The Relationship between Emotional Arousal and Cognition

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

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Abstract

The interaction between emotion and cognition is pivotal for everyday functioning. Emotional scenes, such as a crime scene in a movie, would grab more attention than a neutral scene, such as a car passing by. Besides, we mostly remember personal events that have an emotional significance, such as the first day of the college. On the other hand, some other emotional events, for instance traumatic experiences, can sometimes be recalled frequently and involuntarily or completely suppressed.

This thesis explores these opposing effects of emotional arousal. The first and second studies utilise a memory-guided attention paradigm to investigate emotional enhancement and impairment effects on attention to the scene pictures known by prior knowledge. The results showed that attention to a target location in the scenes previously known was boosted by emotional arousal induced by an anticipation of a fearful shock into the participant's finger. On the other hand, attention to a target location that was not known beforehand was not affected by the fear of shock.

The third and the last study investigated how emotional arousal induced by negative sound clips would affect ambiguous motion perception. Here participants were able to choose a dominant (i.e., leftward or rightward) direction when they felt emotionally aroused by listening a negative sound clip.

These studies underline the complex relationship of emotional arousal and cognition. Emotional arousal helps to boost attention, memory, and perception to something important for the individual whether it comes from past memories or it dominates by perception. Critical evaluations have been included in the experimental chapters while the general discussion draws a broader conclusion in the interaction between emotion and cognition and discusses some implications.

Table of Contents

1 Chapter 1: Literature Review

1.1 Abstract

In this chapter, research on the interaction between cognition and emotion is reviewed. It is well known that emotionally arousing events are processed automatically, capture attention faster, and are remembered better. This enhancing effect of emotion is attributed to the survival mechanism of an organism in the notion of the threat-related stimuli. According to leading accounts in the field, there is an elevated selective attention towards emotionally significant material. However, emotion can also hinder some aspects of cognition. Therefore, the chapter covers theories and empirical research in order to explain why emotion might sometimes enhance and sometimes impair performance. It was suggested that Arousal-Biased Competition (ABC) Theory (Mather & Sutherland, 2011) might be considered as a good candidate to account for opposing effect of emotional arousal and can potentially explain conflicting findings in the literature. Then, research on the dichotomy of selective attention: bottom-up saliency and top-down goals; and as well as a recently proposed third category: selection history were discussed. In this thesis, I conducted three experiments to test ABC Theory's predictions. Experiment 1 and 2 tested the interaction between arousal and attention based on selection history (i.e., memory-guided attention). Experiment 3 tested the interaction between arousal and ambiguous motion perception.

1.2 Introduction

A considerable amount of literature has suggested that emotional stimuli, such as snakes, spiders, emotional facial expressions, and erotic images, are attended to and remembered better compared to non-emotional stimuli (for reviews, see Bennion, Ford, Murray, & Kensinger, 2013; Hamann, 2001; Öhman & Mineka, 2001; Schupp, Flaisch, Stockburger, & Junghöfer, 2006; Vuilleumier & Pourtois, 2007). This emotion-induced enhancement effect on cognitive processes was observed regardless of the types of stimuli, including images (e.g., Bradley, Greenwald, Petry, & Lang, 1992; Sakaki, Niki, & Mather, 2012), words (e.g., Kensinger & Corkin, 2003; Kleinsmith & Kaplan, 1963; Sharot & Phelps, 2004), facial expressions (e.g., Eastwood, Smilek, & Merikle, 2001; Fox et al., 2000; Fox, Russo, & Dutton, 2002), narratives (e.g., Cahill & McGaugh, 1995) and autobiographical memories (e.g., D'Argembeau, Comblain, & Van der Linden, 2003; St. Jacques & Levine, 2007).

From an evolutionary perspective, emotional arousal is considered to have evolved in order to adaptively regulate behaviour in accordance with the environmental changes, helping individuals to avoid threats and to acquire food for their own survival and as well as to approach potential mates for survival of the species (e.g., Lang, Bradley, & Cuthbert, 1997; Öhman, Flykt, & Esteves, 2001). According to the Biological Preparedness theory (Seligman, 1971), for instance, phobias arise from a selective set of biological associations that the organism is evolutionarily prepared to learn, leading to the rapid acquisition of fear, where the conditioned stimuli (CS) is biologically significant rather than neutral. Thus, these theories posit that people are more likely to develop fears to some stimuli, such as snakes, spiders, and heights, which have led mortal threats throughout natural history (for a recent review, see McNally, 2016). More recent accounts of the evolutionary psychology argue the brain itself evolved to carry out specific computations in order to regulate behaviour to be biologically successful and, therefore, they focus on the ‘reproduction of the genes’ rather than the ‘survival’ of an individual (e.g., Tooby & Cosmides, 2008). Nevertheless, researchers agree that emotions are not limited to humans; instead they posit that there is a long evolutionary history behind emotions, which are a part of the natural behaviour in many species (e.g., Barkow, Cosmides, & Tooby, 1992; Buss, 1994; Damasio, 2004; LeDoux, 2012; Pinker, 1997). During evolution, specific mechanisms should have been developed in order to optimise the detection of threats and potential rewards (e.g., Bradley et al., 1992; Lang, 2010; Öhman, 2005; Öhman & Mineka, 2001; Seligman, 1971; Vuilleumier, 2005). The purpose of emotion is, therefore, to highlight what is important or relevant (Frijda, 1986); thus, pivotal for survival and functioning. Before explaining how emotion affects cognition, definitions of emotion are described below.

1.3 Emotion and Arousal

Emotion is defined as a mental state associated with the chemical changes in the nervous system, which is associated with thoughts, feelings, behavioural responses; and a degree of pleasure and displeasure (e.g., Damasio, 1998; Ekman & Davidson, 1994; Panksepp, 2005). Despite the substantial amount of literature on emotion, it does not have a single or preferred definition (Cabanac, 2002). For instance, Kleinginna and Kleinginna (1981) listed almost a hundred different definitions of emotion. Oxford Dictionary defines emotion as “a strong feeling deriving from one's circumstances, mood, or relationships with others” (Oxford University Press, 2019). Schacter and Singer (1962) defined emotion as “a state of physiological arousal and of cognition appropriate to this state of arousal. Emotion has been considered to have two core independent dimensions: Arousal and valence. In this circumplex model (Feldman Barrett, Mesquita, Ochsner, & Gross, 2007; Feldman Barrett & Russell, 1998; J. Posner, Russell, & Peterson, 2005; Russell, 1980), emotion is defined based on valence (i.e., pleasure vs. displeasure) and the level of physiological arousal or activation (i.e., calmness vs. excitation); and thus, emotional states which are similar in valence and arousal will have similar effects on cognition (see Figure 1.1). For the purpose of this thesis, I only focused on emotional arousal, leaving out the ongoing discussion on valence (but see Sutherland & Mather, 2018). Some research suggest that, for instance, fearful faces but not happy faces, enhance visual attention (e.g., Becker, 2009) while others suggest positive stimuli, for instance induced by erotic images, which is considered to be highly arousing, also affects attention (for a review, see L. Wang, Kennedy, & Most, 2012). Sutherland and Mather (2018) further discuss whether the positive stimuli, such as happy faces, are as arousing as negative counterparts; and suggest that it is the arousing aspect that drives opposing effects on cognitive processes rather than the valence. When arousal levels are similar, both positive and negative events should affect cognition in a similar manner. In the three studies conducted in this thesis ABC theory (Mather & Sutherland, 2011), which explains arousal-cognition interaction irrespective of the valence, is tested. Therefore, the literature discussed here includes highly arousing information regardless of whether it is positive or negative. It should also be noted that "emotion" and "arousal" have been used interchangeable throughout this thesis.

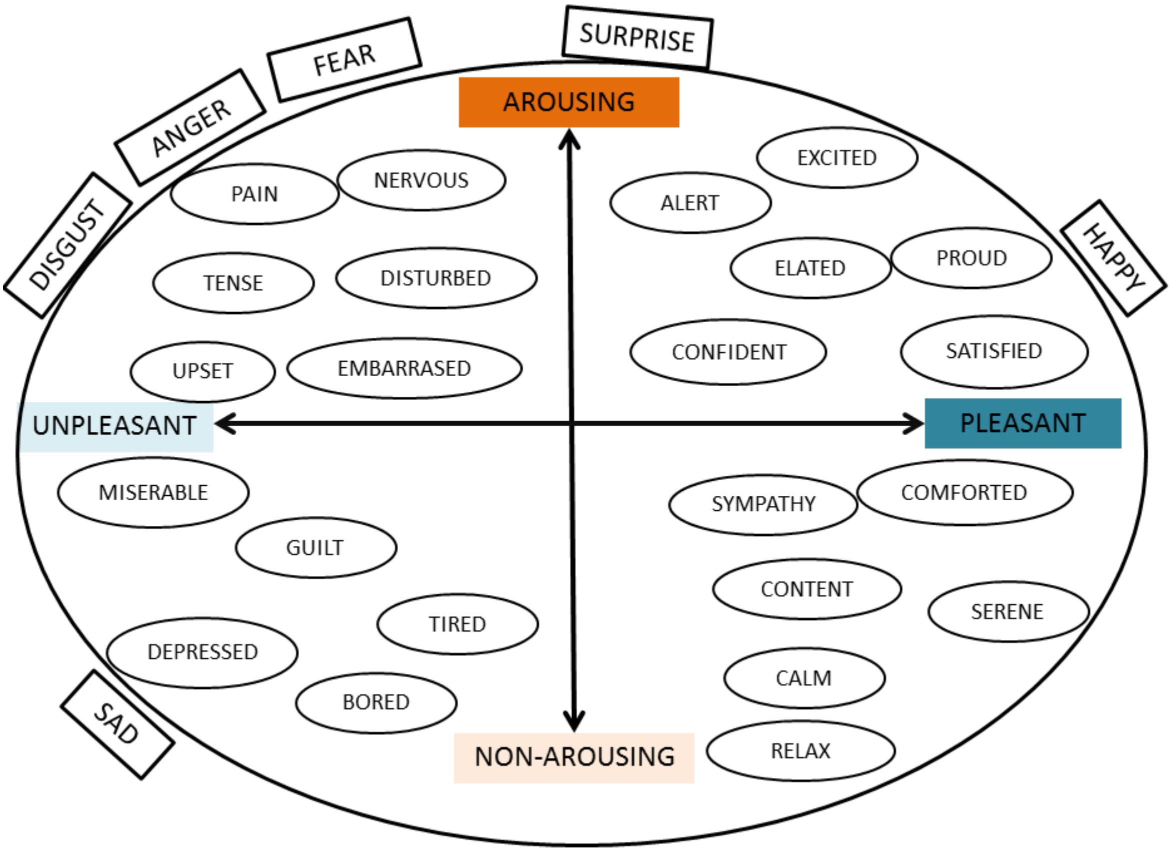

Figure 1.1. *Arousal and valence in the circumplex model of emotion*

1.4 Attentional Bias to Emotional Stimuli

1.4.1 Selective Attention

In everyday life, we are constantly bombarded by various pieces of information. The brain cannot process every bit of information it receives and it has to prioritise what is relevant for the individual. The attentional mechanisms have been considered to help focus on highly relevant items and suppress less important ones (e.g., Allport, 1993; Broadbent, 1958; Bundesen, 1990; Desimone, 1996; Desimone & Duncan, 1995; Neisser, 1967; Treisman, 1969; Tsotsos, 1990). This prioritisation process is called “selective attention”. It means to select the information that is salient (i.e., bottom-up saliency or exogenous attention: discussed later) and/or the information that is relevant to one’s goals (i.e., top-down goals or endogenous attention: discussed later) and to ignore the non-salient or irrelevant ones. Single-cell recordings from monkeys demonstrated that attentional enhancement to salient feature drives from the competitive interactions among neurons representing all of the stimuli presented in the visual field (for a review, see Desimone, 1998). The result of this competition is the suppression of the neural representations of behaviourally irrelevant stimuli in the visual cortex. Thus, there is a constant competition among stimuli or signals to reach out the brain and to grab resources for representations, which has been modelled as "biased competition" by Desimone and colleagues (e.g., Desimone, 1996; Desimone & Duncan, 1995; Desimone, Wessinger, Thomas, & Schneider, 1990; Luck, Chelazzi, Hillyard, & Desimone, 1997). According to the Biased Competition Theory, attentional selection is a process of biasing the most important event and ignoring the mundane ones.

Selection begins with orienting of attention. Orienting is the process of moving attention to a location in space (spatial orienting) or time (temporal orienting). Stimuli or signals at a given location become amplified, and therefore, it is possible to detect an important or relevant stimulus or to orient towards a significant event. Orienting of attention has been divided into three components: engaging, disengaging, and shifting (e.g., M. I. Posner & Peterson, 1990; M. I. Posner, Walker, Friedrich, & Rafal, 1984).

Engagement is one of the key concepts for evidence of attentional selection, which results in the facilitation of attention to process a given stimulus. Disengagement refers to the process of withdrawal of attention from a certain stimulus. Shifting refers to orienting attention from one stimulus or location towards another. Note that different researchers have used different terminologies; and more importantly, methodological issues sometimes make it difficult to distinguish one concept from the other as in the most of the phenomenon studied in cognition and especially in human consciousness.

Nevertheless, research examining the emotional effects on attention demonstrated that emotion affects all of these components. Previous research documented a facilitation of attention (i.e., *engagement*) towards emotional events in *anxious populations* (Amir, Elias, Klumpp, & Przeworski, 2003; Gole, Köchel, Schäfer, & Schienlea, 2012; Koster, Crombez, Van Damme, Verschuere, & DeHouwer, 2004a; Koster, Crombez, Verschuere, Van Damme, & Wiersema, 2006; Massar, Mol, Kenemans, & Baas, 2011; Wilson & MacLeod, 2003), in *depressive groups* (Leyman, De Raedt, Schacht, & Koster, 2007; Mathews, Ridgeway, & Williamson, 1996) and in *healthy controls* (Fox et al., 2000; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2005; Koster, Verschuere, Burssens, Custers, & Crombez, 2007; Mathews, Fox, Yiend, & Calder, 2003; Van Damme et al., 2004). There was also an impaired *disengagement* from emotional stimulus once attention is drawn in *anxiety* (Cocia, Uscătescu, & Rusu, 2012; Fox, Russo, Bowles, & Dutton, 2001; Georgiou et al., 2005; Gole et al., 2012; Koster et al., 2006; Leleu, Douilliez, & Rusinek, 2014; Massar et al., 2011; Salemink, van den Hout, & Kindt, 2007) and in *social anxiety* (Heeren, Lievens, & Philippot, 2011; Moriya & Tanno, 2011), in *post-traumatic stress disorder* (Bardeen & Read, 2010), and in *healthy populations* (Compton, 2000; Koster, Crombez, Verschuere, & DeHouwer, 2004b). Finally, research also found a facilitative *attentional shift* towards emotional material with *depressive* (Mogg, Millar, & Bradley, 2000; Zvielli, Vrijsen, Koster, & Bernstein, 2016), *anxious* (Derakshan, Smith, & Eysenck, 2009; Johnson, 2009), *socially anxious* (Grant & Beck, 2006), *traumatised* (Callinan, Johnson, & Wells, 2015) and *healthy participants* (Cavanagh, Urry, & Shin, 2011; Stormark, Nordby, & Hugdahl, 1995). It should also be noted that not all studies distinguished between engagement and disengagement or attentional shift and there is an ongoing debate whether emotion affects some or all of the aspects of attention (for discussions, see Fox et al., 2001; Mogg, Holmes, Garner, & Bradley, 2008). However, these discussions are beyond the aim of this thesis. In the next section, we will examine selective attention to emotional material in more details.

1.4.2 Selective Attention to Emotional Stimuli

The majority of the literature on emotion and attention interaction comes from studies using threat-related stimuli; and the current consensus generally suggests that highly arousing information, such as snakes, spiders, and emotional faces, are detected faster (e.g., Eastwood et al., 2001; Fox et al., 2000; Frischen, Eastwood, & Smilek, 2008; Juth, Lundqvist, Karlsson, & Öhman, 2005; Öhman, Flykt, et al., 2001; Öhman, Lundqvist, & Esteves, 2001; Williams, Moss, Bradshaw, & Mattingley, 2005). Subsequent studies found that the facilitation effects (as well as emotional impairment effects discussed later) are not limited to threatening information; and arousing stimuli, either negative or positive, produce similar effects on attention when they are equal in their arousal levels (A. K. Anderson, 2005; Bradley, Codispoti, Cuthbert, & Lang, 2001; Most, Smith, Cooter, Levy, & Zald, 2007; Strauss & Allen, 2006). The facilitation of attention by emotion is considered as automatic and pre-attentive (i.e., prior to conscious awareness); therefore arousing stimuli are often more distracting than non-arousing ones when individuals engage in other tasks (e.g., Fox et al., 2002). To examine the effects of emotion on attention, previous research has used several paradigms, such as visual search paradigm, dot-probe task, and attentional blink.

1.4.2.1 Visual search task

In a visual search task (see Figure 1.2A), participants are presented with an array of stimuli and asked to find a target item among distractor items as quickly as possible (for theoritical accounts, see Treisman & Gelade, 1980; Wolfe, 1994, 1998; Wolfe, Cave, & Franzel, 1989). When the target item has a distinguished feature (e.g., different colour) and, thus, is more salient than the other items (i.e., bottom-up saliency), it will have a “pop out” effect among distractors: Participants would detect these salient targets in a short amount of time (typically 100-200 ms). When the array size is increased (i.e., more distractors are included), then the response slows down, so-called "search slopes". These slopes are then examined whether to represent a fast, parallel attentional search or a slow, serial process. Researchers then questioned whether emotional stimuli are processed fast and in parallel or slow and in a serial manner. Öhman, Flykt, et al. (2001) presented threatening (i.e., snakes, spiders) and neutral pictures (i.e., mushrooms, flower) in arrays of different sizes and found that the array size did not affect the speed of detecting the threatening stimuli, suggesting that the search for threatening stimuli was processed in parallel and automatically. Others also found similar results, showing that people attend to emotional stimuli faster than neutral stimuli, – as short as 100 milliseconds (ms) – and that more importantly the search for an emotional stimulus in a crowd is processed in parallel rather than serial, leading to automatic reaction towards such events (Batty, Cave, & Pauli, 2005; Calvo, Avero, & Lundqvist, 2006; Eastwood et al., 2001; Fox et al., 2000; Horstmann & Bauland, 2006).

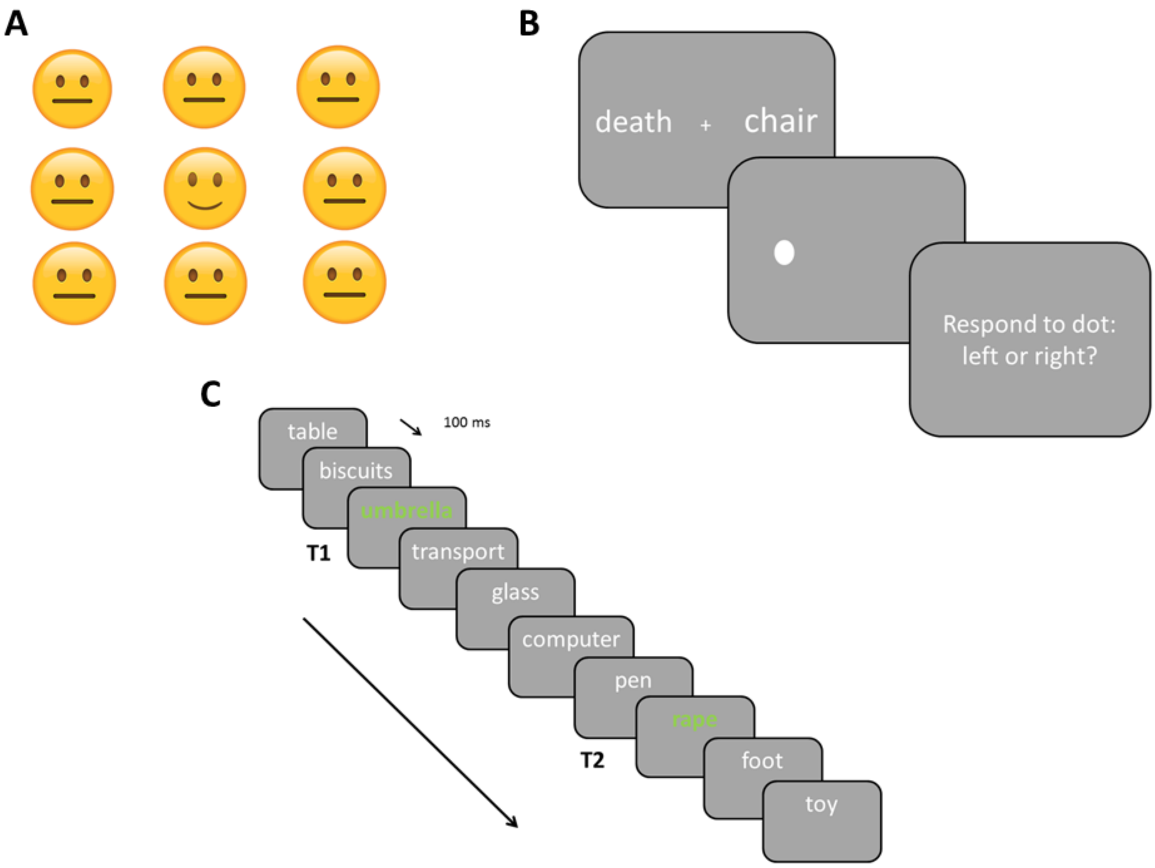

Figure 1.2 *An illustration of a typical visual search (A), dot-probe (B) and attentional blink task (C). In visual search, a smiling face among neutral face will pop-out. In dot-probe, participants will react to faster when the dot appears after the emotional word. In attentional blink, a negative target (i.e., rape) could still be attenuated even if the attentional resources deployed by the first target (i.e., umbrella).*

1.4.2.2 Dot-probe task

In a dot-probe task (i.e., a task which is widely known as attentional cueing paradigms introduced by M. I. Posner (1980)), participants are presented with two stimuli side by side (e.g., one emotional and one neutral word) followed by a dot which can appear in one of the two locations and participants have to respond to the location of the dot (also see Eysenck, 1992). Reaction times to the location of the dot after emotional stimuli compared to the non-emotional counterparts are the indicative of facilitation of attention (see Figure 1.2B). In one of the earlier works on the emotional effects using this paradigm, MacLeod, Mathews, and Tata (1986) found that anxious participants were consistently faster to detect the dot when the dot appeared at the same location as the previous threatening words than when it appeared at the same location as the previous neutral ones, suggesting that these participants preferentially attended to the negative arousing stimuli. Other research using dot-probe paradigm also found attentional biases toward threatening objects, such as snakes and spiders (Lipp & Derakshan, 2005), angry faces (Cooper & Langton, 2006), fearful faces (Holmes, Green, & Vuilleumier, 2005), emotional scenes (Calvo, Nummenmaa, & Hyönä, 2008; Koster et al., 2004b) and an increase selective attention to emotional stimuli after fear-conditioning (Beaver, Mogg, & Bradley, 2005; Koster et al., 2004b; Koster et al., 2007).

Another line of research, which the dot-probe task is useful, concerns the distractibility of the emotional content, which suggests that participants might or might not be faster to react to the emotional stimuli, but they would be slower to disengage from threat-related items. Several studies confirmed impaired disengagement from emotional stimuli in general population (Koster et al., 2004a; Koster et al., 2004b; Koster et al., 2007), and also in people with trait anxiety (Fox et al., 2002; Salemink et al., 2007) as well as in social phobia for social threat words (Amir et al., 1996). These studies suggest that emotion does not always enhance performance to all type of information, but impairs some aspects, which will be discussed later in more details (see Section 1.6).

1.4.2.3 Attentional blink paradigm

Finally, in an attentional blink paradigm (see Figure 1.2C), participants are presented with a rapid stream of visual stimuli: Rapid serials visual presentation (RSVP). Participants' task is to detect targets that are shown in a different colour. If the first target (T1) is presented within few hundred milliseconds before the second target (T2), then T2 is often missed

(Raymond, Shapiro, & Arnell, 1992). "Attentional blink" is therefore the notion that the efficiency to detect T2, which is modulated by the time interval between the two targets (i.e., the number of intervening stimuli between them). Missing T2 is thought to occur since attentional resources are still deployed by T1 and there are not enough sources to process T2 (Olivers & Nieuwenhuis, 2006). In a typical emotional version of this task, when T2 are emotional and T1 are non-emotional, the attentional blink is attenuated such that participants could still perceive emotional T2 (A. K. Anderson, 2005; Keil & Ihssen, 2004; for a review, see Yiend, 2010). Likewise, when T1 are emotional and T2 are neutral, attentional blink for T2 is amplified, because it is harder to disengage from emotional stimuli (Arnell, Killman, & Fijavz, 2007; Most, Chun, Widders, & Zald, 2005; Most et al., 2007). Overall, most studies mentioned above and a considerable amount of others, have demonstrated emotion's facilitation effect on attention, which was attributed to the biological or motivational significance of emotional information.

1.4.3 Brain Mechanisms of Attentional Enhancement of Emotion

The attentional engagement towards emotionally arousing stimuli has been explained by the amygdala in the brain, which is a small, almond-shaped region in the medial temporal lobe that is thought to process emotion (Phelps & LeDoux, 2005; Phelps, Ling, & Carrasco, 2006). The amygdala is widely connected with the sensory areas in the brain (Young, Scannell, Burns, & Blakemore, 1994) and is considered to modulate the visual cortex at multiple stages (Amaral, Behniea, & Kelly 2003). Anatomical studies suggest that there are pathways between amygdala and sensory cortices, which enable the modulations of emotion to facilitate attention and perception (Amaral et al., 2003; Freese & Amaral, 2005, 2006; Hupé et al., 2001; Yukie 2002). Functional brain imaging studies (e.g., Morris, Ohman, & Dolan, 1998) and studies with patients with amygdala damage (e.g., Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004) have further supported a correlation between amygdala and the primary cortex in the enhanced effect of fearful faces and fear-conditioned stimuli.

1.5 Emotion Also Biases Perception

Attention and perception are intertwined which makes it difficult to empirically tease them apart. Thus, it should be noted that some studies in the attention literature mentioned above may be relevant to the emotional effects on perceptual processes (e.g., A. K. Anderson, 2005). For instance, it is possible to interpret the results from studies with the RSVP paradigm, such that attentional resources which are taken up by the item at T1 influences perception of the T2 item rather than attention to the T2 item.

1.5.1 Binocular Rivalry

Previous studies also used paradigms adopted from vision science to examine the effects of emotion on perception. In binocular rivalry, two different images are presented to each eye at the same time; thus, the percept alternates between the two. If one image is more salient than the other, then the salient image dominates perception and the other percept has been suppressed. This rivalry is thought to reflect competition between neurons in the primary cortex (e.g., Blake, 1989) although there is an ongoing debate on the exact underlying mechanisms of this phenomenon (Tong, Meng, & Blake, 2006). Nevertheless, the amount of time the dominant image is perceived then indicates which visual input the brain is selecting for conscious awareness. Using binocular rivalry, emotional faces and scenes and as well as aversively conditioned stimuli have been shown to be predominately perceived compared to neutral stimuli (Alpers & Gerdes, 2007; Alpers & Pauli, 2006; Alpers, Ruhleder, Walz, Mühlberger, & Pauli, 2005; E. Anderson, Siegel, & Feldman Barrett, 2011; Bannerman, Milders, De Gelder, & Sahraie, 2008; Yang, Zald, & Blake, 2007; Yoon, Hong, Joorman, & Kang, 2009). These studies suggest that emotional stimuli have preferential access to perception and consciousness, especially when the attentional resources are limited.

1.5.2 Gabor Filters

Gabor patches have also been useful tools to examine perception. In image processing, Gabor filter, a sinusoidal wave convolved with a Gaussian function, is a linear filter used for edge detection. Its' name is given after Dennis Gabor who won the Nobel Prize in Physics in 1971 (Ash, 1979). Image analysis with Gabor filters is thought to be similar to perception in the human visual system and simple cells in the primary visual cortex of mammalian brains can be modelled by Gabor functions (Dougman, 1980, 1985; Jones & Palmer, 1987; Marčelja, 1980). Unlike other studies using faces, scenes, objects, which needs higher-order representations in the cortical brain regions typically developed in more complex organisms like primates; Gabor patches are low-level stimuli that do not necessarily require higher-order mechanisms in the brain. They are special in the sense that it is possible to keep constant all other features (e.g., size, colour, spatial frequency, temporal frequency), alternating only one at a time (e.g., contrast); thus, allowing high experimental control between conditions.

Phelps et al. (2006) used an attentional cueing paradigm in which observers were presented with a fearful or neutral face cue followed by a Gabor patch with different contrasts (i.e., varying the visibility of them). Observers then had to indicate the orientation of the Gabor patch: Leftward or rightward. The results indicate that observers need less contrast to identify the orientation of the target when a fearful face compared to neutral face precedes it, suggesting the facilitation effect of emotion on low-level perception. In the same study, they further manipulated participants' attention using a peripheral cue (i.e., one of the four quadrants) and a distributed cue (i.e., the same cue on all four quadrants) to examine whether attention and emotional cues interacted with each other. If attention to emotional cues affects perception, then participants should benefit from the peripheral cue, but not the distributed cues. As expected, attention increased the perceptual benefit of emotion when cued peripherally. Given that orientation judgment in such paradigm is thought to reflect the basic functioning of the early visual cortex, these findings suggest that the mechanism of emotion's facilitation effect on perception and interaction with attention might be considered as the modulation of the early visual areas by the emotional brain regions (for a review, see Stanley, Ferneyhough, & Phelps, 2009).

