Effects of Post-encoding Processing on Deliberate and Intrusive Memory for Traumatic Material

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by

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DECLARATION

I, Lone Diana Hørlyck, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

London, 28.09.2017

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ABSTRACT

Following a traumatic event, some individuals might experience distressing involuntary thoughts and imagery, as seen in post-traumatic stress disorder. It is crucial to understand the complex factors that contribute to the occurrence and subsequent treatment of these intrusions. Whilst it has been shown that various factors during the immediate aftermath of an event can alter successful memory storage, little is known about how such post-encoding processes influence intrusive memories for traumatic material. Accordingly, unitary accounts suggest that intrusions behave like strong voluntary memories, whereas a dual representation view predicts that they behave in a complementary way.

This thesis investigated post-encoding processing for traumatic material using behavioural and functional magnetic resonance imaging (fMRI) methods. First, I examined methodologies for assessing intrusive memories in a laboratory setting, demonstrating that short video clips as an analogue trauma induced more intrusions than negative static images. Utilising this method in Chapter 3, I investigated memory for videos immediately followed by either a short break or a second, unrelated video. In two similar experiments, differences between conditions were non-significant. However, when collapsing data across the two studies to gain more power, I showed that deliberate memory performance was significantly reduced for videos immediately followed by another video compared to videos followed by a short break, suggesting disrupted consolidation for the first video. Chapter 4 examined the effects of brief wakeful rest following viewing of traumatic material, a technique thought to enhance consolidation. Here, I demonstrated that, compared to a working memory task, brief wakeful rest decreased intrusive memories and had different effects on deliberate and intrusive memory. In Chapter 5, I used fMRI to show that activity in medial temporal lobe structures, during encoding and its immediate aftermath, predicts deliberate memory, whereas amygdala activity during encoding is associated with memory intrusions. The findings from this thesis highlight the importance of the period in the aftermath of trauma and how its modulation can alter deliberate and intrusive memory in different ways.

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ABBREVIATIONS

AAL	Automated Anatomical Labelling
ABC	Arousal-based competition
ACC	Anterior cingulate cortex
ANOVA	Analysis of variance
APA	American Psychiatric Association
BOLD	Blood-oxygen level dependent
CBT	Cognitive-behavioural therapy
C-Rep	Contextual representation
dmPFC	Dorso-medial prefrontal cortex
DRT	Dual Representation Theory
DSM	Diagnostic and statistic manual of mental disorders
DSSQ	Dundee Stress State Questionnaire
EMDR	Eye movement desensitisation and reprocessing
EPI	Echo planar imaging
FA	False alarm
fMRI	Functional magnetic resonance imaging
FWE	Family wise error
FWHM	Full width at the half maximum
GABA	Gamma-aminobutyric acid
GLM	General Linear Model
HPA	Hypothalamic-pituitary-adrenal
IAPS	International Affective Picture System
IFG	Inferior frontal gyrus
ISI	Inter-stimulus interval
ITI	Inter-trial interval
LTP	Long term potentiation
MANOVA	Multivariate Analysis of Variance
MDEFT	Modified Driven Equilibrium Fourier Transform
MTL	Medial temporal lobe
MVPA	Multivariate pattern analysis

NICE	National Institute for Health and Care Excellence
OCD	Obsessive-compulsive disorder
PANAS	Positive and negative affect schedule
PFC	Pre-frontal cortex
PTSD	Post-traumatic stress disorder
QMI	Questionnaire upon mental imagery
TR	Repetition time
RI	Retroactive interference
ROI	Region of interest
S-Rep	Sensory representation
SPM	Statistical parametric mapping
SSRI	Selective serotonin reuptake inhibitor
STAI	State-trait anxiety inventory
SWC	Small-volume corrected
SWR	Sharp wave ripples
TE	Echo time
TVIC	Test of visual imagery control
VR	Virtual reality
VRET	Virtual reality exposure therapy
VSSP	Visuospatial sketch pad
VVIQ	Vividness of visual imagery
vmPFC	Ventro-medial prefrontal cortex
WM	Working memory

1 INTRODUCTION

‘If you wish to forget anything on the spot, make a note that this thing is to be remembered’

- **Edgar Allan Poe**

1.1 Overview

In this introduction, I will begin by outlining the symptoms and difficulties seen in post-traumatic stress disorder (PTSD) with particular emphasis on altered memory functions associated with the disorder. Influential theories, neural mechanisms and available treatments for PTSD will also be discussed. Next, I will turn to the nature and mechanisms of healthy memory, including the anatomical substrates of memory encoding, consolidation, retrieval and imagery. I will then discuss the effects of emotion on encoding and consolidation of different memory types. Finally, two opposing theories of intrusion development will be presented and the use of an experimental trauma paradigm to investigate post-encoding processing of emotional memory will be outlined.

1.2 Post-traumatic stress disorder

Many people are likely to experience a serious traumatic event during their lifetime. Such events can involve a wide range of occurrences including car accidents, personal assault or a natural disaster. Epidemiological studies put the lifetime probability of an individual experiencing a personal trauma as high as 95% (Kessler et al., 2005). Whilst many people will experience a traumatic event, a large proportion of these individuals will not develop any related mental health issues. However, some will suffer psychological, trauma-related symptoms that, in the majority of these individuals, will diminish over the following weeks. A small number of these individuals will experience persistent symptoms and go on to be diagnosed with post-traumatic stress disorder (PTSD), a debilitating condition following a life-threatening event (Breslau et al., 1998). An American study has estimated the lifetime risk of developing PTSD to be around 8%, (Kessler et al., 1995).

Post-traumatic Stress Disorder (PTSD) is a psychiatric disorder that may develop following exposure to a severe traumatic event involving exposure to serious threat or injury or witnessing the death of others, such as in car accidents, terrorist attacks, physical assaults, rape and war (American Psychiatric Association (APA), 2013). Studies have identified the latter two as being the traumas where victims are most likely to develop subsequent PTSD (Kessler, 1995). PTSD was first included as a psychiatric disorder in the DSM-III in 1980 (APA, 1980; Foa and Riggs, 1995) and is characterised by a range of dissociative, cognitive and emotional symptoms. Among the most prominent symptoms are involuntary and distressing memory intrusions, in which memories of the trauma involuntarily enters consciousness, but patients also display a range of other symptoms involving avoidance behaviour, anxiety and nightmares related to the event (APA, 2013).

The course of the disorder is highly variable. The diagnostic criteria distinguish between acute and chronic PTSD depending on whether symptoms have persisted for more or less than 3 months (DSM-V, APA, 2013). Also, some people develop delayed onset PTSD where onset of symptoms does not occur until at least 6 months after the trauma, although even in these cases some symptoms most likely present immediately following trauma (Andrews et al., 2007). Studies have shown that if an individual develops PTSD following a traumatic event, symptoms tend to persist over extended periods of time and often take a more chronic course (Kessler et al., 1995, Blanchard et al., 2003). Furthermore, the disorder is debilitating to patients, who show significant functional impairment across a range of domains, including professional, social and family difficulties (Rodriguez et al., 2012). Therefore, it is imperative that effective treatments are available for this debilitating disorder.

Apart from being exposed to a severe stressor, diagnosis of PTSD requires four clusters of symptoms to be present; these include persistent intrusion symptoms, avoidance behaviour towards trauma-related stimuli, negative emotions or thoughts, negative alterations in cognition and mood and increased arousal and reactivity (DSM-V, APA 2013). Intrusion symptoms involve re-experiencing of the trauma, which may take different forms of which the cardinal PTSD symptoms are involuntary and distressing memory intrusions related to the trauma, often accompanied by a strong sense of reliving the trauma again in the present (flashbacks). Other intrusion symptoms involve nightmares and increased psychological and physiological reactivity to trauma-related stimuli (DSM-V, APA, 2013). Avoidance behaviour comprises another symptom cluster involving avoidant behaviour towards internal or external trauma reminders such as avoiding the location where the traumatic event happened, avoiding driving a car after an accident or avoiding thinking about the trauma. Negative alterations in cognition and mood cover a wide range of symptoms ranging from difficulties remembering key aspects of the traumatic event (dissociative amnesia) to depression-like symptoms such as self-blame and anhedonia. Finally, patients may show alterations in arousal and reactivity, rendering people unusually aggressive or self-destructive on one hand while having problems sleeping and concentrating on the other (APA, 2013). The pattern of symptoms in PTSD is believed to reflect the effects of longstanding stress on the brain (Bremner, 2006).

1.2.1 Treatments

Current available treatments for PTSD include both psychological and pharmacological approaches, but a lack of understanding of the disorder's underlying mechanisms halts the development of effective treatments (Bremner, 2006). In general, individual psychological treatments with a strong focus on memory for the traumatic event and its meaning, such as trauma-focused cognitive behavioural therapy (CBT) and eye movement desensitisation and reprocessing (EMDR; Shapiro, 1989) have been found to be the most effective treatments (Bisson et al., 2007).

Trauma-focused CBT involves exposure, cognitive therapy and anxiety management. The exposure element aims to create a safe confrontation with the trauma-related memories and stimuli. Hence, in prolonged exposure, a combination of imaginal exposure (e.g. reliving) and in vivo exposure (trauma-related stimuli) is used to reduce distress associated with the trauma. The cognitive component of CBT for PTSD often involves imagery rescripting and is based on the assumption that mental imagery can significantly affect emotion. This is consistent with classical cognitive theory emphasizing the relationship between thoughts, emotions, physiological states and behaviour (Beck, 1979; Beck et al., 1987). Imagery rescripting therefore aims to change meanings associated with mental images so that negative images become less disturbing or are replaced by more positive mental images (Holmes et al., 2007a). The efficacy of using mental images as a target may be explained by findings showing that emotional aspects of traumatic memories are primarily attached to the related mental images (Arntz et al., 2005). In addition, it has been proposed that exposure and imagery rescripting works through strengthening the narrative of the traumatic event and correspondingly reducing memory fragmentation of the trauma (Foa et al., 1995).

In EMDR, trauma memories are desensitised and hence reduced by a process in which the patient produces rhythmic, multi-saccadic eye movements while recalling the trauma memory (Shapiro, 1989). The role of saccadic eye movements in improvement is uncertain. Some have proposed that intrusive memories are held in the visuospatial sketchpad (VSSP) component of the working memory system (Baddeley and Hitch, 1974), and that saccadic movements as a visuospatial task will compete with trauma memory for processing resources (Jeffries and Davis, 2013; Kavanaugh et al., 2001). However several other studies have suggested that the improvement seen with EMDR is merely a result of the exposure elements and is independent of the saccadic eye movement intervention (Renfrey and Spates, 1994, Pitman et al., 1996).

Although a number of studies have found support for EMDR and some have found similar effects of CBT and EMDR (Rothbaum et al. 2005; van Etten and Taylor, 1998) the majority of studies have found that trauma-focused CBT is superior (DeRubeis and Christoph, 1998). This could be explained by the speculations mentioned above suggesting that the effective component in EMDR might be the element of exposure (Renfrey and Spates, 1994). Taken together, cognitive-behavioural therapy (CBT) with exposure is the intervention that has received the most empirical support as an effective treatment of PTSD, both compared to other psychotherapies and compared to psychopharmacological treatments (Bisson et al., 2007; Difede et al., 2014). Hence, it appears that reprocessing, reorganising and desensitising the trauma memory are critical components in successful treatments.

CBT is recommended as a first line treatment in the National Institute for Health and Care Excellence (NICE) guidelines (NICE, 2005). However, despite the empirical support for psychotherapeutic interventions, pharmacological drugs such as selective serotonin reuptake inhibitors (SSRIs), most often used to treat depression and anxiety, continue to be typical first-line treatments used in practice. There is some evidence suggesting that SSRIs are effective in treating PTSD symptoms (e.g. Marshall et al., 2001) but overall, the evidence base for these treatments is lacking (Difede et al., 2014; NICE, 2005).

β-adrenergic receptor antagonists such as propanolol have also been investigated as a potential pharmacological treatment to prevent the development of PTSD, when given at an early stage after experiencing the trauma. The rationale behind this intervention is based on knowledge that release of stress hormones following a traumatic event contributes to the salience of traumatic memories and that this effect can be blocked by propranolol (Cahill et al., 1994). However, results from studies assessing the efficacy of this intervention have been mixed (Pitman et al., 2002; Vaiva et al., 2003; LaBar and Cabeza, 2006). Hence, to provide efficient treatment for people suffering from PTSD, a better knowledge of the underlying mechanisms is needed.

In sum, evidence suggests that psychological treatments are more effective than pharmaceutical treatments and that CBT with exposure is the most effective psychological treatment. In particular, these interventions use imagery to target trauma memory, which in many ways is the central difficulty in the disorder.

However, some symptoms tend to persist after treatment and many patients do not respond to available treatments (Stein et al., 2002, Brady et al., 2000). As a result, understanding the underlying mechanisms of PTSD is of critical importance to informing the development of better treatments and identifying potential therapeutic targets.

1.2.2 Memory alterations in PTSD

As discussed above, a primary symptom experienced by PTSD patients is alterations in memory. These debilitating memory symptoms are most consistently observed in both deliberate and involuntary memory related to the traumatic episode (van der Kolk and Fisler, 1995). Most prominent are frequent and distressing involuntary memories, which are often accompanied by difficulties with deliberate memory processes (van der Kolk and Fisler, 1995), as will be discussed in the following.

1.2.2.1 Involuntary memory alterations in PTSD

Spontaneous or intrusive memories that involuntarily enter consciousness are thought to be a normal phenomenon in daily life (Berntsen and Rubin, 2008). However, spontaneous memories that concern a highly negative event, such as trauma, are often reported as being more salient than other memories and may become highly repetitive and distressing to the individual (Holmes et al., 2005). Indeed, after experiencing a traumatic event, people often report involuntary memories that are typically focused on emotional and perceptual details of the event (Ehlers et al., 2004; Arntz et al., 2005). More recently, it has been suggested that involuntary memories might play a central role in several other psychiatric disorders in addition to PTSD, including obsessive-compulsive disorder (OCD), anxiety and depression (Brewin et al., 2010; Holmes et al., 2010). Cognitive views emphasize the role of these spontaneous memories as maintaining factors in mental disorders (Ehlers and Clark, 2000).

Intrusive memories in PTSD are typically described as being qualitatively different from other memories. Importantly, memory intrusions in PTSD also appear different to the involuntary memories experienced by people who have been exposed to trauma without subsequently developing PTSD (Ehlers, 2010). Intrusive memories in PTSD are often characterised by a strong sense of re-living the trauma in the present. Furthermore, in extreme instances, PTSD patients report dissociating completely from the present (Ehlers et al., 2004). Studies have indicated that aspects of the trauma that are most often remembered is what happened immediately before the trauma or at the beginning of what patients found was the worst part of the trauma, also referred to as 'hotspots' of trauma memory (Holmes et al., 2005; Ehlers et al., 2002). Emotional aspects of the intrusive memories also set PTSD patients apart from others who have experienced trauma; for instance, PTSD patients often report that their intrusive memories are more distressing than trauma-survivors who do not suffer from PTSD (Ehlers, 2010).

Memory intrusions in PTSD may be triggered both by external and internal (such as thoughts, feelings) cues (Brewin, 2001a; Berntsen and Hall, 2004) and it has been suggested that perceptual priming plays a central role in the disorder (Ehlers et al., 2006; Brewin and Holmes, 2003, Ehlers and Clark, 2000). Perceptual priming refers to an enhanced tendency for trauma-related stimuli to trigger memories of the trauma (Schacter, 1992; Sünderman et al., 2013; Ehlers et al., 2006). This enhanced priming can lead to patients feeling that memory intrusions occur with no apparent reason. In addition, people suffering from PTSD might respond emotionally to a situation that is similar to the trauma without consciously recognising the link to the traumatic experience (Ehlers, 2010; Ehlers et al., 2004). Also, memory intrusions in PTSD are often characterised by having a weak temporal organisation and patients may have difficulties recalling details from the trauma. Finally, memory intrusions may show lack of context, resulting in memories not being updated with other (and perhaps contradicting) information (Ehlers et al., 2004).

1.2.2.2 Alterations in deliberate memory in PTSD

Concurrent with these intrusion symptoms, several studies have found that deliberate memory, that is, memories that can be consciously recollected, retrieved and verbalised, is impaired in PTSD compared to both healthy controls and people who experienced trauma without developing PTSD (Johnsen and Asbjørnsen, 2008, van der Kolk and Fisler, 1995). Evidence for this impairment comes from diverse PTSD studies including studies with war veterans (Golier and Yehuda, 2002; Koso and Hansen, 2006), holocaust survivors (Yehuda et al., 2004) and from victims of abuse (Bremner et al., 2004; Jenkins et al., 1998).

People suffering from PTSD may experience trauma-related amnesia, displaying difficulties with voluntary recollection of details from the trauma (van der Kolk and Fisler, 1995, Briere and Conte, 1993). Several studies have also found that deliberate recall of the traumatic experience in PTSD patients tends to be fragmented, poorly organised and characterised by a weak temporal structure (e.g. Halligan et al., 2003; Jones et al., 2003, van der Kolk and Fisler, 1995; Brewin, 2016). For instance, Halligan et al. (2003) investigated impairments in voluntary memory in PTSD based on the cognitive theory of PTSD where it is suggested that PTSD symptoms arise as a result of enhanced data-driven (perceptual and sensory) processing during trauma at the cost of conceptual processing (Ehlers and Clark, 2000). Here, the researchers found that data-driven and self-referent peri-traumatic processing during trauma was associated with subsequent development of PTSD. As it will be described later in more detail, the role of processing both during and in the aftermath of trauma has been the subject of extensive research.

In some instances, PTSD patients will suffer from what is known as psychogenic amnesia, the inability to remember central aspects of the trauma (Golier and Yehuda, 2002). It is not known if psychogenic amnesia is caused by insufficient memory encoding or if it alternatively reflects post-encoding factors such as suppression or forgetting (Golier and Yehuda, 2002). Furthermore, studies have suggested that people who were exposed to trauma as children may show global impairments in voluntary memory (van der Kolk and Fisler, 1995) although this notion has received little empirical support (Evans et al., 2009, Ehlers, 2010).

Taken together, these unusual memory phenomena, including disruptions to voluntary memory and increased involuntary memory experiences, are widely reported by patients and seem to form a primary part PTSD (Brewin and Holmes, 2003).

1.2.3 Neural systems underlying PTSD

Studies investigating the neural underpinnings of PTSD have focused on brain regions involved in fear, arousal and memory, such as the medial temporal lobe

(MTL), amygdala and prefrontal cortex (PFC; LaBar and Cabeza, 2006, Rauch et al., 2006). Generally, studies investigating the neural mechanisms of PTSD have found both structural and functional abnormalities in regions involved in memory processes: for example, smaller hippocampal volumes in PTSD patients are a common finding (Bremner et al., 1995; Francati et al., 2007). However, it remains unclear whether such findings reflect a risk factor for developing PTSD or if hippocampal atrophy is caused by the disorder (Rauch et al., 2006). Studies investigating functional aspects have found excessive amygdala activation and abnormal hippocampal processing, although studies on the latter are inconsistent in how this abnormal processing is expressed (Rauch et al., 2006; Shin et al., 2006). Such hippocampal and amygdala abnormalities may contribute to the development and maintenance of the disorder. However exactly how these regions are involved in trauma processing and subsequent symptom development with memory impairments and intrusions in PTSD is not clear.

1.2.4 Theories of PTSD

Why might some individuals go on to develop PTSD following a traumatic experience? There have been a number of different conceptualisations of PTSD symptoms based on different schools of psychology. For example, PTSD has been conceptualised as an extreme case of conditioning, whereby a range of previously neutral stimuli present during trauma become conditioned to evoke anxiety whereas avoidance symptoms are suggested to arise as a result of instrumental learning (Keane, 1985). Emotional processing theories are based on the assumption that fear is represented in memory structures comprising associated stimulus, behavioural and physiological responses and assigned meanings (Foa and Kozak, 1986). When one element in the structure is activated, this will elicit activation of the rest of the structure, leading to PTSD symptoms (Rauch and Foa, 2006).

Although these theories have contributed to the understanding of aspects of PTSD, cognitive theories offer the most empirically supported and comprehensive conceptualisations of PTSD and have informed successful psychological treatments of the disorder (Brewin and Holmes, 2003). Common to cognitive theories is the focus on alterations in information processing related to the trauma, such as excessive negative appraisal and the role of safety and avoidance strategies in maintaining the disorder (Ehlers and Clark, 2000). Social-cognitive and schema theories have focused on the shattering of fundamental beliefs (schemas) held by the individual about the self and the world following trauma (Janoff-Bulman, 2010, 1989). In this framework, PTSD symptoms may develop when the individual, following trauma, attempts to reconcile the altered assumptions with prior beliefs and schemas. For instance, re-experiencing of the trauma is understood as processing of incompatible elements that are continuously revised until the trauma information has been integrated with the schemas of the individual, referred to as the completion tendency (Horowitz, 1976, 1986). Conflicts arising from this process are expressed as dissociation (Horowitz, 1993; Janoff-Bulman, 2010; Cahill and Foa, 2007) and avoidance symptoms are understood as a response to the stress produced by the completion tendency (Horowitz, 1986, Brewin et al, 2014).

Other theories have focused more on behavioural aspects and suggest that PTSD symptoms are a result of excessive fear conditioning (Dolan et al. 2002). Here, it is hypothesised that patients display particularly strong stimulus-response (S-R) associations and perceptual priming for traumatic material, facilitating triggering of trauma memories that are resilient to extinction (Keane et al., 1985, Cahill and Foa, 2007).

A more recent cognitive theory that has received much attention was proposed by Ehlers and Clark (2000). They suggested that when an individual is exposed to a severe traumatic experience, information processing will shift from a conceptual processing mode towards a data-driven mode that is oriented towards perceptual and sensory details and experiences. Hence, memories created in the data-driven processing mode will be more prone to perceptual priming and less accessible to intentional retrieval, creating the basis for intrusion development (Ehlers and Clark, 2000). In line with this idea, Brewin et al. (1996, 2010)'s dual representation model of PTSD proposed that two complementary memory representations are formed when an event is encoded; one representation comprises sensory details of the event while the other involves contextual information (see also Jacobs and Nadel, 1985).

During a traumatic event, the contextual representation is impaired while the sensory representation is enhanced, resulting in the formation of perceptually rich mnemonic images with poor spatial and temporal context, rendering these memories more likely to be triggered involuntarily. This account will be elaborated further below.

1.3 Healthy memory

In an attempt to understand the factors that might contribute to the memory alterations following a traumatic episode, it is crucial to provide a comprehensive framework for healthy memory on which to place such deficits. The next section describes well-established memory systems with a particular emphasis on the episodic memory system. The neural mechanisms of episodic memory and the processes of encoding, retrieval and consolidation will be discussed. Finally it will be discussed how negative emotion affects episodic memory.

1.3.1 Categories of memory

Over the past few decades, memory research has continued to provide evidence that memory is not a single entity but comprises a number of dissociable systems (Squire and Zola-Morgan, 1996; Squire, 1992; Cohen et al., 1997). Within these long held views, long-term memory is divided into two primary systems, typically including declarative (explicit) memory and non-declarative (implicit) memory.

