://doi.org/10.3389/fneur.2018.01029

Wang, X., Tan, Y., Van den Bergh, O., von Leupoldt, A., & Qiu, J. (2020). Intrinsic functional brain connectivity patterns underlying enhanced interoceptive sensibility. *Journal of Affective Disorders*, *276*, 804–814. https://doi.org/10.1016/j.jad.2020.07.032

Waring, J. D., & Kensinger, E. A. (2009). Effects of Emotional Valence and Arousal Upon Memory Trade-Offs With Aging. *Psychology and Aging*, *24*(2), 412–422. https://doi.org/10.1037/a0015526

Watson, A., Timperio, A., Brown, H., Best, K., & Hesketh, K. D. (2017). Effect of classroom-based physical activity interventions on academic and physical activity outcomes: a systematic review and meta-analysis. *International Journal of Behavioral Nutrition and Physical Activity*, *14*(1), 114. https://doi.org/10.1186/s12966-017-0569-9

Weng, H. Y., Feldman, J. L., Leggio, L., Napadow, V., Park, J., & Price, C. J. (2021). Interventions and Manipulations of Interoception. *Trends in Neurosciences*, *44*(1), 52–62. https://doi.org/10.1016/j.tins.2020.09.010

Werner, N. S., Peres, I., Duschek, S., & Schandry, R. (2010). Implicit memory for emotional words is modulated by cardiac perception. *Biological Psychology*, *85*(3), 370–376. https://doi.org/10.1016/j.biopsycho.2010.08.008

Werner, N. S., Schweitzer, N., Meindl, T., Duschek, S., Kambeitz, J., & Schandry, R. (2013). Interoceptive awareness moderates neural activity during decision-making. *Biological*

Psychology, *94*(3), 498–506. https://doi.org/10.1016/j.biopsycho.2013.09.002

Westermann, R., Spies, K., Stahl, G., & Hesse, F. W. (1996). Relative effectiveness and validity of mood induction procedures: A meta-analysis. *European Journal of Social Psychology*, *26*(4), 557–580. https://doi.org/10.1002/(SICI)1099-0992(199607)26:4<557::AID-EJSP769>3.0.CO;2-4

Weymar, M., Schwabe, L., Löw, A., & Hamm, A. O. (2012). Stress Sensitizes the Brain: Increased Processing of Unpleasant Pictures after Exposure to Acute Stress. *Journal of Cognitive Neuroscience*, *24*(7), 1511–1518. https://doi.org/10.1162/jocn_a_00174

Wiens, S. (2005). Interoception in emotional experience. *Current Opinion in Neurology*, *18*(4), 442–447. https://doi.org/10.1097/01.wco.0000168079.92106.99

Wiens, S., Mezzacappa, E. S., & Katkin, E. S. (2000). Heartbeat detection and the experience of emotions. *Cognition and Emotion*, *14*(3), 417–427. https://doi.org/10.1080/026999300378905

Wild, J., Clark, D. M., Ehlers, A., & McManus, F. (2008). Perception of arousal in social anxiety: Effects of false feedback during a social interaction. *Journal of Behavior Therapy and Experimental Psychiatry*, *39*(2), 102–116. https://doi.org/10.1016/j.jbtep.2006.11.003

Wilson-Mendenhall, C. D., Barrett, L. F., & Barsalou, L. W. (2013). Neural Evidence That Human Emotions Share Core Affective Properties. *Psychological Science*, *24*(6), 947–956. https://doi.org/10.1177/0956797612464242

Wirkner, J., Weymar, M., Löw, A., & Hamm, A. O. (2013). Effects of Pre-Encoding Stress on Brain Correlates Associated with the Long-Term Memory for Emotional Scenes. *PLoS ONE*, *8*(9), e68212. https://doi.org/10.1371/journal.pone.0068212

Woody, S. R. (1996). Effects of focus of attention on anxiety levels and social performance of individuals with social phobia. *Journal of Abnormal Psychology*, *105*(1), 61–69.

https://doi.org/10.1037/0021-843X.105.1.61

Wu, J., Srinivasan, R., Kaur, A., & Cramer, S. C. (2014). Resting-state cortical connectivity predicts motor skill acquisition. *NeuroImage*, *91*, 84–90. https://doi.org/10.1016/j.neuroimage.2014.01.026