1.6 Emotion Does Not Always Enhance Performance

Although previous studies have widely shown that emotional stimuli enhanced attention and perception, as well as memory (see Section 1.7), emotion does not always enhance of all aspects of cognition. Rather, this facilitation effect comes at a cost to other information nearby in space and time (e.g., Carrasco, 2006; Mather et al., 2006; Pestilli & Carrasco, 2005; Strange, Hurlemann, & Dolan, 2003). As briefly mentioned earlier, some studies using attentional blink paradigm found rather an impairing effect of emotion (e.g., Most et al., 2005). Unlike other studies which presented emotional stimuli at T2 and found an enhancement effect (e.g., A. K. Anderson & Phelps, 2001); Most et al. (2005) used emotional scenes (e.g., a crime scene) as distractors in the stream of neutral scenes (i.e., images between neutral T1 and neutral T2) and found that emotional distractors impaired attention to detect the neutral target (e.g., a landscape/architectural photo rotated 90º to the left or right) at the short interval between the two time points (i.e., 200 ms, but not in 800 ms). Similarly, research using cueing paradigm suggests that once attention is shifted to the location of an emotional stimulus, it is more difficult to disengage attention from that location in order to detect the target elsewhere (e.g., Koster et al., 2004b). For instance, Fox et al. (2001)

presented negative, positive, and neutral words followed by a dot. In valid trials, where the target appears at the same location as the words, there was no valence difference in reaction times, suggesting emotion does not result in faster attention shifts to the target location. In contrast, reaction times slowed down when the negative words, compared to neutral and positive words, appeared at a different location than the target, suggesting an impaired disengagement from the negative information.

1.7 The Interaction between Emotion and Memory

Memory begins with encoding processes where a stimulus is first encountered; therefore the factors that affects attention and perception processes will also affect memory encoding and later retrieval (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996). Thus, emotion's enhancing and impairing effects are extensively studied in memory research. For instance, a witness to a crime tends to remember a weapon a perpetrator holds, but forgets the perpetrator's face (Steblay, 1992). Similarly, inherent features of emotionally arousing stimuli (e.g., the colour of the gun) are typically remembered for a long time, whereas memory for between-item associations for arousing stimuli (e.g., bindings between the gun and the perpetrator to identify who is holding the weapon) is impaired (Mather, 2007). Besides, emotional arousal impairs memory for the information that is not relevant to the goals of the observer (Levine & Edelstein, 2009). Encountering emotionally arousing events also induces retrograde amnesia and impairs memory for an event that has occurred before the arousing event (Loftus & Burns, 1982). Furthermore, although emotionally salient aspects are remembered well, memory for nearby neutral information is often impaired (Kensinger, Garoff-Eaton, & Schacter, 2007; Strange et al., 2003). To complicate the story further, exposure to emotionally arousing information sometimes enhances, rather than impairs, memory for nearby neutral information (A. K. Anderson, Wais, & Gabrieli, 2006; Kensinger et al., 2007). The next section provides a review on previous studies and main theoretical approaches that shed lights to the question of why and how emotion has different effects on cognition.

1.8 Theories of Emotion-Cognition Interaction

Historically, emotion has been considered as irrational instances that damage higher order reasoning, and therefore thoughts were superior to emotions in a way of common sense. Philosophical accounts (e.g., De Sousa, 1987) and early psychological theories (Dewey, 1985) proposed that emotion and cognition work in opposition in which emotions have the potential to impair logical judgments and distort the reality. However, contemporary research demolished this idea establishing that emotions have highly adaptive value for the functioning of an organism (Ekman & Davidson, 1994; Frijda, 2016; Öhman, Flykt, et al., 2001).

In his seminal work, Damasio (1994) proposes that emotion-related signals trigger changes in physiological state of a person (e.g., heart rate, blood pressure) that serve as somatic markers which indicate the individual's emotional state. These physiological and experiential information guides individual's responses to the environment. Damasio (1994) also challenged the idea that emotions and cognitive functions are processed separately in the brain. Structures that are thought to be responsible for emotions, which are part of the limbic system, such as the amygdala or the hippocampus, have been shown to be actively involved in cognitive processes, such as memory. Similarly, structures that are thought to be responsible for cognitive functions, such as the prefrontal cortex, have been shown to play a predominant role in processing emotional information. For instance, patients with a damage to the frontal brain regions had impaired learning and decision making alongside with problems processing emotional stimuli despite having intact attention and memory capacities

(Pessoa, 2008). Thus, there has been growing appreciation that emotions have a functional role in cognitive capacities of an individual (Bechara, Tranel, & Damasio, 2000).

Therefore, recent accounts urged the need to move beyond simple dichotomy of “cognition” versus “emotion” (Compton, 2003). For years, emotion is considered as “warm” and cognition is considered as “cold” and they were studied in isolation. However, as mentioned above emotion is not distinct from other processes, such as attention or motivation. Rather, selective attention is regulated by emotional significance (Lang et al., 1997). Emotion is also highly relevant to one’s goal (C. A. Smith & Lazarus, 1990). Therefore, emotionally significant stimuli may capture attention because people would pay attention to what is important for their goals, suggesting motivational significance of emotional stimuli. Emotions, thus, appear to work in coordination with cognitive processing, modulating thoughts, actions, and behaviours of an individual. Damasio (1994) further suggests “when emotion is entirely left out of the reasoning picture … reason turns out to be even more flawed”.

As discussed above, emotions are intertwined with memory, attention, motivation and other cognitive processes. The question, therefore, is how emotion and cognition interacts with each other. Several attempts have been made to explain the complex effects of emotion on cognition. Some of the earliest models considered emotional arousal as the key dimension. In the early 1900s, Yerkes and Dodson (1908) proposed that performance increases with physiological or mental arousal up to the point from which arousal rather decreases performance (i.e., an inverted U-shaped curve). The Yerkes-Dodson law was based on a study requiring mice to discriminate between two boxes (black and white) in relation to the levels of electrical shocks administered when the animal’s choice was incorrect. However, later studies emphasized that the U-shaped curve of arousal effects on performance is present only for complex tasks, and only when the dependent variable is defined as the number of hits rather than the number of errors (Bäumler & Lienert, 1993; for a theoritical discussion, see Hanoch & Vitouch, 2004). Despite these discussions, the U-shaped curve performance has been observed in both human and animal studies investigating the effects of stress (e.g., stress hormone called glucocorticoids) on memory; such that moderate stress during learning enhances subsequent memory whereas high or low level stress either impairs (e.g., Lupien et al., 1997) or has no effect on memory (e.g., Roozendaal, Williams, & McGaugh, 1999). Nevertheless, current views agree that arousal and cognition have more complex interactions than initially claimed.

1.8.1 Attention Narrowing Hypothesis

Easterbrook (1959) explains the mechanisms underlying the relationship between arousal and performance in his cue-utilization theory, which assumes increased arousal leads to a restriction of observed cues, so called narrowing of attention. At a medium level of arousal where performance is optimal, individuals can attend to a larger set of cues whereas higher levels of arousal negatively affect one’s ability to pay attention to or process all of these cues. Since attentional capacity is limited, attention given to the arousing stimulus decreases the amount of attentional resources available to process other nearby information. Therefore, an allocation of attention results in small number of cues in favour of the centre of an event and lower performance levels for the peripheral details.

Supporting attentional narrowing hypothesis, Steblay (1992) pointed to the weapon-focus effect where a witness to a crime remembers the weapon (i.e., central event), but forgets other peripheral details of the scene. Emotional arousal is thought to activate specific brain regions, such as amygdala and the hippocampus, which in turn, leads to narrowed attention and an enhancement of memory for the central aspect of an event (Cahill &

McGaugh, 1995; Hamann, 2001). Narrowing attention, thus, helps individuals to focus on the current goals by eliminating irrelevant information (e.g., LaBar & Cabeza, 2006). Attention narrowing hypothesis, therefore, predicts a trade-off between memory for the central information and peripheral details.

1.8.2 Memory Narrowing

Research has mostly agreed that arousal increases attention to a central event at the cost of other nearby events. However, better memory for the central features than peripheral details under emotion is not only driven by attention during encoding. Several studies have shown that arousal not only modulates attention but also modulates consolidation of emotional information in long-term memory through activation of the amygdala (Cahill, Prins, Weber, & McGaugh, 1994; Dolcos, Iordan, & Dolcos, 2011). Drug infusion studies also revealed that infusing norepinephrine into the basolateral amygdala after encoding enhances long-term memory for the emotional events whereas lesions to the same region after encoding reduces the emotional enhancement (McGaugh, 2004, 2006).

Building on that, early research suggests that emotional arousal enhances memory for the central details at the cost of peripheral details (Burke, Heuer, & Reisberg, 1992; Christianson, Loftus, Hoffman, & Loftus, 1991). In a series of experiments (Burke et al., 1992; Heuer & Reisberg, 1990), participants were presented with two identical stories about a mother and a son visiting the father's workplace (i.e., a gist; the general layout of a scene) using thematic slides. One detail was different to manipulate arousal: the father's workplace is either a hospital (arousing condition) or a garage (neutral condition). For the arousal group, the father is a surgeon who is operating on a victim of a car accident. Both groups then took the memory test. Results showed an increased memory for the plot-relevant gist (e.g., they are going to visit the father) and the central information (e.g., mother was leaning against the wall in the centre of the image) in the arousal condition whereas the pattern was reversed for the background details (e.g., a sink at the background of the father's surgery room) (Burke et al., 1992).

Christianson and Loftus (1991) criticized that previous studies did not equate the details tested in arousing and non-arousing events, which may have led the details of the arousing version be more salient or unique and, therefore, manipulated the to-be-remembered information: a woman injured near a bicycle (arousing) and a woman riding a bicycle (neutral). The results were similar to the findings explained above, supporting the memory narrowing hypothesis for emotional events: Participants were better at remembering the central details (e.g., the colour of the woman's clothing), but not the peripheral details (e.g., the colour of the car driving in the background) in the arousing condition compared to the neutral condition. However, later studies found memory enhancement effect of emotion for both central and peripheral details (Cahill & McGaugh, 1995; Heuer & Reisberg, 1990; Laney, Campbell, Heuer, & Reisberg, 2004; Libkuman, Nichols-Whitehead, Griffith, & Thomas, 1999), memory impairment effect of emotion for both central and peripheral details (Morgan et al., 2004) and as well memory enhancement for peripheral details (Talarico, 2009).

1.8.3 Memory for the Gist vs. Details

One major issue in these early studies on the effects of arousal on the central vs. peripheral details was concerned with the definition of "centre". Christianson and Loftus (1991) defined "central" details as to the participants' spatio-visual attention rather than the relevance to the plot, thus, anything in the background of the scene was considered as peripheral. In their study explained above, the colour of the woman's coat riding a bike was considered as the central information, whereas a car passing by at the background was non-central. On the other hand, Burke et al. (1992) argued that this definition obscured the distinction between memory for the gist and memory for the details of appearance and manner, and suggested that we should define central details as a) details pertaining to the gist and b) the materials central to the visual attention. Similarly, peripheral details were any information that was irrelevant to the plot or background details of the visual field of the participants (for a review, see Reisberg & Heuer, 2004). More importantly, emotion's enhancement effect on memory for an event's both gist and centre has been found in later studies, including autobiographic memories (Berntsen, 2002; Bluck & Li, 2001; Peterson & Whalen, 2001), eyewitness memory (Bornstein, Liebel, & Scarberry, 1998; Steblay, 1992), and episodic memory (Kensinger & Corkin, 2003; MacKay et al., 2004). However, there have been fewer consensuses whether emotion enhances or impairs the peripheral details of an event. For instance, contrary to the early studies, research showed that emotion does not always impair the peripheral details; rather, memory for contextual and peripheral information of emotional stimuli can be also enhanced (D'Argembeau et al., 2003; Kensinger & Corkin, 2003; MacKay et al., 2004).

Reisberg and Heuer (2004) argued that early laboratory research used emotional visual stimulus (i.e., visually induced) which did not represent the real life situations where we become emotional when the events are relevant to our own lives, goals, values, and people that we care about (i.e., thematically induced). When induced thematically arousal without containing a specific visual target (i.e., a narrative depicting an assault), emotion increased memory for both central and non-central information (Laney et al., 2004). They argued that emotional memory narrowing might not occur without the presence of "attention magnet", which is an unexpected or shocking salient sensory stimulus, and concluded that memory narrowing may be a byproduct of the type of surprising sensory stimulus, such as a death body on the ground. Researchers also criticized the weapon focus effect in the eye witness phenomenon, suggesting that the weapon might draw one's attention simply because it is more important or interesting aspect of the visual input (Kramer, Buckout, & Eugenio, 1990; Loftus, Loftus, & Messo, 1987) or the weapon might be considered as unusual rather than threatening (Pickel, 1998).

The pattern of results explained above led researchers to propose that some aspects of an event are better remembered because of its emotional relevance (i.e., rather than the visual saliency), so called memory trade-off (Buchanan & Adolphs, 2002; Reisberg & Heuer, 2004). In a series of experiments, Adolphs and colleagues showed participants emotional and neutral scenes and assessed their gist memory by asking them to recognise or recall the verbal description of the scene: e.g., a dead body had been found in the forest (Adolphs, Denburg, & Tranel, 2001; Adolphs, Tranel, & Buchanan, 2005; Denburg, Buchanan, Tranel, & Adolphs, 2003). Results revealed that emotion has enhanced gist memory but impaired visual details of the images. In contrast, Kensinger, Garoff-Eaton, and Schacter (2006) argued that these studies did not distinguished emotional aspect of the stimuli which are attached to the central stimuli versus peripheral details which consisted non-emotional elements. Therefore, it was not clear from these conflicting results whether memory trade-off occurred for the gist and the details of the emotional aspect of a scene and/or for the gist and the details of the information peripheral to the emotional aspect. They then focused on the visual details of the emotional objects and found no evidence of gist/detail trade-off when they presented the object in isolation; such that visual details as well as the gist of an emotional object were more likely to be remembered than of a neutral object.

Kensinger et al. (2007) further addressed this issue in a series of experiments and found that participants were more likely to remember both the gist and the specific details of negative objects than neutral objects whereas they were more likely to forget the visual details of backgrounds shown with negative objects than with neutral objects; suggesting that the gist/detail trade-off interacts with the central/detail trade-off. More importantly, they showed that emotion enhances or impairs memory for the gist and the details depending on how attention was directed or deployed (e.g., asking participants to focus on the specific details or verbal descriptions), suggesting a need for a better explanation than “narrowing” hypothesis. Turning back to the weapon focus effect, for instance, attention or memory narrowing may occur due to a number of factors: physiological arousal, negative affect, the discrete emotion of fear, or the goal to protect oneself from harm (for a review, see R. L. Kaplan, Van Damme, & Levine, 2012). However, most studies did not differentiate these factors in their experimental manipulations (but see Ritchie, Skowronski, Walker, & Wood, 2006).

1.8.4 Priority-binding Hypothesis

An alternative to the accounts of attention narrowing is priority-binding hypothesis (Hadley & MacKay, 2006; MacKay, Hadley, & Schwartz, 2005). This theory suggests that arousing stimuli elicit emotional reactions that give priority to the associations between arousing feature of the stimuli and the salient aspects of the context that are linked to the arousing stimuli. This results in binding emotional central and peripheral information (i.e., prioritised) better than the non-emotional central and peripheral counterparts. This theory can, therefore, explain why in some studies peripheral information was enhanced alongside with central ones (Heuer & Reisberg, 1990; Libkuman et al., 1999).

Studies using emotional words have conceptualised peripheral information as a) spatial location of the word, b) the ink colour of the word, or c) another neutral word presented at the same time with negative word. These studies found enhanced peripheral information when the central word provoked an emotional response (D'Argembeau & Van der Linden, 2004; Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003; MacKay & Ahmetzanov, 2005; MacKay et al., 2004). Besides, items, as well as their associations with contextual information, are both enhanced by emotion (Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003; Ochsner, 2000). Furthermore, when explicitly instructed to remember the font colour of negative and neutral words, memory for the font colour of negative words was better than memory for the colour of the neutral words (Doerksen & Shimamura, 2001). More importantly, participants were better able to tell which colour was used in a specific emotional word than neutral counterparts, suggesting a strong association between the source (i.e., colour) and the item itself (but see Jurica & Shimamura, 1999).

Overall, these results supported the priority-binding hypothesis, suggesting that associations between the source memory (i.e., central word) and the other peripheral characteristics were prioritised by emotional content. However, colour used in such studies might be intrinsic to the corresponding word and cannot account for the contextual details of a real-world scene. Furthermore, the peripheral details in these studies were different than mentioned above and the results are later interpreted as a general memory enhancement of emotion (Guillet & Arndt, 2009; Kensinger et al., 2007). Besides, others found no difference in memory for the font colour among positive, negative, and neutral words when tested in a consecutive day with a surprise memory task (Dougal, Phelps, & Davachi, 2007), suggesting different effects on memory retrieval after a longer interval (see Section 1.9).

1.8.5 Object-based Binding Theory

As described above, arousal often enhances binding of features within the item (Mather, 2007) and memory of intrinsic features of an object (Kensinger, 2009) at the expense of the associations between items or contextual details. Mather (2007) suggests that the contradictory findings discussed above can be understood by distinguishing between objects that induce arousal and other objects in the same environment. In this object-binding theory, arousal enhances the elements of within-object binding whereas this enhancement effect would be absent in the between-objects binding. The features inherent in arousing stimuli, such as colour or spatial location, can be considered as within-object binding and can be better memorised with arousal. This account can explain some of the conflicting results in the literature mentioned above. Guillet and Arndt (2009) asked participants to learn word pairs and found that associations between central and peripheral words were enhanced by arousal when the two words paired or occurred in the same sentences (i.e., within-object binding).

Mather and Nesmith (2008) presented arousing and non-arousing scene pictures in a modified dot-probe task and found that participants' memory was better for the location of arousing stimuli (i.e., within-item binding) compared to non-arousing pictures. More importantly, the binding of the location to the arousing item did not affect the accuracy of the nearby neutral item (i.e., between-object binding). In a follow-up experiment, they found that memory binding of contextual information is impaired by nearby arousing item (Mather, Gorlick, & Nesmith, 2009). They presented an arousing picture (i.e., a man holding a gun) along with a "bystander" picture, which was equally detailed and perceptually as dominant as the arousing image and found that arousing pictures did not affect the memory for the bystander picture nor the picture-location binding for bystanders (Mather et al., 2009; Experiment 1 & 2). However, seeing an arousing picture in the foreground impaired memory recognition of a pattern shown in the background (Mather et al., 2009; Experiment 3). These results suggest that emotional arousal has different effects on between- vs. within-object memory.

1.8.6 Brain Models of the Emotion-Cognition Interaction

There are a number of theories on the brain mechanisms of emotion and cognition interactions. Since mentioning all of them would exceed the scope of this thesis, I only focused the most influential models in the field. In the following sub-sections, I have briefly reviewed a few of them with their controversies in order to grasp a more comprehensive view of the picture on how emotional arousal affects attention, memory, and perception.

1.8.6.1 Multiple attention gain control (MAGIC) and multiple wave models

The enhanced attention to emotional stimuli is attributed to a specialized pathway in the brain to evaluate emotional salience (Tamietto & de Gelder, 2010). In their MAGIC model, Pourtois, Schettino, and Vuilleumier (2013) propose that amygdala amplifies neural responses to emotional stimuli via sensory pathways and this perceptual modulation is independent of other attentional processes. In contrast, Pessoa and Adolphs (2010) disagree with this modular approach to emotion-perception interaction. On their multiple waves model, multiple brain regions are involved to evaluate emotionally and motivationally significant stimuli, including orbitofrontal cortex, anterior insula, and anterior cingulate cortex alongside amygdala. Here, amygdala helps to prioritise emotional stimuli together with multiple regions; and thus, emotional enhancement effects are not independent from other perceptual and attentional systems.

1.8.6.2 Biased attention via norepinephrine model

Markovic, Anderson, and Todd (2014) further proposed a neurochemical mechanism to explain enhanced biased competition towards emotional stimuli: Norepinephrine released from locus coeruleus. In this model, a pathway called ‘anterior affective system’, which includes the amygdala and the orbitofrontal cortex, based on the recent history of reward and punishment, detects emotional salience. In turn, the amygdala’s recruitment of the norepinephrine released from locus coeruleus helps an additional specialized pathway that further biases attention and memory in favour of the emotionally relevant information.

1.8.6.3 Amygdala modulation hypothesis

As I will discuss in the next section, most studies and theories explained above focused on the memory encoding, rather than the consolidation. The models centred on the amygdala could, however, explain how emotion also affects memory consolidation: The amygdala enhances processes in the hippocampus and other memory-related brain regions in the medial temporal lobes, which results in enhanced memory for emotional events compared to neutral events (e.g., McGaugh, 2004). A number of studies confirmed that the activity in the amygdala and its' functional connectivity with the medial temporal lobe during memory encoding predicts later memory for emotional items but not memory for neutral items (Dolcos, LaBar, & Cabeza, 2004; Richardson, Strange, & Dolan, 2004; Ritchey, Dolcos, & Cabeza, 2008).

This theory has been the focus of various studies, including patients with amygdala damage and drug-infusion studies in rodents as well as in humans. For instance, norepinephrine released in the amygdala during arousal (McIntyre, Hatfield, & McGaugh, 2002) and norepinephrine injected into basolateral amygdala after training (Hatfield & McGaugh, 1999) in rodents and as well as pharmacological manipulations in humans that increase norepinephrine levels (Chamberlain, Muller, Blackwell, Robbins, & Sahakian, 2006) enhanced memory for emotionally arousing events. Amygdala modulation hypothesis can also explain impairing effects of arousal via norepinephrine mechanisms: Enhanced amygdala activity during encoding emotional stimuli is reduced by the administration of the β-adrenergic antagonist, propranolol (Strange & Dolan, 2004). These findings suggest that norepinephrine facilitates the amygdala-mediated enhancement of emotional information.

This interaction can also impair memory for the nearby neutral information of the emotional event. For instance, people showed worse memory for neutral information shown right before an emotional compared with a neutral "oddball" stimulus (Sakaki, Fryer, & Mather, 2014). However, patients with amygdala damage do not show impaired memory for neutral words preceding emotional oddball words, and moreover, a β-adrenergic antagonist prevents this impairment in healthy people (Strange et al., 2003).

1.9 Arousal Effects on Memory Consolidation and Retrieval

As briefly mentioned in the previous section, most studies explained above focused on the encoding phase of memory formation or short-term retention (i.e., usually within half hour in the same experiment session); and therefore, cannot explain arousal effects on the memory consolidation or post-encoding processes (Mickley Steinmetz & Kensinger, 2013; Riggs, McQuiggan, Farb, Anderson, & Ryan, 2011). After initial encoding, neural representation can either be strengthened and the stimuli are remembered later or weakened and simply forgotten. This is called long term memory consolidation (Frankland & Bontempi, 2005; Takashima et al., 2006) and emotion can influence memory by enhancing this storage processes (McGaugh, 2000).

In a classical experiment, Kleinsmith and Kaplan (1963) presented participants with words along with a single-digit number from 2 to 9 and tested memory after a variety of delays ranging from 20 minutes to 1 week. Participants' skin conductance response was measured as an indication of the response to novel or emotional stimuli. Each word was coded as high- or low-arousing depending on the skin resistance drop while the participant saw that word. Results showed an impaired memory for digits paired with arousing words in an immediate recall, but the same digit memory was enhanced after 45 minutes. This interaction was not observed in other studies that categorised stimuli by group norms rather than participants' skin conductance reactions (e.g., S. Kaplan & Kaplan, 1970; Maltzman, Kantor, & Langdon, 1966). These conflicting results were attributed to the opposing effects of stress and arousal: the impairing effects of prolonged stress on the hippocampus and the enhancing effects of arousal on the amygdala (Metcalfe & Jacobs, 1998; Nadel & Jacobs, 1998).

1.10 Evaluation of the Theories

Research testing the theories reviewed above revealed somewhat puzzling findings on the nature of emotional effects on memory. Confirming memory-narrowing hypothesis, emotional arousal has been shown to enhance memory for the central details at the cost of the peripheral details (Burke et al., 1992; Christianson & Loftus, 1991); but when induced thematically, emotion also enhanced non-central information (Laney et al., 2004). Instead of central versus peripheral details, research then defined the gist versus details for emotional stimuli and found that emotion enhances memory for the gist at the cost of the peripheral details (Adolphs et al., 2001). However, memory performance was not impaired, rather enhanced the specific details of emotional objects (Kensinger et al., 2006) and whether emotion enhances or impairs memory for the gist was a result of directing attention to certain aspects during encoding (Kensinger et al., 2007). Rather than the gist versus details, studies then focused on the memory-binding and found that arousal enhances intrinsic features of an object, but does not enhance between-item associations (Kensinger, 2009; Mather, 2007). However, neutral words paired with emotional words were also remembered better (Guillet & Arndt, 2009), suggesting between-item associations were also enhanced. Other research suggests that arousal enhances memory consolidation of emotional events: Arousal induced right after memory encoding has been found to enhance emotional stimuli more than neutral stimuli (Cahill, Gorski, & Le, 2003). However, post-encoding arousal can also enhance memory for the neutral information when tested after a longer time (A. K. Anderson et al., 2006; M. Knight & Mather, 2009).

If an emotional stimulus recruits a separate brain system than neutral stimuli as in the MAGIC model (Pourtois et al., 2013), then it is not clear how emotional arousal could have both enhancing and impairing effects on neutral stimuli. Similarly, multiple waves approach to emotion-cognition interactions (Pessoa & Adolphs, 2010) fails to explain how arousal selectively affects perception as it focuses only on the enhanced perception of arousing stimuli. BANE focuses on how emotionally salient stimuli overthrow less salient stimuli (Markovic et al., 2014), but does not address how arousal induced by these stimuli sometimes enhances and sometimes impairs processing of nearby neutral information. The amygdala-modulation hypothesis is a good candidate to explain both enhancement and impairment effects of arousal in terms of a trade-off effect in which the amygdala focuses resources on to emotional stimuli, leaving less available resources to process and consolidate the neutral stimuli (McGaugh, 2004). However, this explanation fails to explain how norepinephrine-amygdala interactions also enhance memory for non-arousing information (Barsegyan, McGaugh, & Roozendaal, 2014; Roozendaal, Castello, Vedana, Barsegyan, & McGaugh, 2008). Overall, each theory has some caveat and cannot account for both enhancing and impairing effects of emotion. To address these conflicting results, an alternative idea is discussed below: Arousal-Biased Competition Theory (Mather & Sutherland, 2011).

1.11 Arousal-Biased Competition Theory

As we have seen, past research provides substantial information to explain how arousal affects cognition; however, each of these hypotheses is subject to contradictory findings in the literature. Mather and Sutherland (2011) proposed a new theory to explain these puzzling findings. The Arousal Biased Competition (ABC) Theory suggests that arousal (whether elicited by internal thoughts or external stimuli) modulates the strength of competing mental representations, enhancing memory for the information (e.g., item, event) that wins the contest for selective attention. Other stimuli that lose the competition will get even less representation under arousal. This competition for representations begins during perception and carries out into the memory consolidation. Arousal amplifies the effects of competition, improving perception of high priority information and weakening perception of low priority information. During perception, arousal biases competition in favour of the prioritised stimuli, which is either perceptually conspicuous or goal-relevant. Arousal then enhances memory for highly prioritised stimuli (conspicuous or goal-relevant) and impairs less prioritised stimuli (unimportant or goal-irrelevant). In the next section, I explained how priority was determined according to the ABC theory.

A further theory by the same research group, Mather and colleagues explained the brain mechanisms of opposing effects of arousal, focusing on the interaction between norepinephrine and glutamate (Mather, Clewett, Sakaki, & Harley, 2016). The details of this model would exceed the purpose of this thesis; however, it should be briefly mentioned to be able to build upon the brain models explained in previous sections. In this model called Glutamate Amplifies Norepinephrine Effects (GANE), they proposed that norepinephrine released from the locus coeruleus under arousal biases perception and memory in favour of high priority representations at the expense of lower priority representations. When locus coeruleus is active under arousal, increased levels of glutamate at the brain regions (i.e., cortical regions such as parahippocampal place area for scenes) of prioritised representations enhances local norepinephrine release. Glutamate is the brain's primary excitatory neurotransmitter and signals priority: Neurons that process high-priority information release higher glutamate than those that process low-priority information. Then, glutamate and norepinephrine release are mutually amplifying activation of prioritised representations whereas norepinephrine suppression occurs in the regions of weaker representations. Overall, perception and memory selectivity are increased by these noradrenergic mechanisms.