Declarative memory refers to memory systems involving conscious recollection of information that can be declared, or, verbalised (Squire and Zola-Morgan, 1991). Declarative memory is typically divided into semantic memory (what is known) and episodic memory (what is remembered; Tulving, 1983, 1984, 1972). Semantic memory comprises factual knowledge about the world, facilitating the ability to make interpretations of new information (Saumier and Chertkow, 2002). Episodic memory comprises memory for personal events and hence involves recalling a previous experience and the time, place and context in which it occurred (Squire, 2004; Tulving, 1972).

The term implicit memory describes memory types that are not consciously recollected. This category includes priming, where the perception of one stimulus unconsciously activates a set of representations in memory that in turn influences response to another stimulus, for instance enhanced performance as a result of learning without conscious awareness (Squire and Zola, 1996; Schacter, 1987).

Habits and routines are a type of implicit memory, providing the individual with a set of behaviours that are shaped by past experience and can readily be engaged but are outside conscious awareness. Another type of implicit memory is classical conditioning, a type of learning where a new response is learned from associating a stimulus originally coupled to the response with a second stimulus originally unrelated to the response. With learning, the second stimulus becomes associated with the response such as in a classical study by Pavlov, where it was shown that in dogs, the sound of a bell could become conditioned to trigger saliva production in the dogs after training where the sound of the bell was associated with the delivery of food (Pavlov, 1927). Finally, procedural memory describes motor learning and habits not associated with conscious recollection, the feeling of ‘knowing how to do something’, such as riding a bike or playing the violin.

Knowledge about the brain systems underlying different memory systems originally came from studies of patients who had sustained brain damage and subsequently were impaired on certain memory tasks, while other types of memory were unaffected (Squire and Zola, 1996; Scoville and Milner, 1957). For instance, amnesic patients typically show profound impairments in declarative memory while priming and procedural learning is spared (Squire and Zola, 1996). Studies such as these allowed researchers to make deductions on brain function from observed dissociations and demonstrated that specific memory functions can be selectively altered while other memory functions remain intact.

1.3.2 Voluntary memory

1.3.2.1 Neural systems involved in healthy memory

It has long been accepted that the medial temporal lobes (MTL), and particularly the hippocampus, are involved in long-term memory (Eichenbaum and Cohen, 1988; Scoville and Milner, 1957). For example, early neuropsychological studies showed that amnesic patients with damage to the hippocampus and surrounding cortical regions demonstrate drastic impairments in recalling information about personally experienced events (Scoville and Milner, 1957). Recent proposals have highlighted a key framework in setting out how different parts of the MTL memory system, broadly comprising the hippocampus, perirhinal cortex, entorhinal cortex and parahippocampal cortex, function to support memory (Byrne, Becker and Burgess, 2007). For instance, associative memory is known to be supported by the hippocampus, while item memory appears to be dependent on the perirhinal cortex (Brown and Aggleton, 2001).

The general consensus is that the hippocampus forms a major part of the MTL memory system and is critically involved in episodic memory (Tulving and Markowitsch, 1998; Aggleton and Brown, 1999). Episodic memory is characterised by the conscious recollection of personally experienced events that are situated in a coherent spatio-temporal context (Tulving, 1983). Any personal memory will exist as a multimodal and multi-element entity where the individual elements of the memory is integrated to form a coherent whole when the memory is retrieved, often referred to as an engram (Squire, 1986).

It is proposed that the hippocampus play an essential role in supporting this memory process by binding together the constituent parts of an event, stored in various regions of the neocortex. This process is known as associative or episodic binding (Squire, 1992; Bird and Burgess, 2008; Eichenbaum, 1997; Mayes et al., 2007; Damasio, 1989). For example, functional neuroimaging studies show that activity in the hippocampus during encoding correlates with later associative / relational memory success, including remembering that two items were presented as a pair (Kirwan and Stark, 2004; Jackson and Schacter, 2004), remembering the context in which an item was initially viewed (Davachi et al., 2003; Ranganath et al., 2003), and the subjective sense of remembrance or recollection attached to an item's retrieval (Uncapher and Rugg, 2005). Such associative binding of information is thought to support the holistic retrieval of all aspects of an event that provide the rich recollective experience that is the hallmark of episodic memory (Tulving 1985; Horner, Bisby et al., 2015).

At retrieval, presentation of a partial cue is thought to trigger reinstatement of the event memory via pattern completion in the hippocampus and retrieval of individual elements of the memory stored in neocortical areas (Marr, 1971). Pattern completion refers to the process by which a memory in its entirety is recalled from a partial cue, e.g. a single element related to the memory. Hence, it has been proposed that a single element of a memory will induce auto-association in the CA3 region of the hippocampus, facilitating firing of previously associated neurons ultimately leading to an attractor state equivalent to the same pattern of activation as were present at the time when the event was experienced (Marr 1971; Rolls, 2007; McClelland et al., 1995; Carr et al., 2011).

Whilst it is expected that the hippocampus plays a role in episodic retrieval, research seems to highlight that it might be a time-dependent role, where hippocampal involvement is most important for recent memories (Squire, 1992). Evidence from neuropsychological studies have demonstrated that people suffering hippocampal lesions show a temporally graded amnesia where recent memories are abolished (along with the ability to form new memories), while more distant memories may remain intact, showing a gradient of decay to the time of acquisition of the hippocampal lesion (Squire and Alvarez, 1995; Dudai, 2004; Rempel-Clower et al., 1996). Such findings implicate the hippocampus mainly in the encoding and consolidation of new memories (McGaugh, 2000). It has often been argued that memories become independent of the hippocampus with time, as storage is relocated to cortical areas and gradually becomes more alike a semantic memory (Squire, 1992). Conversely, others have argued that even when a distant memory is retrieved, this involves imagining the scene where the event originally took place and this process remains dependent of the hippocampus, regardless of the age of the memory (Nadel, 1995; Nadel and Moscovitch, 1997; Bird and Burgess, 2008).

Dual processing models of memory (Yonelinas, 2002; Gardiner, 1988; Jacoby, 1991) have long distinguished between associative/relational memory processes supporting recollection and memory for single items that can be solved via familiarity. That is, recognition of a single item can be solved by a feeling of familiarity (or *knowing*) in the absence of contextual information whereas recollection (*remembering*) is similar to associative memory as this process involves recollection of source memory. For instance, in a study by Gardiner (1988), participants were presented with a word list and exposed to different encoding conditions. Participants then completed a recognition memory test in which they were required to identify words from the original list that were now mixed with foils and also indicated if they consciously remembered seeing the recognised word at encoding (recollection) or if they recognised it based on familiarity. Results from this study showed that encoding conditions significantly affected performance on the memory test, but only for items that were recollected, whereas there was no difference for items that were recognised based on familiarity (Gardiner, 1988). Hence these results lend support to the idea that familiarity and recollection rely on different underlying mechanisms.

In contrast to hippocampal-dependent associative/relational memory processes, memory for the single elements from an event is thought to be supported by extra-hippocampal structures such as the perirhinal cortex (Barense et al., 2007; Davachi, 2006; Aggleton and Brown, 1999). Studies have shown that patients with selective hippocampal damage that does not include perirhinal cortex can successfully recognise previously encoded faces (Bird and Burgess, 2008). Also, several studies have demonstrated a dissociation between brain activity during encoding and subsequent item and associative or source memory (Davachi and Wagner, 2002; Ranganath et al, 2003). For example, Ranganath et al. (2003) showed that familiarity-based recognition of a previously presented word was associated with activity in the rhinal cortex during encoding while recollection performance (source memory test asking the colour of the word) was predicted by activity in the hippocampus.

The parahippocampal cortex and entorhinal cortex are MTL regions, which have mostly been associated with spatial memory and navigation, although evidence suggests that these areas are also involved in episodic memory. An area within the parahippocampal cortex called the parahippocampal place area responds selectively to visual scenes by representing the geometry of the concrete scene or environment (Epstein and Kanwisher, 1998; Burgess et al., 2002). In a study by Ekstrom and Bookheimer (2007), participants played a game where they acted as 'taxi drivers', navigating in a virtual reality (VR) environment, picking up people and delivering them at landmarks. Following this training, participants were scanned in the MRI scanner while retrieving landmarks, temporal order and spatial associations from the VR environment. Consistent with earlier studies showing that the perirhinal cortex supports item memory, this study showed that perirhinal activity during encoding correlated with memory for landmarks in the VR game (Ekstrom and Bookheimer, 2007). Both activity in the parahippocampal gyrus and the hippocampus correlated with all three memory types but parahippocampal activation in particular was associated with spatial associations, while the hippocampus was associated with memory for temporal order (Ekstrom and Bookheimer, 2007). Hence, this study highlights the functions of different regions in the MTL and show how they work in concert in spatial and episodic memory.

The entorhinal cortex (EC) is also believed to play a role in both spatial navigation and episodic memory. A relatively recent discovery was the identification of cells in the EC, which similar to place cells, fired in response to specific locations in the environment In contrast to place cells however, these cells responded to several different locations with place fields distributed in a hexagonal pattern (Hafting et al., 2005). These cells were names grid cells and are believed to support spatial navigation by providing a metric system in the representation of space and integrating the individual's movements within the spatial representation, a process known as path integration (Moser and Moser, 2008).

In terms of episodic memory, it has been proposed that the EC works as a relay system within and between regions of the MTL and neocortical areas. More specifically, it is suggested that the lateral EC receives object-related information

('What') from the ventral stream via the perirhinal cortex and the medial EC receives spatial information ('Where') from the dorsal stream via the parahippocampal cortex and relays this information to the hippocampus (Schultz et al., 2015; Eichenbaum et al., 2007). Consistent with this, it has been proposed that connections between the lateral EC and perirhinal cortex support familiarity-based memory and item memory, whereas the medial EC and parahippocampal cortex support associative and contextual memory (Eichenbaum et al., 2007).

1.3.2.2 Imagery

Memories can be restructured following encoding or even consolidation and are continuously affected by other knowledge, rehearsal etc. (Dudai, 2004). The flexible nature of memories might also explain why situations that were never experienced can be imagined.

Byrne, Becker and Burgess (2007) proposed a model of spatial cognition involving the role of the hippocampus in episodic memory and mental imagery (the BBB model). The model builds on the idea that egocentric (self-object reference frame) and allocentric (object-object reference frame) representations exist in parallel. Within this model, long-term spatial memory is modelled as allocentric representations in the hippocampus modulated by input from other temporal lobe structures, including object-related information from the perirhinal cortex and spatial-related information from the parahippocampal cortex. In turn, short-term memory and imagination is modelled as egocentric parietal representations of locations. Perception of events is experienced from an egocentric perspective and must therefore subsequently undergo transformation to an allocentric representation. Likewise, imagery and memory retrieval must involve the translation of allocentric representations from long-term memory into egocentric representations (Byrne, Becker and Burgess, 2007). Reciprocal connections within the MTL between place cells in the hippocampus, boundary vector cells in the parahippocampal gyrus and object-recognition cells in the perirhinal cortex connect individual aspects of a scene, enabling pattern completion. When a memory is retrieved or a scene is imagined, pattern completion from partial cues retrieve the allocentric representation related to place cells with place fields corresponding to the location from which the scene will be remembered or imagined. The egocentric representation is formed when information on viewpoint is conveyed by head direction cells (Byrne, Becker and Burgess, 2007).

Consistent with this model, Hassabis et al. (2007) found that brain activity during scene construction, a common feature of imagery, spatial planning and memory retrieval, involved a number of MTL structures including the hippocampus, parahippocampal gyrus and retrosplenial cortex (Hassabis et al., 2007; Hassabis and Maguire, 2007). Ranagatha and Ritchey (2012) proposed that the two object- and location-related representations involving the perirhinal and parahippocampal cortices respectively are elements in large cortical networks supporting different types of memory (familiarity and recollection). Further, different roles in cognition were proposed for these two networks, with the perirhinal cortex being involved with linking items with semantic information and the parahippocampal cortex being involved with matching cues to contextual information.

1.3.2.3 Memory consolidation

Following new learning, memories are thought to initially exist in a fragile state and then, over time, are made stabile through memory consolidation (Dudai, 2004, Wixted, 2004). This phenomenon has been described for centuries and the term 'konsolidierung' was first coined by Müller and Pilzecker in 1900 (Lechner et al., 1999; Dudai, 2004), when they demonstrated that memory for learned material first exists in a malleable state and becomes stabilised in the time following encoding. Since this seminal study, many others have underlined the importance of consolidation and demonstrated how memories are particularly vulnerable to disruption during the consolidation period (Dudai, 2004; Dewar et al., 2009, 2012; Ben-Yakov et al., 2013).

More recent conceptualisations have distinguished between two types of memory consolidation. One, often referred to as synaptic consolidation refers to the short-term processes taking place in the minutes and hours following learning during which the synaptic strength between active neurons during encoding is strengthened (Dudai, 2002), and the learned information is integrated into an engram and becomes more robust to interference (Nadel and Moscovitch, 1997; Dudai, 2002). The idea that memory formation is based on changes in synaptic strength between neurons as a result of experience is long-standing (Marr, 1971, Hebb, 1949, Bliss and Collingridge, 1993). Long-term potentiation, the experience-dependent strengthening of synaptic transmission following high-frequency stimulation, is believed to underlie some of these changes and it has been shown that LTP in the MTL is associated with memory performance (Morris et al., 1990; Bliss and Collingridge, 1993).

In contrast, systems consolidation takes place in the days, weeks and years after learning and refers to the process by which memories becomes independent of the hippocampus and becomes a more distributed representation in neocortical areas (Dudai, 2004; Nadel et al., 2000). During systems consolidation, memories are stabilised through interactions between the hippocampus and the neocortex whereby reactivation of previously acquired associative information promotes long-term memory (Carr et al., 2011). It has been proposed that one mechanism underlying this process is replay of stored representations, in which patterns of activation present during learning are subsequently ‘replayed’ as part of an offline automatic process outside conscious control (Carr et al., 2011; Buzsaki, 1986; Gelbard-Sagiv et al., 2009; Foster and Wilson, 2006; Tambini et al., 2010). Evidence suggests that replay takes place during sharp wave ripples (SWRs) in the hippocampus, which are oscillatory patterns typically present during some phases of sleep and to some extent the awake state in rodents and humans (Buzsaki, 1986; Carr et al., 2011; Wilson and McNaughton, 1994; Axmacher et al., 2008; Deuker et al., 2013).

The standard model of systems consolidation proposes that material is initially registered in parallel in the hippocampus and neocortex but during long-term (systems) consolidation, the memory representation is reorganised and the weight shifts to the neocortex, ultimately rendering the hippocampus independent of the memory (Dudai, 2004). However, it is often debated whether or not episodic memories remain dependent on the hippocampus after long delays (also see description of retrieval mechanisms above). Nadel and Moscovitch (1997) suggested that episodic memories remain dependent on the hippocampus for encoding and retrieval of spatial information. However accounts such as the case of H.M. where retrograde amnesia with a strong temporal gradient was observed would suggest that memories become independent of the hippocampus with time (McClelland et al., 1995).

Offline processes appear to play a critical role in consolidation and evidence suggests that some forms of consolidation rely on sleep while others do not. In the case of declarative memory, studies have suggested a beneficial effect of slow-wave sleep (Marshall and Born, 2007; Stickgold and Walker, 2009). For example, Gais and Born (2004) showed that slow-wave sleep facilitated consolidation of word-pair associates, as demonstrated by a subsequent memory task. Also, Peigneux et al. (2004) found that reinstatement of activity present during spatial navigation during subsequent slow-wave sleep was associated with enhanced subsequent spatial memory.

Studies have investigated how consolidation can be facilitated during the awake state. A number of studies have shown that a brief wakeful rest immediately after new learning can enhance the retention rates of the information (Cowan et al., 2004; Dewar et al., 2007; Dewar et al., 2009). The prevailing view is that a brief wakeful rest might enhance memory via facilitation of memory consolidation processes to reduce subsequent forgetting (Tambini et al., 2010; Wixted, 2004). Consistent with this view, replay of temporal sequences related to previous behaviour has been demonstrated in the wake state in rodents (Carr et al., 2011; Foster and Wilson, 2006). Human studies showing replay in the awake state is lacking, but for instance, Dewar (2012) investigated awake consolidation in humans, assessing the effects of wakeful rest immediately following encoding on memory performance. In this study, participants watched a number of short movie clips and were then either given a brief 10min wakeful rest or were instructed to complete a simple ‘spot the difference’ task for the same duration. They found that both groups performed at a similar level immediately after encoding. However, the wakeful rest group showed less forgetting after a short 15-30 min delay and this difference in performance was also evident after 1 week delay. The authors proposed that such differences in memory performance were due to enhanced consolidation and reduced interference during the brief wakeful rest.

Further studies have attempted to examine the neural structures that might support such post-encoding memory consolidation processes. Ben-Yakov et al. (2011) investigated the importance of post-encoding processing in a study showing participants a series of videos while they were in the MRI scanner. Results showed that bilateral hippocampal and dorsal striatal activity time-locked to the offset of the preceding stimulus predicted memory performance for gist in the videos. In a subsequent study, Ben-Yakov et al. (2013) investigated the effect of disrupting this offline hippocampal processing; here, participants were again presented with a series of videos and each video clip was either presented 'alone' or it was immediately followed by another scrambled or normal video clip. The researchers found that presentation of a video (and to a lesser extent also a scrambled video) immediately following another video impaired memory performance for the first video. Furthermore, this effect was accompanied by reduced offline hippocampal processing of the first video due to retroactive interference, causing the impairment in memory performance (Ben-Yakov et al., 2013).

Taken together, new memories exist in a fragile state and are stabilised through a process of consolidation in the period following encoding. There is substantial evidence that short and long-term consolidation processes are critical to memory. Studies suggest that consolidation processes can be disrupted both immediately following encoding and after several minutes, resulting in impaired memory performance.

1.3.2.4 How is memory affected by emotional experiences?

There is a consensus that emotion is a potent modulator of memory and people often report enhanced memory for emotional events (Cahill and McGaugh, 1995; Brown and Kulik, 1977; Bohannon, 1988; Christianson, 1992). Facilitation of memory by arousing or emotionally negative events has been demonstrated in numerous studies. For instance, Kensinger and Corkin (2003) found in a series of experiments that memory for previously presented emotional words were superior to memory for neutral words. Bradley et al. (1992) showed that arousal facilitated memory performance for emotional picture stimuli for both immediate recall and a follow-up recall test one year after encoding. These findings show that emotion can affect memory performance both in the short and long term. In addition, these studies are consistent with subjective feelings of better memory for negative events, although the subjective sense of recollection is often inflated compared to objective memory measures (Phelps and Sharot, 2008) and it has been suggested that while some memory types are enhanced by emotion, others may be reduced (Rimmelé et al., 2011).

A widely held view is that the amygdala supports emotional memory enhancements via facilitation of key MTL memory structures (McGaugh, 2000; Dolcos et al., 2004). Within a modulation hypothesis (McGaugh, 2004; LaBar, 2007), it is assumed that the amygdala modulates the hippocampus during encoding and subsequent consolidation via two communicative pathways, where one is the strong direct connections between the amygdala and the medial temporal lobe including the hippocampus and the entorhinal cortex. The other pathway is indirect, as the amygdala can modulate hippocampal function by activation of the hypothalamus-pituitary-adrenal (HPA) axis stress response and the resulting production of stress hormones such as glucocorticoids, for which the hippocampus has many receptors (McGaugh et al., 1996; LaBar and Cabeza, 2006; Roozendaal, 2000). The modulation hypothesis has found empirical support, for example from neuropsychological studies showing that people with both unilateral and bilateral lesions to the amygdala displayed impaired memory for emotional stimuli, despite showing preserved memory for neutral stimuli; an effect that was present both compared to healthy controls and patients with other brain damage (Adolphs et al., 1997; 2000; 2005).

In a study conducted in rodents, Bass et al. (2014) investigated the modulation hypothesis experimentally using a paradigm with an object-learning task, in which exposure to some of the objects was associated with electrical stimulation of the amygdala. Subsequently, rats showed enhanced object recognition for the objects that were associated with amygdala stimulation. However when rats were given an injection of muscimol (a $GABA_A$ receptor antagonist known to inhibit pyramidal neuron activity) to the hippocampus, the amygdala facilitation of memory was abolished (Bass et al., 2014), lending further support to the idea that amygdala modulates memory via interactions with the hippocampus. Extending these findings to human studies, Dolcos and colleagues (2004) investigated the neural correlates of encoding for subsequently remembered and forgotten emotional and neutral pictures. Here, it was found that memory performance for emotional stimuli was superior to memory performance for neutral stimuli and that this facilitation of memory was associated with greater activity in both the amygdala and MTL (Dolcos et al., 2004).

In contrast to studies showing that emotion facilitates memory, some research has shown that this effect may not be consistent across all types of memory. Many of the studies showing that negative emotion enhances memory used item memory as their outcome variable (LaBar and Cabeza, 2006). As outlined earlier, there is evidence to suggest that negative emotion and the resulting amygdala activation will facilitate item memory, whilst hippocampal activity is down-regulated and associative /contextual memory impaired (Bisby and Burgess, 2014; Anderson and Shimamura, 2005; Mather et al., 2006; Chiu et al., 2013; Kensinger and Schacter, 2006). Consequently, emotional memories will become more detailed on individual elements of the experience but will also be more fragmented and incoherent. This idea is consisted with the proposal that memory for the gist of the emotional event is enhanced, while memory for details is impaired (Christianson and Loftus, 1991; Adolphs et al., 2005).

Pierce and Kensinger (2011) investigated the effects of positive and negative emotion on associative memory using word pairs as stimuli. This study found that associative memory might be impaired by negative emotion when tested shortly after encoding, whereas the pattern was reversed when tested one week after encoding. A more recent study by Bisby and Burgess (2014) found that negative emotion impaired associative memory for an event, while as item memory was enhanced for negative events, supporting the idea that memory for items and associative memory are reliant on different neural mechanisms. Zlomuzica et al. (2016) investigated the effect of arousal on contextual aspects of episodic memory. In this study, the researchers investigated the effect of different emotional states (pleasant, neutral or anxious states induced by corresponding video clips) on content and contextual aspects of episodic memory encoding using a virtual reality (VR) experimental design. The study found that temporal and spatial memory performance on the VR task was impaired when participants were induced with an anxious emotional state, producing emotional arousal (Zlomuzica et al., 2016).

The studies presented above addressed the influence of memory during encoding. Evidence suggests that negative emotion and the associated physiological correlates can also affect memory consolidation (Phelps, 2004). Hormones released during stress, such as epinephrine and glucocorticoids appear to facilitate systems memory consolidation by facilitating noradrenergic stimulation of the basolateral amygdala (Phelps, 2004; Roozendaal, 2002). For instance, a seminal study conducted in rats showed that the injection of epinephrine after training on a fear conditioning task increased memory retention one day later (Gold and van Buskirk, 1975). This effect was present when epinephrine was administered immediately or 10 minutes post-training but not when administered 30 minutes or 2 hours post-training, suggesting a critical time window for affecting post-encoding processing (Gold and van Buskirk, 1975).