Wu, X., Shi, L., Wei, D., & Qiu, J. (2019). Brain connection pattern under interoceptive attention state predict interoceptive intensity and subjective anxiety feeling. *Human Brain Mapping*, *40*(6), 1760–1773. https://doi.org/10.1002/hbm.24488

Yang, L., & Ornstein, T. J. (2011). The effect of emotion-focused orientation at retrieval on emotional memory in young and older adults. *Memory*, *19*(3), 305–313. https://doi.org/10.1080/09658211.2011.561803

Yang, W. F. Z., Toller, G., Shdo, S., Kotz, S. A., Brown, J., Seeley, W. W., … Rankin, K. P. (2021). Resting functional connectivity in the semantic appraisal network predicts accuracy of emotion identification. *NeuroImage: Clinical*, *31*, 102755. https://doi.org/10.1016/j.nicl.2021.102755

Yarkoni, T., & Westfall, J. (2017). Choosing Prediction Over Explanation in Psychology: Lessons From Machine Learning. *Perspectives on Psychological Science*, *12*(6), 1100–1122. https://doi.org/10.1177/1745691617693393

Yin, Z., Zhao, M., Wang, Y., Yang, J., & Zhang, J. (2017). Recognition of emotions using multimodal physiological signals and an ensemble deep learning model. *Computer Methods and Programs in Biomedicine*, *140*, 93–110. https://doi.org/10.1016/j.cmpb.2016.12.005

Yonelinas, A. P., & Ritchey, M. (2015). The slow forgetting of emotional episodic memories: An emotional binding account. *Trends in Cognitive Sciences*, *19*(5), 259–267. https://doi.org/10.1016/j.tics.2015.02.009

Yoris, A., Esteves, S., Couto, B., Melloni, M., Kichic, R., Cetkovich, M., … Sedeño, L.

(2015). The roles of interoceptive sensitivity and metacognitive interoception in panic. *Behavioral and Brain Functions*, *11*(1), 14. https://doi.org/10.1186/s12993-015-0058-8

Young, E. J., & Williams, C. L. (2010). Valence dependent asymmetric release of norepinephrine in the basolateral amygdala. *Behavioral Neuroscience*, *124*(5), 633–644. https://doi.org/10.1037/a0020885

Zaki, J., Davis, J. I., & Ochsner, K. N. (2012). Overlapping activity in anterior insula during interoception and emotional experience. *NeuroImage*, *62*(1), 493–499. https://doi.org/10.1016/j.neuroimage.2012.05.012

Zamariola, G., Maurage, P., Luminet, O., & Corneille, O. (2018). Interoceptive accuracy scores from the heartbeat counting task are problematic: Evidence from simple bivariate correlations. *Biological Psychology*, *137*, 12–17. https://doi.org/10.1016/j.biopsycho.2018.06.006

Zarubin, V. C., Phillips, T. K., Robertson, E., Bolton Swafford, P. G., Bunge, T., Aguillard, D., … Mickley Steinmetz, K. R. (2020). Contributions of Arousal, Attention, Distinctiveness, and Semantic Relatedness to Enhanced Emotional Memory: An Event-Related Potential and Electrocardiogram Study. *Affective Science*, *1*(3), 172–185. https://doi.org/10.1007/s42761-020-00012-y

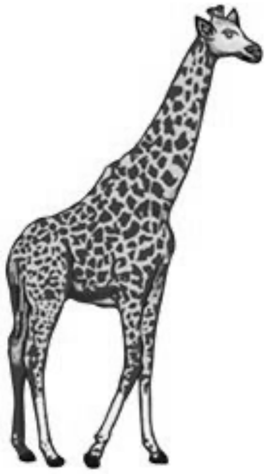
Zhang, X., Ge, T. T., Yin, G., Cui, R., Zhao, G., & Yang, W. (2018). Stress-induced functional alterations in amygdala: Implications for neuropsychiatric diseases. *Frontiers in Neuroscience*, *12*(MAY), 367. https://doi.org/10.3389/fnins.2018.00367

Zimmerman, C. A., & Kelley, C. M. (2010). “I’ll remember this!” Effects of emotionality on memory predictions versus memory performance. *Journal of Memory and Language*, *62*(3), 240–253. https://doi.org/10.1016/j.jml.2009.11.004

Appendices

Appendix A: Examples of Stimuli

Animal Images



Tool Images

Appendix B: Psychopathological Conditions

Please check a list below and indicate if you currently have or have concerns about any of the conditions listed below. If you were diagnosed as one of these conditions in the past 5 years but no longer have them, please also indicate.