1.11.1 What Does Determine Priority?

The ABC theory is built upon Biased Competition Models of attention which suggest that stimuli compete for representations in sensory cortex and a stimulus that is salient or relevant to one's goal initially attracts attention (Buehlmann & Deco, 2008; Desimone & Duncan, 1995; Duncan, 2006; Kastner & Ungerleider, 2000, 2001). As discussed earlier, selective attention is pivotal in cognition (for a recent review, Knudsen, 2018). The selective information and the speed of processing in perception are limited since not all sensory inputs can be processed in parallel and reach consciousness (Marois & Ivanoff, 2005; M. I. Posner, 1980; Pourtois et al., 2013). Therefore, our brains have to deal appropriately with continuous flow of information from various events; and attention and emotion biases and modulates perceptual processes for the most significant or important piece of information (for a recent review, see Pourtois et al., 2013). As described below, bottom-up saliency (e.g., contrast) or endogenous factors, and top-down processes (e.g., goal-relevance and expectations) or exogenous factors can determine priority (for reviews, Bisley & Mirpour, 2019; Fecteau & Munoz, 2006; Hutchinson & Turk-Browne, 2012; Itti & Koch, 2000). Furthermore, recent theoretical accounts (Awh, Belopolsky, & Theeuwes, 2012; Hutchinson & Turk-Browne, 2012; Theeuwes, 2019) suggest a shift from bottom-up and top-down dichotomy: Attention can sometimes neither be bottom-up or top-down, but rather can be driven by prior experiences (see Section 1.11.5). In the next section, I reviewed which factors determine priority and the evidence of the ABC theory on each of these factors. Besides, other elements, such as surprise, emotional and social relevance, reflecting interactions of sensory and cognitive signals, are also discussed below.

1.11.2 Bottom-up Saliency

The basic assumption for bottom-up saliency is that pre-attentive processing is driven by the bottom-up features of a stimulus (such as colour, orientation), prior to the allocation of attention (Burnham, 2007; Corbetta & Shulman, 2002; Theeuwes, 2010). After the initial pre-attentive analysis of a scene, one object is selected on the basis of local feature contrast obtained from its relationship with respect to its surroundings (e.g., Egeth & Yantis, 1997). Bottom-up attention biases the observer towards selecting stimuli that are salient, which stands out from its' environment (Itti & Koch, 2001). This selection process is often investigated with visual search paradigm reviewed earlier. As a reminder, in the visual search, the task is to find a predefined target among a crowd and the relationship between search time and the number of distractors (i.e., search slope) reflects the efficiency of this search (Wolfe, 1998). Selective attention with the visual search paradigm has been subject to a variety of experimental studies (e.g., Eastwood et al., 2001; Fox et al., 2000; Kristjánsson & Campana, 2010; Öhman, Flykt, et al., 2001; Triesman & Souther, 1985) and computational models (e.g., Cave & Wolfe, 1990; Phaf, Van der Heijden, & Hudson, 1990). Several attempts have been made to explain why some stimuli among others attract attention and are automatically detected while others are less conspicuous (e.g., Engel, 1971; Nothdurft, 1992; Triesman & Gormican, 1988; Yantis & Jonides, 1984).

Nothdurft (1991, 1992) suggests that targets in an array will "pop out" when they differ from their surrounds, irrespective of the types of the difference: colour, motion, orientation or luminance. For instance, a vertical line among horizontal line would be salient and easily found whereas a vertical line among other vertical lines is not salient and would require much effort to be detected (Nothdurft, 2000). Using this fundamental notion in determining what draws attention, computational models predict where eye fixations will be on an image by analysing the contrast difference between the centre and the surround at each location in a given image, so-called saliency map models (Berg, Boehnke, Marino, Munoz, & Itti, 2009; Itti & Koch, 2000, 2001; Z. Li, 2002). The saliency map is a retinotopic map which the strength of its' activation is an indicator of how much a particular region should attract attention based solely on bottom-up features in a given image (Walther & Koch, 2007). In saliency maps, the centre-surround contrast is computed for a variety of features, such as colour, orientation, motion at different spatial scales and turned into a global saliency map. The more a stimulus differs from those in its surround (e.g., a tilted line by 45^{o} among 80^{o} tilted lines) the stronger its salience signal. A winner-take-all mechanism then selects that location on the saliency map for allocation of focal attention, which shows the highest activation level in that image.

In these models, a centre-surround contrast mimics the features of local cortical inhibition. Itti and Koch (2000) suggest that incoming information is first assessed by early visual neurons in order to represent the perceptual contrast for a variety of basic visual characteristics at each location. Within each of these feature maps, locations compete for activation through a competition of centre-surround process in which excitement at a specific location leads to further excitement at that location while suppressing its surrounding areas. When the competition contrast is high between centre and surround, then the activation in the centre increases whereas the activation in the surround is inhibited.

The ABC theory predicts that arousal will amplify the effects of contrast by enhancing the activation of the highest contrast and inhibiting the surrounding context (Mather & Sutherland, 2011). This prediction has been directly tested by T. H. Lee, Itti, and Mather (2012) with a visual search paradigm where the target either was salient (a tilted line by 55^{o} among 80^{o} distractors) or non-salient (a tilted line by 55^{o} among 50^{o} distractors). Participants' arousal was manipulated using negative arousing images vs. neutral images during the learning phase, which was followed by a test phase where participants' memory for the target tilted line was tested. Results showed that arousal enhanced memory performance for the target line in the salient condition but impaired it in the non-salient condition, suggesting that arousal enhanced perceptual learning of salient stimuli while impairing perceptual learning of non-salient stimuli.

Sutherland and Mather (2012) also tested the ABC theory's predictions that arousal enhances the perception of the high contrast stimuli (i.e., salient/prioritised) and impairs the perception of low contrast stimuli (i.e., less salient/less prioritised) in a short-term memory paradigm. Arousal was manipulated using sounds briefly presented before a circular array of eight letters. Three of the letters were presented in high contrast dark grey whereas the other five letters were in lower contrast grey. Participants were then asked to report which letters they saw. Participants were more likely to remember high contrast letters than the low contrast letters as expected. More interestingly, hearing an arousing sound prior to the stimuli increased reporting of the high contrast letters and decreased reporting of low contrast letters. Therefore, arousal increased the competition in favour of perceptually salient stimulus while suppressing the representation of the less salient stimulus.

1.11.3 Top-down Goals

Priority is also determined by top-down elements such as goals of an observer. Stimuli that are relevant to one's goal obtain priority over irrelevant stimuli. As we have seen above, bottom-up attention is derived only from low-level image properties, typically using contrast feature. Therefore, this mode of attention is fast, automatic, and task-independent whereas top-down attention is driven by a task or a motive (for reviews, see Belopolsky & Theeuwes, 2010; Pessoa, McKenna, Gutierriez, & Ungerleider, 2002; Theeuwes, 2010; Walther & Koch, 2007). Comparing to bottom-up saliency, its deployment is slow and controlled by volition. M. I. Posner (1980) first described a so-called endogenous cueing procedure (i.e., dot-probe task reviewed earlier), which reflects top-down selection. As a reminder, in this paradigm, observers receive a cue showing them the likely location of the upcoming target. Typically, observers are faster and make fewer errors when the target appears at the cued location compared to when it appears at an un-cued location. Responding to an endogenous verbal cue as in the Posner cueing tasks takes about 200 to 300 ms (Müller & Rabbitt, 1989) whereas exogenous shift to peripheral onset (i.e., bottom-up attention) only takes about 100 ms (Nakayama & Mackeben, 1989). The other essential point here is that observers direct their attention to a particular location in space using their own volitional act when cued endogenously. The assumption here is that information from higher cortical areas needs to be sent to earlier areas in order to guide attention in a top-down manner (Theeuwes, 2018).

Studies testing the ABC theory showed that arousal enhances performance in favour of one's goal (T. H. Lee, Greening, & Mather, 2015; T. H. Lee, Sakaki, Cheng, Velasco, & Mather, 2014) For instance, Sakaki, Fryer, et al. (2014) presented participants image sequences including several neutral objects with no frame and one oddball image highlighted by a black frame. These oddball images were sometimes emotionally arousing and sometimes they were neutral. Participants were instructed to focus on either oddball images (e.g., a banana) or objects that came right before the oddball image (e.g., a ball) in order to manipulate the task goal. The results indicated that emotional oddball images enhanced memory for preceding objects when participants focused on that object. In contrast, memory for the preceding object was impaired by emotional oddball object when participants focused on the oddball images. Thus, there is evidence that emotion also affects cognition depending on the relevance to one's goals, which determined by top-down control (e.g., Lang et al., 1997).

1.11.4 Surprise, Emotional and Social Relevance

Other factors that determine priority, such as unexpectedness or surprise, as well as emotional and social relevance were also considered within the interaction between the bottom-up and top-down attention. For instance, novel and unexpected stimuli create a mismatch between perceptual input and prior knowledge is often prioritised (Itti & Baldi, 2009). Emotionally relevant stimuli are also prioritised through bottom-up features (e.g., Calvo et al., 2008) and top-down goals (K. Y. Lee et al., 2010; Vogt, Lozo, Koster, & De Houwer, 2011). Arousal thus increases the competitive advantage of the emotionally relevant stimuli at the cost of lowering the priority of the neutral stimuli (Mather & Sutherland, 2011). Social relevance is another factor that increases priority of an event. For instance, participants fixated more on the eyes of human faces, which is considered to be the underlying mechanism of this type of priority (Birmingham, Bischof, & Kingstone, 2008). Finally, expectations or prior knowledge is another factor that determines priority can also be deployed by bottom-up features and top-down goals (Theeuwes, 2019), which is a current debate outlined below.

1.11.5 Beyond Bottom-up and Top-down Dichotomy

Although the differentiation of bottom-up and top-down attention has been useful in research related to cognition, recent frameworks suggest a shift from this dichotomy (Awh et al., 2012; Hutchinson & Turk-Browne, 2012; Theeuwes, 2019). In everyday tasks, for instance, low-level features of an object might grab attention in a bottom-up fashion where at the same time fulfilling the aim of the observer via top-down control. Wolfe (1994) argued that a target item appeared among homogeneous background with distractor items in a typical visual search experiment did not reflect the complexity of the real-world tasks: a competition between these two types of attention. Recent computational models, thus, integrated bottom-up and top-down cues in order to understand complex processing of visual attention (Itti &

Koch, 2001; Milanese, Wechsler, Gill, Bostl, & Pun, 1994; Tsotsos et al., 2005; Walther & Koch, 2007). For instance, objects are typically embedded in context with other objects that conveys a general layout of a scene, so-called the gist. Objects can contribute to the general context and interpretation of a scene in a bottom-up fashion while the gist can provide a powerful top-down cue, restricting the possibilities for object identity (Walther & Koch, 2007). Therefore, researchers should address the interaction between stimulus saliency and goal-relevance rather than investigating the two separately.

On the other hand, research also suggests that what appeared to be clearly bottom-up attention, such as attentional capture by abrupt onsets (i.e., sudden appearance of an item in the visual field), depend critically on previously overlooked top-down influences (Folk, Remington, & Johnston, 1992). An object suddenly appeared in the visual field draws attention automatically (Yantis & Jonides, 1990). Theeuwes (2018) argued that such paradigm could reveal whether attention is involuntary but does not ensure that bottom-up and top-down attentions are independent. Attention to a target's sudden appearance among other items, which were already in the visual field, leads to faster reaction times; but is not independent from top-down goals since the aim is to find that target. In a better visual search paradigm (i.e., additional singleton), top-down goals should be orthogonal to the capturing features: a salient target and an independent distractor should be presented (Forster & Lavie, 2008, 2011). Attending to a distractor, therefore, would not help, but damages performance because it would never be the target. In an additional singleton task, the task-irrelevant singleton (e.g., colour) is presented and results in longer reaction times compared to no-singleton trials. Thus, this approach can reveal whether attention is involuntary.

Emotion research also questioned the idea of whether fast, automatic reaction to emotionally arousing stimuli solely depends on bottom-up attention as indicated in early research (Öhman, Lundqvist, et al., 2001). In fact, recent studies, for instance, suggest that automatic attention to facial expressions is not present when participants engage in another task-relevant goal (Hahn & Gronlund, 2007; Stein, Zwickel, Ritter, & Kitzmantel, 2009; Van Dillen, Lakens, & van den Bos, 2011). More importantly, recent research revealed that attention to goal-relevant events could also occur automatically (Folk et al., 1992; Vogt, De Houwer, Moors, Van Damme, & Crombez, 2010). Vogt, De Houwer, Crombez, and Van Damme (2013) presented threatening stimuli together with goal-relevant stimuli and found that attention prioritises stimuli based on goal-relevance and it is automatic even in the presence of threat. These results complicated the story by traditional accounts and challenged the dichotomy of fast, automatic bottom-up attention and slow, voluntary top-down goals.

1.11.5.1 Selection history

As mentioned earlier, traditional accounts suggest selective attention is the result of the interaction between the goals of the observer and the saliency of an object (Carrasco, 2011; Corbetta & Shulman, 2002; Egeth & Yantis, 1997; M. I. Posner, 1980; Theeuwes, 2010). This view has recently been challenged by Awh et al. (2012). They point out that attentional selection can sometimes neither be explained by the stimulus-driven or goal-driven manner; rather they propose that "selection history" can guide attention. Stimulus that receives "value" from the past episodes of attentional selection (i.e., through implicit or explicit learning) affects current attention above and beyond the dichotomy of top-down and bottom-up attention. In a recent review, Theeuwes (2018) defined three components of selection history: priming, reward or acquired fear, and statistical learning.

Priming is determined by past history and is thought to be low-level facilitatory effect on perception (for a review, see Kristjánsson & Campana, 2010). Early examples of research on attention showed that previously attended locations were processed faster compared to unattended location (M. I. Posner, 1980). For instance, Wolfe and colleagues compared performance on pure blocks where a single feature represents the target in the entire block with performance on the mixed blocks where the target's features varied from trial to trial; and found that participants were slower in the mixed blocks (Wolfe, Butcher, Lee, & Hyle, 2003). They concluded that top-down information can be focused on only one dimension instead of two, making the top-down signal higher in the pure blocks. Theeuwes (2018), however, points out that a selection history from trial to trial in the pure blocks might prime and enhance the performance involuntarily (i.e., inter-trial priming). Research confirmed that priming effect was robust even when the observer's goal was irrelevant or inconsistent with the primed cues (Brascamp, Pels, & Kristjánsson, 2011; Hillstrom, 2000; Kristjánsson & Campana, 2010; Kristjánsson, Wang, & Nakayama, 2002; Maljkovic & Nakayama, 1994; Theeuwes & Van der Burg, 2011, 2013). Studies that varied the cued feature from trial to trial were able to distinguish bottom-up priming from goal-driven attention and showed that neither reaction times nor perceptual sensitivity benefitted from the advance cue (Theeuwes & Van der Burg, 2007, 2011). This questions the ability to attribute to the top-down influences for a non-spatial feature when the priming effects were eliminated. Therefore, there has been an ongoing debate on whether the priming effects are bottom-up or top-down (Leonard & Egeth, 2008; Theeuwes, Reimann, & Mortier, 2006; Wolfe et al., 2003) and recent frameworks proposes to define a third category to prioritise attention because selection history can be independent from both physical saliency and one's current goals (Awh et al., 2012; Hutchinson & Turk-Browne, 2012; Theeuwes, 2018, 2019).

Reward is another factor that can determine the priority (for reviews, see Pessoa, 2015; P. Watson, Pearson, Wiers, & Le Pelly, 2019). Several studies have shown a selection bias towards previously rewarded items even when the stimulus is non-salient, task irrelevant and no longer predicts reward (B. A. Anderson, Laurent, & Yantis, 2011; Dayan & Balleine, 2002; Della Libera & Chelazzi, 2006, 2009; Ikeda & Hikosaka, 2003; Kristjánsson & Campana, 2010; Navalpakkam, Koch, & Perona, 2009; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009; Raymond & O'Brien, 2009; Seitz & Watanabe, 2009; Shuler & Bear, 2006). A distractor stimulus that is associated with reward captures attention even when observers are instructed to search for the target; suggesting an independent factor from the top-down control (B. A. Anderson et al., 2011). Pessoa and Engelmann (2010), however, suggest that monetary reward provides motivational significance and enhances perception via goal-directed behaviour. On the other hand, Hickey, Chelazzi, and Theeuwes (2010) showed that performance was higher following a high reward when the target colour remained the same across trials whereas the performance impaired following a high reward by the distractor that had the same colour as the last target. This finding suggests that the rewarded colour captured attention independent of whether it indicated a target or a distractor. They further showed that rewarded colour was automatically biased even when the current goals of the observer was inconsistent.

It is also known that a neutral stimulus can acquire priority after it has been linked to fear as in the fear-conditioning paradigm (Maren, 2001). Threat signals also capture the eyes above and beyond the physical salience (Hopkins, Helmstetter, & Hannula, 2016; Nissens, Failing, & Theeuwes, 2017). Schmidt, Belopolsky, and Theeuwes (2015) conditioned participants to presentation of one colour associated with the delivery of electrical stimulation (i.e. fear or threat) and another colour associated with no shock (i.e., safe). Subsequently, participants responded slower to a target presented with a distractor coupled with the threat-colour than the safe-colour. Similar findings have been shown towards electric shock (e.g., Mulckhuyse, Crombez, & Van der Stigchel, 2013) as well as to loss of money (e.g., Engelmann, Damaraju, Padmala, & Pessoa, 2009) and aversive noise (e.g., Koster et al., 2005). These results are attributable to the motivational significance of the stimuli based on past history.

Contextual cues in the environment can also bias visual attention towards invariant properties of the visual environment (Chun & Jiang, 1998). Studies focused on statistical regularities showed that targets presented in high probability locations are detected faster than low probability locations (Chun & Jiang, 1999; Geng & Behrmann, 2005; Jiang, Swallow, Rosenbaum, & Herzig, 2013). More importantly, recent studies suggest that statistical learning occurs even when the regarding items are irrelevant to the task (Ferrante et al., 2018; B. Wang & Theeuwes, 2018; Zhao, Al-Aidroos, & Turk-Browne, 2013). Theeuwes (2018, 2019), therefore, proposes that statistical learning can produce plasticity with the spatial priority map, which is that the high probability locations of a target are boosted whereas low probability locations of a target are inhibited.

In conclusion, recent frameworks (Awh et al., 2012; Theeuwes, 2018, 2019) suggest that selection history might have been mistakenly taken as top-down attention (Wolfe et al., 2003). However, what is known to be top-down control of visual selection might indeed reflect a "selection history" that is fast, automatic, and effortless (Theeuwes, 2018). This notion received many evidence from the recent studies, which showed that prior knowledge, and past experiences affect attention in very short durations (Patai, Buckley, & Nobre, 2013; Patai, Doalla, & Nobre, 2012; Stokes, Atherton, Patai, & Nobre, 2012; J. J. Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006; J. J. Summerfield, Rao, Garside, & Nobre, 2011). On the other hand, how emotional arousal interacts with prior knowledge regarding visual attention has not been studied yet. Thus, my first aim in this thesis is to test the ABC theory's predictions to examine how emotional arousal affects memory-guided attention.

1.12 Current Study

As we have seen above, emotional events are automatically selected and inherently high-prioritised with strong motivational significance. Teasing apart the 'arousing' and 'priority' in an experimental setting, where emotional and neutral objects are presented, is not always an easy task. When a spider grabs attention faster than a squirrel, it is attributable to both the emotional significance of the spider and its high importance/priority in order to decide to approach to or avoid from it. Thus, arousal and priority are naturally contingent in such stimuli and might need a separation to investigate each of them independently. The other problem in the emotion literature that has been tackled by researchers for years is that emotion does not always enhance, but sometimes impairs cognition as reviewed above. As discussed previously, the ABC theory (Mather & Sutherland, 2011) suggests that arousal enhances memory and perception to the high-priority (but usually neutral) stimuli and it impairs memory and perception to the low-priority stimuli. Ideally, to test the ABC theory's predictions, there needs to be at least one type of stimulus to manipulate arousal and another type of stimuli to manipulate priority, to distinguish between arousing signals and priority signals and to examine the interaction between the two components in a more comprehensive way. Thus, the goal of this project is to test the ABC theory's predictions on memory-guided attention (Experiment 1 and Experiment 2) and motion perception (Experiment 3).

2 Chapter 2: Emotional Arousal Impairs Attention based on Long Term Memory

2.1 Abstract

Recent research reveals that our long-term memory provides predictive information about future events; however, whether and how long-term memory interacts with emotional arousal in guiding attention remains unclear. The current study addressed this issue. Participants completed two sessions (a day apart). In the first session (i.e., a training phase), they saw some scene images that included a target (i.e., the salient memory condition) and other images that did not include the target (i.e., the non-salient memory condition). Participants were asked to detect and learn the locations of the target within scenes. In the next day, participants were presented with a fear-conditioned (CS+) or a non-arousing tone (CS-), followed by the brief presentation of a scene from the training phase (either one from the salient memory condition or one from the non-salient memory condition) or a completely new scene. Their task was to indicate whether the scene included the target key or not. Half of the trials included the target key (a target-present condition) and the other half did not include the target (a target-absent condition). Results revealed that CS+, compared with CS-, led to slower responses in the non-salient memory trials than the salient memory condition. These results suggest that emotional arousal induced by fear-conditioned stimuli impaired the effects of long-term memory in guiding attention.

2.2 Introduction

Arousal-Biased Competition (ABC) theory proposes that emotional arousal sometimes enhances and sometimes impairs perception and memory depending on the priority of the stimulus (Mather & Sutherland, 2011). That is, arousal enhances perception and memory for the information, which is prioritised by individuals' top-down goals and/or by their bottom-up saliency, whereas arousal impairs processing of other events. There is now accumulating evidence that supports the prediction of ABC theory (T. H. Lee et al., 2015; T. H. Lee, Sakaki, et al., 2014; Sakaki, Fryer, et al., 2014; Sutherland & Mather, 2012, 2015). For instance, in one study (Sutherland & Mather, 2012), participants listened to high and low arousing sounds followed by a presentation of an array of letters, some of which drawn with dark grey colour (i.e., high salient stimuli) and others drawn with light grey (i.e., low salient stimuli). Not surprisingly, participants recalled high salient letters more than low salient ones. More interestingly, they remembered more of the high salient letters after hearing a highly arousing sound than hearing a low arousing sound, suggesting that emotional arousal enhances biased competition between the two types of stimuli in favour of more salient stimuli.

Emotion enhances memory and perception, but it comes with a cost to other information nearby space and time (Hurlemann et al., 2005; Kensinger et al., 2007; Mather et al., 2009; Mather et al., 2006; Strange et al., 2003). For instance, emotional arousal impairs memory for events which is not relevant to one's goal (for a review, see Levine & Edelstein, 2009). It is also known that the stronger features of emotionally arousing stimuli (e.g., a gun that perpetrator holds) stays in memory longer whereas between-item associations (e.g., association between the gun and the perpetrator) for arousing stimuli is usually impaired (for a review, see Mather, 2007). Studies that rapidly presented stimuli also showed an impaired perception of neutral stimuli that are presented shortly after emotional stimuli (Arnell et al., 2007; Ihssen & Keil, 2009; Mathewson, Arnell, & Mansfield, 2008; Most et al., 2007; Schwabe et al., 2011). However, emotion does not always impair nearby information. Exposure to emotionally arousing stimuli sometimes enhances memory for the nearby neutral event (A. K. Anderson et al., 2006) and perception for the nearby neutral event in time (Phelps et al., 2006). Taken together, ABC theory can explain these conflicting findings, suggesting that emotional arousal enhances prioritised stimuli at the cost to the mundane ones (Mather & Sutherland, 2011).

Sakaki, Fryer, et al. (2014) directly tested ABC theory's prediction for nearby neutral information, presenting a series of neutral objects alongside with an oddball image (either an emotional or a neutral object) highlighted by a black frame. Participants' goal was manipulated by asking them either to remember the oddball image or the image right before the oddball. The results indicated that seeing emotional oddball images, relative to seeing neutral oddball images, enhanced memory for the preceding object when the goal was to remember that object. In contrast, seeing emotional oddball images, relative to non-emotional oddball images impaired memory of the preceding object when participants focused on the oddball images. Brain imaging studies also supported the predictions of ABC theory (T. H. Lee et al., 2018; T. H. Lee, Sakaki, et al., 2014); such that arousal induced by a fear conditioned tone increased activation in an area responsible for perceptually salient stimuli whereas it inhibits activation in an area responsible for less salient stimuli (T. H. Lee, Sakaki, et al., 2014). Taken together, previous findings suggest that emotional arousal has different effects on cognitive processing depending on the priority, irrespective of whether priority comes from perceptual saliency or goal relevance.

While previous research on arousal and cognition primarily focused on the effects of bottom-up saliency or top-down goal relevance, recent theoretical frameworks suggest that long-term memory can also determine stimulus priority (for reviews, see Awh et al., 2012; Hutchinson & Turk-Browne, 2012; Peelen & Kastner, 2014). Accumulating evidence suggests that prior knowledge guides visual attention irrespective of whether the prior experience is explicitly remembered or implicitly activated (Chun & Jiang, 1998, 2003; Chun & Turk-Browne, 2007; Patai et al., 2013; Stokes et al., 2012; J. J. Summerfield et al., 2006; J. J. Summerfield et al., 2011). For instance, J. J. Summerfield et al. (2006) first asked participants to learn the location of a small target key in natural scenes. Participants then had to detect the target in briefly shown scenes either using their prior knowledge (i.e., memory-guidance) or using a preceding visual spatial cue (i.e., visual-guidance). Results revealed a facilitation effect of memory-guided cues compared with visual-guidance, suggesting a strong effect of yesterday's memories in orienting today's attention.

These results suggest that beyond the dichotomy of stimulus-driven attention (i.e., bottom-up saliency) and goal-directed attention, long-term memory also guides attention. Such effects of memory in attention are considered to have both bottom-up and top-down features (Awh et al., 2012; Theeuwes, 2019). For instance, both memory-guided and stimulus-driven attention rely on external stimuli; however, memory guides attention not because of the sole visual saliency of a stimulus; but rather because it matches with the representations of a prior knowledge. Similarly, both memory-guided and goal-driven attention depends on internal representations; however, memory might also guide attention implicitly without volitional attempts. Besides, memory and attention is generally studied as separate parts of cognition and the notion of memory-guided attention has been suggested as a more integrated approach to understand the brain and the mind (Hutchinson & Turk-Browne, 2012).

The present study aimed to test the interaction between emotional arousal and long-term memory in guiding attention. Given the literature described above suggesting that long-term memory helps to prioritise information in guiding attention and given the ABC theory's predictions (Mather & Sutherland, 2011), we expected that emotional arousal would enhance detection of a previously learnt target, but it would impair detection of the target in which there is no prior spatial memory. To test this prediction, we adapted a paradigm from J. J. Summerfield et al. (2006), consisting two separate sessions in consecutive days. In the first session, participants were trained to detect the target in a scene (i.e., a salient memory condition) or to learn the absence of the target (i.e., a non-salient memory condition). In the second session, participants were first fear-conditioned to a tone (CS+) using electrical stimulation, alongside with a measurement of skin conductance reactions (SCR). They were next shown scenes from the training session or completely new scenes and were asked to find the target in briefly shown images. Scenes from the salient memory condition had predictive information about the location of the target whereas other scenes either had no prior location memory in the non-salient condition or no memory at all (i.e., new scenes).

As mentioned above, the memory-guided attention paradigm used in Experiment 1 and 2 (See Chapter 3) was adopted from J. J. Summerfield et al. (2006). In this study, they compared facilitative effects of long-term memory on attention vs. facilitative effects of visual cue on attention. Participants had first learnt the locations of a small target key that were placed in a randomly selected location in natural scenes (i.e., the learning phase). On the following day, they were asked to complete two different tasks: a memory-guided task and a visually guided task. In the memory-guided task, participants were first shown a scene from the learning phase without the target key and could use their memory to predict where the target would appear (i.e., cue presentation). In the visually guided task, they saw scenes that were completely new, but a small box in a randomly selected area indicated where the target would appear (i.e., cue presentation). The duration of cue presentations were varied: 100 ms, 500 ms, and 900 ms. After the cue presentation, the target scene, which the same scene as the cue scene, but with the target key was presented for 100 ms and participants had to decide whether the scene included the target key or not in both tasks. Performance in valid trials (2/3 of all trials in this task) where the cue correctly predicted the location of the target compared with performance in neutral trials where no spatial information was provided about the location of the target (e.g., target-absent trials from the learning task for the memory-guided task or no small box was provided for the visually guided task). The brain regions involved in both types of attentional orienting were then characterized. Behavioural results showed a main effect of cue for both memory and visual cues: Participants were faster in valid trials than neutral trials. RTs were also faster in the memory-guided task than visually guided task. There was also an interaction between the type of task and the type of cue: The validity effect was stronger in the memory-oriented task that in visually oriented task. Strong effect of cue presentation duration was also observed; suggesting fastest responses in 900 ms and slowest responses occurred in 100 ms. Participants were highly accurate: 90% accuracy for both memory orienting and visual orienting.

In the first two experiments in this thesis, we used the memory-guided attention task explained above adopted from J. J. Summerfield et al. (2006) since we were interested in prioritised and non-prioritised location memory. Therefore, we have not used visually guided cues. Cue presentation was not varied and was always 100 ms in order to be able to analyse accuracy data avoiding ceiling effects. We did have valid trials (i.e., salient memory), which participants knew where the target key would appear and neutral trials (i.e., non-salient memory) where participants did not study the location of the target key. However, we had the number of trials equal across these two conditions and did not aim to calculate a validity effect. This is because we have conceptualised valid trials as salient/prioritised memory and neutral trials as non-salient/non-prioritised memory. Additionally we used fear-conditioning paradigm to manipulate participants' arousal level. Other details of the methodology will be explained in the method section.