Why might negative emotion affect different types of memory in such opposing ways? One idea that can explain these contradictory findings is the notion that stress hormones such as cortisol may have differential dose-dependent effects on the hippocampus and memory performance, where low and high levels of cortisol impairs memory while moderate stress hormone levels may facilitate memory, reflecting an inverted U-shaped function (LaBar and Cabeza, 2006; McGaugh and Roozendaal, 2002; Joëls et al., 2006; Kim and Diamond, 2002; McEwen, 1999). However the involved processes may be too slow to explain the different effects of emotion on memory in experimental studies. Another proposal is that hippocampal processing is reduced during extreme stress, causing impairments to hippocampus-dependent contextual/associative memory while memory for single items might be enhanced via facilitation of the structures associated with item memory, such as the perirhinal cortex (Jacobs and Nadel, 1985).

In summary, the effects of negative emotion on memory have been widely investigated and many studies have found that negative emotion facilitates memory. However there is evidence that this facilitation is specific for retrieval of single items and perceptual-based memory, while memory for associations and context may be impaired by negative emotion. Furthermore, emotion might also modulate memory at the level of consolidation, although it is not known whether these influences mirror those seen during encoding.

1.4 How does intrusive imagery arise?

As outlined above, the effect of emotion on deliberate memory has been relatively thoroughly investigated. The mechanisms underlying the development of intrusive memories and the relationship between intrusions and deliberate memory are less studied. In general, two alternative views about intrusion development have been suggested; one is a unitary account and the other is known as the dual representation theory.

1.4.1 Unitary account view

One view is a unitary theory suggesting that intrusions are supported by emotional memory enhancements in the same way as deliberate memory. The unitary account is based on the idea that traumatic memory is inherently the same as non-emotional episodic memory and that there is no qualitative differences in encoding and processing between trauma memories and non-emotional memories (Hall and Berntsen, 2008; Talarico et al., 2004; Berntsen and Rubin, 2014; see Figure 1.1). What distinguishes trauma memories from other memories is that trauma memories will be subject to emotional facilitation, resulting in stronger encoding and consolidation of the traumatic material (Hall and Berntsen, 2008). This facilitation concerns the memory as a whole and hence this theory assumes that both intrusive and episodic memory is dependent on the same neural systems (Rubin et al., 2008a; 2008b).

This view also emphasizes that spontaneous memories – emotional or not – are inherently a normal phenomenon, except that emotionally negative memories will be noticed more because they are more distressing (Berntsen and Rubin, 2008). In line with ordinary memories, it is argued that memory intrusions are not more sensory (Greenberg and Rubin, 2003) or emotional in nature than other autobiographical memory, which is already characterised by being highly visual and emotional (Berntsen and Hall, 2004; Hall and Berntsen, 2008). This view emphasizes facilitated retrieval in the occurrence of memory intrusions; because emotionally negative memories are more salient and are rehearsed more than other information, there will be more cues in the environment that are likely to trigger involuntary memories of the trauma compared to the number of cues for less salient information rendering highly negative memories more likely to be spontaneously retrieved. Also, within this view, it is argued that traumatic memories become landmark memories that shape other autobiographical memory.

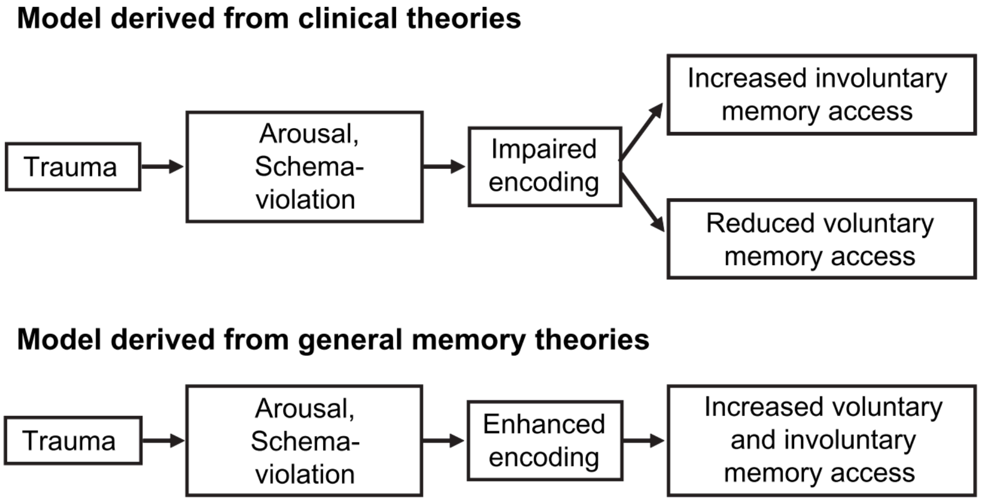

Figure 1.1. Overview of the DRT and unitary accounts of intrusion development. Top panel shows the foundation for theories suggesting that encoding during trauma is impaired, such as the dual representation theory. Bottom panel shows the foundation for theories proposing that memory intrusions rely on enhanced encoding, including the unitary theory. Adapted from Hall and Berntsen (2008).

1.4.2 Dual representation account

In an alternative view, Jacobs and Nadel (1985) suggested that there were two memory systems involved in the encoding of memories; the taxon system, which encodes sensory and affective information related to an experience, and the locale system that places the memory in a spatio-temporal context and is dependent on the hippocampus (O'Keefe and Nadel, 1978). The authors hypothesized that a lack of encoding in the locale system is related to childhood amnesia and that this form of encoding is similar to the conditioning underlying phobias, which can be reinstated during times of high stress where the hippocampus – and consequently taxon encoding – becomes impaired. Subsequent to this early work, the theory has been elaborated as a more comprehensive theory of PTSD and intrusion development and assimilated with more recent research findings. Hence, based on the BBB model mentioned previously, Brewin et al (2010) proposed in this dual representation theory that during encoding of an event, two parallel representations will be formed; one system is the contextual representation system (C-reps), which supports voluntary and deliberate retrieval of declarative information (Brewin et al., 2010). The C-reps allow flexible manipulation of the stored information and, critically for episodic memory, places the event in a temporal and spatial context. It is believed that these processes are mediated by the classical MTL memory system (Brewin 2001; Brewin et al., 2010). In particular, C-reps comprise the spatial properties of the scene related to an episodic event, in the form of allocentric representations and reliant on the hippocampus and surrounding medial temporal lobes (Brewin et al., 2010; O'Keefe and Nadel, 1978; Byrne et al., 2007). When the memory is retrieved, an egocentric image of the memory is formed in short-term memory, a process supported by the precuneus (Burgess et al., 2002; see Figure 1.2).

In parallel with the encoding of C-reps, a more perceptually rich, lower-level representation of the event will be created as a sensation-based representation (S-rep). Under normal circumstances, the S-reps are only transient and will quickly become inaccessible (Brewin et al., 2010). Hence, the S-reps are closely related to the affective, sensory properties and egocentric representations of the memory and can be reactivated by both bottom-up mechanisms such as priming and top-down by associations. Under normal circumstances, moderately salient events will enhance both types of representations and ensure stronger encoding (Brewin et al., 2010).

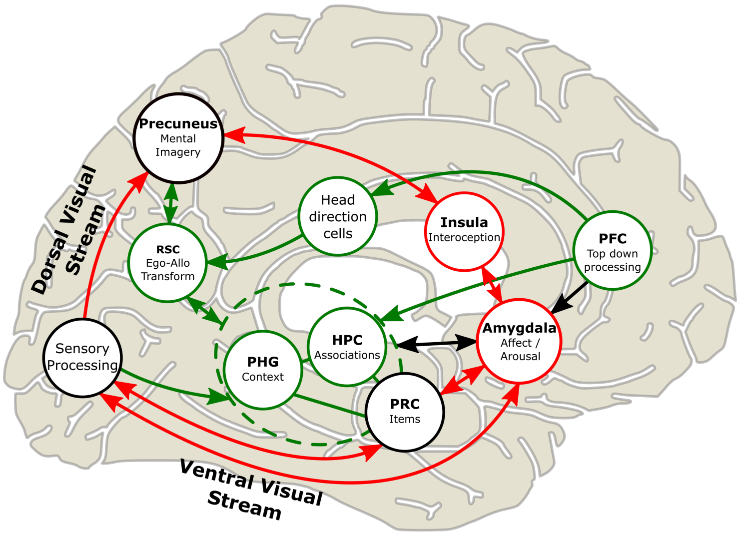

Figure 1.2 Schematic presentation of the dual representation theory and proposed associated neural structures. According to the DRT, two memory representations are formed following encoding of an event. A contextual representation (marked in green) is created in the perirhinal cortex and bound to its corresponding context in the parahippocampal gyrus in the hippocampus. When a memory is voluntarily retrieved, an allocentric representation of the scene in which the experience took place will be created through pattern completion in MTL structures and transposed with an egocentric viewpoint of the event in the precuneus. The other proposed representation is a sensory representation, believed to be facilitated for emotionally negative content. Here, sensory and affective aspects of the event are upregulated via the amygdala, resulting in highly sensory and emotional memories with poor contextual encoding, rendering these representations more likely to involuntarily intrude. Reproduced with permission from Bisby and Burgess (2017).

However, in situations in which the individual is exposed to extreme stress, S-reps will be facilitated via the amygdala and become more enduring while C-reps will be impaired via down-regulation of the hippocampus (Brewin, 2013). These more enduring S-reps may then be activated by associated sensory experiences or emotional states, leading to involuntary retrieval of perceptually rich and affective memories with a sense of reliving the traumatic experience (Brewin et al., 2010; see Figure 1.1). Whereas the unitary account is in line with what is known about the effect of emotion on deliberate memory (for items at least), the DRT is consistent with the clinical presentation of PTSD where there is typically a discrepancy between the presentation of strong negative memory imagery without context (intrusions) on one side, and poor deliberate memory on the other. In addition, the dual representation theory is in line with findings from imaging studies showing decreased hippocampal processing and increased amygdala processing in PTSD (Rauch et al., 2006; Shin et al., 2006; Brewin et al., 2001).

1.5 Methodological challenges in PTSD research

Fundamentally, there are two ways to study memory mechanisms PTSD: either by studying PTSD patients, which will typically involve retrospective accounts of the trauma, or by modelling PTSD-like symptoms in healthy volunteers. One significant challenge when using PTSD patients is that these studies will generally rely on retrospective self-report accounts of the trauma, which introduces a number of problems as such accounts may be influenced by recall bias, subjective interpretations and are heterogeneous and poorly controlled (Frissa et al., 2016). Also, retrospective accounts will often have poor accuracy and are difficult to verify (Candel and Merckelbach, 2004).

Importantly, peri-traumatic encoding factors and processing modes appear to be important predictors for the subsequent experience of the trauma and risk of developing PTSD (Ozer et al., 2003; Holmes and Bourne, 2008). These challenges bring forward a need for a prospective, controlled and ethical method to investigate the development of intrusive memories (for a review see Holmes and Bourne, 2008).

1.5.1 Empirical studies on trauma memory

1.5.1.1 Trauma paradigm

The trauma film paradigm is a method to investigate the development of intrusive memories that satisfies the demands outlined above. In this paradigm, healthy volunteers are exposed to short videos containing traumatic and distressing scenes. These scenes are meant to produce intrusions as part of a stress-response tendency that can be considered a mild form of the response that may produce clinical flashbacks in psychiatric disorders (Holmes, 2004; Horowitz, 1975). These videos all contain material that is in line with the DSM-V criteria for a traumatic experience in so far that they comprise scenes of "actual or threatened death or serious injury" (Holmes and Bourne, 2008; American Psychiatric Association, DSM-V). Naturally however, these scenes will have limited personal relevance to the viewers, a factor that most likely affects emotional involvement and intrusion development (Holmes and Bourne, 2008; Krans, 2013a). Nevertheless, this paradigm has demonstrated its value in inducing memory intrusions in study participants. After the encoding session, participants are instructed to keep a diary of any intrusive memories related to the videos they may have over the course of the next 7 days (for a review, see Holmes and Bourne, 2008). When participants return after one week, other measures, such as tests of deliberate memory can be collected.

Importantly, apart from providing a method for controlled and prospective encoding of "traumatic" experiences, the trauma video paradigm also offers the opportunity to manipulate intrusion development. Experiments have directly manipulated peri- or post-traumatic processing by giving participants a concurrent cognitive task during or immediately following encoding demonstrating that intrusion development can be both enhanced and decreased using different types of manipulations. For example, Bourne et al. (2010; also Holmes et al. 2004; Brewin and Saunders, 2001; Stuart et al., 2006) found that participants had *fewer* memory intrusions when they were carrying out a visuospatial tapping task during encoding of the videos. This effect was not likely to be a result of increased distraction during encoding, as another group carrying out a verbal task during encoding had *more* intrusions and decreased deliberate memory for the videos. Measures of voluntary memory showed the opposite effect; here, participants in the verbal task group showed poorer performance on the verbal memory task compared to participants assigned to visuospatial tapping during encoding and a control group. Hence, studies such as these demonstrate the possibilities offered by the experimental trauma paradigm in the manipulation of peri-encoding and post-encoding factors.

1.5.1.2 Manipulating analogue trauma consolidation

The trauma video paradigm has also been used to study the role of post-encoding processing by introducing tasks or manipulations *after* encoding. For example, Holmes et al. (2009) demonstrated that playing the computer game 'Tetris' (a visuo-spatial task) 30 minutes after encoding of experimental trauma reduced subsequent memory intrusions compared to a control group, who did not perform a task. The mechanism underlying this finding was hypothesized to be the introduction of competition for visuo-spatial resources between the visuo-spatial task and trauma memory representation. However, to rule out the possibility that the observed effect was due to a general competition for attentional resources, Deeprose et al. (2012) demonstrated that carrying out a visuo-spatial task (complex finger-tapping) either immediately or 30 minutes after encoding also reduced memory intrusions, compared to both a control group who did not carry out a task and a control group carrying out a verbal task, counting backwards in threes (Deeprose et al., 2012). Hence, there are empirical studies demonstrating the use of the trauma paradigm to investigate and manipulate post-encoding processing after experimental trauma.

1.6 Can enhanced consolidation improve trauma symptomatology?

In this thesis, I set out to investigate how post-encoding processing of emotionally negative information can affect subsequent deliberate and involuntary memory. For this purpose, I used different techniques to enhance or impair the post-encoding processing of experimental events, including retroactive interference and wakeful rest. As outlined in the literature review, for neutral information it is well described that modulation of consolidation affects subsequent memory and there is evidence to suggest that different memory types may be affected differently by modulating consolidation processes. However less is known about the role of post-encoding processing in memory intrusion development, which will be the focus of this thesis.

Studying the roles of post-encoding processing and consolidation in intrusion development carries clinical implications as the period following encoding could offer a target for secondary prevention of PTSD following trauma. This is particularly important as current treatments leave a significant portion of patients with chronic PTSD symptoms and the mechanisms underlying the most effective available treatments (CBT with exposure) are not fully understood. Hence, neuroscience research on mechanisms underlying intrusion development and how development of these intrusions might be prevented could help identifying new psychological interventions and explain the mechanisms underlying effects of current treatments (Holmes et al., 2014). Secondly, from a basic science perspective, investigating the role of post-encoding processes in intrusion development contributes to the understanding of how memory systems work and how they can be manipulated.

This thesis investigated the role of post-encoding processing in intrusion development and emotional memory, using behavioural methods and fMRI. In the first experimental chapter (Chapter 2), I investigate two different methodologies for assessing intrusive memories in a laboratory setting. Chapter 3 investigates the role of retroactive interference in intrusion development based on previous studies investigating retroactive interference effects on neutral information. In Chapter 4, I investigate if a brief period of wakeful rest following encoding may enhance consolidation, thereby affecting intrusive and deliberate memory. Finally, In Chapter 5, I used fMRI to assess neural correlates of intrusion development.

2 EXPLORING TECHNIQUES TO STUDY MEMORY INTRUSIONS AND DELIBERATE MEMORY

2.1 Overview

As outlined in Chapter 1, the mechanisms that contribute to intrusive memory development are poorly understood. Whilst there is a general consensus that memory consolidation plays a critical role in the formation of episodic memories, the significance of its role in intrusive memories is less known. Typically, studies assessing consolidation processes and their disruption use some form of manipulation in the period following encoding of novel stimuli, including words (Trammell and Clore, 2014), images (Takashima et al., 2006) and short video clips (Nielson and Powless, 2007). Whilst such techniques have been influential in understanding memory processes, investigating intrusive memory development for emotional events has proved more complex. To recreate the emotional response that might be triggered during distressing events, studies investigating intrusive memories often use short clips of traumatic material (Holmes et al. 2004; 2009; Krans et al. 2013a; James et al., 2015; Meyer et al., 2013; Bourne et al., 2010; 2013; Brewin and Saunders, 2001; Bisby et al., 2009), although a few studies have also attempted to induce intrusions via static images (Krans et al. 2013b; Pearson and Sawyer, 2011; Bywaters et al., 2004). The aim of this experimental chapter was to assess and contrast these techniques for investigating intrusive and deliberate memory for traumatic materials and their potential use to examine consolidation processes in subsequent chapters.

2.2 Introduction

Emotion is known to be a potent modulator of memory with a range of studies demonstrating that emotionally negative experiences are remembered better than neutral events (Brown and Kulik, 1977; Cahill and McGaugh, 1995; LaBar and Cabeza, 2006). Many studies investigating the effects of emotion on memory have concerned themselves with using memory for individual elements of an event as their measure for memory performance. However, some studies have suggested that emotional facilitation of memory does not occur for all aspects of an event. For example, when participants are asked to report on the gist and specific details of an emotional event, increased memory is only observed for the gist rather than details of the event (Adolphs et al., 2005). It is therefore important to consider that episodic memories not only include information about the individual elements or items of the event but also the associations between these elements (Horner et al., 2015). Taking such subtle differences into account is clearly important when attempting to understand how intrusive memories develop following a traumatic event.

Many scientists have made the case that item and associative memory are dissociable processes (Gardiner, 1988; Jacoby and Dallas, 1981; Yonelinas, 2002) and rely on different neural systems (Rugg and Yonelinas, 2003; Eichenbaum, 2004). That is, memory for single items can be supported by simple recognition processes or familiarity-based judgements that are thought to rely extrahippocampal areas, including perirhinal cortex (Aggleton and Brown, 1999; Davachi, 2006; Barense et al., 2007; Eichenbaum et al., 2007; Mayes et al., 2007; Montaldi and Mayes, 2010). In contrast, memory for associations between items or items and their context rely on the hippocampus (O'Keefe and Nadel, 1978; Cohen and Eichenbaum, 1993; Burgess et al., 2002; Davachi, 2006; Eichenbaum et al., 2007), and their holistic retrieval contributes to recollection, a hallmark characteristic of episodic memory (Tulving, 1983).

Recent studies have attempted to elucidate these dissociable forms of memory for emotional stimuli. For example, Mather and Knight (2008) showed that emotional harbinger cues were related to impaired associative memory compared to neutral cues. In this study, participants were first presented with negative and neutral images each preceded by a tone. During this phase of the experiment, participants learned which tones were 'emotional harbingers', predicting negative images. Next, participants learned associations between the emotional harbinger tones and digits presented on the screen. Results from this study demonstrated impaired associative memory performance on tone-digit associations where the tone had predicted emotionally negative stimuli in the previous phase of the experiment, pointing to a selective impairment in associative memory for negative information (Mather and Knight, 2008).

Other studies have demonstrated differential effects of emotion on different memory types. Touryan et al. (2007) conducted a study in which participants were presented with emotionally neutral or negative picture stimuli with an unrelated visual object embedded in the periphery of each picture stimulus during encoding. Subsequent memory tests showed that item memory for emotional negative pictures was enhanced compared to neutral pictures, whereas associative memory (matching the original stimulus and peripheral object mixed with foils) performance for emotionally negative pictures was impaired. Consistent with this finding, a study by Rimmelé et al. (2011) also found enhanced recognition memory for negative compared to neutral visual stimuli whereas associative memory (matching the visual scene with one in four colour frames the pictures had been presented with) was impaired for negative compared to neutral information. Furthermore, during the recognition test participants also indicated whether they consciously recollected having seen the original image before or if it seemed familiar to them (the remember/know paradigm). Interestingly, the subjective experience of remembering a picture was higher for negative items compared to neutral items but performance on the associative memory test was lower for negative than for neutral scenes, indicating that the subjective sense of remembering was more associated with the negative items themselves rather than the scene as a whole (Rimmelé et al., 2011; Yonelinas and Ritchey, 2015).

Also, to examine the contrasting effects of emotion on dissociable aspects of memory, Bisby and Burgess (2014) investigated the effect of negative emotion on item and associative memory in a series of experiments. One of these experiments involved presenting healthy volunteers with paired associates of emotionally negative or neutral pictures (pairs could be either two negative pictures, two neutral pictures or a combination of both). Immediately after encoding, participants completed a recognition memory test and an associate memory test. The recognition memory test consisted of participants viewing images on the screen and judged whether the presented picture was 'Old' or 'New'. The associative memory test was an alternative forced choice multiple choice test with four alternative picture descriptions where participants were instructed to indicate which paired associate a presented picture had been paired with during encoding (Bisby and

Burgess, 2014). This study showed that while recognition memory for negative items was enhanced compared to neutral items, associative memory for pairs including a negative item at encoding was impaired. In line with such dissociable memory systems and the neural structures that support them, it has been proposed that negative items might up-modulate the amygdala to enhance item memory encoding, whilst disrupting the hippocampus and associative encoding (Bisby et al., 2016; Kensinger and Schacter, 2006; Yonelinas and Ritchey, 2015).

Interestingly, whilst the dissociation between item and associative memory is well established in the general memory literature, these ‘types’ of memory for traumatic material and related intrusive memory development are yet to be clearly investigated. However, as described in Chapter 1, a dual representation account (Brewin, 2008, Brewin et al., 2010) of intrusive memories does consider this distinction and proposes that while associative memory will be impaired by strong negative affect, item memory and more implicit memory forms such as memory intrusions may be facilitated, dissociating these memory types. Within this view, it is suggested during encoding of an episodic event, two parallel representations of the event are formed; one is a contextual representation and is supported by the hippocampus, while the other encodes lower-level sensory and emotional aspects of the event. It is proposed that during psychological trauma, lower level processing of sensory and emotional aspects of the event will be facilitated via the amygdala while contextual processing of the event, supported by the hippocampus, is impaired (Brewin et al., 2001; 2010) As a result, associative memory for emotionally negative events is impaired while sensory memory for single aspects of the event is enhanced (Brewin et al., 2010).

In contrast, unitary accounts predict that that negative affect will facilitate a stronger memory trace compared to neutral information, where recall for all aspects of the memory are enhanced through stronger encoding and more subsequent rehearsal of the event (Rubin et al., 2008a; 2008b). Hence, it follows from this account that both memory for contextual details (associative memory) and item memory should be enhanced by negative affect (Talarico et al., 2004).