		Do you currently have it?	Did you have it in the past 5 years?
1.	**Major depression/Bipolar disorder**	Yes No	Yes No
2.	**Panic disorder**	Yes No	Yes No
3.	**Specific phobias (e.g., snake, spider, fear)**	Yes No	Yes No
4.	**Post-traumatic stress disorder**	Yes No	Yes No
2.	**Schizophrenia**	Yes No	Yes No
3.	**Social/General anxiety disorders**	Yes No	Yes No
4.	**Autism**	Yes No	Yes No
5.	**Eating disorder**	Yes No	Yes No
6.	**Obsessive Compulsive Disorder**	Yes No	Yes No
7.	**Personality disorder**	Yes No	Yes No
8.	**Seizure**	Yes No	Yes No
9.	**Parkinson's disease**	Yes No	Yes No
10.	**Peripheral neuropathy**	Yes No	Yes No
11.	**Huntington's disease**	Yes No	Yes No
12.	**Strokes**	Yes No	Yes No
13.	**Tourette's Syndrome**	Yes No	Yes No

Appendix C: Supplementary Analyses

Positive and Negative Affect

Negative affect was not significantly different after the picture viewing task ($M = 13.5$, $SD = 4.41$) than baseline ($M = 13.9$, $SD = 5.01$), $t(33) = .508$, $p = .615$. Positive affect was also not significantly different after the task ($M = 24.3$, $SD = 6.89$) than baseline ($M = 25.6$, $SD = 6.59$), $t(33) = 1.77$, $p = .087$.

Manipulation Checks

Most of the participants reported not expecting a memory test (94%). On a 7-point Likert scale, participants generally reported trusting that the beeps presented during the heart rate feedback condition represented their own heartbeats ($M = 5.6$, $SD = 1.46$).

Correlations

There was no significant correlation between the negativity bias in memory (calculated by subtracting positive memory from negative memory) during the heart rate feedback blocks and the baseline to post-task increase in either positive or negative affect, or the degree of trust that the played tones are one's heartbeats (Table C.1).

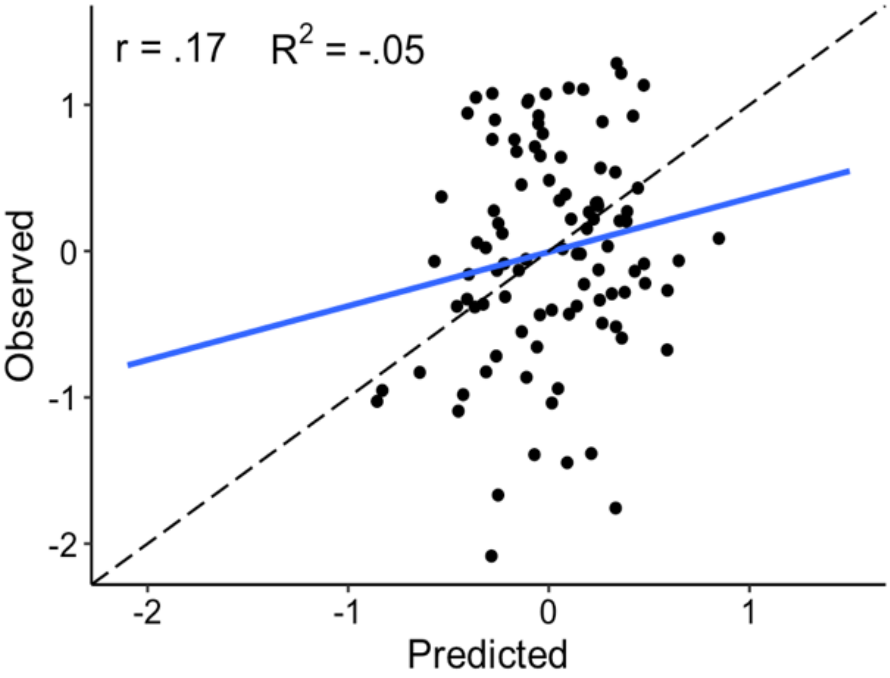
Table C.1
Correlations between negativity bias in memory and manipulation checks