If arousal enhances attention to high-priority information and impairs low-priority information as ABC theory suggests, then CS+ should lead to faster reaction times to detect the target in the salient memory condition and should lead to slower reaction times in the non-salient memory condition and no effect of arousal in the no memory condition. In other words, we expected that participants would react faster to CS+ trials than CS- trials in the salient memory condition both in the target-present and target-absent conditions; but this effect would be stronger in the target-present trials since the target key could provide a salient information. We also expected that they would react slower to CS+ trials than CS- trials in the non-salient memory condition when the target key was absent. However, we thought that the key-present trials might provide bottom-up saliency for the detection of the target key even in the absence of a memory cue and the impairment effect of arousal might then disappear in this condition. We predicted that there would be no arousal effect in the new memory condition, but we used this condition for exploratory reasons and did not have specific predictions for the target-present and target-absent trials.

2.3 Method

2.3.1 Participants

Forty-five undergraduate and graduate students at the University of Reading were invited to the study. The sample size was determined to ensure to detect the small-to-medium sized effects (Cohen's f = .24) that were observed in a prior study on the ABC theory (Sakaki, Fryer, et al., 2014). Two participants could not complete the first session (see Procedures) due to a program failure. One participant had a sleep deprivation before the second session and showed skin conductance reactions even in the neutral (CS-) tone (see Procedures). Therefore, data from these participants were excluded before data analyses. Thus, the analyses were conducted on data from 42 participants (26 females, 16 males, M_{age} = 24.19, SD = 4.46, age range = 18-35). All participants had normal or corrected-to-normal vision. The study was approved by the University Research Ethics Committee of the University of Reading (UREC 15/17), and all participants signed an informed consent form and were fully debriefed after the study.

2.3.2 Design

We employed a 3 (memory: salient memory, non-salient memory, no memory) X 2 (arousal: CS+, CS-) X 2 (target type: target-present, target-absent) within-participant design. All participants completed two sessions that took place on two consecutive days.

2.3.3 Stimuli

Stimuli included 144 photographs that depicted indoor scenes (e.g., kitchen; bathrooms; 91 images) or outdoor landscapes/scenes (e.g., forests; 53 images), which were obtained from online open sources through the Internet and randomly assigned to one of the conditions for each participant. Additional 12 scenes were used in the practice trials. For each scene, there were three different versions. The original scene was used as a picture of dimension 1000 x 750 pixels in 32-bit colour in the first version for non-salient memory images in the training phase (see Procedures). In the second and third versions, a small yellow key was embedded within the scene, but the dimension of the target key differed, such that a smaller key (15 x 29 pixels) was used in the second version (i.e., a training phase) and a bigger key (25 x 49 pixels) was used in the third version to decrease the task difficulty considering the duration of the scenes (see test phase in Procedure). The location of the key was determined to ensure that the key did not capture attention through its' bottom-up saliency. For each scene, we first randomly determined the location of the key. We then used a Graph-Based Saliency algorithm (Harel, Koch, & Perona, 2007) in Matlab R2013a (The Mathworks Inc, 2013a) which allowed us to find the most salient areas of images and ensured that the key was not embedded at one of them in the resulting scene. When the key was detected in one of the three most salient areas in the image, the key location was reallocated to another randomly determined location and we ran the algorithm again. This procedure was repeated until the key was embedded in a non-salient area. The stimuli were presented on a screen (resolution of 1680 x 1050 pixel) using Psychtoolbox (Brainard, 1997; Pelli, 1997) in Matlab R2013a (The Mathworks Inc, 2013a).

2.3.4 Mood Questionnaires

We have used couple of forms in order to measure participants' overall mood, including the State and Trait Anxiety Inventory (STAI, Spielberger (1983)), the Center for Epidemiologic Studies-Depression Scale, Radloff (1977), the Positive Affect and Negative Affect Scale (PANAS, D. Watson, Clark, and Tellegen (1988)), and the Intolerance of Uncertainty Scale (IUS, Buhr and Dugas (2002)). Besides, we also asked participants to indicate how many hours they slept the day before the test session (i.e., second day of the study), how many hours they sleep in general, how they evaluate their overall stress level using a 9-point Likert scale (1: extremely low; 5: moderate level; 9: extremely high), and how they evaluated their relative stress on the test day (see Session 2) comparing to general stress level (1: much lower; 5: same as usual; 9: much higher).

2.3.5 Procedures

2.3.5.1 Session 1.

Participants first filled out TAI, CES-D, and IUS after consent given. Following the instructions, they next completed six blocks of visual search task. In each block, they viewed

96 scenes in a randomized order for each block. Half of the scenes included a small yellow key (i.e., the salient memory condition) and the other half did not include the target key (i.e., the non-salient memory condition; see Figure 2.1A). Participants were asked to find the target key and learn its locations as much as possible. They were also instructed to pay attention to images that did not include the target and try to remember the absence of the target for these images.

For each scene, participants were asked to use the left and right button of a mouse to indicate whether they have found the target key or not in the scene; if they found the key, they used the left button of the mouse to indicate that they have identified the target key. To ensure that they memorised the location of the target key in each scene, when they pressed the left button, the mouse cursor appeared and they had to drag the cursor to the location of the key and to click on the left button again to save their response and to move to the next trial. When they did not find the target key, they were asked to press the right button of the mouse and move to the next trial. The available search time decreased with the blocks progressed as done in previous studies (e.g., Stokes et al., 2012; J. J. Summerfield et al., 2006) since participants would need less time with practice. This procedure ensured each participant spent roughly similar amount of time in a given scene. The maximum duration of each scene was randomly determined within a range of 16-24 s in the block 1, 12-20 s in the blocks 2 and 3, 10-18 s in block 4 and 5, and 8-16 s in the last block. Participants were encouraged to respond within these time windows. After a response has been made or after the available search time has expired, participants were presented with a fixation cross for 500 ms, followed by the next trial.

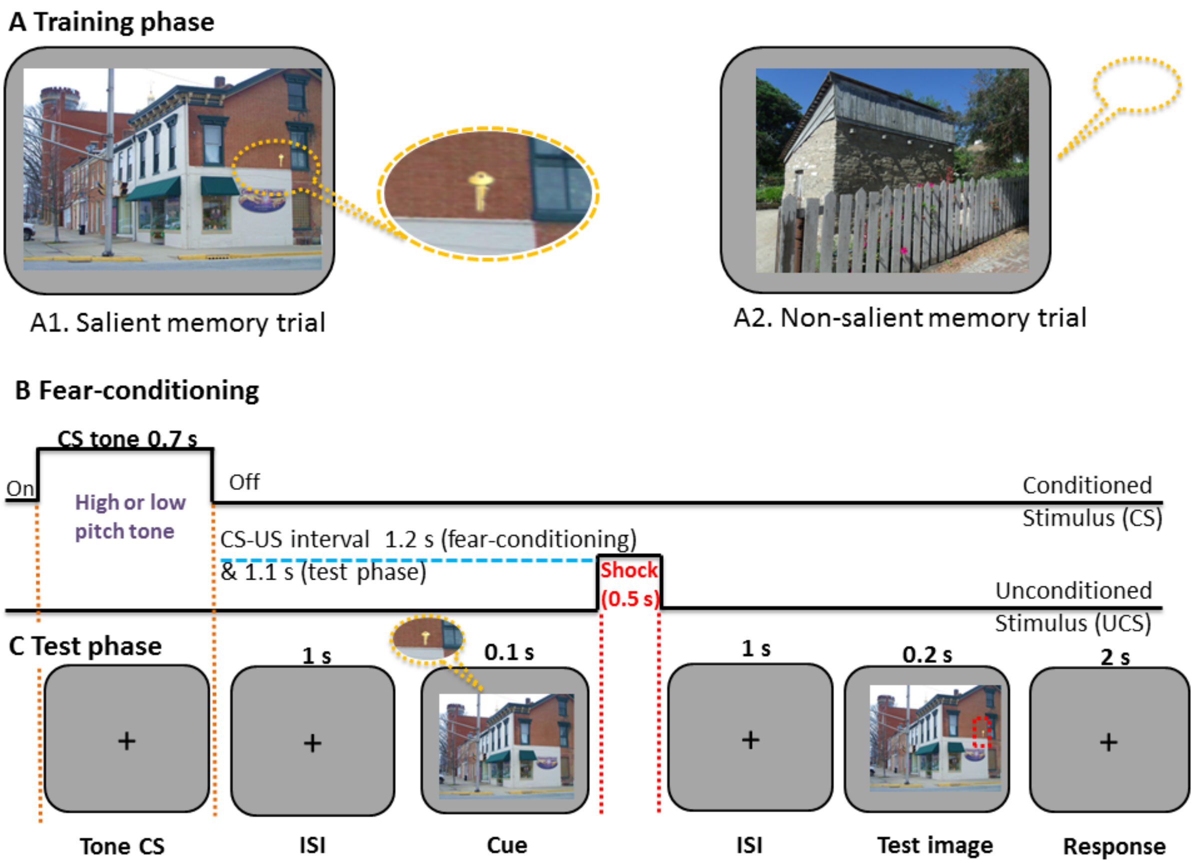

Figure 2.1. *(A) Example stimuli used in the training phase, where participants were asked to indicate whether they detected the target (**A1**; the salient memory condition) or not (**A2**; non-salient memory condition). Schematic illustration of (**B**) a single trial in the fear-conditioning phase and (**C**) a single trial in the test phase from the salient memory condition. The interval between the CS+ and electrical stimulation (shock) was similar (but not the same) between (B) the fear conditioning phase and (C) the test phase. The red square was drawn for presentation purpose only to show the yellow target key on the 'Test image'; participants saw all scenes without the red square.*

Participants completed the second session on the next day. In the second session, participants first completed SAI and PANAS forms (Time 1) upon arrival. They were then completed a fear-conditioning task, where they learned associations between a tone and electrical stimulation (UCS) delivered to the ring finger of their left hand (see Figure 2.1B). There were two tones that differ in their pitches and one of them sometimes led to electrical stimulation (CS+) and the other tone never led to electrical stimulation (CS-). The assignment of the two tones to the CS+/CS- conditions was counterbalanced across participants. A trial began with the presentation of one of the two tones for 700 ms, followed by a 1200 ms inter-stimulus interval (ISI). Then, the shock were administered for 500 ms if the trial was one of UCS and/or followed by a fixation cross for 10 s. Participants pressed either the right or left arrow key with their right hand to indicate whether the tone was high- vs. low-pitched irrespective of whether they received a shock or not. The task included 30 trials: 10 trials for the CS+ with UCS condition, 10 trials for the CS+ without UCS condition, and 10 trials for the CS- condition. Prior to the fear-conditioning task, participants were informed which tone would lead to shock but were unaware of the probability of the shock. We also asked participants to rate how much they felt uncomfortable about receiving the shock using a 9-point Likert scale (1: not at all uncomfortable -9: extremely uncomfortable) before the fear condition task (Time 1) and after the visual search task at the end of the session (Time 2).

After fear conditioning, participants were asked to complete the test phase (see Figure 2.1C). To prevent fatigue, we had split the test phase into three blocks (48 trials in each block) and participants were instructed to take a short break between blocks. In each trial, they were first presented with either the CS+ or CS- tone for 700 ms, followed by a 1000 ms fixation cross. Participants were then presented with a “cue” scene without the target key (i.e., first version of the scene used in the training phase) for 100 ms, followed by another 1000 ms fixation cross (ISI). This followed by the same cue scene for 200 ms (a “test image”). This test image sometimes included the target key and sometimes did not include the target key. If participants saw the target in the test image, they were instructed to press “1” using the number pad in the keyboard as soon as possible. If they did not find the target key, they pressed “2”. They had to make a response within 2 sec; if they missed it, the fixation cross automatically disappeared and participants saw a warning instruction to respond faster. The next trial started after a jittered 1-4 s inter-trial interval (ITI), but it was longer for shock trials (5 s).

There were 96 old memory trials, which participants saw in the training phase and 48 additional trials constituted completely new images. Half of the trials included scenes with the target key (target present trials) and half of them did not include the key (target absent trials). Target condition was counterbalanced across memory conditions, such that half of the salient memory trials included the target and half of them did not include the target key. Likewise, half of the non-salient memory trials included the target key. The same procedure was applied for the new trials (i.e., half target present, half target absent). To prevent extinction, in some trials (i.e., booster trials: 16 trials per block), participants were given shock to their finger during the first ISI. After the test phase, participants were asked to rate how uncomfortable was the shock using the same 9-point Likert scale as in Time 1 and they also filled out demographic form, SAI and PANAS (Time 2).

2.3.6 Electric Shock and Skin Conductance

Administration of the electrical stimulation was performed using the Powerlab system and LabChart version 7 (ADInstruments Ltd, Chalgrove, Oxfordshire, UK). In order to measure the manipulation of emotional arousal, participants' SCR were recorded from the middle and index fingers of their left hand at 1000 Hz sampling rates during the fear conditioning task.

Prior to the second session, the amplitude and frequency of "highly unpleasant but not painful" level of electrical stimulation was determined for each participant (M = 3.61 mA, SD = 2.04; M = 78.42 Hz, SD = 96.77) to account for individual differences of unpleasantness depending on the strength of the shock. The level determined was then used throughout the fear conditioning phase. To prevent habituation to the shock, after the fear-conditioning task, participants were asked whether they still felt “highly unpleasant but not painful” with the shock or whether they would like to increase it. Some participants (N = 7) asked the experimenters to slightly increase the level of stimulation to make the shock “highly unpleasant but not painful” and therefore we increased the level of stimulation for this subset of participants (the averaged increase of shock was small: 0.6 mA and 37.96 Hz). This procedure ensured that the administration of stimulation was subjectively felt arousing for all participants throughout the experimental session.

2.3.7 SCR Analysis

Data acquisition for one participant in fear-conditioning task and for two participants in during test phase were failed; therefore, the data were analysed on 41 and 42 participants, respectively, using MATLAB R2013a (The Mathworks Inc, 2013a). SCR data epochs were extracted from a time window between 0 and 10 s after CS tone onset, and baseline-corrected between 0 and 1 s. The peak SCR amplitude was taken between 2 and 10 s from the trial-by-trial average SCR epoch as a function of CS tone. Data from the first trial were removed as responses in this trial could reflect orientation response (J. Li et al., 2017).

2.4 Results

Results from booster trials were excluded from all analyses (both fear-conditioning and the test phases) since we were interested in the effects of emotional arousal induced by anticipation of shocks, rather than the effect of the shock per se.

2.4.1 Training Phase

To test participants’ performance during the training phase, reaction times and accurate responses were analysed using two separate repeated measures ANOVAs with an independent variable of blocks. The analyses revealed the main effects of blocks for accuracy, F (5,205) = 3.94, $p < .01$, $\eta_p^2 = .09$, and for reaction times, F (5,205) = 123.73, $p <$

.001, η_p^2 = .75, suggesting that participants' performance improved across six training blocks as reflected by increased accuracy and decreased reaction times (see Figure 2.2A). The percentage of scenes where participants correctly identified the target key (*M* = 94.08 %, *SD* = 23.60) and the percentage of scenes where they correctly identified the absence of the target (*M* = 98.67 %, *SD* = 11.46) were all above 90 % across all blocks. These results indicate that participants successfully learned the target's location in each scene as observed in other studies with a similar paradigm (Patai et al., 2012; Stokes et al., 2012; J. J. Summerfield et al., 2006).

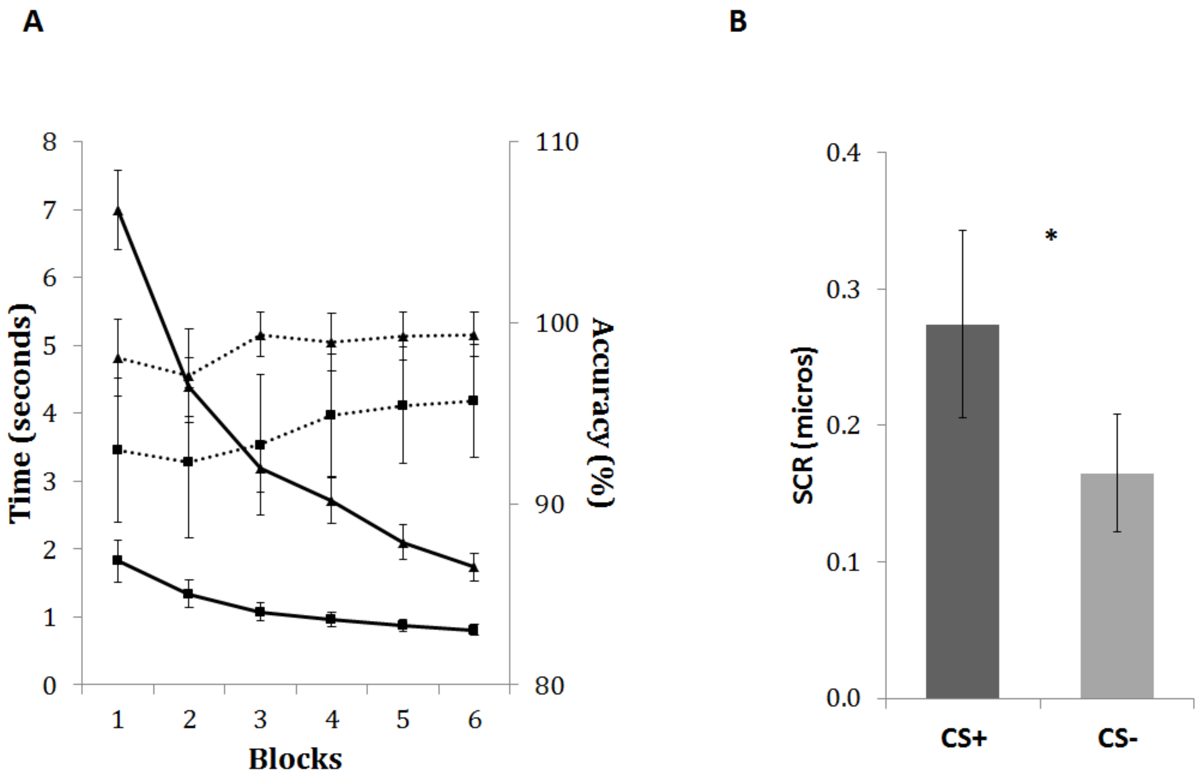

Figure 2.2. (A) *Participants' performance improved over the six blocks in the training phase. The figure includes the RTs (solid line) and the accuracy (dashed line) for the detection of the presence (squared line) and the absence (triangle line) of the target key within each scene.* ***(B)*** *Participants' SCR was higher in the CS+ condition compared to the CS- condition during the fear conditioning phase.* * $p < 0.05$

There was a significant difference in the SCR collected in the fear-conditioning phase between CS+ and CS- trials, t (40) = 2.11, $p < .05$, Cohen's $d_z = 0.33$, indicating that participants had a higher SCR when they heard the CS+ tone ($M = 0.27$, $SE = 0.07$) compared to the CS- tone ($M = 0.16$, $SE = 0.04$; see Figure 2.2B). Thus, participants acquired fear response to the CS+ tone. Furthermore, there were also significant differences in the SCR between CS+ and CS- conditions during Block 1, t (39) = 2.08, $p < .05$, Cohen's $d_z = 0.33$, and Block 3, t (39) = 2.22, $p < .05$, Cohen's $d_z = 0.34$. SCR difference in Block 2 was marginally significant, t (39) = 2.22, $p = .07$, Cohen's $d_z = 0.29$. We also analysed participants' subjective ratings of unpleasantness for shock and found that they reported stronger negative feelings towards electric shock at Time 2 ($M = 3.95$, $SD = 1.45$) relative to Time 1 ($M = 2.93$, $SD = 1.37$), $t(40) = 4.30$, $p<0.001$, Cohen's $d_z = .67$. These results suggest that participants' emotional arousal was maintained or even increased over the course of the experiment.

2.4.2 Mood

Data from mood questionnaires showed normal and near-to-normal distributions for all scales and also questions for stress and sleep (see Table 2.1 and also see Appendices for normality histograms: Appendix 1 for TAI, Appendix 2 for SAI Time 1; Appendix 3 for CES-D, Appendix 5 for relative stress level, Appendix 6 for relative sleep hours). Some participants scored higher than a cut point of 39-40 in TAI ($N = 17$) and SAI scales (Time 1; $N = 13$), which has been suggested to detect clinically significant symptoms (R. G. Knight, Manning, & Spears, 1983). However, there are clinical studies suggesting false positives when standard (low) cut-off scores were applied (Zich, Attkinson, & Greenfield, 1990). Four participants had a SAI (Time 1) score of 1 SD above the mean and ten participants had a TAI score of 1 SD above the mean. For CES-D, 14 participants scored higher than the cut-off point of 16 and only seven of them had 1 SD above the sample mean. For IUS, 8 participants had a score of higher than 1 SD above the mean. Nevertheless, none of these questionnaires' results did correlate with the SCR results, (rs < .3, ps > .2), suggesting the manipulation of emotional arousal was not affected by participants' baseline mood or their emotional traits. We also identified participants who had both high depression score and high TAI scores (N = 10) and compared them with the remaining participants on their SCR difference scores (i.e., CS+ trials – CS- trials). There was no significant difference in SCR difference score between the two groups (p > .3). This suggests that participants who had either high anxiety and/or high depression scores did not differ in their emotional arousal level evoked by the CS+ tone than participants who reported low in those scales.

Table 2.1. Means, standard deviations, minimum and maximum values of Mood Scales

Questionnaires	Mean	SD	Minimum	Maximum
TAI	38.31	8.52	23	59
CES-D	12.98	7.33	0	29
IUS	56.95	13.50	32	84
SAI-Time 1	36.83	5.60	24	52
SAI-Time 2	39.93	6.63	27	54
PAS*-Time 1	30.05	6.58	18	48
PAS-Time 2	27.05	7.74	13	46
NAS*-Time 1	13.15	2.61	10	20
NAS-Time 2	12.98	7.33	10	20
Sleep last night	7.33	1.09	5	10
Sleep in general	7.43	1.02	5	10
Stress on the test session	3.79	1.75	1	7
Relative Stress	4.55	1.96	1	9

* PAS: Positive Affect Scale and NAS: Negative Affect Scale

2.4.3 Performance in the Test Phase

Given that we had a time-window of 2 sec to respond, any response provided after 2 seconds was excluded (1.4 % of all trials). Additionally, trials with scene images that the participant failed to find the key more than 3 times (i.e., half of the time) during the training phase were also excluded from the analyses (0.84 % of all trials) to allow us to examine the effects of emotion on visual search performance based on strong long-term memory. The mean reaction times were obtained for each participant for each condition.

Our prediction was that participants would be quicker to detect the target in the salient memory condition under emotional arousal and they would be slower to detect the target in the non-salient memory condition under emotional arousal. More specifically, we expected a main effect of memory and an interaction effect between memory and arousal, with no main effect of arousal; similar to what has been found in the literature testing ABC theory (Sutherland & Mather, 2012). We also predicted a main effect of target type and an interaction between memory and target type with no interaction effect between target type and arousal. We also expected a three-way interaction. A repeated-measures ANOVA with memory condition (salient, non-salient and no memory), arousal (CS+ or CS-) and target type (target present and target absent) was performed on the mean reaction times using IBM SPSS Statistics for Windows (IBM Corp, 2017). This analysis showed a main effect of memory, $F(2,82) = 4.23$, $p < .05$, $\eta_p^2 = .09$ and a main effect of target type, $F(1,41) = 9.77$, $p < .01$, $\eta_p^2 = .19$ with no main effect of emotion ($p > .80$). We also observed a significant interaction between emotion and memory, $F(2,82) = 4.09$, $p < .05$, $\eta_p^2 = .09$ and a significant interaction between memory and target type, $F(2,82) = 23.40$, $p < .001$, $\eta_p^2 = .36$, with no significant interaction between emotion and target type and with no three-way interaction (*p*s > .40).

Subsequent tests for the main effect of memory revealed that participants performed slower in the salient memory condition ($M = 790.95$ ms, $SD = 116.53$) and in the no-memory condition ($M = 787.38$ ms, $SD = 112.55$) than the non-salient memory condition ($M = 765.95$ ms, $SD = 122.09$), $t(41) = 2.14$, $p < .05$, Cohen's $d_z = .34$ and $t(41) = 3.30$, $p < .01$, Cohen's $d_z = .51$, respectively. There was no significant difference in performance between the salient memory condition and the no memory condition ($p > .70$). In terms of the effects of the target type, participants were faster in the target present trials (M = 757.38 ms, SD = 105.69) than in the target absent trials (M = 799.76 ms, SD = 132.21), $t(41) = 3.68$, $p < 0.01$, Cohen's d_z = .55. The significant interaction effect between emotion and memory revealed that in the non-salient memory trials, participants were slower in the CS+ condition (M = 778.80 ms, SD = 129.79) than the CS-condition (M = 753.57 ms, SD = 126.41), $t(41) = 2.05$, $p < .05$, Cohen's d_z = .32 (see Figure 2.3A). This suggests an impairment effect due to emotional arousal when participants did not have a salient memory whereas there was no arousal difference in salient memory trials or no-memory trials (ps > .2).

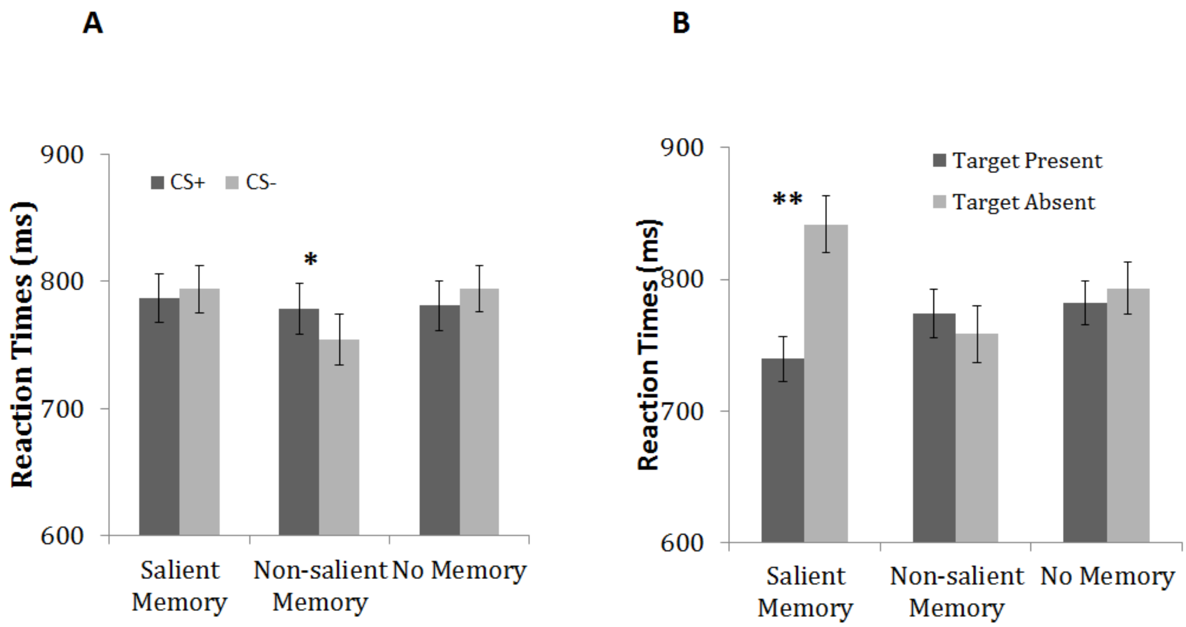

Figure 2.3. (A) *During the test phase, there was a significant interaction between arousal and memory-salience, such that CS+ impaired performance in the non-salient memory condition.* ***(B)*** *There was also a significant interaction between memory-salience and target type, such that participants performed the best in the target present condition whereas they performed worst in the target absent condition among salient memory trials. Error bars represent the standard error of the mean (SEM). * p < .05 ** p < .001.*

In order to examine the interaction effect between memory and target type, we have combined the arousal trials and found that participants were faster in the salient memory condition when the target key was present (M = 739.3 ms, SD = 113.21) than target absent condition (M = 841.5 ms, SD = 139.96), $t(41) = 6.62$, $p<0.001$, Cohen's $d_z = 1.02$ (See Figure 2.3B). There was no target type difference in neutral memory and no-memory conditions (ps > .3). Finally, although we did not have a significant three-way interaction, we have illustrated the means with standard error bars from all conditions in Figure 2.4 in order to examine each condition separately. As shown in Figure 2.4, the impairment effects due to CS+ in the non-salient memory condition were similar across the target present vs. the target absent trials.