Due to methodological constraints, studies examining intrusive memory development in the laboratory have been unable to dissociate different aspects of deliberate memory. For instance, studies investigating intrusive memory occurrences often use a trauma film paradigm in which participants are exposed to one or more audio-visual clips with emotionally negative content (Holmes et al., 2004; 2009; Pearson, 2012; Pearson et al., 2012). Whilst this method provides a more immersive experience than other methods, deliberate memory is normally tested for the static scenes or for sentences referring to aspects of the clips and has provided mixed results. For example, Holmes et al. (2004) carried out a series of experiments in which participants watched a trauma film comprising emotionally negative video clips while simultaneously carrying out a visuospatial pattern tapping task or a control condition (no task or verbal distraction). In the week following encoding, participants kept a diary of memory intrusions and completed a cued recall memory test at the end of the week. Results from these studies found that carrying out a visuospatial task during encoding reduced the number of intrusions, while the verbal task enhanced them. In contrast, no differences in deliberate memory performance were observed between the different groups (Holmes et al., 2004). Subsequent studies have replicated the finding that a visuospatial task reduced intrusions, while results for deliberate memory is less consistent. For instance, in a more recent study by Bourne et al. (2010), it was investigated whether the effect of Holmes et al. (2004) could be explained by distraction during encoding. For this purpose, participants carried out one of two tasks during encoding, where one was a visuospatial tapping task and the other was a verbal interference task. Again, this study showed that carrying out a visuospatial task during encoding reduced the number of subsequent intrusions. Critically, this effect was not present for the group carrying out a verbal interference task, suggesting that the specific cognitive resources engaged during a peri-traumatic task predict subsequent intrusion development (Bourne et al., 2010). Furthermore, this study also showed an effect of task on deliberate memory, with better memory performance in the verbal interference group than in the visuospatial tapping group, showing opposite effects for memory intrusions and deliberate memory (Bourne et al., 2010).

Other studies have introduced manipulations immediately *following* encoding to disrupt post-encoding processing and memory consolidation. In a widely described study by Holmes et al. (2009), healthy volunteers viewed emotionally negative video clips immediately followed by either an intervention (playing the visuo-spatial computer game 'Tetris') or a control condition. Again, participants kept a diary of involuntary memories associated with the trauma film one week following encoding. Participants also completed a recognition memory test one week after encoding in which participants were required to answer with 'True' or 'False' to a number of statements relating to the trauma film they had seen one week earlier (Holmes et al., 2009). Similar to previous reports investigating peri-traumatic processing, this study showed that playing 'Tetris' immediately after viewing experimental trauma reduced the number of reported memory intrusions but had no affect on recognition memory performance (Holmes et al., 2009). Taken together, it is unclear whether unlike involuntary memory, deliberate memory performance is unaffected by manipulations to encoding or consolidation of traumatic material or whether a lack of change is related to the specific tasks used to assess memory.

Using methods more similar to typical memory tests, others have used emotional pictures to assess intrusive memory development (Pearson and Sawyer, 2011; Pearson et al., 2012; Krans et al., 2016). For instance, Krans et al., (2013b) carried out a study similar to the one by Holmes et al. (2004) in which participants were shown emotional pictures, while concurrently carrying out either a verbal task or a visuospatial task. Furthermore, half of the participants were given a written narrative before the presentation of each picture. Intrusions were measured using an intrusion diary and on follow-up a week after encoding, participants were tested on both recognition memory and contextual memory. For the recognition test, participants were presented with pairs of pictures showing similar situations and were instructed to indicate which of the two pictures they had seen previously during encoding. In the contextual memory test, participants were presented with pictures from encoding and asked about the corresponding narrative for each picture (only results from the group who had received a narrative were used for analysis). Results from this study showed that participants who had been given narratives of the pictures reported more intrusions and scored higher on the recognition memory test than the group who did not read narratives for each picture (Krans et al., 2013b). Furthermore, the visuospatial condition was related to impaired associative memory performance compared to the verbal task and no task. The researchers argued that these results contradicted the dual representation theory and supported a unitary account (Krans et al., 2013b). However, the 'contextual details' given to participants appeared to enhance emotional impact and salience of the pictures, perhaps to a larger extent than providing associative information, which makes the results more difficult to interpret.

In this first set of exploratory experiments, the aim was to examine whether different paradigms could be used to elicit intrusive memories and which different aspects of deliberate memory could be assessed. As such, this method could then be implemented, along with various manipulations, within all subsequent experiments within this thesis. As identified, two main techniques to investigate emotional memory and memory intrusions involve the use of emotional images (such as images from the International Affective Picture System (IAPS); Lang et al., 2005) or short audio-visual clips ('trauma films') as stimuli. Given the benefits of using a paradigm that more closely fits typical memory research (i.e. static images that can easily be paired and tested in different ways), the first exploratory experiment attempted to investigate deliberate and intrusive memories for static images. Using a similar design to Bisby and Burgess (2013; see below for a detailed description), memory for items and associations could be assessed separately and this could be related to intrusive memories reported for those images. Further, based on the predictions from different views, if dissociable forms of memory are affected in opposing ways in line with a dual representation account, it was expected that item memory for negative images would be enhanced and associative memory would be reduced, an imbalance that should predict intrusive memory reports. However, if memory is generally facilitated by negative emotion, all forms of memory should be boosted and potentially positively correlated.

2.3 Exploratory experiment 2.1: Using static images to assess trauma memory

The first experiment aimed to investigate the effects of negative emotion on intrusion development, item and associative memory performance using neutral and negative static images. The study design was the same as design used in Bisby and Burgess (2013). That is, participants encoded pairwise associates made up from either two neutral pictures or a combination of neutral and negative pictures. To also incorporate a measure of intrusive memory, a one-week interval between the encoding and the test session was added whereas Bisby and Burgess (2013) used a shorter 10 min delay.

From the two theories of intrusive memory outlined above, two contrasting predictions for this experiment could be formulated. For both accounts, it could be predicted that recognition memory performance for negative items would be enhanced compared to neutral items and that a recognition memory for a neutral image that was associated with a negative image during encoding would show the lowest performance, due to salience of the negative event (Figure 2.1). Further, from the unitary account it was expected that memory performance on the associative memory test would follow the same pattern as recognition memory, demonstrating enhanced associative memory for negative items compared to neutral items.

In contrast, the DRT would predict that scores on the associative memory test would be lower for negative compared to neutral items, hence showing opposite effects of emotion on recognition and associative memory (Figure 2.1). More specifically, it was predicted that performance would be impaired when a neutral associate was to be retrieved from a negative cue (NegNeut). For negative associates that were retrieved from a neutral cue (NeutNeg), it was expected that associative memory would be facilitated compared to the NegNeut condition due to salience of the negative associate, which therefore might be more easily retrieved. Finally, retrieving a neutral associate from a neutral cue (NeutNeut) would show the best performance (Figure 2.1). In short, the prediction based on the DRT would be to see opposing patterns in performance on the recognition memory test and the associative memory test.

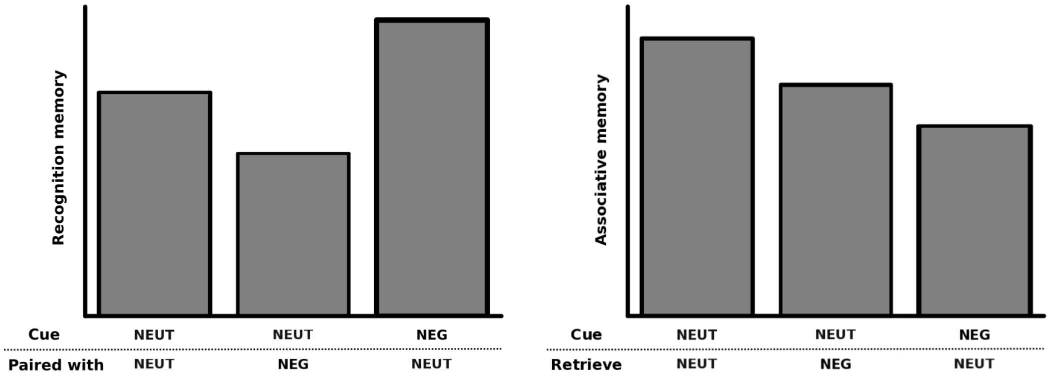

Figure 2.1. Expected pattern of recognition and associative memory performance. Hypothesized pattern of memory performance for neutral and negative items on a recognition memory test (left) and an associative memory test (right). Based on the DRT, it was expected that opposing patterns would be observed for recognition and associative memory for negative and neutral information.

2.3.1 Method

2.3.1.1 Sample size estimation

Based on effect sizes reported in a previous study by Bisby and Burgess (2014), the G*power software package was used to conduct a power analysis yielding an approximate required sample size of N=18 for the experiment (power level of 80%, α=0.05).

2.3.1.2 Participants

Seventeen healthy volunteers (11 females) aged 18-35 years (M=22.88, SD=-4.22 years) were recruited from the student population at University College London (UCL). The UCL research ethics committee approved the studies and all volunteers gave written informed consent prior to participating in the study. To take part, volunteers were paid 7.50 pounds per hour. Participants with a history of psychiatric or neurological disorders were excluded from the study via self-report.

2.3.1.3 Stimuli

The stimuli consisted of 90 pictures (45 neutral, 45 negative) taken from International Affective Picture System (IAPS; Lang et al., 2005). Negative images could typically depict a negative scene such as an injured person or an accident, whereas neutral images would reflect everyday situations of people shopping, eating etc.

2.3.1.4 Intrusion diary

To record intrusive memories, participants filled out a written, pen-and-paper intrusion diary, detailing any spontaneous memories related to the presented pictures they experienced over the next 7 days, until they returned for the follow-up session a week later. Participants were instructed that an intrusive memory was a visual image or thought about a picture they had seen during encoding that came to mind spontaneously without purposefully trying to retrieve the information with or without identifiable triggers. Participants were instructed to report all picture-related spontaneous memories in the diary with a different entry for each memory specifying the content of the memory and what picture it was related to. For each intrusion, participants were required to specify 1) what they spontaneously remembered 2) in what situation the memory occurred and 3) which picture the memory was related to.

If participants had days with no spontaneous memories, they were still required to make an entry in the diary noting that they had not experienced any picture-related spontaneous memories on that day. This was done to ensure that participants were compliant in carrying out the task. Participants also made ratings indicating how distressing and vivid they experienced the memories. Participants were instructed to write down intrusions immediately after they occurred or as soon as possible, and as a minimum to fill out the diary at the end of each day. Upon return a week later, information recorded in the intrusion diary was checked by the experimenter to ensure that participants had understood and completed the task in accordance with the given instructions and that the experimenter understood the match between memory intrusion and picture.

2.3.1.5 Questionnaires

Participants' mood was assessed prior to and following viewing of the emotional stimuli. To assess anxiety, participants completed the state-trait anxiety (STAI) inventory (Spielberger et al., 1983). The STAI-T consists of 20 self-report items for evaluating trait anxiety (e.g. 'I am a steady person', 'I feel like a failure') and responses are made on a 4-point Likert scale ranging from 'Almost never' to 'Almost always'. The state anxiety inventory (STAI-S) also consist of 20 items (e.g. 'I feel relaxed, 'I am presently worrying over possible misfortunes') and responses are given on a 4-point Likert scale ranging from 'Not at all' to 'Very much so'. Scores range from 20-80 with higher scores being indicative of higher anxiety levels.

To examine mood changes, the positive and negative affect schedule (PANAS) questionnaire (Watson et al., 1988) was filled out. The PANAS questionnaire is a self-report inventory consisting of words that describe feelings and emotions that are either positive (e.g. 'Interested, Excited, Strong') or negative (e.g. Distressed, Upset, Ashamed) including 10 items each. Ratings are given on a 5-point Likert scale ranging from 'Very slightly or not at all' to 'Extremely'.

2.3.1.6 Procedure

2.3.1.6.1 Encoding

At the start of the encoding session, participants completed the trait (STAI-T) and pre-encoding state STAIS and PANAS questionnaires. For encoding, participants were presented with randomly ordered pairs of images on the screen. The pairs could either be a combination of two neutral (NeutNeut) pictures or a combination of one negative and one neutral picture (NegNeut or NeutNeg, depending on which picture was used as a cue picture during the test session; NegNeut = cue with negative image, retrieve neutral image and vice versa). The pictures were presented on a black background on the screen for a duration of 4 seconds. Participants were instructed to try and imagine a link between the two pictures. There were 90 encoding trials in total (30 of each condition). After stimulus presentation, participants gave a rating indicating how plausible they thought it was that the pictures would occur in an event together. Each trial was followed by an inter-trial interval (ITI) of 1 second in which a fixation cross was presented in the middle of the screen before the next trial. Finally, the second part of the state questionnaires was filled out immediately after encoding.

2.3.1.6.2 Intrusion diary

Following the encoding session, participants received instructions on how to fill out the diary over the next 7 days until returning for the follow-up session.

2.3.1.6.3 Memory tests

The memory test was conducted at follow-up on day 8 and consisted of both a recognition memory (item memory) test and an associative memory test. On each trial of the test, participants were presented with a picture on the screen and were instructed to judge whether they recognised the picture or not (participants were instructed to respond with 'Old' if they recognised the picture from encoding and respond with 'New' if not). There were 135 trials with 45 new pictures interleaved with 90 old pictures. If the presented picture was 'Old', participants were given a second question, comprising the associative memory test. Here, they again saw the image cue and were asked which other picture the presented picture had been paired with during encoding. Volunteers would make their response by choosing a paired associate in an alternative forced choice question comprising four written descriptions with one correct answer and 3 foils in addition to a fifth answer option indicating 'I don't know'.

2.3.1.6.4 Statistical analysis

All statistical analyses were carried out using SPSS 22.0 software. A repeated-measures ANOVA was used to investigate the relationship between the three conditions (neutral cue with neutral associate, neutral cue with negative associate or negative cue with neutral associate) for both recognition and associative memory performance. All follow up tests were performed using t-tests with Bonferroni correction. The relationship between number of reported intrusions and measures of deliberate memory was also investigated with correlation analyses.

2.3.2 Results

2.3.2.1 Recognition memory

Trials from both the recognition and associative memory tests were separated into three conditions: 1) remembering a neutral picture that had been shown with another neutral picture during encoding (NeutNeut), 2) remembering a neutral picture that had been shown with a negative picture during encoding (NeutNeg) and 3) remembering a negative picture that had been presented with a neutral picture during encoding (NegNeut).

A corrected recognition memory score was calculated by subtracting the number of false alarms from the total number of hits (correctly recognised pictures). A repeated-measures one-way ANOVA on corrected recognition memory scores showed a main effect of condition, $F(2,32)=15.03$, $p<.001$, $\eta^2=0.48$ (Figure 2.2a). Further analysis with follow up t-tests showed better recognition of negative item cues (NegNeut) compared to both neutral item cue conditions (NeutNeg, $t(16)=4.43$, $p<.001$, $d=1.08$; NeutNeut, $t(16)=3.77$, $p<.01$, $d=0.72$). Analysis also showed better recognition performance for item cues that had been paired with another neutral associate at encoding (NeutNeut) compared to neutral items that had been paired with a negative associate (NeutNeg, $t(16)=3.05$, $p<.01$, $d=0.91$).

2.3.2.2 Associative memory

Participants generally performed very poorly (i.e. at or below chance) on the associative memory test, during which they were instructed to identify the paired associate from four descriptions when cued with a previously recognised picture. A repeated-measures ANOVA revealed no differences in associative memory scores across the three conditions, $F(16)=0.52$, $p=0.60$, $\eta^2=0.032$ (Figure 2.2b). The overall proportion of correct responses was 0.21 (chance level was 0.25, excluding the 'Don't know' response option). Due to the low performance scores, a one-sample t-test was carried out, which showed that the across conditions, the mean performance was not significantly different from a 0.25 chance level performance (t(16)=1.27, p=0.22, d=0.31).

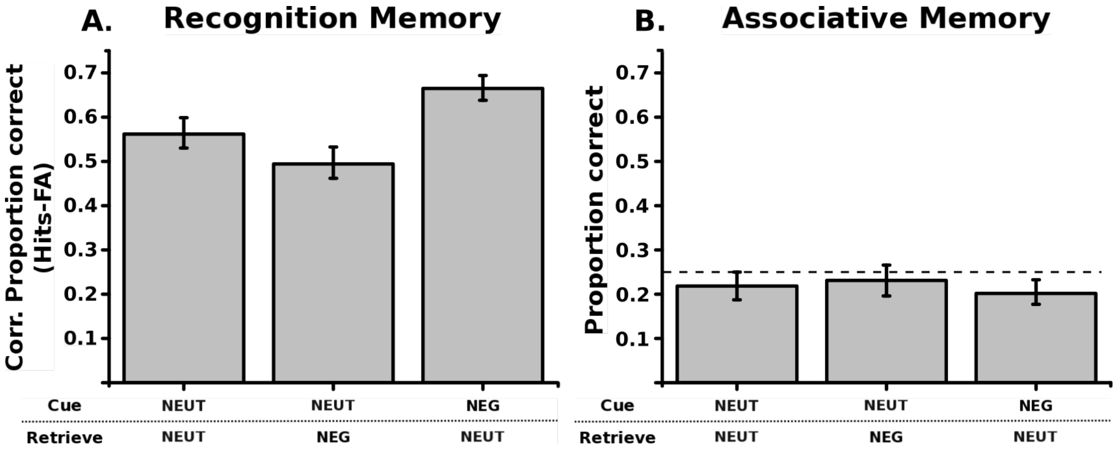

Figure 2.2. Mean performance on tests of recognition and associative memory. During encoding, participants were presented with pairs of pictures. For the recognition memory test, participants were presented with a cue picture (cue valence indicated above the dashed line) and were instructed to indicate whether or not they recognised the picture from the encoding session (A). Figure shows corrected scores (hits minus false alarms). If participants correctly recognised the picture, they were then asked to recollect the paired associate in the associative memory test (B). Valence cue indicated above the line. Valence of paired associated indicated below the line. Error bars show SE. The dashed line on figure B indicates chance level on the associative memory test.

2.3.2.3 Intrusions

The number of reported intrusions that were correctly filled in and could be matched with pictures amounted to 96%. Participants experienced a mean number of 3.58 (SD=4.71, Md=1) intrusions over the week during which they filled out the diary, although few people reported relatively many intrusions while 10 out of 17 participants only reported 1 or zero intrusions. There were no significant correlations between intrusions and any conditions of item or associative memory performance (all p's >.38) or between intrusions and subjective ratings (all p's > .14)

2.3.2.4 Subjective ratings

A paired-samples t-test revealed that state anxiety measures (STAI-S) increased from pre- to post-encoding, t(19)=4.72, p<.001, d=1.05. The same was the case for the PANAS negative affect scale, t(19)=3.47, p<.01, d=0.76. In contrast, the positive scale showed an decrease from prior to encoding of the trauma videos to after, t(19)=2.55, p<.05, d=0.57 (see Table 2.1). Looking at the relationship between measures of affect and memory, there was a medium positive correlation between trait anxiety and recognition memory performance for negative items but this relationship did not reach significance, r=0.46, p=0.07. Furthermore, the difference in positive affect from pre- to post encoding was associated with overall associative memory performance which was probably driven by a positive correlation between difference in positive affect and retrieving a negative associate from a neutral cue (r=0.55, p=0.02) and perhaps to a lesser extent retrieving a neutral associate from a negative cue, although this effect did not reach significance, r=0.45, p=0.07.

Table 2.1 Means (SD) of questionnaire measures of positive and negative affect and anxiety in Experiment 2.1.

	N=29		
	Pre	**Post**	**Sig.**
Trait anxiety	39.00 (9.55)	n/a	n/a
State anxiety	31.20 (7.45)	41.35 (8.79)	p<.001
Positive affect	31.60 (8.24)	28.25 (9.39)	p<.05
Negative affect	11.75 (2.02)	15.00 (4.11)	p<.01

2.3.3 Discussion

The goal for this experiment was to investigate a potential experimental design using static neutral and negative images as a way to assess the effects of negative emotion on different aspects of deliberate memory (item recognition and associative memory) and memory intrusions. Results generally showed that static images only led to a small number of intrusive memories. Further, whilst recognition memory was enhanced for negative images, associative memory performance was poor and at or below chance, suggesting that this paradigm might not be optimal for assessing these aspects of memory following such a delay introduced in the current study.

Consistent with previous studies (Burke et al., 1992, Touryan et al., 2007, Mather and Knight, 2008, Rimmelé et al., 2011, Cahill and McGaugh, 1995) results showed enhanced item recognition for negative images. That is, participants recognised a greater number of negative images after 1 week compared to neutral images. This result also replicates the findings of Bisby and Burgess (2013), who used a similar design to this study. This study found the same pattern of results with better item recognition for negative than for neutral images when the test was conducted immediately after encoding. This suggests that this memory effect is consistent in the time following encoding and does not reflect reduced temporal decay of neutral information compared to negative information.

Recognition memory for neutral images was worse when the image had previously been shown with a negative associate at encoding (NeutNeg) compared to recognition of neutral images previously shown with another neutral associate (NeutNeut). Reduced recognition for neutral images when paired with a negative image might reflect attentional competition between the two images. For example, it is well established that negative stimuli usurp attentional processing at the cost of neutral stimuli (Talmi, 2013; Mather, 2007; Mather and Sutherland, 2011). Mather and Sutherland (2011) coined the term arousal-biased competition (ABC) to describe these processes where events associated with high arousal are prioritised both during perception, consolidation and memory retention. It is proposed that arousal is critical to increased attention during perception and further downstream, in memory formation and consolidation, the events that received the most attention during encoding will be processed more (Mather and Sutherland, 2011).

In the context of the present study, participants' attention might have been drawn to the negative image during encoding resulting in reduced processing and hence poorer recognition for the neutral image. Therefore, this facet of the results further demonstrates that negative items may take precedence over neutral items.

Disappointingly, associative memory performance was below chance level and there were no significant differences between conditions on memory scores. Nevertheless, it should be noted that from visual inspection it appeared that the numerical pattern for associative memory performance was directly opposite to the pattern observed for item memory, albeit not significant. By visual inspection, a pattern of numerically better memory performance was observed for trials where a negative associate was retrieved from a neutral cue and lower performance when a neutral associate was retrieved from a negative cue (Figure 2.2b) although this difference was non-significant. As it was the case with recognition memory, this pattern of associative memory performance is the same as in the previous study by Bisby and Burgess (2013) where participants were tested immediately after encoding. This identical pattern shows that the lack of significant effects in the current study compared to the study of Bisby and Burgess could be due to forgetting over time. Hence, low memory performance in the current study could be a factor of forgetting or temporal decay, a normal and adaptive process (Schooler and Hertwig, 2011).

For the intrusion data, a significant problem encountered was that over half the participants reported only one or zero intrusions. This could be due to lack of emotional response to the traumatic stimuli for some participants, which has been shown to be associated with fewer reported intrusions (Clark et al., 2015). However, previous studies using static images to investigate intrusion development found similar or lower rates of memory intrusions to this study (e.g., Krans et al., 2013b, 2016; Pearson et al., 2011; Pearson, 2012). It would have been interesting to investigate the number of intrusions in each condition and investigated their relationship with recognition and associative memory scores. However, because many participants had very few intrusions, it was difficult to perform further analyses on these data.