Variable	1	2	3	4	5
1. Negativity Bias – Heart rate feedback condition					
2. Negativity Bias – Control	-.14				
3. Trust in Presented Heartbeats	-.10	.13			
4. Increase in Positive Affect	.00	.20	-.10		
5. Increase in Negative Affect	.02	-.04	**.50***	**-.43***	
6. Depression Score	-.25	.19	-.31	.15	-.33

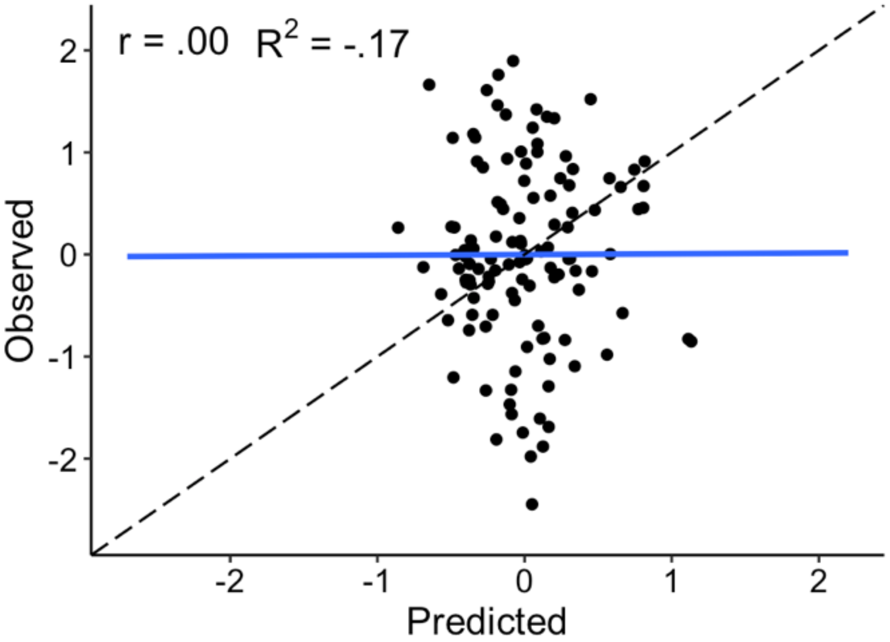
* $p < .05$

Appendix D: Predicting Intelligence for Middle-Aged and Older Adults

Intelligence — Middle Aged Adults.