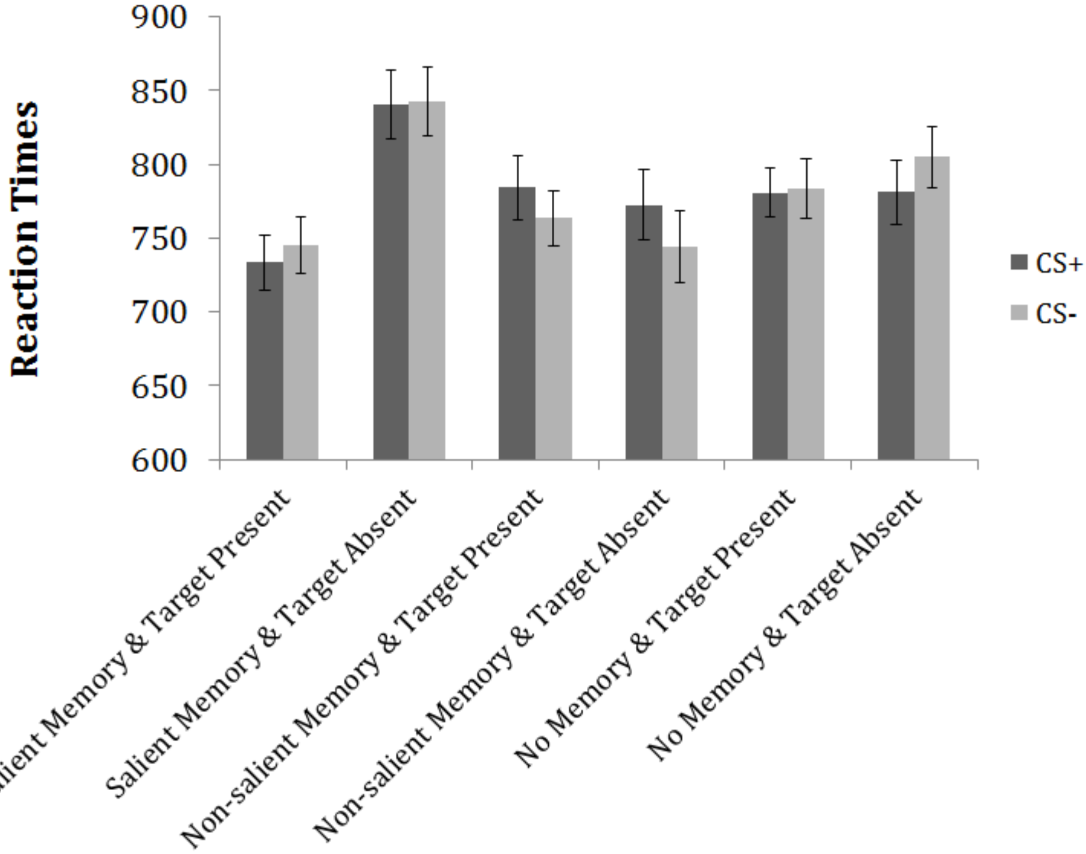

Figure 2.4. *Interaction among arousal, memory saliency, and target type. Participants performed the best in the salient memory condition when the key was present whereas they performed the worst in the salient memory condition when the key was absent. Error bars represent the standard error of the mean (SEM).*

We also examined the mean accuracy of the performance and found that participants' performance was low in the non-salient memory and new memory conditions when the target key was present, suggesting an incongruency effect (see Table 2.2): They made more errors to identify the target key when they did not have a location memory. However, location memory helped them to recognise the target key as well as to reject the presence of the target.

Table 2.2. Means and standard deviations of participants' accuracy performance (%) in each condition

Condition	Mean (%)	SD
CS+/Salient Memory/Target Present	66.98	18.62
CS+/Salient Memory/Target Absent	91.93	13.15
CS+/Non-Salient Memory/Target Present	39.25	20.90
CS+/Non-Salient Memory/Target Absent	97.29	6.15
CS+/New Memory/Target Present	44.40	21.58
CS+/New Memory/Target Absent	96.30	7.22
CS-/Salient Memory/Target Present	74.93	14.29
CS-/Salient Memory/Target Absent	91.99	12.64
CS-/Non-Salient Memory/Target Present	44.16	18.69
CS-/Non-Salient Memory/Target Absent	96.18	6.85
CS-/New Memory/Target Present	40.55	18.71
CS-/New Memory/Target Absent	94.19	7.31

A repeated-measures ANOVA with memory condition (salient, non-salient and no memory), arousal (CS+ or CS-), and target type (target present and target absent) was performed on the mean accuracy performance. This analysis showed a main effect of memory, $F(2,82) = 48.45$, $p < .001$, $\eta_p^2 = .54$ and a main effect of target type, $F(1,41) = 368.93$, $p < .001$, $\eta_p^2 = .90$ with no main effect of emotion ($p > .44$). We also observed a significant interaction between emotion and memory, $F(2,82) = 4.02$, $p < .05$, $\eta_p^2 = .09$ and a significant interaction between memory and target type, $F(2,82) = 74.11$, $p < .001$, $\eta_p^2 = .64$, with no significant interaction between emotion and target type ($p > .11$) and with no three-way interaction ($p > .07$). Pairwise comparisons for the main effect of memory revealed that participants performed more accurately in the salient memory condition (M = 81.46 %, SE = 1.13) than both in the non-salient memory condition (M = 69.22 %, SE = 1.23) and the no memory condition (M = 68.86 %, SE = 1.35), ps < .001. There was no significant difference in performance between the non-salient memory condition and the no memory condition (p > .80). In terms of the target type, participants were more accurate in the target present trials (M = 94.65 %, SD = .97) than in the target absent trials (M = 51.71 %, SE = 1.80).

The significant interaction effect between emotion and memory reflects that participants were less accurate in the salient memory trials in the CS+ condition (*M* = 79.45 %, SD = 11.05) than the CS- condition (*M* = 83.46 %, *SD* = 8.28), $t(41) = 2.07$, $p < 0.05$, Cohen's $d_z = .39$ (see Figure 2.5), but there was no arousal difference in the non-salient memory trials or the no-memory trials (*p*s > .11). These results suggest there was an impairment effect of arousal when participants had a salient memory. Since this includes both target-present and target-absent trials, bottom-up saliency of the presence of the target key might have been interfered to participants' decisions.

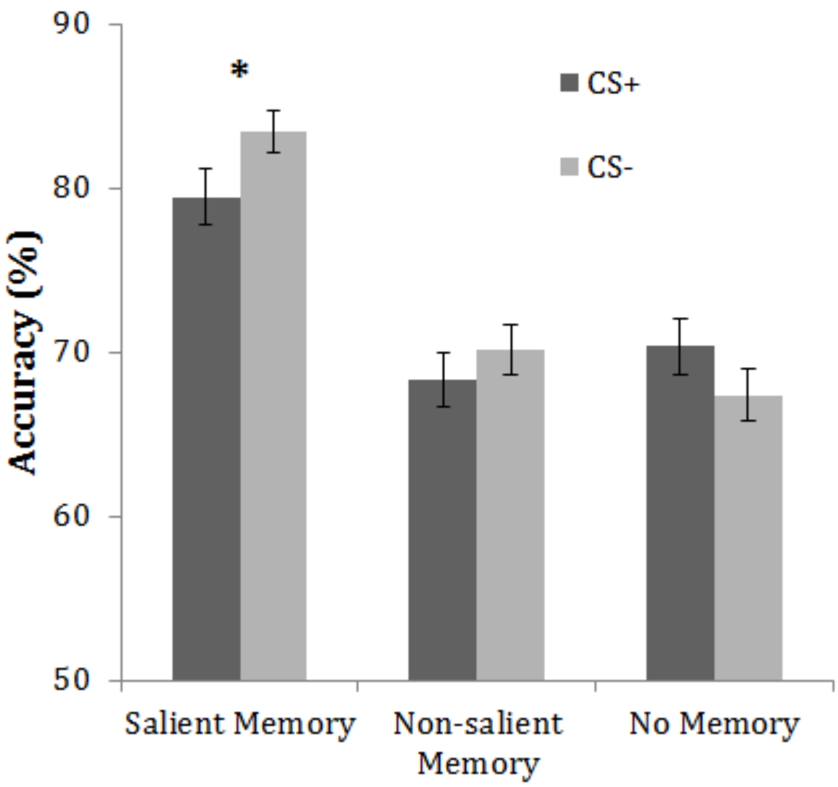

Figure 2.5. *There was a significant interaction between arousal and memory-salience, such that participants performed less accurately in the arousing condition than non-arousing condition in the salient memory trials. Error bars represent the standard error of the mean (SEM).* * $p < 0.05$

The significant interaction effect between memory and target type was due to that participants were more accurate in the target absent condition than the target present condition in all memory types (*p*s < .001); however, the difference between the target types was lower in the salient condition (See Table 2.3).

Table 2.3. Mean and standard deviations of accuracy (%) in each condition

Condition	Mean (%)	SD
Salient Memory/Target Present	70.95	12.64
Salient Memory/Target Absent	91.96	11.52
Non-Salient Memory/Target Present	41.70	15.84
Non-Salient Memory/Target Absent	96.73	5.04
New Memory/Target Present	42.48	17.39
New Memory/Target Absent	95.24	6.01

2.5 Discussion

In this study, we tested the prediction of the ABC theory (Mather & Sutherland, 2011) using a memory-guided attention paradigm adapted from a previous study (J. J. Summerfield et al., 2006). According to the ABC theory and past research (T. H. Lee et al., 2015; Sakaki, Fryer, et al., 2014; Sutherland & Mather, 2012, 2015), emotional arousal enhances high-priority information whereas it impairs low-priority information. Our results did partially confirm the emotional impairing effect on the non-prioritised stimuli, but we did not observe emotional enhancement to prioritised stimuli in reaction times. More specifically, we found that the speed of the detection of the target key was impaired by the CS+ tone when the target key's location was not predicted by prior memory. Participants' arousal level measured by SCR yielded greater responses in the CS+ cues than CS- cues, confirming that participants acquired fear responses in CS+ condition.

However, the effects of arousal in non-salient memory should be evaluated cautiously. Response interference (Lupker, 1979; Stins, Polderman, Boomsma, & de Geus, 2007) that refers to the phenomenon where response times to a target stimulus are longer in the presence of distractor stimuli (i.e., the target key in this case) might have caused the impairment effect in this condition. Since we have collapsed the key-present and key-absent trials, the presence of the key might have distracted the participants in this non-salient memory condition. Furthermore, we are unsure whether this condition has created low priority information as participants have also studied these images in the training sessions. Nevertheless, we have conceptualised the non-salient memory as to reflect the absence of a location memory for the target key.

Our results suggested that participants made more errors in the CS+ condition than the CS- condition in the salient memory trials. This finding contradicts the prediction of the ABC theory (Mather & Sutherland, 2011), which suggests an emotional enhancement effect on salient events. Therefore, these results were not consistent with our prediction that arousal would enhance priority signals based on long-term memory. However, this should be evaluated cautiously: Although participants did make more errors in the arousing condition when they know where to look at, they were also faster to respond. This suggests that there might be a speed-accuracy effect on participants' responses. Thus, they might have reacted faster in the salient memory condition at the cost of making mistakes.

Previous studies have shown that emotionally arousing events are remembered better than non-emotional events (Bradley et al., 1992; Kensinger & Corkin, 2003; LaBar & Cabeza, 2006; Sakaki, Fryer, et al., 2014; Talmi, 2013). However, these studies focused on the effects of memory at the time of encoding or consolidation. In contrast, the effect of emotional arousal on memory retrieval has been less examined. A few relevant literature shows that acute stress impairs memory retrieval both in animals (de Quervain, Roozendaal, & McGaugh, 1998) and in humans (Kuhlmann, Kirschbaum, & Wolf, 2005; Kuhlmann, Piel, & Wolf, 2005). It has been also shown that emotional arousal impairs executive function (Kuhbandner & Zehetleitner, 2011) and negative mood impairs retrieval of episodic memory (Ellis, Thomas, McFarland, & Lane, 1985) and semantic knowledge (Sakaki, Gorlick, & Mather, 2011). Therefore, our findings extend this literature suggesting that emotional arousal might also impair attentional performance based on long-term memory cues.

It is not surprising that past experiences serve as a basis of our expectation in a given environment. Places or objects that were previously important are often prioritised during visual search (e.g., Chun & Jiang, 1998; Jiang, Swallow, & Rosen, 2013). Besides, long-term memory possibly affects current attention with a more complex manner than bottom-up saliency or top-down goals (e.g., Hutchinson & Turk-Browne, 2012). This complex system made somewhat difficult to disentangle the enhancement and impairment effects of emotional arousal in our design. Although we have seen an impairment effect of arousal, we did not observe emotion-enhancement effect on salient memory condition, which is inconsistent with our prediction. There might be number of reasons of why one of our predictions was not supported.

First, in the second session, the duration of the test image might be too short to detect the target key in the incongruent trials as mentioned above. This is especially true for the new images which they have never seen before. In fact, participants had much lower hit rates (below 50%) to detect the target key in both new images and non-salient images in which they did not have a location memory. Furthermore, the target key was always placed in a peripheral location because of the algorithm that we used (i.e., we avoided to place the target in the most salient areas). Although this procedure was used to ensure that the locations of the target are equally non-salient for all images, it might have made the task difficult, which might be one of the reasons to yield the complex effects of emotional arousal on memory-guided attention observed in the study. Second, we used both correct and incorrect responses to test reaction times since we did not have a sufficient number of trials to separate them where participants made correct responses vs. incorrect responses. Therefore, we designed our second study to aim to use only correct responses. Finally, in the salient memory condition, participants' reaction times were faster when the key was present than when the key was absent (see Figure 2.4), but the effects of emotional arousal on these conditions are not clear. Besides, accuracy results that suggest that participants made more errors in the salient memory conditions under emotional arousal complicated the interpretation of the results. Looking at Figure 2.4, it seems like there is a pattern of emotion-enhancement effect on salient memory trials in the target present condition for reaction time data, which did not reach significant level unlike our predictions. Therefore, in the second study (see Chapter 3), we have examined the emotion-enhancement effect with some modifications in the design.

As mentioned above, performance in target present and target absent trials heavily differ than each other with a congruency effect between memory saliency and target type; and thus, complicate the interpretation of the results. Examining the means of each condition (see Table 2.2), it is evident that participants did not have trouble to reject the presence of the target key in both the CS+ and the CS- condition when they knew where to look at. However, it seems like they made more errors when the target key was present, but when they did not have memory cues for the location of the target (i.e., incongruent trials). This might suggest that the duration of the test image might be too short to detect the target, especially in the congruent trials. Therefore we have decided to use target absent trials as catch trials in the second experiment and only focused on the target-present trials. Another explanation might be that participants were expecting the shock at the time of the presentation of the test image in CS+ trials, which might be distracting and potentially affect their attention to the target key. That is why in our second experiment, we decided to administer the shock after the test image presentation (see Chapter 3). The duration of the ITI in the test phase might have been short to allow the skin conductance to come back to its' baseline level, so we have increased ITI in the next experiment. Also the number of trials was small and inconsistent across conditions. Specifically, arousing condition had smaller number of trials (i.e., 8/9) than the non-arousing condition (11/12) since we excluded the booster trials. This has been addressed and equalised in Experiment 2.

In summary, our results only partly confirmed one of the predictions that emotional arousal would impair memory-guided attention for the less salient, less important event, which supports ABC framework. However, we did not find emotional enhancement effect for the salient memory condition. On the contrary, our accuracy results showed an impairment effect for the salient memory trials. The complexity of our design might have hindered some of the effects; thus, we aimed to improve the design in a follow-up study in the next chapter.

3 Chapter 3: Emotional Arousal Enhances the Impact of Long-Term Memory in Attention

3.1 Abstract

Previous research reveals that long-term memory guides attention but it remains unclear how it interacts with emotional arousal in guiding attention. In Chapter 2, we have found an emotional impairment effect on memory-guided attention; however, the results were somewhat complex to explain due to the number of problems in the experiments (i.e., the small number of trials per condition and the low accuracy in performance). To address these issues, we made some modifications into our task. As in Chapter 2, participants were first asked to learn the locations of a target key embedded within scenes (i.e., training phase). In the next day, participants were presented with a fear-conditioned (CS+) or a non-arousing tone (CS-), followed by the brief presentation of a scene from the training phase, and asked to indicate whether the scene included the target key or not. The target was presented at the same location as the training phase. Unlike in Chapter 2, here, we have not used new images and have only focused on salient memory, which the key was present in the training session vs. non-salient memory, which the key was absent. Besides, we have only analysed data from key-present trials in the test phase and used the key-absent trials in the test phase as catch trials. Results revealed that CS+, compared with CS-, led to faster target detection, suggesting that arousal induced by CS+ enhanced the effects of long-term memory in guiding attention. Our results are consistent with recent findings that arousal amplifies the effects of priority and extend them to another source of priority-- long-term memory.

3.2 Introduction

It is well established that emotionally arousing stimuli, such as snakes, spiders, emotional facial expressions, and erotic pictures, are preferentially processed compared with non-emotional stimuli (for reviews, see Öhman & Mineka, 2001; Schupp et al., 2006; Vuilleumier & Pourtois, 2007). For instance, emotionally arousing stimuli are detected faster than non-emotional stimuli (e.g., Eastwood et al., 2001; Fox et al., 2002; Joshua & Reinke, 2008). Emotionally arousing events are also much more memorable than mundane events (LaBar & Cabeza, 2006; Mather, 2007; Talmi, 2013). This emotion-induced enhancement effect was observed irrespective of stimulus types, including pictures (e.g., Bradley et al., 1992; Sakaki et al., 2012), words (e.g., Kensinger & Corkin, 2003) and autobiographical memories (e.g., St. Jacques & Levine, 2007).

Recent research suggests that arousal induced by emotional stimuli affects not only the way we process that emotional stimuli but also the way we process other stimuli nearby in time or space (Hurlemann et al., 2005; Kensinger et al., 2007; Strange et al., 2003). For example, previous research with rapid serial visual presentation (RSVP) indicates that people show impaired perception of neutral stimuli that are presented shortly after emotional stimuli (A. K. Anderson, 2005; Arnell et al., 2007; Ihssen & Keil, 2009; Mathewson et al., 2008; Most et al., 2005; Schwabe et al., 2011; S. D. Smith, Most, Newsome, & Zald, 2006). However, emotional arousal does not always impair processing of other stimuli nearby in time or space (for a review, see Levine & Edelstein, 2009). For example, exposure to emotionally arousing information sometimes enhances memory of a nearby neutral event (A. K. Anderson et al., 2006; Kensinger et al., 2007) and perception for a nearby neutral event in time (Phelps et al., 2006; Zeelenberg & Bocanegra, 2010).

Arousal-biased competition (ABC) theory was proposed to explain these conflicting results (Mather & Sutherland, 2011). According to the ABC theory, arousal enhances perception and memory of high-priority information, which determined by bottom-up saliency or top-down goals of the observer, whereas it impairs perception and memory for low-priority information. Research confirmed the predictions of the ABC theory both for bottom-up saliency (e.g., T. H. Lee et al., 2018; T. H. Lee, Sakaki, et al., 2014; Sutherland & Mather, 2012; Sutherland & Mather, 2015) and for top-down goals (e.g., T. H. Lee et al., 2015; Sakaki, Fryer, et al., 2014).

Long-term memory is also an important factor that determines stimulus priority (for reviews, see Awh et al., 2012; Hutchinson & Turk-Browne, 2012; Peelen & Kastner, 2014; Theeuwes, 2019): attention is driven not only by our top-down goals or bottom-up visual inputs, but also by one's memory about prior experience. Consistent with this view, prior experiences and expectancies based on knowledge guide visual attention and modulate cognitive performance, irrespective of whether the experiences are deliberately remembered or automatically activated (Chun & Jiang, 1998, 2003; Chun & Turk-Browne, 2007; Henderson & Hollingworth, 1999; Moores, Laiti, & Chelazzi, 2003; Olivers, 2011; Patai et al., 2012; Rosen, Stern, Michalka, Devaney, & Somers, 2016; Stokes et al., 2012; J. J. Summerfield et al., 2006; J. J. Summerfield et al., 2011).

The present study aimed to investigate the interaction between emotional arousal and long-term memory for spatial locations of objects in guiding attention. Following up from the first experiment, we have used a similar task with some modifications. As in Chapter 2, participants learned the locations of a target embedded within natural scenes, where half of the scenes included the target (salient memory condition), whereas the other half did not include the target (non-salient memory condition). However, we have not used new images at all as the accuracy to detect the target was below chance level. In the second session, participants were first presented with a fear-conditioned tone that predicted electrical stimulation (i.e., CS+) or a neutral tone, which did not predict the electrical stimulation (CS-). Their skin conductance reactions (SCR) were recorded to confirm that they acquired fear responses. They were then shown scenes from the first session and asked to find the target. Since target-present and target-absent trials yielded a congruency effect which complicated the saliency effect based on memory, we have not modelled target absent trials in this second experiment and used them as catch trials. Finally, we have had some modifications of the duration of the stimuli and number of trials (see Procedures). The idea was similar to Chapter 2: Scenes from the salient memory condition should provide predictive information about the location of the target, but those in the non-salient memory condition should not provide any information about the location of the target. If arousal enhances attention to high-priority information as the ABC theory suggests, CS+, relative to CS-, should lead to faster reaction times to detect the target in the salient memory condition and arousal should impair performance in the non-salient memory condition. Specifically, we predicted that participants would react faster to CS+ trials than CS- trials in the salient memory condition whereas they would react slower to CS+ trials than CS- trials in the non-salient memory condition. We also predicted that they would react to salient memory condition faster than non-salient memory condition in CS+ trial, but this effect would be absent in the CS- condition.

3.3 Method

3.3.1 Participants

Forty-seven undergraduate students at the University of Reading were invited to the study. As in Chapter 2, the sample size was determined to ensure to detect the small-to-medium sized effects (Cohen's f = .24) that were observed in a prior study on the ABC theory (Sakaki, Fryer, et al., 2014). One participant pressed a key even before the stimuli were presented in more than 1/3 of the trials during the test phase (see Procedures); data from this participant were excluded before data analyses. Thus, the analyses were conducted on data from 46 participants (38 females, 8 males, M_{age} = 19.35, SD = 1.49, age range = 18-24). Acquisition of SCR failed for four participants due to technical problems. Therefore, SCR analyses did not include these participants' data. All participants had normal or corrected-to-normal vision. The study was approved by the University Research Ethics Committee of the University of Reading (UREC 15/17), and all participants signed an informed consent form approved by the Ethics Committee.

3.3.2 Design

We employed a 2 (memory: salient memory, non-salient memory) X 2 (arousal: CS+, CS-) within-participant design. All participants completed two sessions that took place in two consecutive days.

3.3.3 Stimuli and Material

Stimuli included 136 images chosen from those used in Chapter 1. As mentioned, there were originally 144 images; however, we have excluded 9 of them for the number of reasons: 3 images had red tones in them yielded very salient locations of the yellow key; 3 images that depicted some boards written words on them which might distract the participants; 2 images depicted baby rooms, which might attract emotional reactions; and 1 image which had scaled down and distorted the size ratio and looked odd or artificial. Other details were exactly the same and we have asked participants to fill out the same forms.

3.3.4 Procedures

3.3.4.1 Session 1.

The procedures were the same as those used in the session 1 in Chapter 2 (see Figure 3.1A).

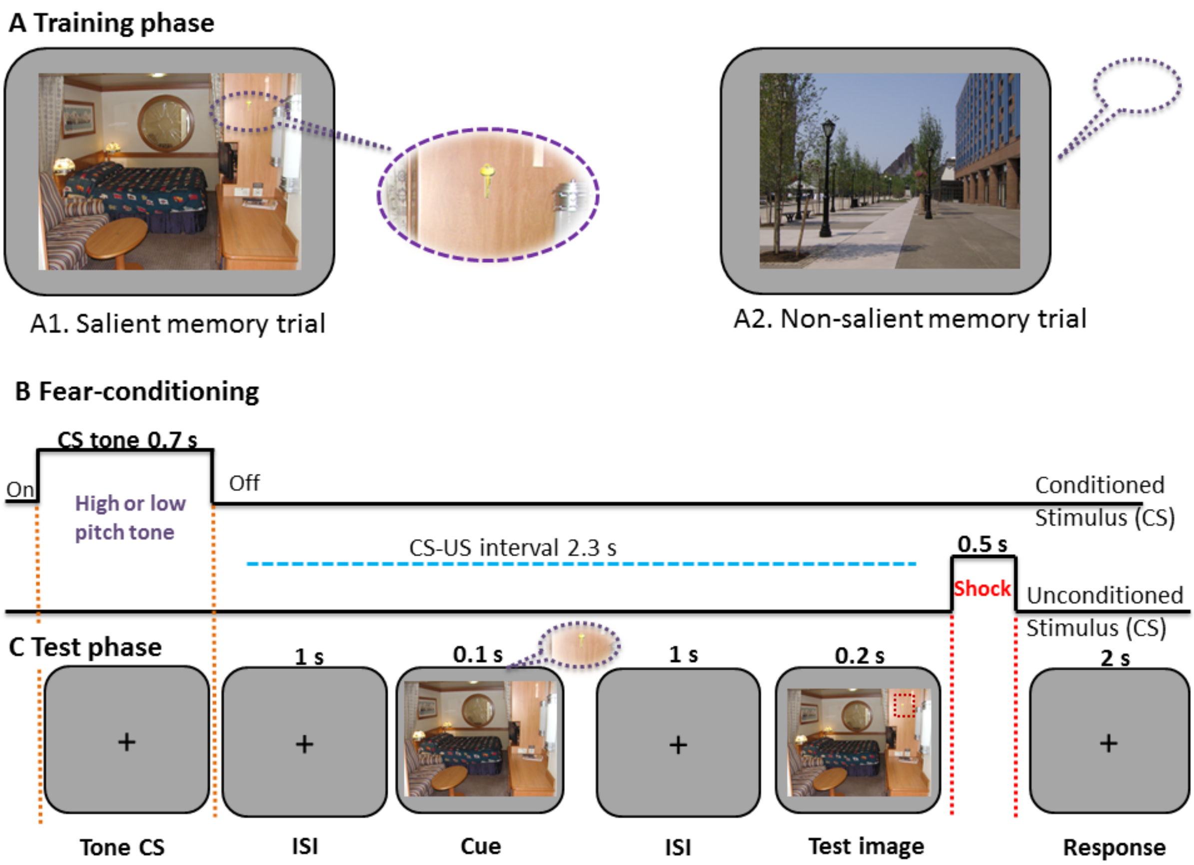

Figure 3.1. *(A) Example stimuli used in the training phase, where participants were asked to indicate whether they detected the target (**A1**; the salient memory condition) or not (**A2**; non-salient memory condition). Schematic illustration of (**B**) a trial in the fear conditioning phase and (**C**) a trial in the test phase from the salient memory condition. The interval between the CS+ and electrical stimulation (shock) was identical between (B) the fear conditioning phase and (C) the test phase. The red square was drawn for presentation purpose only to show the yellow target key on the 'Test image'; participants saw all scenes without the square.*

3.3.4.2 Session 2.

On the following day, participants completed the second session similar to what they did in Chapter 2. However we have made some modifications. In the fear-conditioning task (see Figure 3.1B), we used a longer ISI between the end of the tone and the start of the shock (2300 ms) in order to make the interval consistent with the test session. This was not considered in the first experiment. Next, participants completed a test phase (see Figure 3.1C) similar to what they did in Chapter 2. Since, we have not used new images; they saw the same 96 images that they saw in the training phase. To prevent fatigue, we had split the test phase into three blocks (32 trials in each block). Two-thirds of the trials included the scenes with the target key (64 trials; key present trials). In order to ensure that participants engaged with the task, we have still included trials where participants saw scenes that did not include the key (32 trials; key absent trials). Among the 64 key-present trials, 32 trials included scenes from the salient memory condition (13 trials with CS+, 13 trials with CS-, and 6 booster trials) and the other 32 trials included scenes from the non-salient memory condition (14 trials with CS+, 13 trials with CS-, and 5 booster trials). A single trial was similar to what has been described in Chapter 1. However, shock came after the test image to prevent participants' distractibility as oppose to during the test image in Chapter 2. ITI has been increased to 8 sec for booster trials and 2-8 sec jittered interval for other trials.

After the test phase, we assessed participants' explicit memory for the location of the target key. This was not measured in the first experiment and we were unsure how strongly participants remembered the locations of the target. In this explicit memory test, a trial began with the presentation of a scene without the target key. Participants indicated whether the scene included the key or not based on their memory. When they thought the scene included the key, they were asked to press the left button of the mouse and the target key appeared at the centre of the screen. Then, they were asked to drag and move the key to the location where they thought it was before. In contrast, when they thought that the scene did not include the key, they pressed the right button of the mouse and moved to the next trial. Feedback indicating whether the response was correct or incorrect was provided after participants made the initial decision in each trial. The duration of the trials was self-paced and there was no time-limit.

3.3.5 Electric Shock and Skin Conductance

Administration of the electrical stimulation was performed with the similar procedure in Chapter 2 using the Powerlab system and LabChart version 7 (ADInstruments Ltd, Chalgrove, Oxfordshire, UK). During the fear conditioning task, participants' SCR were also recorded from the middle and index fingers of their left hand at 1000 Hz sampling rates.

Prior to the session, we determined the amplitude and frequency of "highly unpleasant but not painful" level of electrical stimulation for each participant (M = 3.91 mA, SD = 2.22; M = 52.41 Hz, SD = 42.68). The level determined was used throughout the fear conditioning phase. To prevent habituation to the shock, after the fear-conditioning task and after each block of the test phase, we asked participants whether they still felt "highly unpleasant but not painful" feelings to the shock. Some participants (N = 14) asked the experimenters to slightly increase the level of stimulation to make the shock "highly unpleasant but not painful"; therefore, in these occasions, we increased the level of stimulation for this subset of participants (the averaged increase of shock was 0.46 mA and 9.33 Hz). Four participants rather asked the experimenters to decrease the level of stimulation because they felt too uncomfortable with the initial level and therefore we adjusted the level of stimulation for the small number of participants (the average change was 0.25 mA and 5.35 Hz). This procedure ensured that the administration of stimulation was subjectively felt "unpleasant but not painful" for all participants throughout the experimental session.