2.4 Exploratory experiment 2.2: Using videos to study trauma memory

Results from Experiment 2.1 highlighted several challenges in investigating deliberate and intrusive memory for negative material using static images. Static images produced very low numbers of intrusions across participants. In addition, what appeared to be floor effects on the associative memory test were significant concerns. Therefore, drawing meaningful conclusions from the results of Experiment 2.1 was difficult. As detailed in Chapter 1 (see section 1.5.1.1), another method that has been used to investigate intrusion development is the trauma film paradigm using audio-visual video clips (Holmes et al., 2004; Bourne et al., 2010; Krans et al., 2009a; 2009b; 2009c; 2013a; Holmes and Bourne, 2008). These stimuli are complex, multimodal and carry a narrative and are therefore more similar to real-life events than pictures, producing more ecological validity (James et al., 2016). Consequently, it is reasonable to assume that these stimuli might have a greater emotional impact on volunteers than the use of static pictures. Experiment 2.2 aimed to use short emotional video clips as stimuli to elicit intrusions.

However, using video stimuli also introduces new challenges, primarily because it is more challenging to assess memory performance on complex stimuli. As mentioned above, the use of video clips to investigate intrusive memories is well established and has been used in several previous experiments (Holmes et al., 2004; Bourne et al., 2010; Krans et al., 2009a; 2009b; 2009c; 2013a; Holmes and Bourne, 2008). For the present study, a larger number of videos were used to maximise statistical power. In addition, a mix of emotionally negative and neutral videos was used, in which neutral videos could serve as a baseline of memory performance to contrast with negative clips. Previously, only a small number of studies have included a neutral comparison condition when examining an experimental trauma paradigm.

Therefore, Experiment 2.2 assessed deliberate memory performance and memory intrusions for negative events using an adapted design from previous studies, with more negative clips and a neutral control condition.

Here, I used a between-group design to assess the effectiveness of using of a number of emotional and non-emotional audio-visual clips to investigate memory intrusions and deliberate memory. Encoding sessions were identical for the two groups but for one group, the follow-up deliberate memory test was given immediately after encoding while the other group completed follow-up one week after encoding. The immediate follow-up group worked as a pilot to assess how distressing participants found the videos before measuring intrusions. Also, having two groups allowed investigation of how deliberate memory changes over time.

For this study, participants watched 20 video clips (10 negative, 10 neutral) and deliberate memory performance was assessed either immediately following encoding (same day) or after a one-week delay to observe how memory changed over time. In addition, participants in the group with the one-week delay test also kept a diary of video-related memory intrusions in the week between encoding and test. It was predicted that memory performance in the immediate test group would be superior to the group completing the test after one week. In terms of intrusions, the two models outlined previously again made different predictions: Based on the dual representation theory, a negative correlation between deliberate memory performance and memory intrusions would be predicted, while the unitary account would predict a positive relationship between deliberate memory performance and intrusions.

2.4.1 Methods

2.4.1.1 Sample size estimation

Based on an effect size from a previous study investigating post-encoding interventions and intrusions (Holmes et al., 2009) of d=0.91 a sample size estimation was calculated using the G*power 3.1 software (Faul et al., 2007). This analysis indicated a required sample size of N=40 to achieve an 80% power level at $\alpha=0.05$.

2.4.1.2 Participants

A total of 37 volunteers (21 females) aged 18-40 years (M=25.3, SD=6.3) were recruited for the study. The UCL research ethics committee approved the studies and all volunteers gave consent prior to participating in the study. Volunteers were compensated 7.50 pounds per hour to take part. Participants with a history of psychiatric or neurological disorders were excluded from the study.

2.4.1.3 Stimuli

Stimuli included 20 audio-visual clips involving either emotionally negative or neutral events (see the Appendix, Table A1 for a list of videos). The videos were of realistic events in which most were real-life episodes and a minority were realistic film clips. There were 10 neutral and 10 negative videos and each video had a duration of 50-60 seconds. Neutral videos would include scenes of people engaging in everyday activities such as buying a coffee, having a barbeque or going to the supermarket. Negative videos comprised traumatic scenes of accidents, traumas and violence, such as the aftermath of a traffic accident, people fighting violently or a person being assaulted.

2.4.1.4 Intrusion diary

The intrusion diary used to record participants' intrusive memories over 1 week was the same as reported in Experiment 2.1.

2.4.1.5 Questionnaires

As in Experiment 2.1, subjective mood and trait assessments were carried out using the state-trait anxiety (STAI) inventory (Spielberger, 1984) and the positive and negative affect schedule (PANAS) questionnaires (Watson et al., 1988).

2.4.1.6 Procedure

2.4.1.6.1 Encoding

Prior to presentation of the videos, participants were briefed about the nature of the videos and completed anxiety trait and the first part of the state questionnaires. Participants watched a total of 20 video clips (10 neutral, 10 negative) presented in the middle of the screen on a black background (see Figure 2.3). The videos were presented in a randomised order in a darkened room and sound was delivered through headphones. Participants were instructed to watch the presented videos carefully but without actively rehearsing the material and to imagine that they were at the scene, watching the events unfold (similar to the procedure in James et al., 2015). This was done to ensure a higher personal involvement in the films and hence greater emotional response to the stimuli, which has been associated with more reported intrusions in the experimental film paradigm (Clark et al., 2015). Each clip ended with a 1 second ITI during which a white fixation cross was displayed on the screen. After watching each video, participants were asked to make subjective valence ('How happy or sad did the video make you feel?') and arousal ('How upset did the video make you feel?') ratings of the videos on a Likert scale ranging from 1-7, anchored by 1 as the most negative/low arousal and 7 as the most happy/high in arousal.

2.4.1.6.2 Intrusion diary

As in experiment 2.1, participants in the one-week delay group filled out a memory diary over the 7 days between encoding and test, detailing any spontaneous memories of the material presented at encoding they experienced over the week.

2.4.1.6.3 Memory test

One group of participants completed a memory test for the clips on the same day as encoding (Immediate group, N=18) whereas another group were required to keep a diary of any video-related involuntary memories they might have over the following week and completed the deliberate memory test upon return to the laboratory on Day 8 (Delay group, N=19). For the memory test, participants were presented with pictures from the videos they had previously seen during encoding and each picture was accompanied by a question relating to the video. The memory test comprised a total of 100 written questions (5 from each video) asking about details ('What does the woman take out of her bag?') or gist (e.g. 'What happens next?') from the videos and participants were instructed to type their answers on the screen (Figure 2.3).

2.4.1.6.4 Statistics

Statistical analyses were conducted using SPSS Statistics V. 22.0 software. Pre- and post-encoding anxiety measures and memory for intruding vs. non-intruding videos were assessed with paired-sample t-tests. Where assumptions of normality were violated, data were analysed with Mann-Whitney U tests. Mixed ANOVAs with group as a between-subject factor (delay, immediate) and emotion as a within-subject factor (neutral, negative) were used to analyse subjective video ratings and deliberate memory performance. Finally, the relationship between variables was assessed with Pearson's correlations and Spearman's correlations, as appropriate.

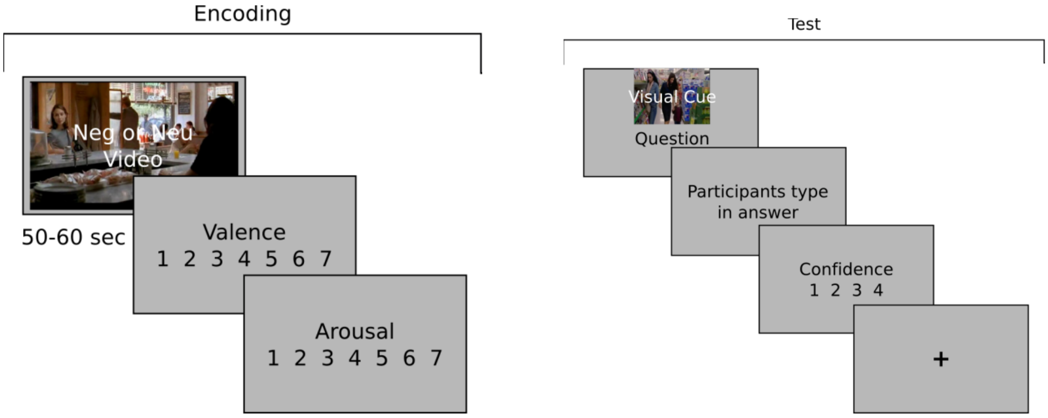

Figure 2.3. Experimental design of the exploratory video experiment A) During the encoding session, participants watched 20 short videos and gave subjective valence and arousal ratings on a 1-7 Likert scale after each video. B) For the test session, participants were given 100 cued recall questions (5 for each video) and were cued with a still frame from the corresponding video. Participants were able to type in their answers and gave confidence ratings for their answers after each trial.

2.4.2 Results

2.4.2.1 Subjective ratings

Subjective ratings for negative and neutral videos were analysed by carrying out separate 2x2 repeated measures ANOVAs for valence and arousal ratings across videos with group as a between-subjects factor (immediate, delay) and emotion (neutral, negative) as a within participants factor. As expected, the ANOVA for valence revealed a main effect of emotion, F(1,36)=395.96 p<0.001, η^2=0.92 which was due to lower valence ratings for negative compared to neutral video clips (see Figure 2.4). The main effect of group (F(1.36)=0.22, p=0.64, η^2<0.01 and the group x emotion interaction (F(1,36)=0.002, p=0.96, η^2<0.001) were not significant. Likewise, an ANOVA for arousal ratings with group as a between participants factor revealed a significant main effect of emotion, F(1,36)=269.41, p<0.001, η^2=0.88 which was due to higher arousal scores for negative compared to neutral videos. The main effect of group (F(1,36)=0.72, p=0.40, η^2=0.02) and the emotion x group interaction (F(1,36)=4.17, p=0.05, η^2=0.10) were not significant.

Table 2.2. Means (SD) of questionnaire measures of anxiety, positive and negative affect of Experiment 2.2.

	Immediate Group N=18		**Delay Group N=20**	
	Pre	**Post**	**Pre**	**Post**
Trait anxiety	37.42 (10.66)	n/a	35.60 (7.76)	n/a
State anxiety	29.72 (6.81)	46.35 (10.95)	28.89 (5.84)	47.22 (12.35)
Positive affect	33.28 (8.60)	23.19 (10.32)	32.26 (6.79)	26.16 (8.50)
Negative affect	14.17 (6.84)	20.75 (8.06)	12.05 (2.09)	20.79 (7.74)

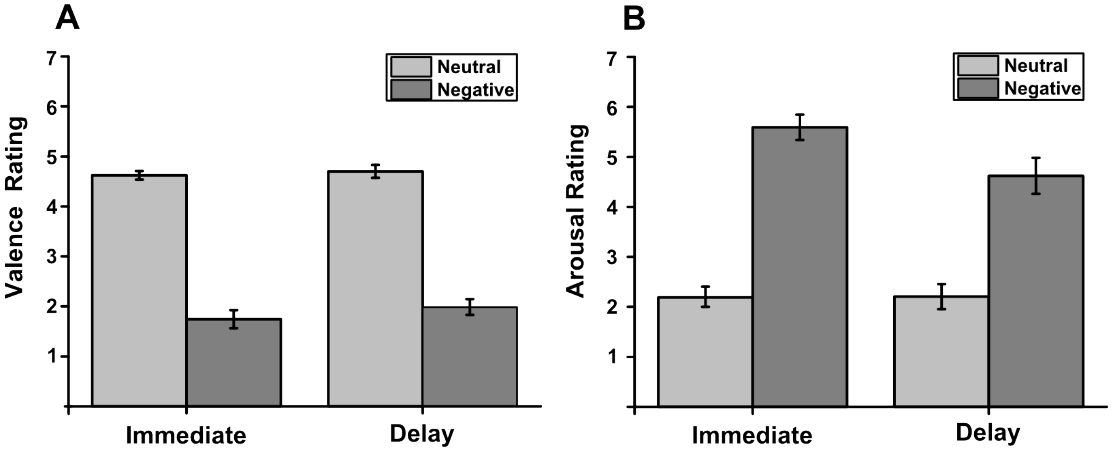

Figure 2.4. Subjective video ratings of valence and arousal in Experiment 2.2. A) Mean valence ratings for neutral and negative videos for the Immediate and Delay group. B) Mean arousal ratings for neutral and negative videos for the Immediate and Delay group. Error bars represent SE.

2.4.2.2 Intrusive memories

Only participants in the Delay group recorded intrusions in the week between encoding and follow-up. 87% of the total number of intrusions could be precisely matched with specific videos. Intrusions that were not matched to a video were omitted from further analyses. Three participants from this group did not complete the diary and were omitted from further analysis. Participants in Delay group experienced an average of 6.67 (SD=5.81, Md=3) negative intrusions over the week from encoding to the test session.

As participants rated each clip for valence and arousal, further analyses were performed to examine differences in ratings between those clips that later intruded versus clips that did not intrude. When comparing the data for intruding versus non-intruding videos, participants had higher arousal ratings for videos that intruded (M=5.21, SE=0.43) than those that did not intrude (M=4.62, SE=0.48; t(13)=2.48, p=0.03, d=0.66). There were no differences between clips that intruded and those that did not intrude on valence ratings (t(13)=1.55, p=0.15, p=0.41) or deliberate memory scores (t(13)=0.70, p=0.50, d=0.19).

2.4.2.3 Deliberate memory

First, performance on the cued memory recall test for negative and neutral videos was analysed. Three cases were not included in the analysis because of missing data from the memory test leaving N=17 in the immediate group and N=15 in the delay group. A 2 x 2 repeated measures ANOVA with emotion (neutral, negative) as a within participant factor and group (immediate, delay) as a between participant factor revealed a significant main effect of group $F(1,33)=11.16$, $p<0.01$, $\eta^2=0.25$, reflecting better memory performance for the Immediate than for the Delay group (see Figure 2.5). By visual inspection, memory performance was numerically greater for negative compared to neutral items but this difference was not significant, $F(1,33)=2.71$, $p=0.11$, $\eta^2=0.08$, nor was the emotion x group interaction $F(1,33)=1.88$, $p=0.18$, $\eta^2=0.05$.

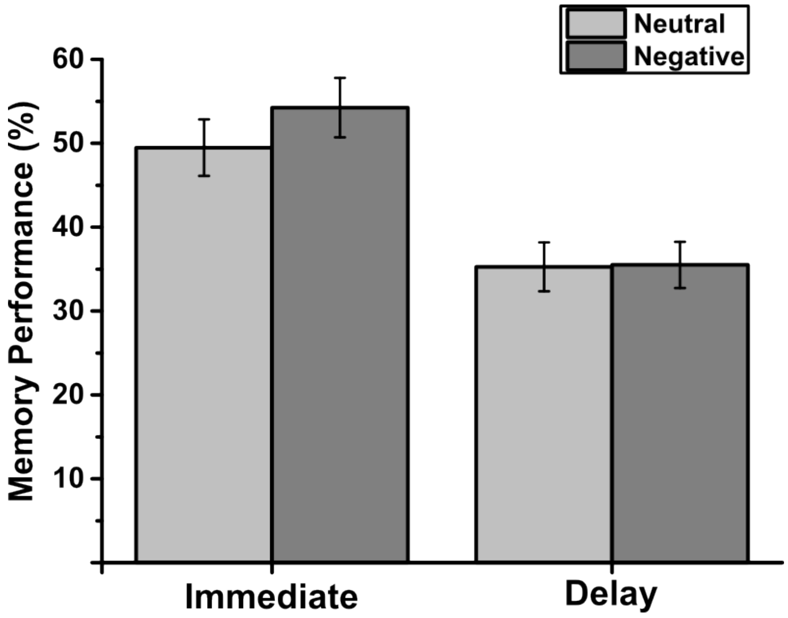

Figure 2.5. Mean memory performance on cued recall test in Experiment 2.2. Memory performance for neutral and negative items for participants who were tested on the same day as the encoding session (Immediate) and the group that were tested after 7 days (Delay) groups. Error bars show SE.

2.4.2.4 Relationship between deliberate memory and subjective ratings

Further correlation analyses were performed on each group separately to assess the relationship between subjective ratings and memory performance. These analyses were done separately for neutral and negative videos. For participants tested immediately following encoding (immediate group), a significant positive correlation was found between memory performance and valence rating ($r(16)=0.55$, $p<0.05$) reflecting better deliberate memory performance for negative video clips rated as less negative (no correlation was found between neutral clips and deliberate memory; $r(16)=0.18$, $p=0.49$; Figure 2.6). Similarly, the relationship between arousal and deliberate memory performance for the negative videos showed a significant negative correlation ($r(16)=-0.46$, $p=0.05$) due to better memory performance when clips were rated less arousing (again no significant correlation was observed between deliberate memory and arousal for neutral clips; $r(16)=-0.08$, $p=0.76$). Hence, these results indicate that participants who found the negative videos more disturbing performed worse on the memory test immediately following encoding.

For the Delay group however, the opposite pattern was apparent (Figure 2.6). Analysis showed a negative correlation between deliberate memory performance and valence, ($r(15)=-.53$, $p=0.03$; no correlation for neutral clips, $r(15)=-.11$, $p=0.67$). There was also a significant positive correlation between memory performance and arousal for negative videos ($r(15)=0.598$, $p=0.01$; no correlation for neutral clips, $r(15)=0.28$, $p=0.27$). Hence, in contrast to the immediate group, these results indicate that participants who found the negative videos more upsetting or sad showed better memory after a longer delay of 1 week.

To further assess the apparent switch in the relationship between subjective ratings and memory performance between the immediate and delay groups, correlation coefficients were transformed using Fishers r-to-z transformation for each group, transforming the sampling distribution of Pearson's r to the normally distributed z. This analysis showed that there was a significant difference between the valence-memory performance correlation for the Immediate and Delay group, $z=3.25$, $p<0.001$. Likewise for the arousal-memory correlation, there was a significant difference between the correlation coefficients for the Immediate and the Delay group, z=-3.22, p=0.001. Hence, these results further support that the relationship between subjective distress and memory performance shifted from a negative relationship when participants were tested immediately to a positive relationship when participants are tested with a one-week delay.

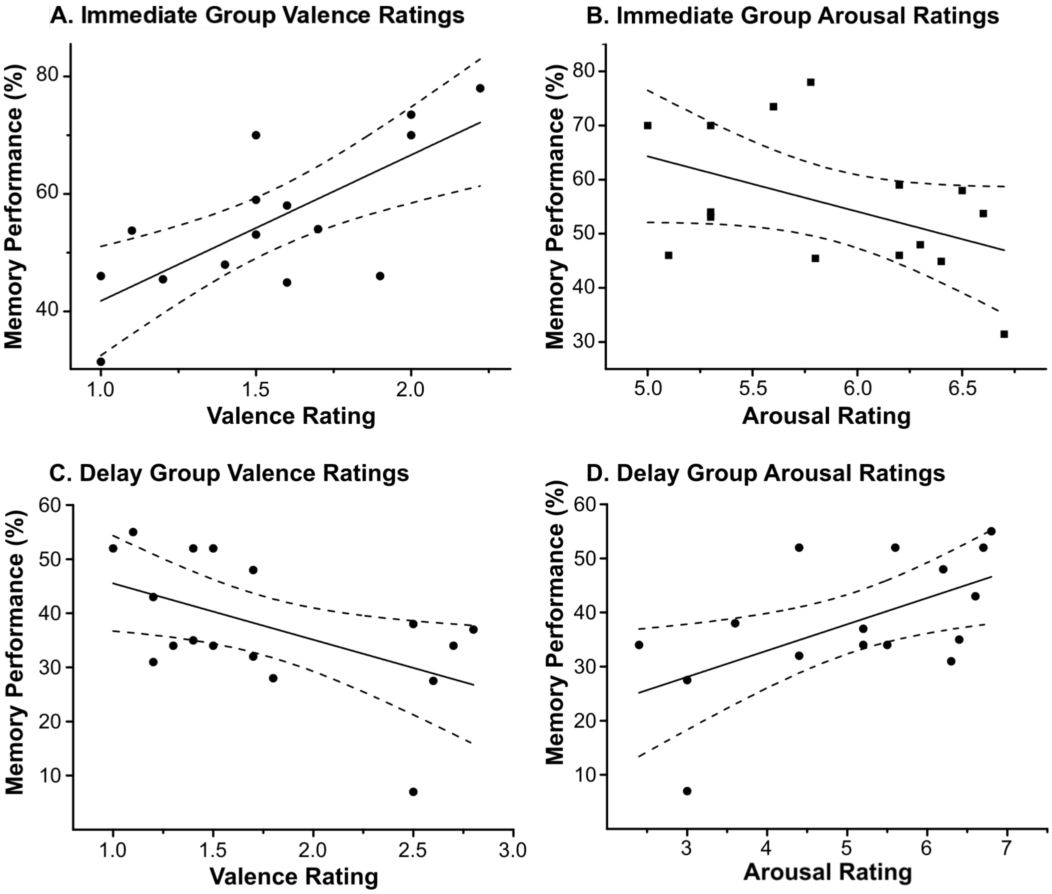

Figure 2.6. Relationship between memory performance and subjective video ratings in Experiment 2.2. Correlations between valence ratings and memory performance (A and C) and correlations between arousal ratings and memory performance (B and D) for the group who were tested on the same day as encoding and the group who were tested after 7 days.

2.4.2.5 Relationship between deliberate memory and intrusions

The relationship between intrusions and deliberate memory performance for negative items was also assessed. The intrusion data were not normally distributed and hence, a non-parametric test (Spearman's rank correlation coefficient) was used for this analysis. A positive relationship between the number of reported intrusions and memory performance for negative items ($r_s(13)=0.65$, $p=0.008$) was found, indicating that overall, volunteers with better memory scores also experienced more spontaneous memories of negative items (Figure 2.7). There was no significant relationship between the valence ratings and the number of reported intrusions ($r_s(14)=-0.20$, $p=0.46$), or between arousal ratings and intrusions ($r_s(14)=0.10$, $p=0.72$).

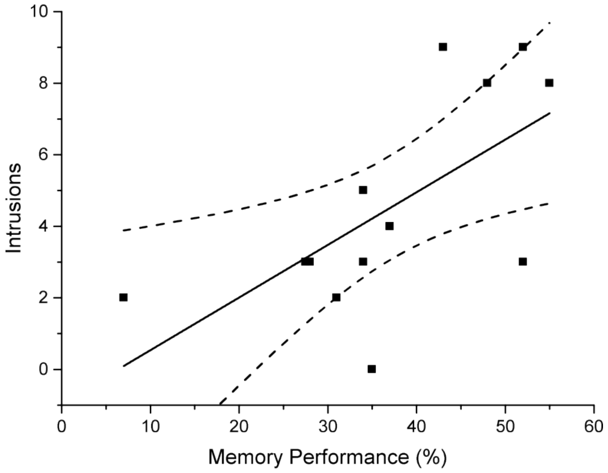

Figure 2.7. Relationship between memory intrusions and deliberate memory performance in Experiment 2.2. A correlation analysis revealed a positive correlation between deliberate memory performance on a cued recall test and the number of intrusions after one week

2.4.2.6 Relationship between questionnaire measures and intrusions

As intrusions were not normally distributed, Spearman's rho was used to assess the relationship between measures of affect and the number of reported memory intrusions. There was no significant relationship between intrusions and difference in state anxiety from pre- to post encoding, $r_s(13)=-0.13$, $p=0.65$. The same was the case for the relationship between intrusions and difference in positive affect (PANAS-pos), $r_s(13)=-0.36$, $p=0.18$ and negative affect (PANAS-neg), $r_s(13)=0.11$, $p=0.69$. Likewise, the correlation between memory intrusions and trait anxiety was non-significant, $r_s(14)=0.10$, $p=0.72$.