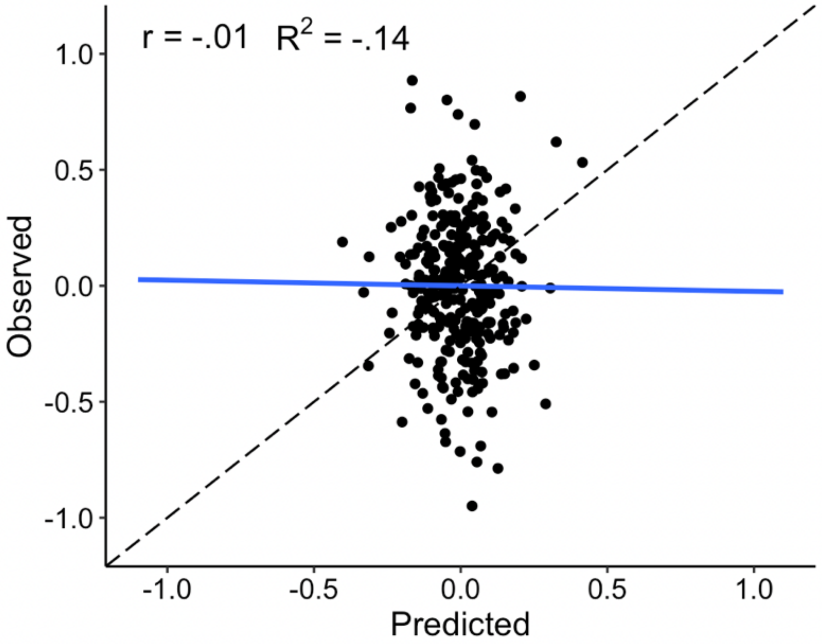


Intelligence – Older Adults

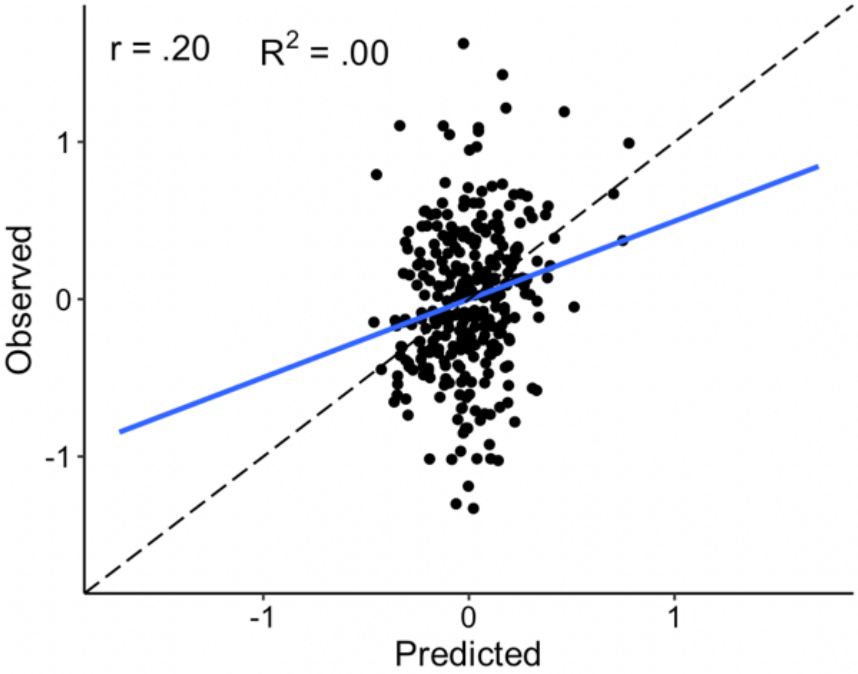


Appendix E: Predicting Associative Valence Memory

Emotional Enhancement Effect — All Ages

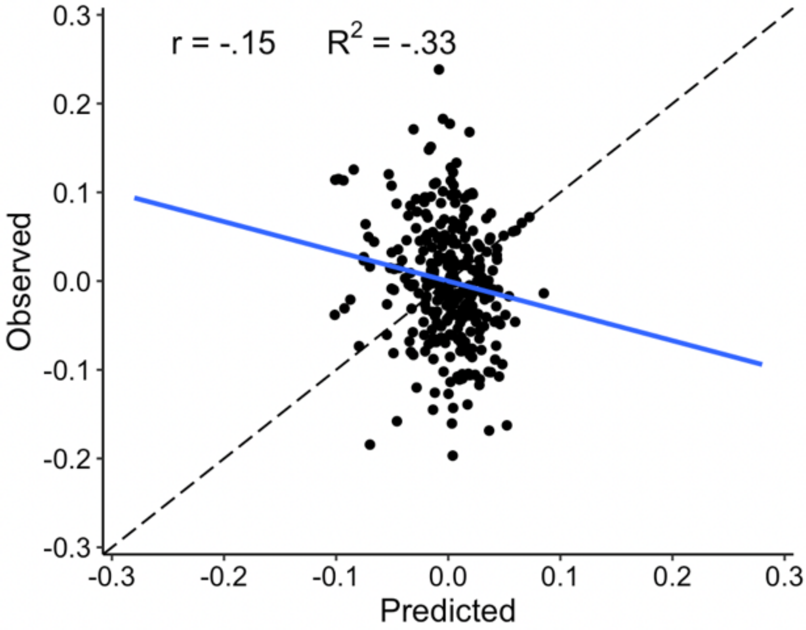


Positivity Bias — All Ages



Appendix F: Predicting Background Memory

Emotional Enhancement Effect — All Ages



Positivity Bias — All Ages