3.3.6 SCR Analysis

SCR data epochs were analysed in the same manner as Chapter 2. More specifically the data were extracted from a time window between 0 and 10 s after CS tone onset, and baseline-corrected between 0 and 1 s. The peak SCR amplitude was taken between 2 and 10 s from the trial-by-trial average SCR epoch as a function of CS tone. Data from the first trial were removed as responses in this trial could reflect orientation response (J. Li et al., 2017).

3.4 Results

Results from booster trials were excluded from all analyses (both fear-conditioning and the test phases) because we were interested in the effects of emotional arousal induced by anticipation of shocks, rather than the effect of the shock per se.

3.4.1 Training Phase

Reaction times and accuracy during the training phase were analyzed using two repeated measures ANOVAs with an independent variable of blocks in order to test participants' performance over time. The analyses revealed the main effects of blocks in accuracy, F (5,235) = 11.14, $p < .001$, $\eta_p^2 = .19$, and in reaction times, F (5,235) = 150.69, $p < .001$, $\eta_p^2 = .76$. These findings suggest that participants' performance improved across six training blocks as reflected by increased accuracy and decreased reaction times (see Figure 3.2A). The percentage of scenes where participants correctly identified the target key (M = 97.56%, SD=1.18) and the percentage of scenes where they correctly identified the absence of the target (M=94.25%, SD=1.31) were also above 90% across all blocks. These results indicate that participants successfully learned the target's location in each scene as observed in other studies with a similar paradigm (Patai et al., 2012; Stokes et al., 2012; J. J. Summerfield et al., 2006)

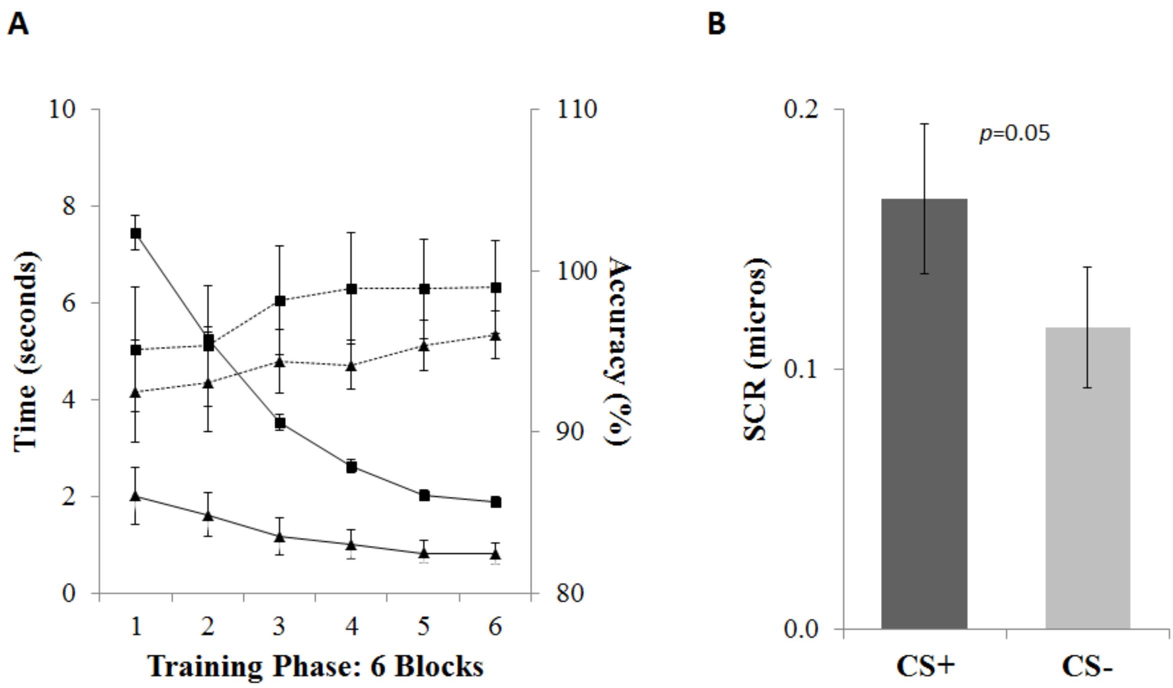

Figure 3.2 (A) *Participants' performance improved over the six blocks in the training phase. The figure includes the RTs (solid line) and the accuracy (dashed line) for the detection of the presence (squared line) and the absence (triangle line) of the target key within each scene.* ***(B)*** *Participants' SCR was higher in the CS+ condition compared to the CS- condition during the fear conditioning phase. Error bars represent the standard error of the mean (SEM). ** $p < 0.01$*

3.4.2 Fear-conditioning Phase

SCRs were greater in the CS+ trials (M = 1.68, SD=0.19) than in the CS- trials (M = 1.2, SD=0.15; see Figure 3.2B), t (41) = 1.96, p = .05, Cohen's d = 0.42. Thus, participants acquired fear response to CS+ tone. We also analysed participants' subjective ratings of being uncomfortable for shock and found that they reported stronger negative feelings towards electric shock at Time 2 (M = 4.33, SD = 1.51) relative to Time 1 (M = 3.27, SD = 1.72), t(41) = 3.35, p<0.001, Cohen's d = .66. These results suggest that participants maintained or even increased their negative feelings towards shock over the course of the experiment.

3.4.3 Mood

Data from mood questionnaires showed normal and near-to-normal distributions for all scales and also questions for stress and sleep; histograms were very similar to what has been shown in Chapter 1 (see Table 3.1 for the means and standard deviations). None of these questionnaires' scores did negatively correlate with the SCR difference results which was obtained by subtracting the average SCR to the CS- trials from the average SCR to the CS+ trials, (rs < .2, ps > .3), except CES-D, r = .29 p < .05, suggesting that participants who scored higher in depressive symptoms had a smaller difference in their SCR between CS+ and CS- conditions (see Appendix 6).

Table 3.1. Means, standard deviations, minimum and maximum values of Mood Scales.

	Mean	SD	Minimum	Maximum
TAI	37.74	9.24	24	60
CES-D	10.89	8.91	0	35
IUS	57.26	18.11	30	102
SAI-Time 1	37.98	7.08	24	51
SAI-Time 2	39.52	6.79	26	52
PAS*-Time 1	28.33	6.74	17	46
PAS-Time 2	25.65	8.74	10	50
NAS*-Time 1	12.82	2.81	10	22
NAS-Time 2	12.98	3.64	10	26
Sleep last night	7.36	1.19	4.5	10
Sleep in general	7.65	1.08	6	11
Stress on the day	7.65	1.08	1	7
Relative Stress	4.63	1.57	1	7

* PAS: Positive Affect Scale and NAS: Negative Affect Scale

3.4.4 Performance in the Test Phase

Given that our main focus was on the effects of emotional arousal on the target detection based on long-term memory, our analyses focused on performance in the target present trials in the test phase. The average accuracy of participants' response in the catch trials (i.e., target absent trials) was high (M = .89, SD = .31), confirming that participants engaged with the task. For key-present trials, trials with scene images where the participant failed to find the target key more than 3 times (i.e., half of the time) during the training phase were excluded from the analyses reported in this section (1.39% of all trials) to allow us to examine the effects of emotion on visual search based on strong long-term memory.

The mean reaction times from trials where participants made correct responses during the test phase were obtained for each participant for each condition. One participant was excluded due to not having any correct responses in the CS+ trials of the non-salient condition. Our prediction was that participants would perform better in the salient memory condition under emotional arousal and they would perform worse in the non-salient memory condition under emotional arousal. We expected a main effect of memory and an interaction effect between memory and arousal, with no main effect of arousal as seen in the previous studies (Sutherland & Mather, 2012). A repeated-measures ANOVA with arousal (CS+ or CS-) and memory condition (salient or non-salient) was performed on these mean reaction times using SAS Proc Mixed procedures (SAS 9.4; SAS Institute, Raleigh, NC, USA). This analysis showed a significant interaction between memory and arousal (see Figure 3.3), $F(1,44) = 10.18$, $p < .01$, $\eta_p^2 = .25$, with no significant main effects (ps > .10). Subsequent simple effect tests revealed that when participants were presented with the CS+ tone, they were faster to identify the target key in the salient memory trials (M = 505.98 ms, SD=268.45) compared to the non-salient memory trials (M = 592.24 ms, SD = 281.76), $t(44) = 3.46$, $p < .01$, Cohen's $d_z = .52$. In contrast, the difference between the two memory conditions was not significant in CS- trials ($M_{salient}$ = 593.54 ms vs. $M_{non\text{-}salient}$ = 541.76 ms; p > .07). In addition, in the salient memory condition, participants were faster to identify the target key in the CS+ condition (M = 505.99 ms, SD = 268.45) than the CS- condition (M = 593.54 ms, SD = 275.15), $t(44) = 2.71$, $p < .01$, Cohen's $d_z = .40$, but there was no significant difference between CS+ and CS- trials in the non-salient condition (p >.10). These results suggest that, consistent with our hypothesis, emotional arousal induced by CS+ enhanced the target detection based on long-term memory.

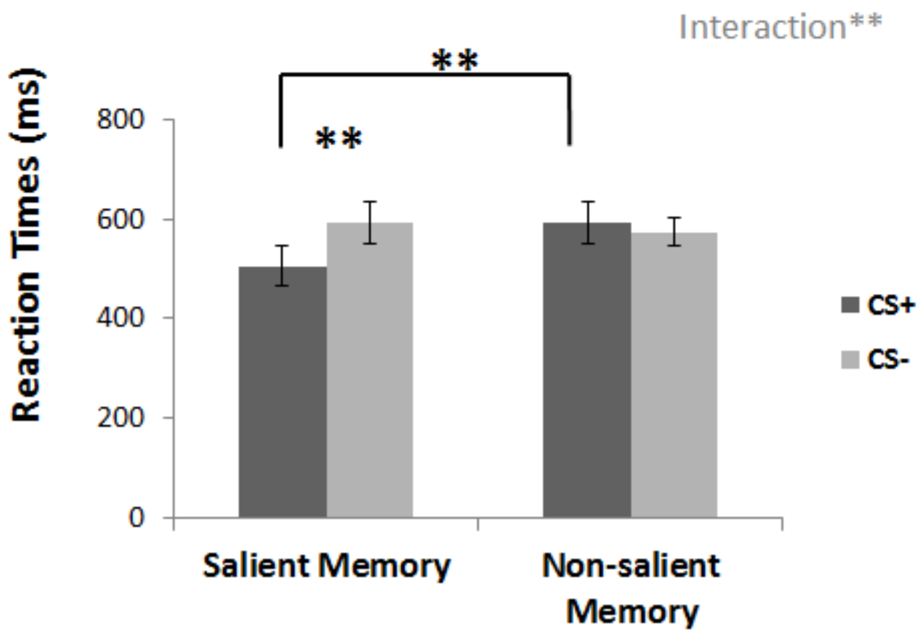

Figure 3.3. *During the test phase, there was a significant interaction between arousal and memory-salience, such that CS+ facilitated the detection of the target key in the salient memory condition. Error bars represent the standard error of the mean (SEM). ** $p < 0.01$*

We have further analysed participants' accuracy responses. A repeated-measures ANOVA with arousal (CS+ or CS-) and memory condition (salient or non-salient) was performed; and there was a significant main effect of memory, $F(1,44) = 94.70$, $p < .001$, $\eta_p^2 = .68$, and a marginally significant effect of arousal, $F(1,44) = 3.60$, $p < .07$, $\eta_p^2 = .08$, reflecting that participants were more accurate to identify the target key in the salient memory trials (*M* = 78.68 %, SE = 1.71) compared to the non-salient memory trials (*M* = 64.54 %, SE = 1.65). They were also more accurate in CS+ trials (*M* = 72.77 %, *SE* = 1.64) compared to CS- trials (*M* = .70.44, *SE* = 1.62). However, there was no significant interaction effect ($p > .20$). Therefore, the arousal-by-saliency interaction in the reaction times cannot be simply explained by the speed-accuracy trade-off (e.g., Reed, 1973).

Since we have had an issue with the low accuracy performance in Experiment 1, we have further tested whether accuracy in all conditions differ than chance level with four separate one-sample t-tests. Results revealed that participants' correct responses were above chance level for all conditions: CS+ non-salient memory, $t(44) = 7.88$, $p < .001$; CS+ salient memory, $t(44) = 16.52$, $p < .001$; CS- non-salient memory, $t(44) = 7.92$, $p < .001$; and CS- salient memory, $t(44) = 13.76$, $p < .001$.

Table 3.2. Means and standard deviations of accuracy (%) in each condition

Condition	**Mean (%)**	**SE**
CS+/Salient Memory	80.78	1.83
CS+/Non-Salient Memory	64.39	1.99
CS-/Salient Memory	76.96	1.91
CS-/Non-Salient Memory	63.59	1.77

3.4.5 Explicit Memory Test

As described above, our results from the test phase suggest that CS+ facilitated the detection of the target key when it appeared at the location predicted by long-term memory relative to the CS- condition. To see whether this significant difference was simply due to the fact that participants had better memory for the target location for scenes presented in the CS+ condition than in the CS- condition, we analysed performance in the explicit memory test. During this task, participants correctly identified whether or not the scene included the target in 62% of the salient memory trials. For the scenes that the participant correctly identified as it included the target key in Day 1 (i.e., training phase), we calculated the distance between the original location of the target key learned in Day 1 and the location that the participants recalled in the explicit memory test with the following Euclidian formula:

$$Distance = \sqrt{(diffx^2 + diffy^2)}$$

, where *diffx* refers to the difference between the original location and the retrieved location in the horizontal dimension and *diffy* refers to the difference between the original location and the retrieved location in the vertical dimension. This distance measure did not show a significant difference between CS+ (M = 110.55, SD = 90.08) and CS- (M = 106.34, SD = 75.10) trials ($p > .60$). Thus, reaction times results from the test phase were not readily explained by the difference in memory strength between those used in the CS+ condition than those used in the CS- condition. Additionally, we have conducted a 2 (arousal: CS+ or CS-) x 2 (explicit memory accuracy: accurate or wrong) repeated-measures ANOVA on the mean reaction times in the test phase in order to test whether the explicit memory interacts with arousal. This analysis confirmed a significant main effect of emotion, $F(1,44) = 9.64$, $p < .01$, $\eta_p^2 = .18$, showing faster reaction times to detect the target under arousal (M = 589.07, SE = 40.65) compared to CS- condition (M = 699.06, SE = 61.25). However, there was no main effect of explicit memory accuracy nor an interaction between arousal and explicit memory accuracy (*p*s > .50), suggesting that explicit memory performance did not affect the reaction times in the test phase to detect the target based on long-term memory.

3.4.6 Meta-analysis across Experiment 1 and Experiment 2

The two studies in Chapter 2 and Chapter 3 showed somewhat different results, but they were not contradictory to each other. In Chapter 2, Experiment 1 revealed an emotional impairment on memory-guided attention whereas Experiment 2 revealed an emotional enhancement effect where each of them supported one of our hypotheses. Therefore, we combined these two studies to conduct a meta-analysis in order to examine the emotional arousal effects on participants' reaction times based on long-term memory. We have only included target present trials from Experiment 1 to be consistent with Experiment 2. Difference scores of SCR, reaction times of memory for arousing condition (CS+/salient memory – CS+ non-salient memory), of memory for non-arousing condition (CS-/salient memory – CS-/non-salient memory), of arousal for salient memory (salient/CS+ – salient/CS-), of arousal for non-salient condition (non-salient/CS+ – non-salient/CS-) were first calculated for each study. Then, we have used the "meta" package in software R (Schwarzer, 2007) to calculate a fixed effect model for each of the difference scores. Fixed effect models assume that there is one true effect size that underlies all the studies in the analysis and is recommended when the number of studies are small (Borenstein, Hedges, Higgins, & Rothstein, 2010). Results revealed a significant effect of SCR ($z = 2.75$, $p < 0.01$), confirming that participants showed higher SCR in the CS+ condition than in the CS- condition. There was also a significant effect of memory for arousing condition ($z = 2.11$, $p < 0.05$), suggesting that participants performed faster in the salient memory condition when they heard the CS+ tone than when they heard the CS-tone across the two studies. Thus, it appears that arousal enhances the detection of the target based on long-term memory.

3.5 Discussion

According to the ABC theory (Mather & Sutherland, 2011), emotional arousal favours processing of high-priority information over low-priority information. While previous studies on the ABC theory predominantly focused on priority signals determined by goal-relevance or bottom-up saliency (T. H. Lee et al., 2018; T. H. Lee et al., 2015; T. H. Lee, Sakaki, et al., 2014; Sakaki, Fryer, et al., 2014; Sutherland & Mather, 2012, 2015), an increasing number of studies suggest that individuals' long-term memory is also a critical factor affecting information's priority. In the present study, we tested whether emotional arousal favours stimuli that have high-priority based on long-term memory, by presenting a fear-conditioned (CS+) or a neutral tone (CS-) during the memory-guided attention paradigm used in previous research (J. J. Summerfield et al., 2006). We found that the detection of a target key was facilitated by the CS+ tone than the CS- tone when the target key was presented at the location predicted by prior memory. Participants' arousal level measured by SCR yielded greater responses to CS+ cues than to CS- cues, confirming that participants acquired fear responses to the CS+ tone. Furthermore, the meta-analysis combining Experiment 1 (see Chapter 2) and Experiment 2 explained above confirmed an emotional enhancement effect on memory-guided attention. Thus, these results are consistent with our prediction that arousal not only interacts with priority signals determined by top-down goals or bottom-up saliency but also with priority signals determined by long-term memory.

The human visual system (but see for auditory system, Zimmermann, Moscovitch, & Alain, 2017) is highly sensitive to familiarity in the environment so that the brain can prioritise and use its resources accordingly (e.g., Chun & Jiang, 1998; Chun & Jiang, 2003; Rosenbaum & Jiang, 2013). Thus, long-term memories allow the brain to distinguish between old and new information to modify representations of the environment. Places or objects that were previously important are often prioritised during visual search, even though observers may not be aware of the previous exposures (e.g., Jiang, Swallow, & Rosen, 2013). Past experiences, therefore, serve as a basis of our expectation in a given environment. Locations that were once important in the past will preserve its importance in the future, giving ways to know where to attend. Expectations and prior knowledge therefore help to reduce the "computational burden" among stimuli to be perceived at a time (C. Summerfield & Egner, 2009). Emotional arousal is known to enhance prioritisation processes (Mather & Sutherland, 2011). Therefore, it is plausible to expect that arousal also enhances attending to a previously learnt location, possibly via reducing the number of competitions for representation in a given scene and at a given time. Consistent with the above literature, the results from the current study suggest that emotional arousal interacts with attention guided by long term memory.

Previous studies have shown that emotion affects episodic memory, such that emotionally arousing events are remembered better than non-emotional events (e.g., Bradley et al., 1992; Hurlemann et al., 2005; Kensinger & Corkin, 2003; Kensinger et al., 2007; LaBar & Cabeza, 2006; Sakaki, Fryer, et al., 2014; St. Jacques & Levine, 2007; Talmi, 2013). These findings have been typically explained by factors associated with learning or consolidation, such as the enhanced attention to emotional materials during learning or the amygdala's modulation effects on the hippocampal activity during learning and consolidation (for reviews, see Talmi, 2013; Turkileri & Sakaki, 2017). In contrast, the effects of emotional arousal on memory retrieval have been less examined in the literature. A few relevant literatures show that prolonged negative mood impairs retrieval of episodic memory (Ellis et al., 1985) and semantic knowledge (Sakaki et al., 2011). Emotional arousal also typically impairs the executive function (Kuhbandner & Zehetleitner, 2011) which is required to deliberately retrieve contextual details of previous memories (Dobbins, Foley, Schacter, &

Wagner, 2002). Taken together, these findings suggest that emotional arousal may impair memory retrieval and therefore hinder the effects of memory cues that evoke one's long-term memory concerning the location of the target key. In contrast, we found that emotional arousal rather facilitates the effects of the memory cues in guiding one's attention.

These results suggest that emotional arousal may have different impacts on memory cues depending on the strength of associated memory. When associations between cues and to-be-retrieved memories are relatively weak, individuals would need to exert deliberate efforts to retrieve associated memories when they are presented with cues. This deliberate process would be related to the prefrontal cortex and the executive function (Dobbins et al., 2002) which can be impaired by arousal (Kuhbandner & Zehetleitner, 2011). Thus, emotional arousal may reduce the effects of memory cues in this context. In contrast, when the links between cues and to-be-retrieved memories are strongly formed after repeated exposure as we have done in Session 1 in this study, associated memories can be retrieved automatically and rapidly with few cognitive resources (McDaniel & Einstein, 2000; McDaniel, Einstein, Guynn, & Breneiser, 2004). Emotional arousal may not impair this automatic retrieval process. Rather, once memories are retrieved, emotional arousal may amplify the effects of these memories in guiding one's behaviour via the selective enhancement effects on high-priority information. However, in the current study, we did not systematically manipulate the memory strength. Future research should manipulate strength of the cue-target associations and test whether emotional arousal has different effects depending on the memory strength.

Another related question concerns whether arousal equally enhances the effects of explicit memory (i.e., memories that participants are consciously aware of) vs. implicit memory (i.e., memories that participants are not necessarily consciously aware of). During our experiment, we tested participants' explicit memory about the location of the target for each scene and examined whether the CS+ tone has similar facilitative effects on the target detection irrespective of the performance in the explicit memory test. In this analysis, we found that CS+ had similar impacts on the target search irrespective of whether participants could explicitly retrieved the association between the scene and the target key. Additionally, we have confirmed that participants' accuracy performance in the explicit memory task (i.e., when they were asked to identify whether the target key had previously been present or absent) did not facilitate reaction times in the test phase. Together with the fact that the cues were presented only for a very short presentation (100 ms) in the test phase, these results suggest that the effects of arousal on the memory-guiding cues are at least partly due to the implicit memory derived from previous experiences and do not necessarily rely on explicit memories. However, we asked participants to locate the target key in the explicit memory task only when they had correctly identified the scene as target-present. Thus, the number of trials per cell was small in this analysis. Likewise, we did not experimentally manipulate nor measure whether participants explicitly vs. implicitly remembered the location of the target key during the test phase. Therefore, it is unclear if emotional arousal has stronger or even opposite effects on implicit vs. explicit memory cues. Future research should manipulate the cue presentation duration systematically together with arousal and test this issue.

Another question concerns the lack of the significant effects of emotional arousal in the non-salient memory condition. According to the ABC theory, emotional arousal should impair attention to low-priority information (Mather & Sutherland, 2011). One prediction that can be made is therefore that arousal should impair the target detection in the non-salient memory condition because the location of the target key has lower priority in this condition compared with the salient memory condition. However, while we found an impairment effect of arousal in the non-salient condition in Experiment 1, we neither saw the same effect in the current study nor in our meta-analysis. This lack of significant effects may be due to the fact that we used the same target key across all trials and therefore the target key itself gained goal-relevance over the course of the experiment, which may have obscured the impairing effects of arousal due to lack of long-term memory. Future research could manipulate the target type and/or target locations to overcome this issue.

Furthermore, we did not compare the effects of arousal on the memory-guided attention task vs. the visual-guided attention, where visual search is enhanced by a salient cue (Patai et al., 2012; Rosen et al., 2016; Stokes et al., 2012; J. J. Summerfield et al., 2006). Therefore, it is unclear whether the interaction between emotional arousal and memory-guided attention are smaller or larger than those with perceptual saliency documented in the literature.

In summary, this study provides evidence for the role of arousal on memory-guided attention. Our findings suggest that emotional arousal interacts with prior knowledge and one's expectations to guide current attention, supporting the ABC framework. More generally, the results indicate that emotion makes us even more likely to be biased by the information that has once been prioritised based on memory.

4 Chapter 4: Effects of Emotional Arousal on Ambiguous Motion Perception

4.1 Abstract

Arousal induced by emotional events sometimes enhances and sometimes impairs perception of subsequent emotionally neutral stimuli. Recently proposed theories suggest that these conflicting results reflect different effects of emotional arousal depending on stimulus saliency: such that emotional arousal enhances perception of salient stimuli but impairs perception of low-salient stimuli. In this study, we tested this prediction by examining the effects of emotional arousal on motion perception. We used two Gabor patches that drifted in opposite directions (one drifted to the left and the other drifted to the right) and superimposed one over the other. To examine the effects of saliency, we manipulated their contrast levels so that the two Gabor patches had only a small difference in their contrast levels and therefore the motion direction of the superimposed stimulus became ambiguous. Before each trial, arousal was manipulated by presenting a sound clip. Results showed that hearing an emotionally arousing sound enhanced the perception of the high-contrast motion direction over the low-contrast motion direction. The effects of arousal were not observed when there was no ambiguity in the direction of motions when the two Gabor patches had a clear difference in their contrast levels. These results are consistent with recent notions that emotional arousal interacts with saliency in perception, and suggest that emotional arousal induces a reduction on ambiguity in favour of high salient stimuli.

4.2 Introduction

Traditional accounts on cognition claimed that the early visual system is independent of other cognitive processes and is not affected by individuals' expectations or emotional states (e.g., Pylyshyn, 1999). However, a growing body of research suggests that emotional states of perceivers actually play an important role in early perception (e.g., Alpers & Gerdes, 2007; E. Anderson et al., 2011; Becker, 2009; Bocanegra & Zeelenberg, 2009; Phelps et al., 2006). In a brain imaging study, participants were presented with the faces in the centre surrounded by places (e.g., buildings) and it was found that negative faces increased the activity in the brain area that is responsible to represent scenes (i.e., parahippocampal place area), suggesting that emotion biases gating early visual inputs and alters perceptual encoding (Schmitz, Rosa, & Anderson, 2009). These effects of emotion on perceptual processing have been associated with the amygdala's modulation in sensory areas in the brain (A. K. Anderson, Chrristoff, Panitz, De Rosa, & Gabrieli, 2003; A. K. Anderson & Phelps, 2001; Vuilleumier, 2005; Vuilleumier et al., 2004).

Behavioural studies further provide evidence that emotion affects perception (E. Anderson et al., 2011); however, the results from these studies are rather inconsistent (see Mather & Sutherland, 2011, for a review). For instance, Phelps et al. (2006) presented participants with fearful faces or neutral faces prior to low spatial frequency (LSF) Gabor patches at different contrast levels, and examined whether emotional experiences induced by fearful faces alter the contrast threshold. Their results showed that participants' contrast sensitivity was improved after exposure to fearful faces than neutral faces, suggesting that emotional arousal induced by fearful faces enhances individuals' ability to perceive a subsequent non-emotional stimulus. In contrast, other studies reveal that emotional arousal impairs perception of a subsequent non-emotional stimulus (e.g., Bocanegra & Zeelenberg, 2009). In a rapid serial visual presentation (RSVP) paradigm, for example, presenting arousing taboo words, relative to less arousing words, impaired perception of a subsequent non-arousing word (Mathewson et al., 2008).

The arousal-biased competition (ABC) theory addresses this puzzle and suggests that emotional arousal enhances memory and perception of high-priority stimuli but impairs memory and perception of low-priority stimuli; the stimulus priority is determined by bottom-up saliency or top-down goal relevance (Mather & Sutherland, 2011). Consistent with this theory, accumulating evidence indicates that arousal has different effects on cognitive processes depending on stimulus' priority (T. H. Lee et al., 2018; T. H. Lee, Sakaki, et al., 2014; Sakaki, Fryer, et al., 2014; Sutherland & Mather, 2015). For instance, when participants briefly heard an arousing sound, they reported high-salient letters more than low-salient letters (Sutherland & Mather, 2012). However, most of these studies used high-level stimuli that require complex processes beyond basic visual features, such as faces, scenes, objects or letters (but see T. H. Lee et al., 2012). Therefore, the question of whether and how emotional arousal interacts with saliency in low-level visual perception still needs to be explored.

Gabor patches are low-level perceptual stimuli that drive early visual activity and enable researchers to examine how the early vision works in a controlled fashion by altering low-level features, such as contrast, size, and spatial frequency. Previous research examined individuals' perception of ambiguous motion by superimposing one moving Gabor patch over the other (Adelson & Movshon, 1982; Levinson & Sekuler, 1975; VanRullen, Reddy, & Koch, 2005). When the two Gabor patches have the same contrast and the same temporal frequency but differ in motion directions (e.g., one moves to the left and the other moves to the right), the two motion directions cancel out each other and perceivers typically see a stationary flicker without any motion (e.g., Levinson & Sekuler, 1975). In contrast, when the two patches differ in contrast levels, individuals are more likely to perceive the direction of the higher contrast patch (i.e., dominant direction) over the low-contrast one (Levinson & Sekuler, 1975; VanRullen et al., 2005).

Employing a similar paradigm, the present study aimed to investigate the interaction between emotional arousal and perceptual saliency in ambiguous motion perception. In our experiment, we manipulated participants' arousal presenting arousing vs. non-arousing sound clips. After each sound, participants were shown two Gabor patches that moved in different directions, which were superimposed one over the other. Their task was to decide the direction of the overall motion. For some trials, the two Gabor patches had a clear difference in their contrast levels (i.e., a low ambiguous condition) while for the other trials, they had only a small difference in their contrast levels (i.e., a high ambiguous condition). If arousal enhances signals of high-priority inputs as the ABC theory suggests, hearing arousing sounds relative to non-arousing sounds, should lead to the detection of the dominant direction (high contrast patch) when the motion direction is highly ambiguous. In contrast, in the low ambiguous condition, we expect that the high-salient signal is too strong that participants should always perceive the dominant direction irrespective of arousal levels. Therefore, we have used the low ambiguity condition as a control condition and did not expect a specific arousal effect on these trials. Besides, this condition was a good indicator whether participants understood the task and thus, we based our final sample examining participants' responses in this condition.