2.4.3 Discussion

Experiment 2.2 investigated the use of short emotionally negative video clips to induce memory intrusions and contrasted deliberate memory for those clips with memory for neutral video clips. In the current experiment, it was demonstrated that short emotional videos were able to induce memory intrusions and that the number of reported intrusions showed a positive correlation with deliberate memory. There were no differences in deliberate memory performance for neutral and negative information. However surprisingly, within the negative category, there was a difference between the Immediate and Delay groups in the relationship between subjective ratings and deliberate memory.

The finding that deliberate memory performance did not differ between negative and neutral clips contrasts the well-established finding that memory is enhanced for negative over neutral stimuli (Cahill and McGaugh, 1995; Brown and Kulik, 1977; Kensinger and Corkin, 2003; Bradley et al., 1992; Bohannon, 1990; Christianson, 1992). Why might the current study demonstrate similar memory accuracy between neutral and negative events? Speculatively, subtle differences in methodology might have contributed to the lack of memory differences. For example, the current design utilised a combination of short video clips and a cued recall memory test in which participants were shown a static image and asked a 'what happened next' question. This design differs from typical memory tests in which recognition of images or recall of single items are tested (e.g. Pierce and Kensinger, 2011; Burke et al., 1992). The temporal dynamics of memory are considered an important aspect of providing a coherent spatio-temporal context and is supported by the hippocampus (MacDonald et al., 2011). The current task may therefore have tested more hippocampal dependent memory, which might not be facilitated by negative emotion in the same way as item recognition (Bisby et al., 2016).

Deliberate memory performance was significantly lower when tested after one week than when tested immediately after encoding. These results reflect the common finding that declarative memory tends to decrease over time (Schooler and Hertwig, 2011). The temporal decay was present for both neutral and negative information, suggesting that both were subject to normal forgetting processes. However, within the negative video category, a different pattern emerged. Here the relationship between subjective distress and memory performance showed a distinct change between immediate and delayed groups. That is, deliberate memory performance was worse for more distressing videos when memory was tested immediately after encoding. However, when memory for the video clips was tested one week after encoding, this pattern was reversed, showing that deliberate memory performance was better for clips rated as more distressing. This shift in the relationship between subjective ratings and memory performance might reflect findings showing that memory for neutral information show faster temporal decay than memory for emotional stimuli (Mather and Sutherland, 2011). Hence, more distressing scenes might have been more strongly consolidated over time, whereas less distressing scenes remembered better immediately after encoding might be forgotten more rapidly. However from this follows that memory performance for neutral videos should be worse than for negative videos, which was not found here.

Finally, results from the current experiment also show a positive relationship between overall deliberate memory performance and the number of reported intrusions. At face value, the positive relationship runs against the prediction of a dual representation model (Brewin et al., 2010). Under this model, deliberate (associative) memory should reflect C-reps, which should be weakened by stronger emotional content, while intrusions should reflect S-reps, which should be strengthened by stronger emotional content. It is possible that strongly encoded negative videos might be subject to more rumination and thereby contribute to intrusions. That is, memories already prominent in memory might tend to intrude more (Rubin et al., 2008b). To square this with the dual representation model, however, would require that these intrusions were not a good model for the pathological negative intrusions seen in PTSD.

2.5 Comparison of the picture and video experiments

2.5.1 Subjective ratings

First, an analysis was carried out to confirm that there were no differences between the two groups in baseline trait anxiety between participants in the two studies. Here, an independent samples t-test showed no differences in trait anxiety between the picture (M=39, SD=9.80) and the video experiment (M=36.06, SD=8.93), t(51)=1.12, p=0.27.

To investigate if there were any differences in emotional impact between the picture study and the video study, one-way ANOVAs were conducted for each of the state measures with Time (pre, post) as a within-subject variable and Group (picture, video study) as a between group factor. Ratings from the video study were collapsed across the Immediate and Delay groups. The analysis for the STAI-state data showed a main effect of time, F(1,51)= 77.01, p>.001, confirming results from previous analyses with each study independently, showing that state anxiety was significantly increased from pre- to post-encoding. In addition, the Time x Group interaction was significant, F(1,51)=4.97, p=0.03, reflecting a higher rise in state anxiety in the video experiment than in the picture experiment. Likewise, the analysis for the PANAS negative scale of affect showed a significant main effect of time (F(1,50)=42.02, p<.001) and a significant Time x group interaction, F(1,50)=8.61, p<0.01, also reflecting an increase in negative affect from pre- to post-encoding. Finally, the analysis for the PANAS positive affect scale showed a main effect of time, F(1,50)=25.95, p<.001 while the time x group interaction did not reach significance, F(1,50)=2.87, p=0.10.

2.5.2 Intrusions

A Mann-Whitney test was performed to directly compare the number of intrusions reported between the first experiment using picture stimuli and the second experiment using video stimuli. This analysis showed a significant difference between experiments with a greater number of intrusions reported in the 7 days following short emotional video clips (M=5.67, SD=5.81, Md=3) compared to static images (M= 3.58, SD=4.71, Md=1; U=78.5, p=0.04).

2.6 General discussion

In this first experimental chapter, different techniques to examine intrusive memories and deliberate memory performance were tested in two exploratory studies. For this purpose, two different designs were used. First, emotional images were used as a way to more closely examine dissociable aspects of memory and their relationship with intrusive memory development. Second, short video clips were then used to potentially increase intrusive memory reports from participants and a cued recall memory test was added to test deliberate memory. Overall, these two experiments demonstrated that videos were more likely to facilitate intrusion development than static images. Deliberate memory findings were mixed, but mostly showed non-significant effects.

2.6.1 Intrusive memories

Contrasting the number of intrusive memories reported by participants across the two experiments, participants reported markedly more intrusions after watching short emotional clips compared to static images. In experiment 2.1, emotional images seemed to be a poor method for generating intrusive memories with a number of participants reporting very few instances of spontaneous memories. Similarly, other studies using static images to measure intrusions have also shown that participants report very few intrusions (e.g., Pearson et al., 2011; 2012). Given that the majority of participants reported zero or one intrusions, this would suggest that static images are not a strong technique to assess intrusions.

Audio-visual clips may have produced more intrusions due to being more immersive and similar to real world events, containing complex, multimodal scenes with a narrative component. Furthermore, each stimulus had a much longer duration when using videos than pictures and each stimulus was thereby more likely to make an emotional impact on the viewer. Participants showed a larger change in anxiety levels between pre and post encoding in the video study than in the picture study which is consistent with participants in the video study reporting more intrusions. These results are consistent with previous studies, where experiments using video stimuli generally tend to report higher numbers of memory intrusions than studies using emotional picture stimuli (e.g. Holmes et al., 2004; Bourne et al., 2010).

2.6.2 Deliberate memory

The two experiments generated different deliberate memory results; Experiment 2.1 showed better recognition memory for negative images compared to neutral images but this effect was absent in Experiment 2.2. The findings of Experiment 1 are consistent with the widely demonstrated finding that memory for emotional events is often facilitated compared to neutral information. Why might this effect be absent in Experiment 2.2? Studies have suggested that emotion influences different memory types in different ways (Anderson and Shimamura, 2005). The memory test in Experiment 2.1 was a recognition memory test putting demands on the familiarity judgments whereas the memory test in Experiment 2.2 was a cued recall test requiring the conscious recollection of the scene to answer the question. These two memory types have been shown to rely on different neural mechanisms and can be affected differentially (Rimmelé et al., 2011; Yonelinas, 2002). In fact, the cued recall memory test used in Experiment 2.2 is probably more similar to the associative memory test in Experiment 2.1 in terms of engaged resources, as answering the questions requires recalling the scene where the 'event' took place, which places demands on the hippocampus and episodic binding, also required in associative memory. However, memory performance on the associative was so poor that it is not meaningful to compare this to the memory test in Experiment 2.2.

2.6.3 Theoretical implications

For the video study (Experiment 2.2), it would be consistent with the dual representation theory if there was a positive correlation between item memory and intrusions and consistent with a unitary account if there is a positive relationship between associative memory and intrusions. Answering the cued recall memory test used in this study should require the conscious recollection of event and its context. Hence, the finding from this study showing a positive correlation between memory intrusions and deliberate memory performance support a unitary account of intrusion memory development, although it should also be mentioned that the majority of questions asked participants about aspects related to the gist of the video rather than details. Some studies have shown that memory for gist is enhanced by negative emotion, while memory for details is impaired, consistent with an interpretation of recollection as requiring detailed re-experience of an event, which familiarity-related processes could not support (Christianson and Loftus, 1991; Adolphs et al., 2005). However, such an interpretation of recollection versus familiarity is hard to square with the assumptions of the dual representation model (Brewin et al., 2010) in which gist would more naturally be thought of as a more abstract contextual representation. Taken together, the results presented in this experiment favour a unitary account.

2.6.4 Limitations

Investigating intrusion development prospectively requires the use of experimental stimuli, which has a high emotional impact on participants. Often, experimental stimuli will lack personal relevance, rendering experimental stimuli less likely to intrude (Kavanagh et al., 2001). It appeared that the picture stimuli used in the static picture study (Experiment 2.1) did not elicit sufficiently strong responses to produce memory intrusions in the majority of participants. Using videos in Experiment 2.2 was more successful, as the number of reported intrusions increased markedly. However video stimuli does not in the same way allow separate assessment of item and associative memory as images, which is attractive when investigating the effects of emotion on different aspects of deliberate memory.

Another challenge was the low individual variability on memory tests in both studies, which increases the chances of type II error. Hence, it would be beneficial to develop a more sensitive memory test that increases the overall spread in scores between those with lowest and highest performances. This challenge extends to the measure of memory intrusions, which was characterised by many participants reporting few intrusions and only a few reporting many. This effect was less pronounced in Experiment 2.2 but extended across both studies.

2.6.5 Conclusions

Overall, results from the above studies suggest that using video stimuli was the most appropriate design to induce memory intrusions. Using videos in intrusion memory research is a well-established method that allows ethical, controlled, and prospective 'trauma' exposure while giving the opportunity to introduce peri- or post-traumatic manipulations of intrusion development (Holmes and Bourne, 2008; Holmes et al., 2004).

Consistent with studies showing that emotion can facilitate memory, the recognition memory test in Experiment 2.1 showed better memory for negative videos compared to neutral videos. In contrast, there were no differences in memory performance between neutral and negative items in the associative memory in Experiment 2.1 and the cued recall memory test in Experiment 2.2.

3 THE EFFECTS OF IMMEDIATE POST-STIMULUS ENCODING ON MEMORY FOR TRAUMATIC MATERIAL

3.1 Overview

From the experiments in Chapter 2, it was established that the use of short video clips, as opposed to static images, best elicited memory intrusions in an experimental trauma paradigm. As highlighted in Chapter 1, the period immediately after encoding (i.e. consolidation) is important following both neutral and traumatic events (e.g. Ben-Yakov et al., 2013; Dewar et al., 2012; Deeprose et al., 2012). Previous studies demonstrate that tasks performed during this critical window can impact subsequent intrusive memories for related events (Holmes et al., 2004; 2009; Holmes and Bourne, 2008; Deeprose et al., 2012). Research has also shown that the experience of naturalistic scenes immediately after encoding of short video clips can reduce memory for these previously seen clips, possibly through disruptions of post-stimulus consolidation (Ben-Yakov et al., 2013). The current chapter therefore aimed to further investigate how exposure to new information immediately after the encoding of traumatic material can influence deliberate memory and intrusions.

3.2 Introduction

Following learning, new memories go through a period of transformation and stabilisation often referred to as consolidation (Muller and Pilzecker, 1900, reviewed in McGaugh, 2000 and Dudai, 2004). Consolidation involves changes both over the short and long term: as outlined in Chapter 1, short-term changes occurring in the minutes to hours after encoding is known as synaptic consolidation and more long-term consolidation is also known as systemic consolidation (p.42-43).

One long-standing idea in the field of consolidation research is that post-encoding processing involves reactivation of the learned material and that this process is critical to successful memory consolidation (Müller and Pilzecker, 1900, reviewed in Lechner, 1999). Over the years, this idea has been elaborated and empirically supported; for instance, some studies have indicated that the mechanism underlying this reactivation may be ‘replay’, an automatic process in which a sequence of activation present during learning is replayed in the same or reversed order (Carr et al., 2011; Buzsaki, 1986; Gelbard-Sagiv et al., 2009; Foster and Wilson, 2006; Tambini et al., 2010). Sharp-wave ripples (SWRs) are hippocampal network patterns

(~110–250 Hz ripples superimposed on ~0.01–3 Hz sharp waves) most often identified during wake immobility, slow-wave sleep and consummatory behaviour (Buszaki, 1986). SWRs have been associated with hippocampal replay and memory consolidation of hippocampal-dependent memories, e.g. from studies showing reinstatement of exploration-related activation during subsequent sleep (O'Neill et al., 2010).

Rodent studies have investigated replay in spatial navigation, indicated by activation of place cells in a sequence corresponding to a route previously travelled by the rodent (Carr et al., 2011). These studies show that hippocampal replay during rest correlates with subsequent memory (Carr et al., 2011; O'Neill et al., 2010). Critically, interruption of hippocampal replay has been shown to impair memory performance (Ego-Stengel and Wilson, 2010; Girardieu et al., 2009). Emerging evidence suggests that replay also plays a significant role in human memory consolidation (Peigneux et al., 2004; Tambini et al., 2010). Consistent with this finding, Rasch et al. (2007) demonstrated that the introduction of an odour cue related to a previous event presented during subsequent slow-wave sleep enhanced subsequent memory performance for the event while this effect was not present if the cue was presented at other stages of sleep. Another study found that ripples in the perirhinal cortex, but not hippocampus post-encoding correlated with memory for single items (Axmacher et al., 2008), which is consistent with the idea that associative memory, but not memory for items is dependent on the hippocampus.

Along with the idea of consolidation follows that new memories exist in a fragile state in the time following encoding (Bouton, 1993; Tulving and Pstoka, 1971; Dudai, 2004). During this time, memories might be considered vulnerable to internal and external factors that could disrupt consolidation and potentially lead to a weakened memory representation. Returning to the landmark study of Müller and Pilzecker (1900, in Wixted, 2004), they demonstrated that memory recall of a list of nonsense syllable pairs was impaired by presentation of a second list of syllables in between encoding and test of the first list of syllables, particularly if the second list was presented immediately after learning (Müller and Pilzecker, 1900 in Wixted, 2004; Wixted and Cai, 2013). The phenomenon that new learning is more vulnerable to interference by other information was coined retroactive inhibition, or, retroactive interference (Dudai, 2004; Tulving and Psotka, 1971). Although the findings of Müller and Pilzecker were opposed for a number of years, the idea of retroactive interference remain influential today (Wixted, 2005) and retroactive interference has been demonstrated in a number of studies (e.g. Dewar et al., 2012).

In a series of studies using functional imaging and naturalistic scenes in the form of audio-visual clips, Ben-Yakov et al. (2011; 2013) demonstrated the importance of post-encoding processing to subsequent memory performance and then investigated the effects of introducing a new stimulus immediately following a previous stimulus on this processing and subsequent memory performance. More specifically, Ben-Yakov et al. (2011) found that post-encoding hippocampal and dorsal striatum activity time-locked to stimulus offset (ending of the video clip) was associated with better subsequent memory performance, demonstrating the significance of post-encoding hippocampal processing in memory consolidation (Ben-Yakov et al., 2011). Building on this study, Ben-Yakov et al. (2013) investigated the effects of introducing a second event, immediately following the previous event, on memory performance and post-encoding processing. Participants were shown short video clips while in the MRI scanner and each clip was followed either by a second video clip, a 'scrambled' video clip with indiscernible visual information or they were given a rest period. 20 minutes after encoding, participants completed a cued recall test outside the scanner where each trial consisted of a visual cue from one of the videos and a corresponding question, for which participants could type in their answer. Results from this study showed that presentation of a second stimulus immediately following the first stimulus impaired memory for the first stimulus. This effect was present both when the interfering stimulus was a video clip and a scrambled clip but was more pronounced for the normal video clip. This behavioural effect was associated with reduced offline processing (Ben-Yakov et al., 2013).

The studies by Ben-Yakov et al. (2011; 2013) used non-emotional stimuli in their experiments. It is unclear how these results would translate to the emotional and trauma memory literature or how retroactive interference from further real-life events could affect intrusion development.

Some evidence from retrospective PTSD studies have suggested that post-encoding factors do indeed play a role in subsequent development of PTSD symptoms; for instance, Schönenberg et al. (2005) investigated whether ketamine administration shortly after trauma had an impact on subsequent acute and long-term (one year post-trauma) PTSD symptoms. Ketamine is used as a sedative and analgesic and is therefore often administered to trauma victims, but is also known to induce dissociative states (Schönenberg et al., 2005). Results from this study showed that ketamine administration was associated with PTSD symptoms such as re-experiencing and avoidance both acutely and at one year post-trauma, suggesting that post-encoding factors known to modulate cognitive processing present in the immediate aftermath of trauma can affect PTSD symptom development both in the short and long term (Schönenberg et al., 2005; 2008).

As outlined in Chapter 1, analogue trauma paradigms using healthy participants and presentation of emotionally negative stimuli constitute a useful method to directly investigate peri- or post-encoding factors believed to influence trauma memory and memory intrusions. Consistent with the above findings from PTSD patients, studies such as these have highlighted the importance of the consolidation window and how tasks during this period can alter subsequent intrusive memory reports. For instance, Holmes et al. (2009) showed that carrying out a visuo-spatial task (the computer game 'Tetris') 30 minutes after encoding of experimental trauma videos reduced the number of reported intrusions in the week following encoding compared to a 'No task' control group. This study did not find any differences between the two groups on a recognition memory task (Holmes et al., 2009). The researchers concluded that the effect showing reduced intrusions was due to competition for visual-spatial resources.

However, it is possible that the occurrence of intrusions could also reflect other processes than competition for visuo-spatial resources. In a more recent study, Deeprose et al. (2012) demonstrated that employing complex finger-tapping either immediately or 30 minutes after encoding also reduces memory intrusions, compared to a 'No task' control and, critically, also compared to a verbal control task (counting backwards in threes; Deeprose et al., 2012). Unlike playing Tetris, it is not so clear that finger tapping would compete for the same visual resources as the consolidation of a trauma video.

A recent study by Das (et al., 2016) investigated the role of N-methyl D-aspartate receptor (NMDAR) dependent memory consolidation in intrusion development in an analogue trauma paradigm. NMDARs play a critical role in LTP and hence in memory consolidation (see above) and so administration of an NMDAR antagonist (nitrous oxide) was expected to block memory consolidation. Here, it was found that nitric oxide inhalation immediately following encoding of a trauma video was associated with a faster reduction in intrusive memories compared to a control group who inhaled medical air, suggesting that disruption of memory consolidation modulated memory intrusions (Das et al., 2016). This study demonstrates that altering post-encoding processing in other ways than competition for resources can affect subsequent development of intrusive memories.

Taken together, consolidation processes modulate memory following learning and evidence suggests that disruption of these processes results in reduced strength of memory traces. Post-encoding processing also appears to have an impact on trauma memory, with impaired post-encoding processing resulting in more memory intrusions. It has been demonstrated that one way to impair consolidation is the presentation of a second stimulus immediately following a previous stimulus, thereby reducing post-encoding processing and memory performance for the stimuli presented first. However the effects on memory for emotionally stimuli and memory intrusions in this context is not known. These questions are the topic of the current chapter.

As detailed in Chapter 1, different accounts make opposing predictions about the nature of intrusion development and hence also the effects of post-stimulus disruptions to consolidation. The dual representation theory (DRT) proposes that impaired hippocampal consolidation would reduce deliberate memory while memory intrusions would increase (Brewin et al., 2010). As mentioned previously, Ben-Yakov et al. (2013) found that presentation of a second video immediately following another video resulted in reduced post-encoding processing of the stimulus in the posterior hippocampus. Hence, in terms of the DRT, it would be expected that for events that are immediately followed by another event, hippocampal processing is down-regulated and contextual representations reduced relative to events not followed by another event, resulting in reduced deliberate memory performance. The DRT emphasizes a relative strengthening of sensory representations compared to contextual representations in intrusion development. It is not known how immediate presentation of a second video would affect sensory representations, which are likely modulated by the amygdala. However, Ben-Yakov et al. (2011) found that primarily the hippocampus and dorsal striatum was involved in post-encoding processing, suggesting that sensory representations might be unaffected by the intervention and therefore relatively strengthened compared to contextual representations when these are impaired, consistent with the DRT.

In an alternative view, a unitary view of intrusion development proposes that emotional memories are more strongly encoded than other events, explaining accounts of people often having a sense of strong remembrance of emotional information (Hall and Berntsen, 2008; Berntsen and Hall, 2004; Talarico et al., 2004; Rubin et al., 2008). It is argued that because these memories are more strongly encoded, they will intrude more often. Therefore, this view would predict that if deliberate memory were impaired by disruption to consolidation processes, intrusions would also be reduced in a similar manner. Hence, if memory performance were reduced for events that are immediately followed by another event compared to videos followed by a break, these videos would also be associated with fewer intrusions.

3.3 Experiment 3.1

Experiment 3.1 aimed to examine whether post-stimulus encoding would affect memory for previously viewed traumatic material. Therefore, the current experiment used a similar design to previous studies (Ben-Yakov et al., 2013) in which participants were presented with short video clip (50-60 seconds) that was immediately followed by either a second video clip or by a resting period of 16 seconds. This yielded a within-subject condition of video position (Immediate or Interval) in addition to a video valence condition (Neutral or Negative). Further, participants were either assigned to congruent emotional clip group or an incongruent emotional clip group. In the congruent group, both clips in a block had the same valence (Neutral-Neutral or Negative-Negative) and in the incongruent group blocks consisted of mixed valence clips (Neutral-Negative or Negative-Neutral). Participants kept a diary of intrusive memories over the following week and were then required to return for a cued recall test where they answered questions about the videos.

3.3.1 Methods

3.3.1.1 Sample size estimation

A power analysis conducted in G*power based on an effect size of 0.28 reported in a previous study (Ben-Yakov et al., 2013) provided an approximate sample size of N=30 required for the experiment ($1-\beta=0.80$, $\alpha=0.05$).

3.3.1.2 Participants

Forty-five participants (33 females) with an age of 18-40 years (M=24.02, SD=5.69) were recruited for Experiment 3.1. The UCL research ethics committee approved the studies and all volunteers gave informed written consent prior to participating in the study. Participants were paid 7.50 pounds per hour. Participants with a history of psychiatric or neurological disorders were excluded from the study.