4.3 Method

4.3.1 Participants

Fifty-three undergraduate and postgraduate students at the University of Reading were invited to the study. The sample size was determined to ensure to detect the small-to-medium sized effects (Cohen's f = .24) that were observed in a prior study on the ABC theory (Sakaki, Fryer, et al., 2014). Three of them withdrew from the experiment after the practice session due to the discomfort of audio clips and/or the length of the experiment (i.e., 1 hour in total) (see Procedures). Two of the remaining participants were excluded from analyses due to a program failure. In addition, seven participants consistently indicated that they viewed a non-dominant motion direction in the low ambiguous condition (i.e., control condition) throughout the session. More specifically, in the low ambiguous condition, these participants chose the non-dominant (i.e., low-contrast) motion direction more than 50 % of the time during a practice session ((i.e., during which when we did not have any sound stimuli; see Procedure; M = 80.48 % of trials), as well as during the main task (M = 77 % trials in the arousing trials; M = 81.43 % trials in the non-arousing trials), suggesting that these participants failed to detect the salient signal or did not understand the instruction of the task. Therefore, data from these seven participants were excluded from the analyses. Thus, our analyses were conducted on data from 41 participants (34 female, 7 male; M_{age} = 21.56, SD_{age} = 3.45, age range = 18-31). All participants had normal or corrected-to-normal vision and normal hearing. The study was approved by the University Research Ethics Committee, and all participants signed an informed consent form.

4.3.2 Stimuli and Apparatus

Visual stimuli were generated using MATLAB and the Psychophysics toolbox (Brainard, 1997) and presented on a computer with a gamma-corrected Iiyama 15-inch

Vision Master Pro 1411 monitor (85-Hz refresh rate; resolution of 1024 x 768 pixels). Target stimuli were created with superimposing two identical Gabor patches onto each other (sinusoidal gratings enveloped by a 3 Cycles/deg Gaussian; see Figure 4.1). These Gabor patches moved to opposite directions with the temporal frequency of 10 Hz. In the high-ambiguous condition, one of the Gabor patches had a contrast of 56% while the other had a contrast of 44%. In the second condition (i.e., low ambiguous condition), the ratio of the contrasts of the two patches was 70/30% so that participants would be able to detect the direction of the dominant contrast (i.e., the direction of 70% contrast patch) most of the time.

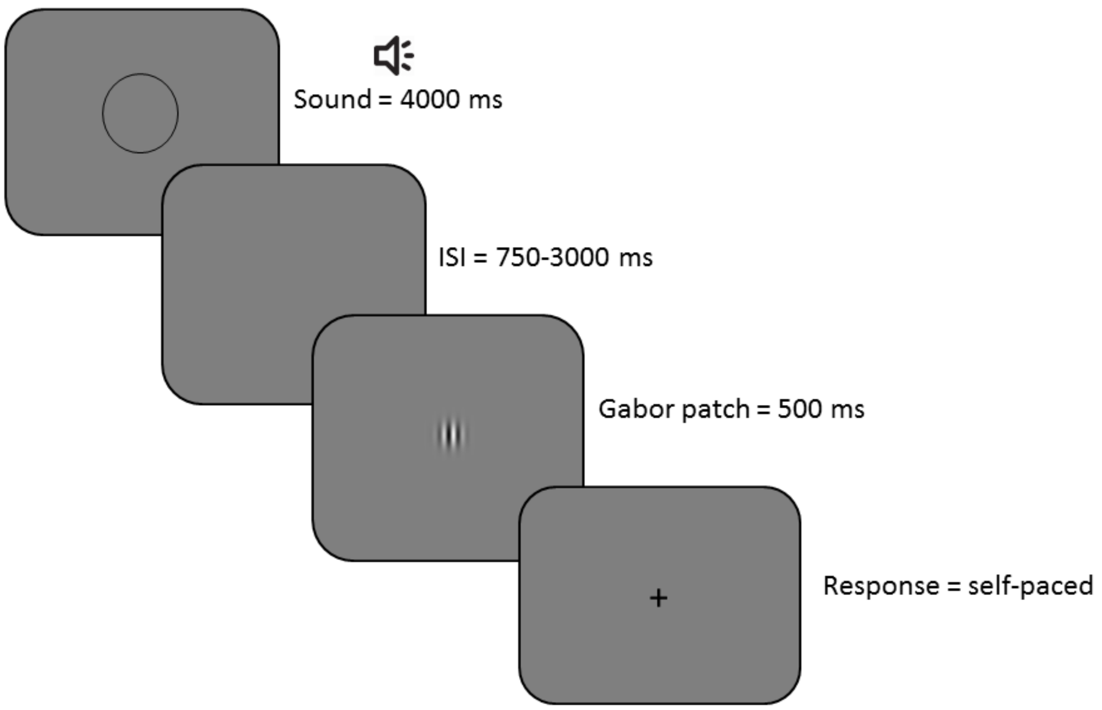

Figure 4.1. *Illustration of a single trial. Participants' task was to indicate whether the briefly presented target was moving to the left or right direction.*

Participants' emotional arousal was manipulated using sound clips. We obtained 200 sound clips from the International Affective Digitized Sounds (Bradley & Lang, 2000), previous studies (Sakaki, Ycaza-Herrera, & Mather, 2014), and online open sources. All of them were modified using Audacity (Audacity, 2012) so that they lasted for 4 seconds. These sound clips were rated by eight participants (5 female, 3 male; M_{age}= 31.87, SD_{age}= 7.19) with regards to their subjective arousal levels (1: not at all arousing – 9: extremely arousing) and valence (1: highly negative – 9: highly positive). Based on these ratings, 60 highly arousing negative sounds ($M_{arousal}$ = 7.32, $SD_{arousal}$ = 0.44, $M_{valance}$ = 2.28, $SD_{valence}$ = 0.61) and 60 low arousing neutral sounds ($M_{arousal}$ = 2.51, $\mathrm{SD}_{\mathrm{arousal}}$ = 0.83; $M_{valence}$= 4.93, $SD_{valence}$ = 0.40) were selected for our study. High arousing sounds included crying babies, domestic violence, and a car crash, while low arousing sounds included daily conversations in a restaurant and environmental sounds.

4.3.3 Procedure

The session started with a familiarization phase, which included 40 trials. During this phase, participants saw a non-ambiguous stimulus with a contrast ratio of 90/10% with various temporal frequencies (i.e., 5, 10, and 20 Hz) in order to ensure they understood the procedure and experienced the stimuli in advance. We next asked participants to complete a practice session (i.e., baseline measurement) with 60 trials. During the practice session, participants completed 30 trials in the high ambiguous condition and 30 trials in the low ambiguous condition in a randomized order. The contrast levels we used were the same as those used in the main task but we did not present any sound clips during this practice session to allow us to ensure that the participants were able to identify the high-contrast direction over the low-contrast direction when they did not hear any sound clips.

In the main task, participants completed three blocks; each block included 10 trials for each four condition in a randomized order (120 trials in total). For each ambiguity condition, half of the trials started with high arousing sounds and the other half included low arousing sounds. Each trial began with a sound clip for 4 sec and a presentation of a light grey circle (1.5^{o} x 1.5^{o} cm) which was placed in the centre of a uniform grey background, serving as a fixation guide, followed by a blank screen (in order to avoid after effect of the fixation cross) jittered between 750-3000 ms. We used a blank screen after the fixation guide to avoid any possible after-effect of the circle on the test stimuli (i.e., Gabor patches). The two superimposed Gabor patches were then presented for 500 ms, followed by the inter-trial interval for 4 sec, during which participants were asked to judge the motion direction irrespective of the sound types. Whether the dominant direction was leftward or rightward direction was randomly determined for each trial. After the main task, participants were asked to listen to all of the sound clips again and rate each of them in their arousal levels (1: not at all arousing – 9: extremely arousing).

4.4 Results

4.4.1 Sound Ratings

Participants showed higher arousal ratings for sound clips used in the arousing condition (M = 6.94, SD = 1.57, *Median* = 7.22) than those used in the non-arousing condition (M = 1.71, SD = .83, *Median* = 1.45), $t(40) = 22.58$, $p < .001$, 95% CI [4.76, 5.70], Cohen's $d_z = 3.52$. However, there were also large individual differences in the ratings of the sounds between the arousing and non-arousing conditions, such that the difference in the average arousal score between the conditions varied across participants from 0.80 to 7.75 (M = 5.23, SD = 1.48). To take into account these individual differences, for each participant, we categorized sound clips into two categories based on the median of his/her arousal ratings.

Five participants had a median of 1, leaving no room for low arousing condition; however, we did not exclude these participants so that we can still estimate the effects of ambiguity for these subset of participants in the main analysis (see Section 4.4.3).

4.4.2 Baseline

Results from the baseline session showed that participants chose the dominant direction more often in the low ambiguous condition (M = 78.54 %, SD = 22.15) than high ambiguous condition (M = 57.64 %, SD = 17.42), $t(40) = 6.362$, $p < .001$, $d_z = .99$, 95% CI [-27.53, -14.26], confirming that the ambiguity manipulation was successfully applied.

4.4.3 Main task

Participants' choice during the main task was coded as "1" when they selected the direction of the Gabor patch with a stronger contrast and "0" when they selected the direction of the patch with a weaker contrast. A hierarchical generalized linear model (HGLM) analysis was then performed on the participants' mean direction choices using SAS Proc Glimmix procedures (SAS 9.4; SAS Institute, Raleigh, NC, USA). Level-1 unit is each trial and Level-2 unit is each participant. Predictors included arousal (arousing vs. non-arousing), ambiguity (high ambiguous vs. low ambiguous) and the interaction between arousal and ambiguity. We also included random effects for participants, random participant slope for ambiguity, random participant slope for arousal, and random participant slope for the interaction between ambiguity and arousal. This analysis[1] showed a main effect of ambiguity, $F(1,36) = 11.67$, $p < .001$, and a significant interaction between ambiguity and arousal (see Figure 4.2), $F(1,36) = 5.66$, $p < .05$, with no main effect of arousal ($p > .10$). Subsequent simple effects analyses revealed that when participants heard more arousing sounds, they were better at choosing the dominant direction in the high ambiguous condition (M = 64.92

[1] Results including whole sample showed a main effect of ambiguity ($t(42) = 6.06$, $p < .001$) with no main effect of arousal ($p = .85$) nor an interaction effect between ambiguity and arousal ($p = .15$).

%, *SD* = 16.12 %) compared with the non-arousing condition (*M* = 58.96 % , *SD* = 19.57 %), *t* (36) = 2.44, *p* = .05, 95% CI [1.02, 10.90], Cohen's d_z = 0.40. In contrast, there was no effect of arousal in the low ambiguity condition as predicted (*p* = .61).

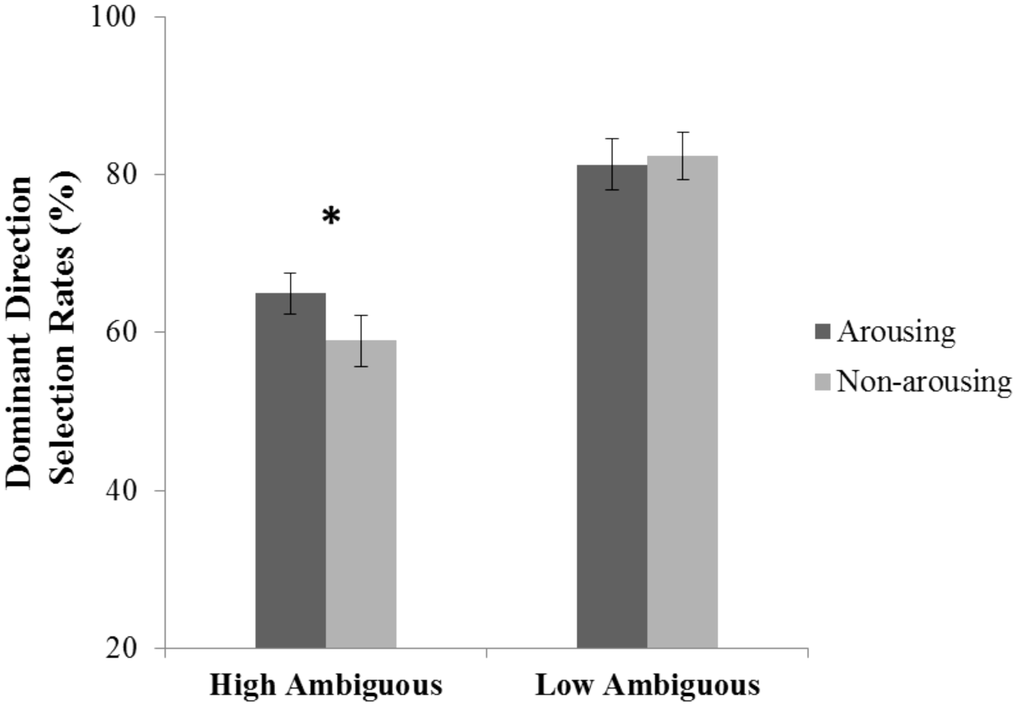

Figure 4.2. *Results showed that there was a significant interaction between arousal and ambiguity, such that emotional sounds facilitated the detection of the dominant direction in the high ambiguous condition. Error bars represent within-subjects standard error of the mean (SEM). * p < .05*

4.5 Discussion

In the present study, we tested the prediction of the ABC theory that arousal enhances high-salient inputs over low-salient inputs and found that when participants received two motion inputs (one from a high-contrast stimulus and another from a low-contrast stimulus), they were more likely to perceive the high-contrast direction over the low-contrast direction under arousal. Thus, these findings are consistent with our prediction that arousal interacts with saliency in perception even when the high- and the low-salient inputs are otherwise identical. The results are also in line with previous findings, which suggest that emotion enhances visual perception (Bocanegra & Zeelenberg, 2009; T. H. Lee et al., 2012; Phelps et al., 2006; Zeelenberg & Bocanegra, 2010). However, a note of caution is due here since we only had a marginally significant effect of emotional arousal on the highly ambiguous stimuli.

Recent research suggests that our emotional states influence what we perceive (E. Anderson et al., 2011), perhaps a notion that has recently been fully acknowledged (for a review, see Pessoa & Ungerleider, 2004). Emotional stimuli affect attention automatically (Öhman, 2002; Vuilleumier, Armony, Driver, & Dolan, 2001) and do sometimes so even without conscious awareness (Morris et al., 1998; Whalen, 1998). Such effects of emotion on attention are explained by the amygdala's modulation on the visual cortex (e.g., Vuilleumier et al., 2001) as well as the role of the top-down attentional mechanisms on emotional stimuli (Pessoa et al., 2002). Attention also alters the appearance of a stimulus, which mediates changes in perception of higher-level aspects, such as subjective feeling (for a recent review, see Carrasco & Barbot, 2019). Thus, there is growing appreciation on the complex interaction among attention, perception and emotion; and our results further supported that emotional arousal alters low-level perceptual processes.

Studies on visual perception reveal that emotion makes people to overestimate the distance from a balcony ledge (Stefanucci & Storbeck, 2009) and the steepness of a hill (Stefanucci, Proffitt, Clore, & Parekh, 2008). Emotion also affects our time perception, such that participants under emotional arousal believed more time or less time had passed than actually did (Droit-Volet & Gil, 2009; Wittmann, 2009; Yamada & Kawabe, 2011). These findings suggest that changes in arousal and attention have an important impact on temporal judgments and contribute to emotional distortions of perception within the context of internal clock models of time perception (for a recent review, see Lake, LaBar, & Meck, 2016). Our results, therefore, are line with a broader research suggesting that emotion also facilitates early processing of visual features such as colour and brightness via attentional gain and cost (Bocanegra & Zeelenberg, 2009; Ferneyhough, Kim, Phelps, & Carrasco, 2013; T. H. Lee et al., 2012; Phelps et al., 2006; Song & Keil, 2013). We expand these findings and suggest that emotional arousal also modulates ambiguous motion perception.

The main challenge faced by vision researchers is the question of how the brain computes a global percept from many isolated local cues that is evident in the small receptive field size of neurons in early visual cortex (Adelson & Movshon, 1982; Fennema & Thompson, 1979; Marr & Ullman, 1981). Thus, there is an ongoing debate whether we perceive the world as a continuous flow of information or in discrete episodes (Crick & Koch, 2003; Harter, 1967; Holcombe, Clifford, Eagleman, & Pakarian, 2005; Kline, Holcombe, & Eagleman, 2004; Purves, Paydarfar, & Andrews, 1996; Shallice, 1964; VanRullen & Koch, 2003; VanRullen, Reddy, & Koch, 2006). It has been suggested that the visual perception involves interpretation of the sensory data in accordance with the sensory sampling of the world (Leopold, Wilke, Maier, & Logothetis, 2002). When a stimulus is ambiguous or contradictory, vision lapses into a chain of continually alternating percepts; switching very few seconds (e.g., 100 ms; VanRullen & Koch, 2003) between two or more visual interpretations of the stimulus. This phenomenon is called 'wagon-wheel illusion', which is thought to show a neural temporal sampling process, leading to the perception of reversals in the same way as the discrete snapshots of a movie camera (Andrews & Purves, 2005; Crick & Koch, 2003; Purves et al., 1996; Simpson et al., 2000; VanRullen & Koch, 2003; VanRullen et al., 2006). VanRullen et al. (2005) suggest that the perception of reversals is linked to fluctuations in the frequency of the temporal sampling process and motion information is perceived in discrete episodes at a rate between 10 and 15 Hz.

We have successfully created such bi-stable motion stimulus, in which both possible percepts correspond to the same object, differing only in their contrasts, and are perceived as identical stimuli moving at the same speed and changing only in direction. However, as described in the method section, we had a small subset of participants who constantly perceived the non-dominant motion direction. These observers reported the motion direction of the higher contrast component either at chance level or perceived the motion direction of the lower contrast component (i.e., a non-dominant direction) in many trials. If the motion perception occurs in snapshots of 100 ms in duration (VanRullen et al., 2006), then these subset of participants might have experienced a switch from the dominant direction to the non-dominant direction within the time window of 500 ms duration of the stimuli and they possibly reported the second or third percept (i.e., non-dominant direction). Alternatively, they might have been unsure about the percept and simply guessed the direction. We have anecdotal evidence from some participants, suggesting they found the task difficult to perform. Besides, we did not have an explicit option to select if the observer was unsure of the motion direction. Future research should incorporate such option to understand perceptual experiences of these participants (e.g., Hupé & Rubin, 2003). Besides, our results should be interpreted cautiously and should be replicated before drawing conclusions. For instance, the design of the current study can be improved using actual and perceptual changes between the two motion directions as VanRullen et al. (2005) did. In that case, emotional arousal could decrease the perceptual changes if it helps to enhance dominant direction suggested by ABC theory (Mather & Sutherland, 2011).

In a different line of research on binocular rivalry, it is widely accepted that the bi-stability arises from active competition between two rivalries, which is implemented via reciprocal inhibition between the two percepts (e.g., Blake, 1989; Laing & Chow, 2002; Lehky, 1995). Neuroimaging studies with binocular rivalry and ambiguous figures revealed a frontoparietal network of activity that is typical to switch-related responses (e.g., Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998). Recent neuroimaging studies on wagon-wheel illusion showed that the perceptual switches are elicited by the area called MT/V5, which is commonly referred to as the human motion complex and as well as the frontoparietal regions that are involved in more general aspects of visual perception such as attentional selection and processing of perceived salience (Sterzer, Russ, Preibisch, & Kleinschmidt, 2002). In an MEG study, ambiguous bistable apparent motion is observed in a component at around 160 ms after the frame change, the magnitude of which depended on the perceived motion whereas the brain responses to less ambiguous and physically unambiguous motions did not evoke such a component (Kaneoke, Urakawa, Hirai, Kakigi, & Murakami, 2009). The differential activity evoked by the ambiguous stimuli suggests that the competitive neural activities for the two possible percepts exist even when one dominant image is continuously perceived. A further study with a focus on brain-imaging can reveal how brain areas responsible for emotional arousal (e.g., locus coeruleus) can alter signals to early visual cortex, for instance focusing on the right and left MT/V5 using such motion perception paradigm.

In summary, this study provides evidence for the role of arousal in ambiguous motion perception. Our findings suggest that emotional arousal interacts with bottom-up saliency in favour of high salient signals, supporting the ABC framework. More generally, the results indicate that emotional arousal overrides ambiguity towards the salient feature of the information at hand.

5 Chapter 5: General Discussion

5.1 Abstract

In three experiments, I have examined the effects of emotional arousal on memory-guided attention (Experiment 1 and Experiment 2) and on ambiguous motion perception (Experiment 3). According to the Arousal Biased Competition (ABC; Mather & Sutherland, 2011) theory, arousal should enhance memory and perception of something important or relevant and should impair memory and perception of other stimuli. Our results confirmed the arousal-enhancing effect on both attention guided by long-term memory (Chapter 3) and ambiguous motion direction (Chapter 4), but the impairing effect that we found in the first study (Chapter 2) was somewhat confounded by the low accuracy results. Therefore, the findings partially confirmed the ABC theory's predictions. Nevertheless, the results are in line with the broader literature that suggests emotional enhancement to perception and attentional guidance. In this chapter, I discuss some of the strengths and limitations of the three studies and provided some implications and suggestions for the future.

5.2 Summary of the Findings

In the first two experiments, we have measured participants' performance on memory-guided attention with a visual search task while manipulating their emotional arousal with a fear-conditioning paradigm. There is a growing interest towards the notion that long-term memory guides attention (Awh et al., 2012; Hutchinson, Pak, & Turk-Browne, 2015; Hutchinson & Turk-Browne, 2012; Patai et al., 2013; Patai et al., 2012; Stokes et al., 2012; J. J. Summerfield et al., 2006; J. J. Summerfield et al., 2011); but to our knowledge, these are the first two studies that have tested arousal effects on attention guided by past experience. In the first study (Chapter 2), we observed an emotional impairment effect on the reaction times to a target that have not previously been studied (i.e., non-salient memory). However, the results were somewhat problematic due to the small and unequal number of trials across conditions. Participants' accuracy was also low when the memory was not strong (i.e., non-salient memory) or when new images were used, suggesting a speed-accuracy trade-off (Reed, 1973). To address these issues, we made some modifications into our visual search task in the second study (Chapter 3). Specifically, we omitted new images and decided to compare performance between the salient memory condition which participants knew exactly where the target would appear with performance of the non-salient memory condition which participants were presented without the target (i.e., they did not have prior knowledge about the location of the target). Results revealed that participants were faster to react to the targets of the salient memory trials under emotional arousal, suggesting that arousal induced by CS+ enhanced the effects of long-term memory in guiding attention. These findings are consistent with recent findings that arousal amplifies the effects of priority (T. H. Lee et al., 2018; T. H. Lee, Sakaki, et al., 2014; Sakaki, Fryer, et al., 2014; Sutherland & Mather, 2012, 2015, 2018) and extend them to another source of priority-- long-term memory.

In the last experiment (Chapter 4), we used an ambiguous motion perception task and manipulated participants' arousal level with negative arousing sound clips. We created ambiguously moving stimuli using two Gabor patches superimposed onto each other and manipulated the contrast levels: highly ambiguous vs. less ambiguous. Results revealed that hearing an emotionally arousing sound enhanced the perception of the high-contrast motion (i.e., dominant or prioritised) direction over the low-contrast motion direction. This effect was absent in the less ambiguous condition as participants perceived the high contrast direction most of the time when they heard both arousing and non-arousing sound clips. These results confirmed the ABC theory's predictions and expanded further, suggesting emotional arousal induces a reduction of ambiguity in favour of the high-prioritised stimuli. To our knowledge, this is the first study which has tested the prediction of the ABC theory on such low-level motion perception stimuli (but see T. H. Lee et al., 2012).

The ABC theory proposes that emotional arousal sometimes enhances and sometimes impairs attention and perception depending on the priority of the stimulus (Mather & Sutherland, 2011). This theory has now been confirmed by a number of studies (T. H. Lee et al., 2015; T. H. Lee et al., 2012; T. H. Lee, Sakaki, et al., 2014; Sakaki, Fryer, et al., 2014; Sutherland & Mather, 2012, 2015, 2018). Our results from the three studies, therefore, expand upon these findings and further suggest that arousal not only interacts with bottom-up saliency and top-down goals but also affects priority signals a) based on long-term memory in guiding attention and b) based on low-level visual features.

5.3 Critical Evaluation

5.3.1 General Strengths

This thesis has provided a deeper insight into the effects of emotional arousal on cognition. Past research focused on the effects of emotion on attention, memory, and perception separately. However, it is known that cognitive processes are complex in their nature and all aspects of cognition are intertwined with one another. Here, we have combined attention and memory to better understand the manifold effects of emotional arousal. We have also tested how arousal affects ambiguous motion perception. More importantly, we do not envisage cognition and emotion as separate phenomena; rather we consider emotion as part of cognition that serves for the best interest of the individual.

5.3.1.1 Experiment 1 & 2

In the first two experiments, we used a visual search task adapted from previous studies (Patai et al., 2012; Stokes et al., 2012; J. J. Summerfield et al., 2006; J. J. Summerfield et al., 2011) and successfully confirmed that the selection history from past experiences can guide attention. We carefully selected the images, avoiding salient pictures that would evoke emotional responses or would distract participants; such as, luxury places, nursery room, messy offices, famous or familiar landscapes, and as well as the pictures including bright colours (e.g., red colour), which the yellow target key would pop out. More importantly, we placed the target key in the locations where the target would not draw attention automatically, avoiding the most salient areas in each scene using a saliency algorithm (Harel et al., 2007). Therefore, our results cannot be explained by the sole bottom-up saliency during memory encoding or visual search, but rather it should be attributed to the encoding and retrieval of each spatial location and as well as learning the absent of the target. The findings of the first two studies add to the ever-expanding field of emotion studies as well as recently proposed selective attention based on selection history.

Recent accounts of selective attention (Awh et al., 2012; Hutchinson & Turk-Browne, 2012; Theeuwes, 2019) highlight the need to depart from the dichotomy of bottom-up saliency and top-down goals and further suggest a new category based on past experiences:

selection history. We have successfully confirmed that participants have learnt the spatial locations of the target key over the six blocks during training phase and were able to retrieve their knowledge during the test phase. Past research using a similar paradigm also suggested that memory guides attentional orienting within a short time window (e.g., J. J. Summerfield et al., 2006). Our two studies expand upon these findings suggesting an emotional enhancement effect of orienting attention based on prior knowledge.

We also successfully manipulated participants' arousal level using fear-conditioning. The level of electrical stimulation was calibrated by the experimenter for each participant, asking participants to test different levels and agreeing the most suitable level at which they felt unpleasant but not painful. We started testing with the lowest intensity, slightly increasing the level until they felt unpleasant. Participants were also encouraged to try higher levels and to turn back if necessary. This ensured that all participants subjectively felt emotionally aroused, which was evident in both SCR difference between CS+ and CS- trials and participants' subjective ratings before and after the experiment. The two tones used as CS+ and CS- were counterbalanced across participants, ensuring that there were no differences between the arousing vs. non-arousing stimuli except for the association with shock.

Since mood and subjective feeling affect one's performance, they may modulate the effects of arousal. Therefore, we used mood questionnaires and subjective ratings of overall health, sleep quality, and stress level. Results showed a normal distribution for these measurements, confirming the generalizability of our findings to the population. More importantly, the SCR results of arousal were not modulated by mood states. Overall, this work contributes to existing knowledge of emotion research by providing new insights towards memory-guided attention.

5.3.1.2 Experiment 3

In our last experiment, we created ambiguous motion stimuli using Gabor patches. These are useful tools to measure low-level features of perception with a controlled fashion. We then showed that participants were able to perceive the dominant direction in the low ambiguous condition, but this dominance became ambiguous when we altered the contrast levels of the two Gabor patches without changing other features, such as phase, temporal or spatial frequency. The method used here might be applied to the brain imaging studies of emotion to explore how emotion-related brain regions interact with early visual areas (i.e., MT/V5). Therefore, the insights gained from this study should lead to new research to further investigate neural correlates of the interaction between emotional arousal and vision.

We manipulated participants' arousal with short sound clips, which have been widely used in the literature (e.g., Sutherland & Mather, 2012). One problem with using such stimuli is the variety of individual differences in arousal to each sound even though they are taken from a standard database (Bradley & Lang, 2000). This was evident in participants' subjective judgements that were collected after the main task. Therefore, we modelled participants' own ratings in our analysis using a hierarchical approach. The methods applied here should be useful in other experimental studies to deal with random effects of individual differences as well as other factors including stimuli (Murayama, Sakaki, Yan, & Smith, 2014).

5.4 General Limitations

In all three studies, we focused on the arousal aspect of emotion; however, valence is another important feature that might affect cognitive processes. ABC theory (Mather & Sutherland, 2011) does not provide a distinctive prediction based on valence; rather suggests that experiencing emotional arousal of either valence should enhance attention and perception to the prioritised stimuli. There are studies showing that positive and negative material affects cognition differently (Becker, 2009); however, it is unclear whether positive stimuli that have been used in these studies were as equally arousing as negative stimuli. Sutherland and Mather (2018) presented high and low salient letters alongside with a positive arousing, negative arousing, and neutral sounds and suggest that arousal, but not valence, amplifies the effect on priority. Nevertheless, it should be noted that our results are limited to negative arousing events.

In the first two experiments, we measured participants' memory performance; however we did not compare memory cues with current visual cues unlike previous studies using a similar paradigm (e.g., J. J. Summerfield et al., 2006). In this study, participants were presented with a memory cue as an image that they have seen before and a visual cue as a new image showing the likely location of the target. The researchers then compared the performance with memory cues and visual cues and found a faster respond to memory cues. In our studies, since we only had memory cues, it might be possible that the saliency of the presence of the target key in the test image also guided attention. Without making a comparison between visual cues and memory cues, it is difficult to overcome the potential bottom-up saliency of the target. However, it should be noted that unlike previous studies mentioned above, we placed the target in less salient areas in a given scene; thus, the target key should not grab attention in the first saccade or so, which typically occurs within 200 ms (i.e., the duration of the test image). Nevertheless, it would be interesting to compare arousal effects on visual-guidance vs. memory-guidance on attention.

In the first two studies, the most important limitation lies in the fact that we failed to find an impairing effect of arousal. Although the first study initially suggested that arousal impaired reaction times to less salient stimuli, we approached this finding cautiously due to the low accuracy results in the same condition alongside some problems in the design discussed in Chapter 2. Additionally, neither the second study nor the meta-analysis of the two studies revealed an arousal-impairment effect on attention guided by memory, despite our predictions. Therefore, it seems likely that the effects of arousal on enhancement for attention to cues predicted by long-term memory are stronger than the effects of arousal on impairment for attention to cues not predicted by long-term memory. A further study should test this prediction directly using a different paradigm.

A main weakness of Study 3 was the inability to interpret why a small number of participants constantly chose the non-dominant direction even in the absence of any sound manipulation and when the stimuli was less ambiguous. These observers reported the motion direction of the higher contrast component either at chance level or in some cases they may have reliably seen the motion direction of the lower contrast component (i.e., non-dominant direction). If the motion perception occurs in snapshots of 100 ms in duration as suggested by VanRullen et al. (2006), then these participants might have seen the switch from dominant direction to non-dominant direction within the time window of stimulus duration (i.e., 500 ms) and might have had difficulty choosing which direction to report. We have anecdotal evidence from some participants that they saw double direction or no obvious direction throughout the session. Therefore, further work is needed to replicate this finding. Overall, in spite of its limitations, this thesis adds to our understanding of the emotional arousal on attention, memory, and perception.

5.5 Implications

Our findings confirmed that past experiences influence current attention and that arousal interacts with prior knowledge. Extensive research focused on whether emotion affects bottom-up saliency or top-down goals. However, these studies did not consider past experience that is an important part of our everyday functioning. We rely on our memories almost anytime whether driving a car or even when using language. Our results further imply that past experiences can be retrieved in a very short amount of time and can be considered almost automatic. However, this is distinct from fast, automatic attention based on bottom-up features; and thus, needs to be explored separately. This is a notion that has only recently been acknowledged (e.g., Theeuwes, 2019). The current data highlights the importance of memory-guided attention and would lead to more research exploring the interaction between emotion and prior knowledge in guiding attention.

An implication of this thesis is the possibility to consider emotional stimuli as motivationally significant. Past research has predominantly focused on the emotional materials that are thought to have evolutionary significance (such as snakes, spiders, fearful faces); however, emotionally arousing stimuli could also indicate a rather goal-relevant drive and may not derive solely from evolution. In fact, some aspects of the Evolutionary Theory have recently been challenged. For instance, new evidence from animal behaviour rejects the idea that organisms behave for "the good of the species" as initially suggested by the notion of 'group selection'; but rather they behave to pass on as many copies of their genes as they can (Sapolsky, 2017). Therefore, the notion of survival and the "selfish gene" (Dawkins, 2006) are no longer thought to be in the centre of the evolution. Rather, both animals and humans should show cooperative behaviours in order to increase their success of reproductivity. Therefore, emotion research should re-evaluate and potentially update their emphasis on the survival mechanisms to explain fast, automatic attention to historically called 'threat-related' stimuli.

Throughout this thesis, there was a focus on the arousal rather than valence. This is because past research using emotional objects, such as snakes, spiders, emotional faces, fails to tease apart; a) valence from arousal and b) saliency from emotionality. In such studies, emotional objects are inherently salient; therefore, it is unclear whether emotional states of the observers or the saliency of the object drives the enhancement effects on cognition. Here, we manipulated participants' emotional arousal using fear-conditioning and negative arousing sounds. Unlike past research using negative objects, these manipulations were independent from the target stimulus; and thus, our findings should lead to more research separating arousal and saliency.

Besides, most research used facial expressions; but faces are unique in terms of their motivational significance in social reciprocal relationships. Moreover, other research suggests facial expressions are predominantly affected by low level image manipulations (for a recent review, see Murphy, Gray, & Cook, 2017). Therefore, it is unclear whether the attentional enhancement effects of emotional facial expressions derive from bottom-up features of saliency or top-down guidance to the relevance of social interactions. Nevertheless, the experimental designs using facial expressions cannot separate arousal from priority. The ABC theory, on the other hand, successfully distinguishes between priority and arousal; and they place the arousal in the centre. Here, as long as one stimulus is equally arousing as another, they should both reflect similar effects on cognition, irrespective of whether they are coming from bottom-up features, motivational goals or social-relevance. Therefore, new research in emotion-cognition interactions should carefully consider these aspects when designing new experiments.

Going back to the point on the circumplex model of emotion, both valence and arousing aspects are inherent in a negative stimulus (e.g., snakes, spiders, fearful faces) and the ABC theory suggests that arousal, but not valence is the driving force of the opposing effect on cognition. Since we have only focused on negative arousing stimuli, future work is needed to examine the effect of valence, potentially using positive aspects of emotion, in attentional guidance or in perception. According to the ABC theory, the results revealed here should be similar when positive highly arousing stimuli are used.

Emotions are typically conceptualized as fitting into discrete categories: fear, anger, sadness, or joy whereas affect is often conceptualized as varying along two dimensions: pleasantness and activation (Russell & Feldman Barrett, 1999). Unlike negative emotions that narrows a person's attention to promote quick and decisive action, some researchers suggest that positive emotions can broaden people's mind and personal resources that would have long-term benefits (e.g., Fredrickson, 2001). For instance, psychologically resilient people are found to utilise positive emotions to recover from negative ones (Tugade & Fredrickson, 2004). However, other research using positive affective pictures did not find any difference between negative and positive valence (L. Wang et al., 2012). These conflicting results can be partly attributable to the difficulty of defining what is emotion since different studies used different definitions. In this work, we focus on the 'affect', but future work should also test whether and how distinct categorical emotions influence attentional guidance or motion perception.

It should also be noted that a positive state might be more difficult to induce in an experimental setting than a negative state, such as fear; and also negative stimuli (e.g., snakes, spiders, crime scenes) might be considered more arousing than positive ones (e.g., baby faces, people hugging each other). In fact, few picture contents, except erotic stimuli, reliably evoked high levels of skin conductance (Bradley et al., 2001). Research used erotic images as positive stimuli for an attempt to equalise arousal level in accordance with negative images, such as a crime scene. However, erotic movies, for instance, are found to be disgusting for some women more than men (Koukounas & McCabe, 1997). Therefore, there might be more individual differences in the emotional responses to such materials, depending on the age, gender, and culture. However, a snake in the grass would trigger fear responses (perhaps in different degrees) for most people in modern societies irrespective of the individual characteristics (unless they own a pet snake, in which they would fall towards the very rare end of the normal distribution). On the other hand, the typical context of positive emotions is not a life-threatening situation as oppose to negative situations. Thus, positive affect might also depend on the individual's motivation more than negative affect. For instance, a positive arousing state could include listening to one's significant others' voice as a counterpart to negative arousing sound clip used here. Therefore, I believe the implications of this thesis would be thought-provoking for positive psychology researchers to use more elegant manipulations of positive valence to replicate these findings of emotion on memory-guided attention or motion perception.

Brain imagining studies using memory-guided attention paradigm (e.g., J. J. Summerfield et al., 2006) found an interaction between brain areas which are attributed to the retrieval of spatial memories with parietal-frontal network for attentional orienting. In this thesis, we only focused on behavioural performance; however, future research should investigate neural correlates of arousal on attention based on selection history. In their recent model, Mather et al. (2016) predicts that norepinephrine released from the locus coeruleus under arousal amplifies glutamate level in the cortex, which is responsible for exciting the saliency signals. This interaction between norepinephrine and glutamate further enhances the effects of arousal on specific brain regions that are related to the prioritised/salient event. This theory was recently tested with a neurocomputational model and confirmed that emotional arousal can modulate memory in opposite ways via the local/synaptic-level noradrenergic mechanisms (Sakaki, Ueno, Ponzio, Harley, & Mather, 2019). Future brain-imaging research should test these predictions using a paradigm based on selection history as done in this thesis. For instance, a modified memory-guided attention paradigm can be used to explore how the locus coeruleus interacts with glutamate signals in parietal-frontal areas using functional magnetic resonance spectroscopy—a non-invasive technique used to measure such neurochemicals in the brain.

A further study could also test this model on early visual areas using low-level perceptual stimuli as used in Study 3. Until recently, early sensory brain areas (i.e., early visual cortex) have been thought to be independent of higher-order mechanisms, such as motivation or emotion. However, recent works (for a review, see Phelps, 2006) suggest that brain areas, such as the amygdala, has connections throughout the brain and is involved in various cognitive processes. Our results from Study 3 also suggest a possibility of the influence of norepinephrine from emotional brain areas, such as amygdala and locus coeruleus, towards the visual cortex—possibly motion areas: MT/V5. A modified motion perception task could reveal whether glutamate signals on one hemisphere of the MT/V5 regions are amplified when participants perceive the dominant direction under emotional arousal while glutamate signals on the other side of the hemisphere are further supressed.

As mentioned earlier, one of the limitations in Study 3 was that we did not address perceptual change between the two motion directions (e.g., a perceptual switch from the dominant to the non-dominant direction; for instance, from left to right side; or vice versa) during ambiguous motion perception as suggested in previous studies (VanRullen & Koch, 2003; VanRullen et al., 2005, 2006). The main idea of these previous studies is the notion that motion perception is perceived in discrete snapshots of 100 ms, rather than being continuous. They manipulated the two superimposed Gabor patches as to reflect an actual change of direction (e.g., a physical change of the dominant side from left to right or right to left) and a perceptual change (e.g., only a perceptual change of dominance from left to right side or from right to left side without an actual physical change). Their results revealed that people experienced perceptual switches between temporal frequency of 10-15 Hz, but not in the 5 or 20 Hz. Attention to a small target within the moving stimuli further interrupted the perceptual switch. One interpretation from these studies could be that if emotion amplifies signals towards the dominant stimuli, then people should switch from the dominant direction percept more quickly and frequently under arousal. Therefore, we might expect that using actual and perceptual changes with longer duration of stimulus presentation (i.e., 1-2 seconds) as done in the studies mentioned above, arousal effects should amplify the perceptual switch without affecting perception of the actual switch. Alternatively, it is also possible that arousal would enhance the dominant direction signals and would not allow further perceptual switch to the other direction, as indicated by their attentional interruption findings, which results in less frequent perceptual switch. This latter hypothesis seems more plausible if emotion enhances perception and amplifies perceptual benefits of attention (Phelps et al., 2006). When a dominant direction is perceived, more attentional resources would be gathered to enhance that direction and would not allow for a quick perceptual switch to the other non-dominant direction under emotional arousal. I believe a further study using such manipulation would both shed light on arousal effects on motion perception and also imply whether motion perception is discrete or continuous,—which is a current debate in vision science. Therefore, further work is needed to explore how arousal affects temporal judgments.

Vision scientists have applied physical phenomenon into their research and have been highly influential not only in psychology but also in computer science in recent years. However, they have mostly focused on the bottom-up features that rely on the external sensory input—e.g., data-driven approach. Gibson (1966) suggested that what you see is what you get: The pattern of light reaching the eye, known as the optic array, contains all the visual information necessary for perception. According to this view, perception of the stimulus may not depend on prior knowledge or past experience. Conversely, Gregory (1970) suggested that perception is about making the best guess or a hypothesis testing of what we see. He explained that past experience related to a stimulus helps us make these inferences. In a more extreme view from cybernetics, we see what we expect to see as the eye movement is almost exclusively under top-down control (Chernyak & Stark, 2001). Although later research agreed that there is an interaction between these two processes as reviewed in the first chapter, the influence from computer science and the applicability of the bottom-up concepts into Artificial Intelligence (AI) led to more research on the stimulus-driven approaches. Today, the difficulty, yet, is to apply human consciousness (Shanahan, 2010) and possibly top-down concepts such as self-awareness, imagination, value, intentionality, or the capacity of suffering into computers to construct a more autonomous AI. For instance, research with animals, infants, adults and robots suggests that the mechanism of empathy, which is thought be innate, is actually obtained through social interaction (Heyes, 2018). Consequently, what makes a human special is how we learn things working collectively with others, showing reciprocal relationship in a functioning society, having internal goals, motivation, and higher-order mechanisms of emotion rather than having a simple input-output system. That is why we still have the "hard problem of consciousness" shared by philosophy, psychology, neuroscience, and computer science. I believe new research on emotional and motivational significance, the effect of prior knowledge and how they interact with low-level perception will both help to understand human behavior and how the brain works, as well as how to apply these concepts into computers.

Finally, the findings of this thesis might have important implications for future clinical practice. Emotional arousal not only interacts with memory encoding, but also guides attention in the retrieval of memories. Therefore, clinical interventions should carefully consider how traumatic events in the past can affect current attentional resources and potentially damage ongoing cognitive processes. They should also consider the complex nature of memory, perception, and attention under emotional arousal. Our results highlight the importance of a more holistic approach to cognition; rather than only focusing on one element, such as negativity bias in many anxiety studies in the past. Furthermore, our sample characteristics reveal that there are a number of students who are dealing with subclinical anxiety or depression. Studies have shown a high risk for mental health problems with the start of the university (Reavley, McCann, & Jorn, 2012). Therefore, education policies should address these increasing problems in youth.

5.6 Conclusion

This thesis contributes to our understanding of the complex effects of emotional events on cognition. The three studies provide the first evidence of emotional arousal on memory-guided attention and on ambiguous motion perception. The results confirmed the predictions of ABC theory (Mather & Sutherland, 2011), suggesting that emotional arousal increases attention to a past event that has been prioritised. Arousal also enhanced perception to the high salient signals by low-level featured stimuli. This work confirmed and extended the literature on emotion and cognition interactions.

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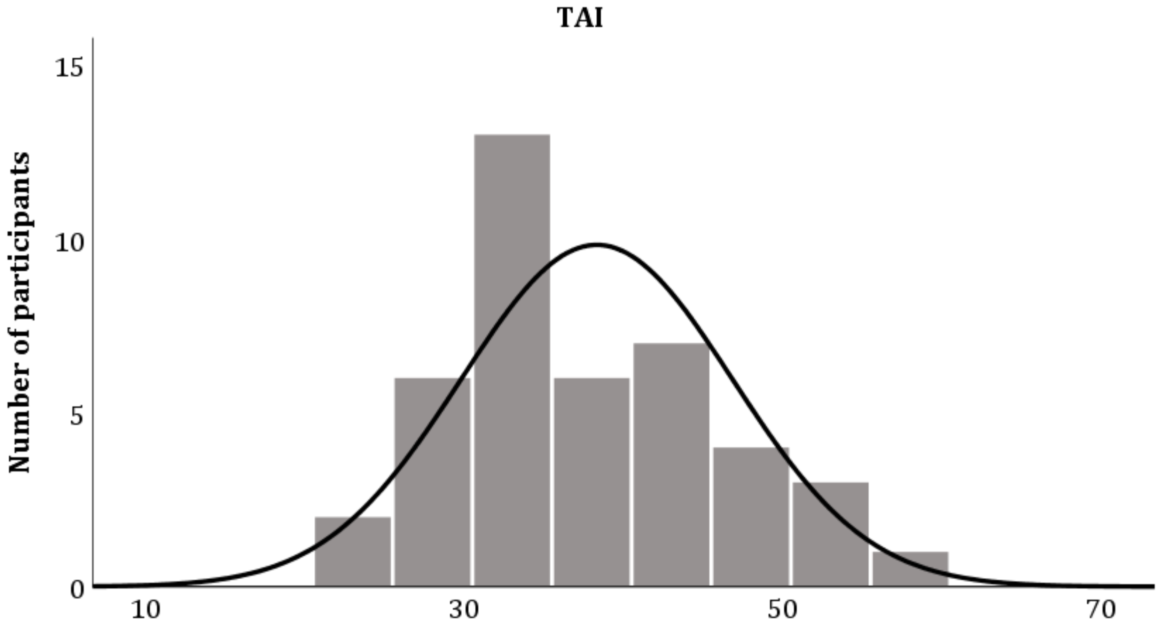
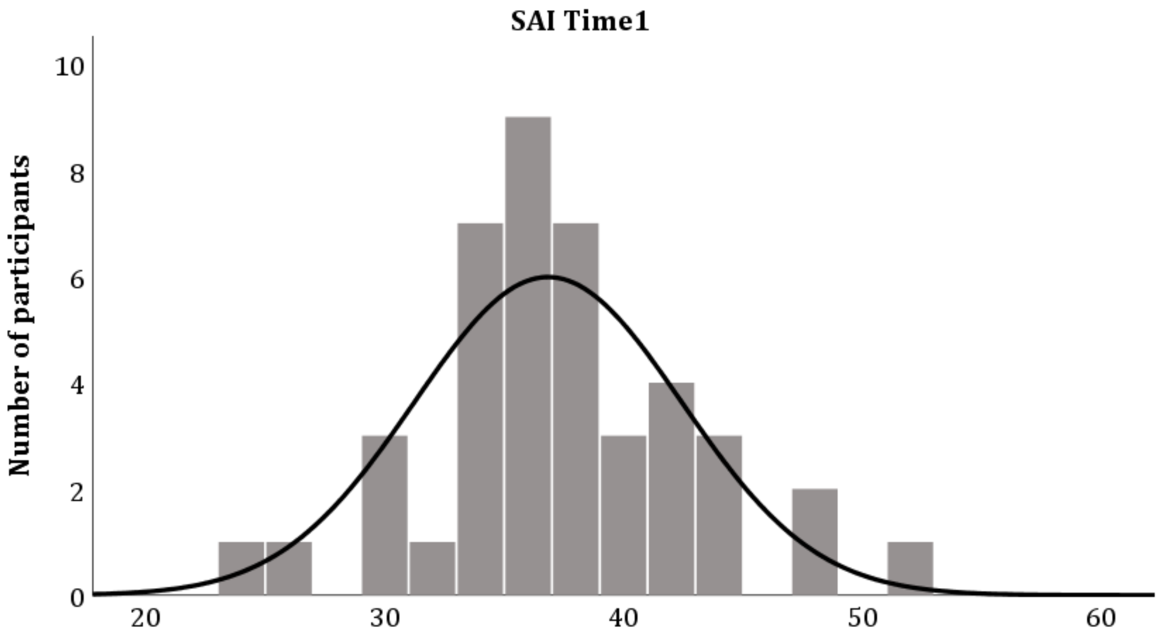
Appendices

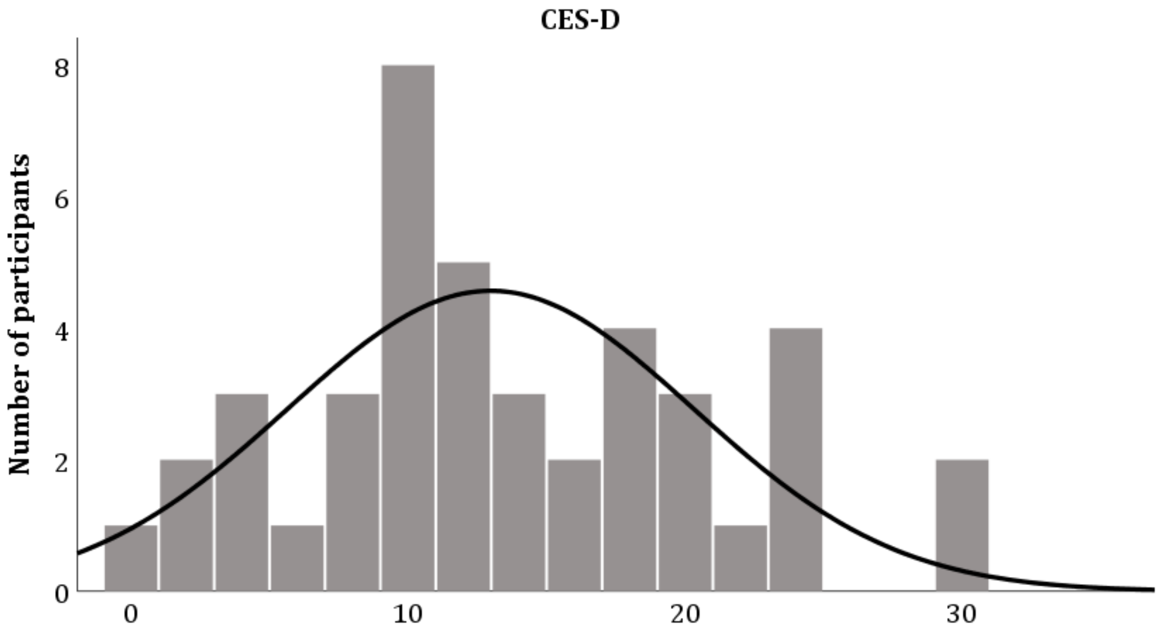
Appendix 1



Appendix 2



Appendix 3



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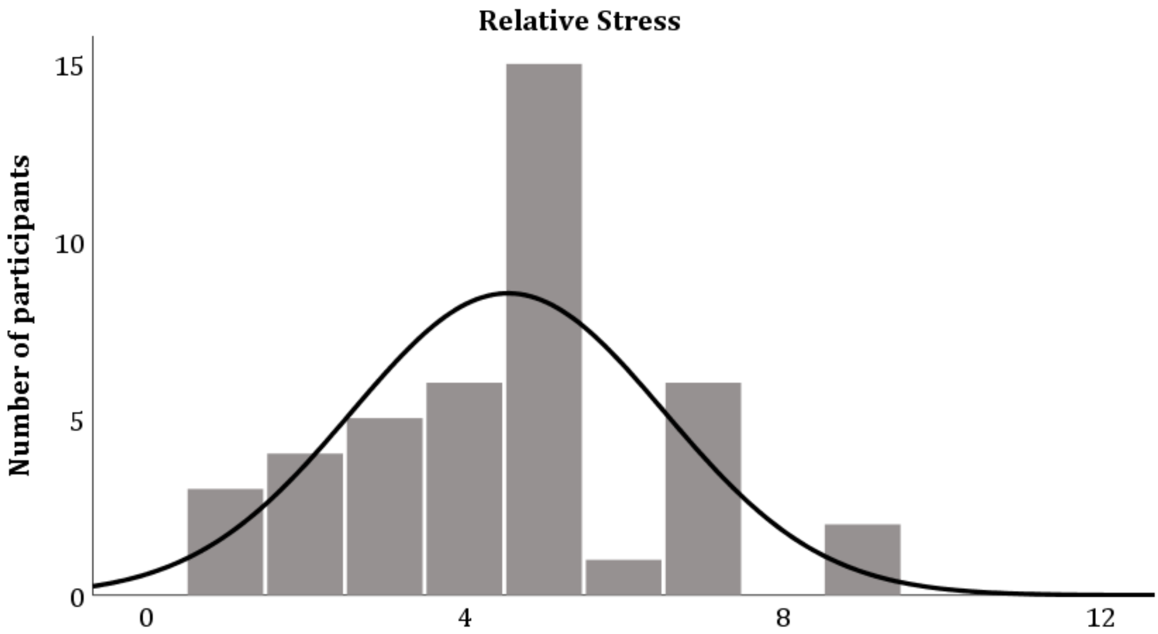

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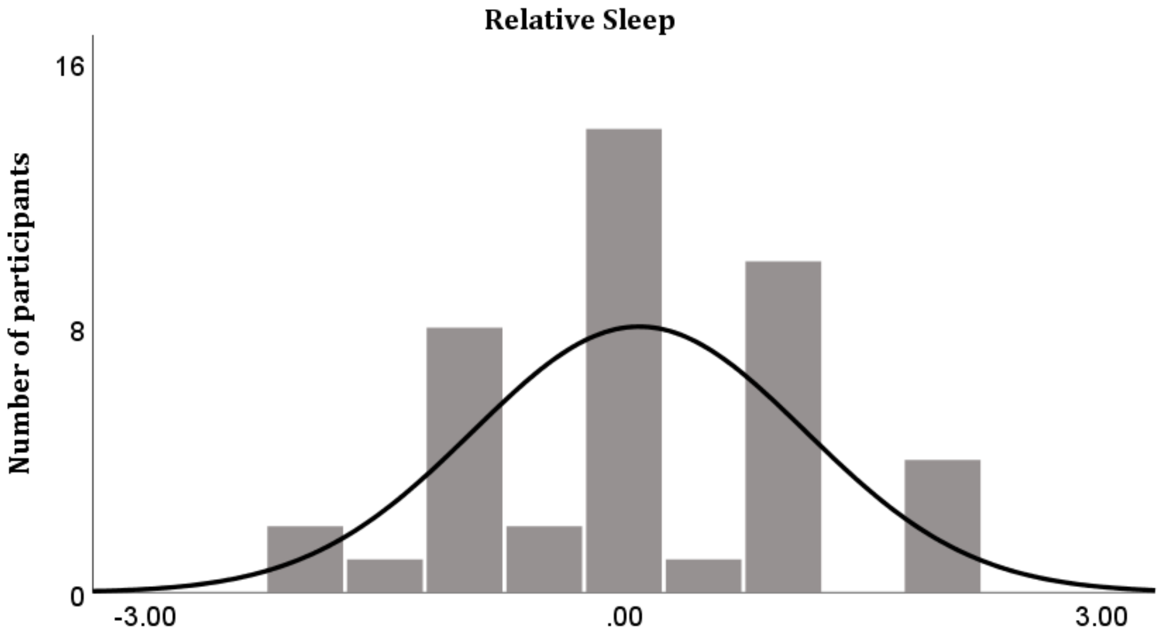

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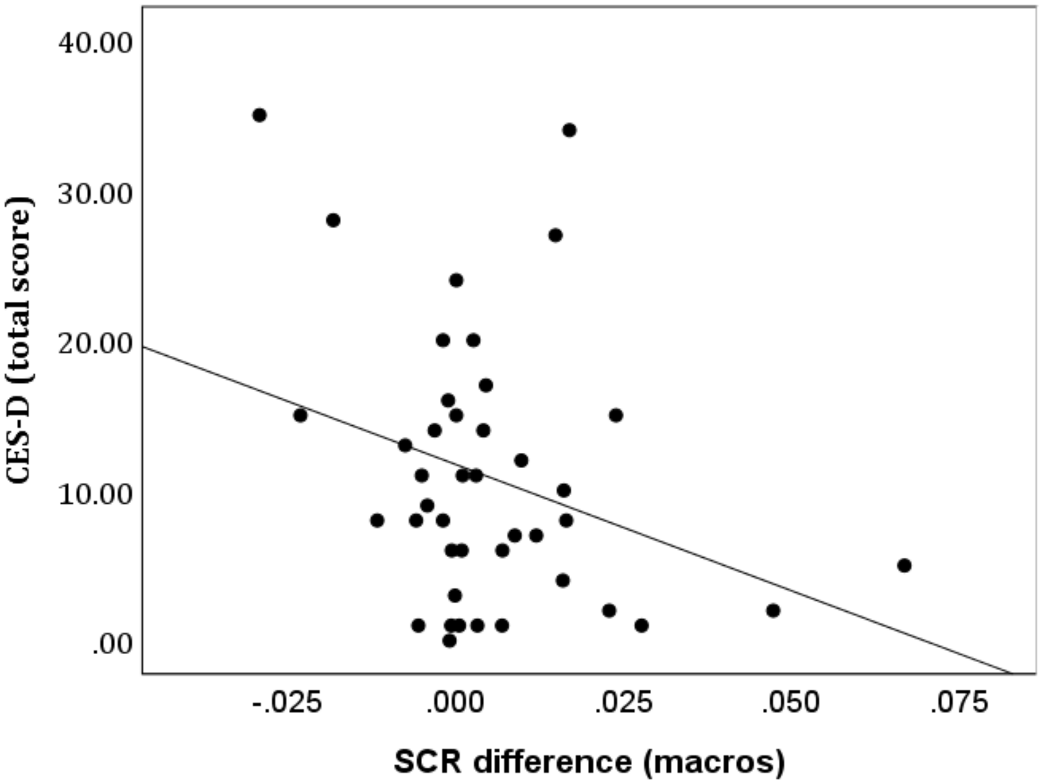
40.00
30.00
20.00
10.00
.00
CES-D (total score)
-.025
.000
.025
.050
.075
SCR difference (macros)