3.3.1.3 Stimuli

A total of 20 video clips (10 neutral, 10 negative), each with a duration of 50-60 seconds were used for Experiment 3.1. These videos were the same videos as the stimuli used in Experiment 2.2 in the previous chapter (see appendix table A1 for a list of videos used). Neutral videos comprised scenes from everyday life whereas negative videos involved traumatic events of car accidents, violence and assaults.

3.3.1.4 Intrusion diary

Following encoding, participants were required to keep a written intrusion diary, detailing any spontaneous memories relating to the clips for a 1-week period. Participants were instructed that an intrusive memory was a visual image or thought about a video or part of a video that came to mind spontaneously without purposefully trying to retrieve the information. Participants were asked to report details of each spontaneous memory so it could be identified which video it was from. Participants also made ratings indicating how distressing and vivid they experienced the memories. Participants were instructed to write down intrusions immediately after they occurred or as soon as possible, and as a minimum to fill out the diary at the end of each day.

3.3.1.5 Questionnaires

Subjective mood was measured using the state-trait anxiety (STAI) inventory (Spielberger, 1984) and the positive and negative affect schedule (PANAS) questionnaires (Watson et al., 1988).

The STAI-T consists of 20 items assessing trait anxiety from self-report (e.g. 'I am a steady person', 'I feel like a failure'). Responses to each of the 20 items are given on a 4-point Likert scale ranging from 'Almost never' to 'Almost always'. Likewise, the STAI-S contains 20 items for evaluating state anxiety (e.g. 'I feel relaxed, 'I am presently worrying over possible misfortunes') and here, responses are given on a 4-point Likert scale ranging from 'Not at all' to 'Very much so'. On both inventories, the scores range from 20-80 with higher scores being indicative of higher trait or state anxiety levels.

The PANAS questionnaire is a self-report inventory comprising 20 words describing emotions that are either positive (e.g. 'Interested, Excited, Strong'; 10

items) or negative (e.g. Distressed, Upset, Ashamed; 10 items). Ratings are given on a 5-point Likert scale ranging from 'Very slightly or not at all' to 'Extremely'.

In addition, mental imagery was assessed using the shortened questionnaire upon mental imagery (QMI; Sheehan, 1967), Gordon's test of visual imagery control (TVIC; Gordon, 1949) and Marks' vividness of visual imagery questionnaire (VVIQ; Marks, 1973).

Marks' VVIQ includes 16 items in blocks of 4 where participants are instructed to imagine specific scenes and rate on a 5-point Likert scale how vivid the imagined scene is to them (lower scores indicate that the image is imagined vividly) (Marks, 1973). The shortened questionnaire upon mental imagery is a short form of Bett's original 150-item questionnaire that assesses an individual's capacity for clear and vivid mental imagery in different sensory modalities, rated on a 7-point Likert scale, with lower scores indicated that participants imagine mental imagery more clearly and vividly (Sheehan, 1967). Finally, Gordon's TVIC is a short assessment tool of 12 items used to evaluate the ability of an individual to control and manipulate imagined scenes and objects. Again, lower scores reflect higher control of the imagined material (Gordon, 1949).

3.3.1.6 Experimental protocol

3.3.1.6.1 Encoding

Prior to start of the encoding session, participants were informed about the nature of the videos and completed anxiety trait and the first part of the state questionnaires. Participants watched a series of videos presented in pairs with the second video in a pair following the first after a short, 2 second ISI. Each of these video pairs were followed by a longer ITI of 16 seconds (Figure 3.1). During the ISI and ITI, a white fixation cross was presented in the middle of the screen on a grey background. The total duration of the encoding session was approximately 25 minutes. As in the video Experiment described in Chapter 2 (Experiment 2.2), participants were instructed to watch the presented videos carefully but without actively rehearsing the material and to imagine that they were at the scene, watching the events unfold (similar to the procedure described by James et al., 2015). Participants were assigned to one of two groups. In one group, clip pairs were congruent across emotion (Neutral-Neutral or Negative-Negative), whereas another group of participants encoded mixed pairs (Neutral-Negative or Negative-Neutral). Participants encoded 10 blocks of clip pairs with a total of 20 videos. Participants completed the STAI-T, Marks' VVIQ, shortened QMI, Gordons TVIC, pre-STAIS and pre-PANAS before encoding and the post-STAIS and post-PANAS after encoding.

3.3.1.6.2 Intrusion diary

Following the encoding session, participants received instructions on how to fill out the diary over the next 7 days until returning for the follow-up session.

3.3.1.6.3 Memory test

On day 8, participants returned for a computerised cued recall memory test. During test, a picture cue with a still frame from a video and a corresponding question were presented on the screen in a randomised order and participants were able to type in their answer and were instructed to respond with 'can't recall' if they did not know the answer. The test comprised 6 questions for each video, yielding a total of 120 questions. Questions were typically related to the gist of the video clip, such as 'What happens after the woman enters the shop?'. The memory test was self-paced and after each question, participants made a rating indicating how confident they were that their response was correct on a Likert scale ranging from 1 (not at all confident) to 4 (very confident).

Each correct answer was awarded a score of 1 (or 0.5 for less adequate correct responses) and a total score was calculated as a percentage of the total number of questions. Hence each participant would acquire 4 scores, one for neutral and negative questions in each condition (immediate or interval position).

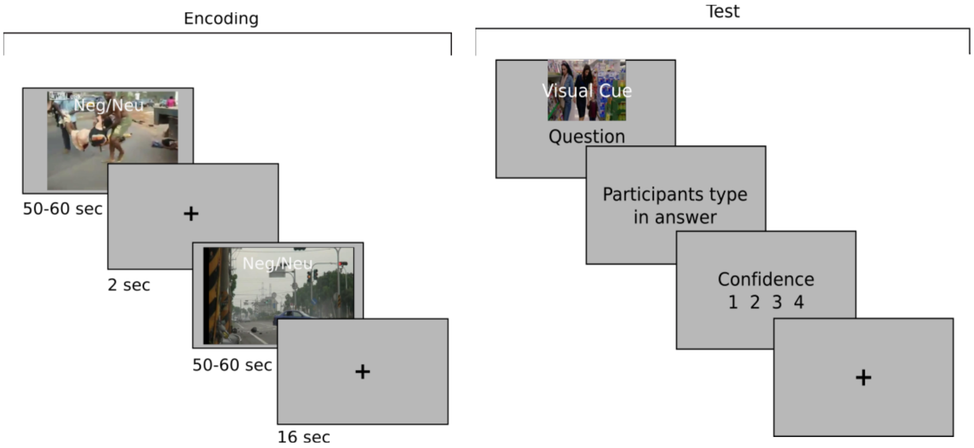

Figure 3.1. Experimental design in Experiment 3.1. Encoding session: Participants watched blocks of two videos with a duration of 50-60 seconds in close succession with an ISI of 2 seconds. Each block was followed by a longer 16 second ITI. **Test session:** Participants were presented with a question and a visual cue from the corresponding video. Participants were instructed to type in their answers when they were ready. After each given response, participants indicated on a 1-4 Likert scale how confident they were that their response was correct. This was followed by a 1 second ITI where a fixation cross was shown in the middle of the screen

To prevent interference from the subjective ratings during encoding, participants made valence and arousal ratings for each video upon returning for the second session. On this occasion, participants were cued with 4 still frames from a video shown simultaneously on the screen. Participants were instructed to try and remember how they felt when they had watched the video and indicate their subjective mood and arousal ratings measured on a 7 point Likert scale by pressing a key anchored by 1 as the most negative/low arousal and 7 as the most happy/high in arousal.

3.3.1.6.4 Statistical analysis

All statistical analyses were carried out using SPSS Statistics V. 22.0 software. The deliberate memory data was analysed using a 2x2x2 mixed ANOVA with group (congruent versus incongruent pairs) as a between participant factor and condition (neutral-neutral or negative-negative for the congruent group and neutral-negative or negative-neutral for the incongruent group) and position (Immediate or Interval) as within-participant factors. The relationship between deliberate memory performance and intrusions was investigated using Pearson's rank correlation. Likewise, the relationship between memory variables and questionnaire measures was assessed using correlational tests. For all statistical tests, we ensured that assumptions were satisfied. Intrusion data were not normally distributed and hence these data were analysed with non-parametric tests. The alpha-level was set at 0.05 for all analyses. Power analyses were carried out using G*power software.

3.3.2 Results

3.3.2.1 Subjective ratings

For subjective valence ratings of the presented videos, a 2x2 mixed ANOVA with emotion (neut, neg) as a within-participant factor and group (congruent, incongruent) as a between-participant factor revealed a main effect of emotion, $F(1,31)=696.56$, $p<0.001$, $\eta^2=0.96$. This effect reflected that on average, participants across the two groups rated negative videos ($M=1.77$) as being sadder than neutral videos ($M=4.59$). The main effect of group, $F(1,31)=0.47$, $p=0.50$, $\eta^2=0.02$ and the emotion x group interaction were not significant, $F(1,31)=0.03$, $p=0.87$, $\eta^2=0.001$.

For arousal ratings, a 2x2 mixed ANOVA with emotion (neut, neg) as a within-participant factor and group (congruent, incongruent) as a between-participant factor showed a main effect of emotion ($F(1,35)=140.02$, $p<0.001$, $\eta^2=0.80$), reflecting that negative videos ($M=5.41$) were rated as significantly more arousing than neutral videos ($M=2.26$). The main effect of group, $F(1.35)=0.62$, $p=0.44$, $\eta^2=0.02$ and the emotion x group interaction were not significant, $F(1,35)=0.011$, $p=0.92$, $\eta^2<0.001$

3.3.2.2 Deliberate memory performance

As negative and neutral clips were used in a way that produced an unbalanced design to clearly assess emotion, cued recall scores were first analysed using a 2x2x2 mixed ANOVA with group (congruent versus incongruent pairs) as a between participant factor and condition and position as within-participant factors. For the congruent group, the factor of condition included 2 levels of whether two neutral (neutral-neutral) or two negative (negative-negative) clips had been seen in succession. For the incongruent group, the factor of condition determined whether clips seen in succession were viewed in the order neutral-negative or as negative-neutral. Whilst this design removes a general effect of emotion from the analysis, it allows examination of how the congruency of clip valence, the order of valence and the position of the clip from a pair can affect deliberate memory performance.

This analysis showed a non-significant group x order interaction ($F(1,37)=3.84$, $p=0.058$, $\eta^2=0.09$). Likewise, the interactions of order x position ($F(1,37)=2.92$, $p=0.10$, $\eta^2=0.06$) and group x order x position ($F(1,37)=2.98$, $p=0.09$, $\eta^2=0.08$) were non-significant. However given our a priori hypotheses about how position should affect memory performance, we further explored the data by performing a separate ANOVA on congruent and incongruent groups.

For the congruent pair group, a 2x2 ANOVA of condition and position on deliberate memory performance showed non-significant main effects of order ($F(1,17)=3.25$, $p=0.09$, $\eta^2=0.16$) and position ($F(1,17)=3.66$, $p=0.07$, $\eta^2=0.17$), condition x position interaction, $p>0.90$; Figure 3.2, left panel.

For the incongruent pair group, a further 2x2 ANOVA of condition and position showed a significant condition x position interaction ($F(1,20)=4.31$, $p=0.05$, $\eta^2=0.17$; main effects of condition and position, $p>0.30$; Figure 3.2, right panel). Further analysis of this interaction showed that this effect reflected worse memory for neutral clips relative to a preceding negative clip (clip 2 minus clip 1) compared to negative clips preceded by a neutral clip ($t(20)=2.08$, $p=0.05$).

A second 2x2x2 ANOVA with group (congruent, incongruent) as a between subjects factor and position (immediate, interval) and emotion (neutral, negative) as within subject factors showed a main effect of emotion, $F(1,38)=8.34$, $p<0.01$, $\eta^2=0.18$, which was due to lower memory performance for neutral compared to negative videos. The main effect of position F(1,38)=0.83, p=0.37, $\eta^2=0.02$ and the position x emotion interaction F(1,38)=1.82, p=0.19, $\eta^2=0.05$ were non-significant.

In summary, by visual inspection a decrease in memory performance for the first compared to the second clip in a pair was observed for all pairs except from when a negative video preceded a neutral. However, this difference was only significant in the incongruent condition when a neutral video was followed by a negative video. When a neutral clip was immediately followed by a negative clip, there was a decrease in memory for the neutral clip relative to the first clip.

In addition, there was a main effect of emotion, reflecting better memory performance for negative compared to neutral videos.

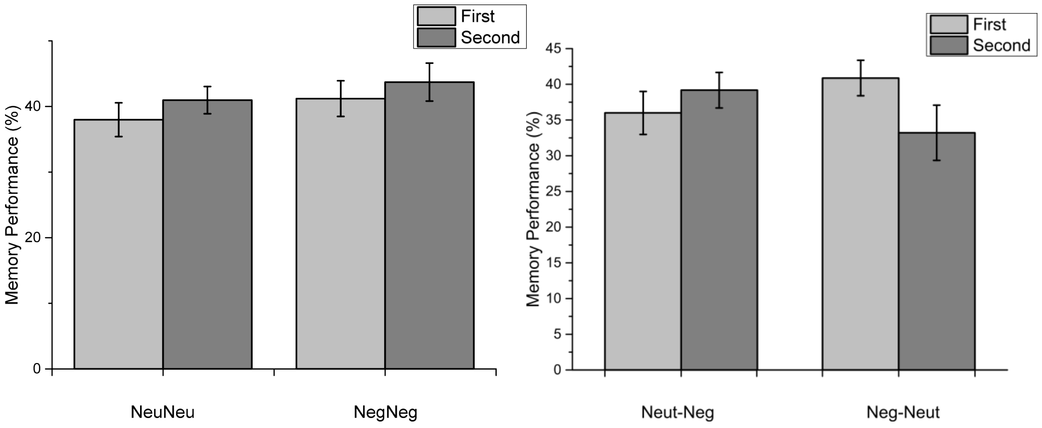

Figure 3.2. Mean memory performance on a cued recall memory test in Experiment 3.1. Left panel: Memory performance for the congruent-emotion group, showing memory performance for the first and second video in the Neutral-Neutral condition and the Negative-Negative condition. **Right panel:** Memory performance for the incongruent-emotion group, showing memory performance for the first and the second video in the Neutral-Negative and the Negative-Neutral condition. Error bars show SEM.

3.3.2.3 Intrusions

Two participants were omitted from the analysis of the intrusion data, as they did not fill out the diary. Overall, 89% of reported intrusions by participants could be matched with specific videos. Videos that could not be matched to a specific video were omitted from further analysis. A 2x2 repeated measures ANOVA with position (immediate, interval) as a within-subject factor and group (congruent, incongruent) as a between-subject factor showed that the main effect of position was not significant, F(1,40)=0.26, p=0.61, $\eta^2<0.01$ (Figure 3.3). The same was the case for the main effect of group, F(1,40)=0.23, p=0.64, $\eta^2<0.01$ and for the position x group interaction, F(1,40)<0.01, p=0.95, $\eta^2<0.01$.

Analyses investigating the relationship between subjective ratings (valence or arousal) and the number of reported memory intrusions across condition and group showed no significant relationship between intrusions and valence ratings for negative videos, r(34)=0.26, p=0.12. Likewise, the correlation between intrusions and overall arousal ratings for negative videos was non-significant, r(34)=-0.27, p=0.11.

3.3.2.4 Relationship between intrusions and questionnaire measures

Pearson correlations were used to assess the relationship between the overall number of intrusions and measures of affect. The correlation between trait anxiety (STAIT) and intrusions was positive but non-significant, r(32)=0.31, p=0.07. Likewise, there were no significant correlations between intrusions and difference in state anxiety (r(34)=-0.05, p=0.77), positive affect (r(33)=0.18, p=0.29) and negative affect, r(33)=-0.18, p=0.30.

3.3.2.5 Relationship between intrusions and memory performance

Looking at the relationship between intrusions and memory performance, a partial correlation between these two measures with the effect of condition held constant showed no significant relationship between deliberate memory performance and memory intrusions, r(75)=0.15, p=0.19.

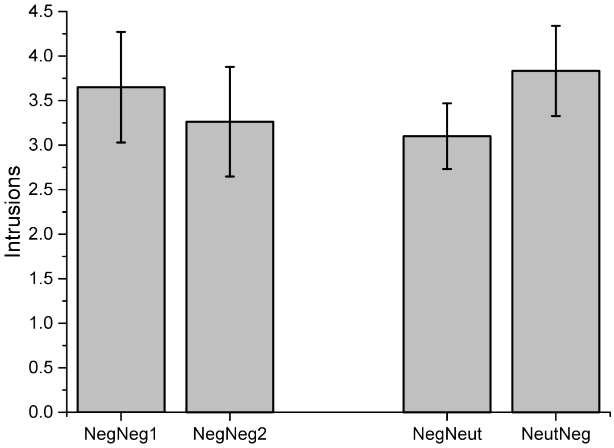

Figure 3.3. Mean number of reported intrusions in Experiment 3.1. The figure shows the mean number of intrusive memories in the congruent-emotion (NegNeg1 and NegNeg2) and the mixed emotion (NegNeut and NeutNeg) condition. NegNeg1 shows the number of intrusions for the first video in the pair with two negative videos and NegNeg2 intrusions for the second video in the pair with two negative videos. Error bars show SD.

3.3.2.6 Questionnaires

The relationship between memory variables (intrusions and cued recall memory scores for neutral and negative items) and imagery scores (Shortened QMI, Marks' TVIC and Gordons VVIQ) was investigated with Pearson's correlations but none of these were significant (all p's > 0.05; see table 3.1).

An analysis of trait anxiety scores showed no differences in baseline anxiety levels between the congruent and incongruent group, t(36)=0.08, p=0.93, d=0.03. State anxiety was analysed using a 2x2 mixed ANOVA with group as a between participants factor and time (pre-encoding, post-encoding) as a within participant factor. This analysis revealed a main effect of time (F(1,38)=50.36, p<0.001, η^2=0.57) reflecting an increase in state anxiety from before encoding of the video clips to after encoding. The main effect of group (F(1,38)=0.33, p=0.57, η^2<0.01) and group x time interaction (F(1,38)=1.14 p=0.29, η^2=0.03) were both not significant.

The PANAS inventories measuring positive and negative affect before and after encoding of the trauma videos were analysed with 2x2 mixed ANOVAs with group (congruent, incongruent) as a between group factor and time (pre-encoding, post-encoding) as a within-subject factor. For the positive affect scale, this analysis revealed a main effect of time (F(1,37)=12.08, p=0.001, $\eta^2=0.25$) reflecting a decrease in positive affect scores after viewing the trauma videos compared to before viewing. There was no main effect of group (F(1,37)=0.58, p=0.45, $\eta^2=0.02$) or group x time interaction (F(1,37)=0.27, p=0.61, $\eta^2<0.01$). For the PANAS scale of negative affect, the analysis also showed a main effect of time (F(1,37)=26.42, p<0.001, $\eta^2=0.42$), reflecting higher scores of negative affect after encoding compared to before. The main effect of group was non-significant (F(1,37)=1.00, p=0.32, $\eta^2=0.03$) and the group x time interaction was also non-significant (F(1,37)=0.13, p=0.72, $\eta^2<0.01$).

Table 3.1. Means (SD) of questionnaire measures of anxiety, positive and negative affect and visual imagery during Experiment 3.1.

	Congruent Group N=20		**Incongruent Group N=24**	
	Pre (SD)	**Post (SD)**	**Pre (SD)**	**Post (SD)**
Trait anxiety	40.13 (9.92)	n/a	39.87 (9.08)	n/a
State anxiety	33.12 (10.36)	47.69 (13.46)	32.33 (8.57)	51.71 (11.25)
Positive affect	31.75 (6.04)	25.05 (7.12)	29.13 (9.19)	24.88 (8.70)
Negative affect	12.69 (3.43)	21.50 (8.39)	15.29 (7.89)	23.13 (8.51)
Shortened QMI	80.50 (22.28)	n/a	86.35 (20.97)	n/a
Marks' TVIC	35.90 (9.82)	n/a	41.08 (11.57)	n/a
Gordon's VVIQ	20.11 (6.69)	n/a	24.21 (6.96)	n/a

3.3.2.7 Post-hoc power analyses

Due to the non-significant effects observed in this study, a post-hoc power analysis was conducted based on the effect size for the main effect of interest (position) and sample size to assess if the chosen number of participants was too small to be likely to detect an effect. This analysis showed the power to detect an effect of position was 0.16 for the memory data and 0.08 for the intrusion data, which is very low.

3.3.3 Discussion

This experiment examined the effects of immediate post-stimulus encoding of a consecutive clip on deliberate and intrusive memory for the preceding clip, using emotional stimuli. In general, results for both the deliberate memory and intrusion data were non-significant. For purposes of hypothesis generation and planning of future experiments however, it can be useful to consider systematic patterns in the data as they appear from visual inspection, although no conclusions or claims can be made as effects were non-significant.

For deliberate memory, it was hypothesized that videos presented with a subsequent inter-trial interval of 16s would facilitate memory consolidation and thereby increase memory performance, while as retroactive interference from events (videos) occurring in immediate succession after a preceding event (video) would impair memory for the event (Ben-Yakov et al., 2013). Therefore, it was expected that the video presented as the second video in a pair would interfere with post-encoding processing of the first video in the pair, resulting in a retroactive interference effect.

By visual inspection only, the *numerical* pattern of results were largely consistent with this hypothesis as deliberate memory performance for video clips presented as the first video in a pair was typically numerically reduced compared to video clips presented as the second video in a pair, but effects were statistically non-significant. This visual but non-significant pattern was present in both congruent conditions (Neut-Neut, Neg-Neg) and in the incongruent condition where a neutral video was followed by a negative video (Neut-Neg). However, this visual pattern was absent when a neutral video was followed by a negative video in the incongruent group.

Speculatively, had the differences between conditions by visual inspection been significant, it could have been considered if the absence of the ‘retroactive interference pattern’ in the Negative-Neutral video combination could be due to higher salience of the negative video compared to the subsequent neutral video, taking precedence of processing resources during and following the event (Mather and Sutherland, 2011). This effect would not happen in congruent conditions comprising two same-valence videos, or in the neutral-negative condition, where the patterns by visual inspection were in accordance with a retroactive interference hypothesis (however as mentioned, these differences were non-significant).

Similar to the deliberate memory data, no statistically significant differences were found between conditions in the number of reported memory intrusions over the week between encoding and memory test. By visual inspection, there were some interesting numerical patterns in the data but no significant effects, which may be due to low statistical power in this study. Low power in the intrusion analysis could be attributed to high between-participant variability in the reported intrusive memories.

Also for the intrusion data it is informative to consider patterns that appear by visual inspection for purposes of hypothesis generation to be used as a guide when designing future experiments, despite the lack of statistically significant findings. Interestingly, by visual inspection the numerical pattern of intrusions in the congruent condition was opposite to the corresponding numerical pattern of memory performance, with numerically more memory intrusions for the first video in a pair compared to the second. The numerical pattern in the incongruent condition was less clear, as was the case for deliberate memory performance.

In the following study, these problems were addressed as I attempted to create a stronger and simpler design by increasing the number of stimuli, using congruent conditions only and introducing a baseline condition similar to the baseline used in Ben-Yakov et al. (2013) in which a single video clip was presented alone and followed by an ITI. This baseline condition was added to establish whether effects of a second immediate stimulus on e.g. deliberate memory performance reflected reduced memory in the first video in a pair (indicating a retroactive interference effect) or enhanced memory for the second video in a pair.

3.4 Experiment 3.2

Experiment 3.2 focused on the condition from Experiment 3.1 in which video clips were presented as congruent pairs (either as neutral-neutral or negative-negative pairs). In addition, given the lack of an appropriate baseline to contrast the changes in memory observed in Experiment 3.1, this experiment also included a control condition in which single neutral or negative video clips were viewed without another clip presented immediately afterwards. Therefore, Experiment 3.2 used a similar design to Experiment 3.1, but here, participants watched an increased number of short video clips that were either presented in a pair as in the previous experiment (but only using emotion-congruent pairs) or as a single video clip with a long interval before and after presentation of the video clip.

It was hypothesized that both the videos in the control condition and the videos presented as the second in a video pair would not be subject to retroactive interference effects due to preserved post-encoding processing in the seconds following encoding. Hence, memory performance for the control condition was expected to be similar to the second video clip in a pair and superior to memory performance for videos positioned as the first in a pair.

3.4.1 Methods

3.4.1.1 Sample size estimation

Sample size estimations were the same as for the previous Experiment 3.1 and provided a required sample of approximately 30 (see p. 105).

3.4.1.2 Participants

Twenty-nine participants (17 females) aged 19-40 years (M=24.6 years, SD=6.36) were recruited for Experiment 3.2. The UCL research ethics committee approved the studies and all volunteers gave informed consent prior to participating in the study. Participants were paid 7.50 pounds per hour. Participants with a history of psychiatric or neurological disorders were excluded from the study.

3.4.1.3 Stimuli

In Experiment 3.2, the total number of videos was increased to 60, including 30 negative and 30 neutral videos, each with a duration of 16 seconds, which was shorter than the previous experiment (see the Appendix, Table A2 for a content list). The nature and content of the videos was equivalent to the videos used in Experiment 3.1. There was partial overlap between videos from Experiment 3.1 but videos were shortened for the current experiment.

3.4.1.4 Intrusion diary

The procedure for the intrusion diary was identical to Experiment 3.1.

3.4.1.5 Questionnaires

Participants completed the same questionnaires as participants in Experiment 3.1, including the STAI, PANAS, Shortened QMI, Gordon's TVIC and Marks' VVIQ (see Experiment 3.1).

3.4.1.6 Procedure

3.4.1.6.1 Encoding

Participants watched a randomised sequence of pairs comprising a total 30 neutral and 30 negative videos that were either presented in close proximity with another video (a video pair) with an ISI of 1000 milliseconds, and followed by a 16 second ITI or 'alone' with an interval of 16 seconds preceding and following the video presentation. The general viewing conditions and instructions mirrored those described in Experiment 3.1.

3.4.1.6.2 Intrusion diary

Participants were instructed to keep a record of any memory intrusions from the videos they might experience in the week following encoding until they returned for the follow-up session. This part of the experimental procedure was identical to the intrusion diary procedure in Experiment 3.1.

3.4.1.6.3 Memory test

The memory test was similar to the memory test used in Experiment 3.1: Participants were cued with a still frame from a video presented with a question relating to that video and were instructed to type in their answers on the computer. After each question, volunteers made a confidence rating indicating how confident they were that their response was correct, on a scale from 1-4 (from 'Not at all confident' to 'Very confident'). There were two questions per video and a total of 120 questions for the memory test.

Following the test, subjective valence and arousal ratings of the videos were acquired. For this task, participants were cued with a single still frame from a video in the middle of the screen and made valence and arousal ratings on 7 point Likert scale when they had recalled the video. Both of these tasks were self-paced.

3.4.1.7 Statistical analysis

The statistical analysis procedure was similar to Experiment 3.1, using repeated measures GLMs to assess differences between the different conditions (positions).

3.4.2 Results

3.4.2.1 Questionnaires

A paired-samples t-test revealed that state anxiety measures increased from pre- to post-encoding, t(25)=7.69, p<0.001, d=1.51. The same was the case for the negative affect scale, t(26)=6.02, p<0.001, d=1.16. In contrast, the positive scale showed an decrease from prior to encoding of the trauma videos to after, t(26)=4.45, p<0.001, d=0.42 (Table 3.2)

Table 3.2. Means (SD) of questionnaire measures of anxiety, affect and visual imagery during Experiment 3.2.

	N=29	
	Pre (SD)	**Post (SD)**
Trait anxiety	39.85 (8.87)	n/a
State anxiety	29.70 (6.64)	49.12 (12.15)
Positive affect	32.33 (6.81)	25.81 (7.91)
Negative affect	13.26 (3.99)	21.11 (6.69)
Shortened QMI	85.47(29.55)	n/a
Marks' TVIC	36.70 (11.82)	n/a
Gordon's VVIQ	21.35 (7.96)	n/a

3.4.2.2 Deliberate memory performance

For the memory performance scores, a 2x3 repeated-measures ANOVA with emotion (neutral, negative) and clip position (single, first, second) as within-participant factors was conducted. This analysis revealed a significant main effect of emotion, F(1,27)=122.45, $p<0.001$, $\eta^2=0.82$, which was due to better memory performance for negative compared to neutral items (Figure 3.4). The main effect of position was not significant, F(2,54)=0.90, p=0.41, $\eta^2=0.03$, indicating that there was no significant difference in memory scores across conditions. The emotion x position interaction was also not significant, F(2,54)=0.03, p=0.97, $\eta^2=0.001$.

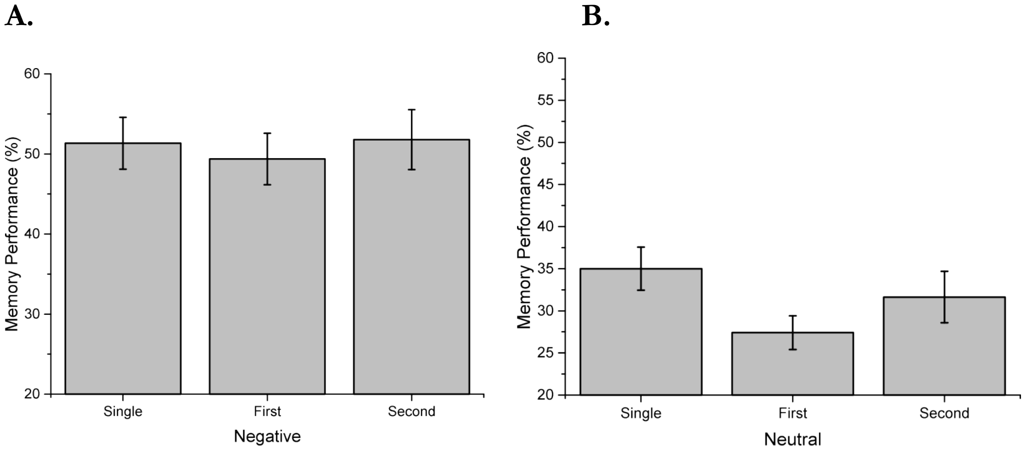

Figure 3.4. Mean memory performance on the cued recall test in Experiment 3.2. Memory performance for A) negative items and B) Neutral items that were presented by themselves, first or second in a pair. Error bars show SEM.

3.4.2.3 Intrusions

An initial assessment showed that 89% of reported intrusions could be matched to specific videos and the rest were omitted from analyses. Normality tests showed that the intrusion data was not normally distributed. Hence, we conducted a Friedman's ANOVA on the number of intrusions recorded for negative clips (single, first and second). This analysis showed that there was no significant difference in the number of reported intrusions for the three conditions, $X^2(2)=1.17$, $p=0.56$ (Figure 3.5).

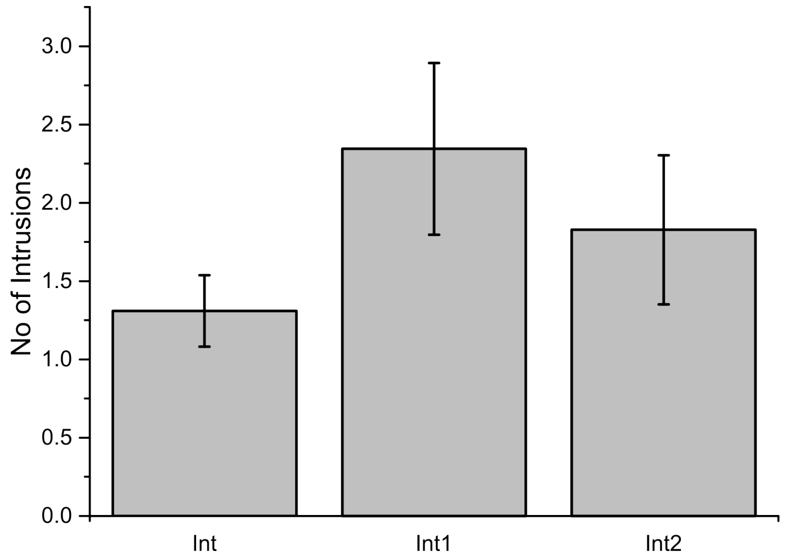

Figure 3.5. Distribution of mean number of reported intrusions in the three conditions in Experiment 3.2. Number of reported intrusions for videos that were presented by themselves, first or second in a video. Error bars show SEM.

3.4.2.4 Relationship between memory measures and measures of affect

As a Shapiro-Wilk test had demonstrated that the intrusion data was non-normally distributed ($p<0.01$), the relationship between intrusions and measures of affect was assessed with spearman's correlations. The correlation between trait anxiety and number of reported intrusions was non-significant, $r_s(25)=-0.14$, $p=0.50$. Likewise, there was no significant relationship between intrusions and pre- to post-encoding differences in state anxiety ($r_s(25)=0.06$, $p=0.79$), positive affect ($r_s(25)=-0.04$, $p=0.85$) or negative affect ($r_s(25)=0.09$, $p=0.65$.

Corresponding analyses were carried out with a Pearson's correlation for affect measures and deliberate memory for negative and neutral videos. For negative memory, these analyses showed no significant relationship between memory performance and affect measures (all p's >0.05). Similarly, there were no significant relationship between memory performance for neutral videos and any measures of affect (all p's >0.05). Due to an error in the script, subjective video ratings could not be interpreted and were therefore excluded from analysis.

3.4.2.5 Post-hoc power analyses

We performed post-hoc power analyses to assess the power of the results. As before, effect sizes of the parameter of highest interest in (position) and the sample size were used. This analysis revealed that the power to detect an effect of position in both the memory data ($1-\beta=0.19$) and for intrusions ($1-\beta=0.39$) was low, which suggests the observed effects were relatively weak. As such, further studies would require larger sample sizes to detect significant effects.

3.4.3 Discussion

Like the first experiment in this chapter (Experiment 3.1), the current study investigated the effect of retroactive interference on deliberate memory and memory intrusions, but using a stronger and simpler design with more trials and only comprising emotion-congruent pairs. Results showed better memory performance for negative compared to neutral videos on the follow-up memory test one week after encoding. In contrast, there were no significant differences between the three conditions (single, first or second video in a pair) for memory performance or intrusions, which was likely due to low statistical power as reflected in the post-hoc power analysis.

Better memory performance for negative events compared to neutral events is consistent with the widely held view that emotion can be a potent facilitator of memory (Cahill and McGaugh, 1995, Dolcos et al., 2004). Some studies have shown that different types of memory are modulated differentially by emotion; in particular, it has been suggested that associative memory performance is impaired, while item memory may be enhanced (Pierce and Kensinger 2011, Madan et al., 2012; Chiu et al., 2013; Guez et al., 2015; Bisby and Burgess, 2014, 2017). These findings appear to contradict the findings in this experiment as the memory test was a cued recall memory test, requiring conscious recall of the scene in which the 'event' took place and associative binding of the constituent parts of the memory. However, many questions used in the current task related to gist in the videos, and studies have shown that memory for gist is facilitated by the amygdala whereas details of complex stimuli are not (Adolphs et al., 2005).

Despite not seeing any significant differences between conditions for either intrusions or deliberate memory, an interesting pattern emerges when visually inspecting the data. By visual inspection, memory performance for the first video in a pair was lower than for a single or second video in a pair. Had this effect been significant, this pattern of results would have suggested that retroactive interference impaired memory performance for videos shown as first in a pair of two, compared to videos shown alone or as second video in a pair. Such a result would have been in accordance with the findings in Ben-Yakov et al. (2013), also demonstrating a retroactive interference effect of presenting a second stimulus immediately after the first.

Interestingly, visually inspecting the intrusive memory reports showed the opposite pattern to deliberate memory performance, with a numerical increase in intrusions for the first video in a pair compared to a single or second-video position. Had these differences between conditions been significant, the results would have been consistent with a dual representation account of involuntary memory. The DRT proposes that involuntary memories arise when negative events are not adequately encoded as ‘normal’ episodic memories comprising a strong contextual representation (C-reps). In turn, this will facilitate a relative strengthening of lower-level sensory and emotional representations (S-reps), resulting in memory intrusions (Brewin, 2010). Although the visual pattern of results is in accordance with this theory, the differences were non-significant.

I had hoped that a higher number of videos would give more statistical power in the study. However, a lower number of average intrusions were observed in Experiment 3.2 than in Experiment 3.1. It is possible that using shorter videos reduced the sense of a narrative and that this may have reduced the subsequent occurrence of intrusions. Likewise, the adjusted deliberate memory test in this experiment did not increase differences between conditions and remained non-significant.

3.5 Experiment 3.1 and 3.2 combined

To some extent, Experiment 3.1 and 3.2 could be combined and analysed as a whole. This was done to achieve more power and to explore whether the patterns present by visual inspection would reach statistical significance when data from the two studies were combined. More specifically, data from the congruent condition (NeutNeut and NegNeg) in Experiment 3.1 and the corresponding data from the first and second position conditions in Experiment 3.2 (NeutNeut or NegNeg) were used for this analysis, while data from the incongruent condition in Experiment 3.1 and the single condition in Experiment 3.2 were not included in these additional analyses.

3.5.1 Deliberate memory

A mixed 2x2x2 ANOVA with experiment (3.1, 3.2) as a between group factor and position (First, Second) and emotion (Neut, Neg) as within-subject factors revealed a significant main effect of position, $F(1,39)=68.82$, $p<0.001$, $\eta^2=0.64$ reflecting that across emotional valence of the videos, participants showed better deliberate memory performance for the second video compared to the first video in a pair. The main effect of emotion was also significant, $F(1,39)=7.00$, $p=0.01$, $\eta^2=0.15$, which was due to superior memory performance for negative compared to neutral videos. Finally, the position x experiment interaction $F(1,39)=35.82$, $p<0.001$, $\eta^2=0.48$ was also significant, whereas the emotion x experiment, the position x emotion and position x emotion x experiment interactions were non-significant (all p's>0.6.

3.5.2 Intrusions

A mixed 2x2 ANOVA with experiment (3.1, 3.2) as a between group factor and position as a within-subject factor was used to analyse the combined intrusion data from Experiment 3.1 and 3.2 as the ANOVA is known to be robust to violations of the normality assumption. However, this analysis revealed no significant results; the main effect of position was non-significant, F(1,44)=1.52, p=0.22, $\eta^2=0.03$ as was the position x experiment interaction, F(1,44)=0.10, p=0.75, $\eta^2<0.01$.

3.6 General discussion

This aim of this chapter was to investigate how exposure to a new emotionally negative or neutral 'event' presented immediately after the encoding of another event could influence deliberate memory and memory intrusions.

Unfortunately, neither of the two studies conducted for this purpose yielded statistically significant results. However as mentioned previously, it may be useful to examine systematic patterns in the data by visual inspection for the purposes of hypothesis generation. Also, when data from both experiments were analysed together, deliberate memory performance was impaired for videos that were immediately followed by another video, indicating that the presentation of a second video retroactively interfered with memory for the first video. This finding is consistent with the theory of retroactive interference. Intrusion results did not show any significant effects for either experiment.

3.6.1 Effect of emotion on deliberate memory

Results from both experiments in this chapter showed better memory performance for negative compared to neutral items. This is consistent with the well-established finding of negative memory enhancements (Kensinger and Corkin, 2003; Cahill and McGaugh, 1995). As mentioned previously, evidence suggests that different memory types are differentially modulated by emotion; in particular, it has been suggested that item memory is enhanced while associative memory is impaired (Bisby and Burgess, 2013; Anderson and Shimamura, 2005). The task used in this experiment was a cued recall memory test, believed to place demands on associative memory processes in the recall of scenes from the videos. Hence, from this it could be predicted that memory for this type of information would be impaired. However, it has been suggested that memory for gist and details of complex scenes are also modulated differently by emotion (Adolphs et al., 2005) and hence it is possible that the observed effect was driven by facilitated memory for items related to gist.

3.6.2 Effect of post-stimulus encoding on deliberate memory

When data from the two studies was combined, deliberate memory for events that was immediately followed by another event was generally impaired compared to events that were followed by a short break. This result is also consistent with the pattern observed by visual inspection in each experiment but did not reach statistical significance. Hence, there was evidence of retroactive interference effects in the congruent conditions when data from the two experiments were combined but not when each experiment was analysed on its own. It is possible that the failure to detect significant results when analysing each experiment independently might be due to type II error. Hence, results across these two studies are in accordance with previous studies demonstrating retroactive interference for neutral information (Ben-Yakov et al., 2013) and show that these effects extend to include negative information.

3.6.3 Effect of post-stimulus encoding on intrusive memories

The two experiments above demonstrated that intrusive memories were unaffected by our manipulations of post-encoding processing. The number of intrusive memories reported by participants for the first clip was not altered by the immediate presentation of a second clip, even when directly compared to the number of intrusions for the second clip (Experiment 3.1 and 3.2) or a clip presented alone (Experiment 3.2). These findings contrast with studies reporting that post-encoding factors can indeed modulate memory intrusion development (Holmes et al., 2009, Deeprose et al., 2012). These studies all used specific tasks, whereas presentation of an additional event was used in this experiment. It is possible that the effects of applying a specific task are stronger than introducing a second event in disrupting post-encoding processing, which could explain these findings.

In relation to current views of intrusive memory development outlined in the Introduction, these findings are difficult to interpret within either the dual representation (DRT) or the unitary account. The DRT would predict opposite effects of disrupted post-encoding processing on deliberate memory performance and intrusions, whereas the unitary account would predict that intrusions and deliberate memory would both be reduced by disrupted post-encoding processing. When combining data from the two experiments in one analysis, it was shown that deliberate memory was impaired by the immediate presentation of a second stimulus, while immediate presentation of a second stimulus did not seem to affect the number of reported intrusions. These results are not consistent with either of the above accounts but do indicate that memory intrusion development and deliberate memory performance may rely on different underlying mechanisms.

3.6.4 Limitations

One limitation of these studies is the relatively unspecific deliberate memory test, which contains elements both related to gist and details of the videos. It might be useful to use a memory test that could specifically assess and dissociate item memory and associative memory. Nevertheless, the cued recall memory test used in these experiments should require recollection of the scene and 'mental time travel' to an extent similar to what is normally required during episodic recall (Tulving and Markovitch, 1998).

Another significant limitation in these studies is the high level of random variability in the intrusion reports. These data rely solely on compliance of participants in filling in the diary and it is not possible to control for forgotten entries etc. Also, despite using highly emotionally negative stimuli, the videos have limited personal relevance to the participants and many reported having only few memory intrusions over the week, while a minority reported having many intrusions. This high and random individual variability in intrusion reports sets high demands for large sample sizes to detect potential effects, which was reflected in the lack of statistical power observed in these experiments. Another indication that type II errors might have been made is the observation of systematic and repeated patterns in results across the two experiments in the absence of statistical significant effects.

3.7 Conclusions

In conclusion, results from the current chapter demonstrated that manipulations to post-encoding processes of neutral and negative events could alter deliberate memory performance (Experiment 3.1 and 3.2 combined). There was no effect of disrupted post-encoding processing on memory intrusions, suggesting that intrusions and deliberate memory performance are not modulated in the same way and may rely on different mechanisms. Finally, the presence of systematic patterns in the data in the absence of negative events combined with low observed power may suggest that some of these results did not reach significance due to type II error.

4 THE EFFECT OF BRIEF WAKEFUL REST AFTER VIEWING NEGATIVE EVENTS DISSOCIATES DELIBERATE MEMORY FROM INTRUSIVE IMAGERY

4.1 Overview

New memories exist in a fragile state after encoding where they undergo post-encoding processing and consolidation (Dudai, 2004). As demonstrated in the first experiment in Chapter 3, this consolidation phase offers a window where memory formation can be facilitated or impaired. Studies have demonstrated that wakeful rest during this period can enhance memory performance compared to when another task is performed (Dewar et al., 2012). However it is not known how this intervention could affect memory intrusion development or whether these findings extend to deliberate memory for emotionally negative material. Hence, the current chapter aimed to investigate how a period of brief wakeful rest after viewing negative events might affect subsequent deliberate memory performance and intrusion development.

4.2 Introduction

In the aftermath of learning, memories undergo stabilisation and transformation through consolidation processes (Dudai 2004; Wixted, 2004). Consolidation is thought to occur in the minutes and hours immediately after an event and can continue over many days (systems consolidation; Dudai, 2002). As mentioned in Chapter 1, a distinction exists between synaptic and systems consolidation (see p. 42-43; Dudai and Morris, 1990; Dudai, Squire and Alzarez, 1995). During the consolidation process, memories exist in a fragile state and are more vulnerable to interference from other sources (Dudai, 2004). Numerous studies have shown that consolidation processes can be facilitated or disrupted to enhance or impair memory respectively (Müller and Pilzecker, 1900 in Lechner, 1999; Ben-Yakov et al., 2013; Dewar et al., 2012a; McGaugh, 2002; McGaugh et al., 1996; McGaugh and Roozendal, 2002).

Research has shown that rest can be an important facilitator of memory consolidation processes, which may be due to reduced interference from other information (Wixted, 2004; Mednick et al., 2011). Building on the literature on rodent studies showing improved spatial memory performance for a previously taken route after hippocampal replay of activity present during encoding, Craig et al.

(2015) investigated whether these findings generalise to humans; in their study it was demonstrated that rest following a spatial learning task improved spatial memory performance on two measures of spatial memory (associative spatial memory and temporal order memory). However it should be noted that two other measures of spatial memory did not improve in the rest condition (cognitive map formation and route memory). Nevertheless, a number of other studies have demonstrated that rest benefits subsequent memory performance. For example, studies with amnesic patients have found that more words from a word-learning task was remembered after a short period of rest was given in between encoding and retrieval compared to when carrying out a new task (Cowan et al., 2004; Dewar et al., 2009).

Equivalent findings exist for healthy subjects. For example, Dewar et al. (2012) showed that the benefits of rest also work over the long term. In two studies, volunteers learned two short stories presented aurally and were then either asked to sit quietly and rest for 10 minutes (wakeful rest condition) or they completed a spot-the-difference task. Results showed that wakeful rest following encoding was associated with higher memory performance scores both after 15 and 30 minutes as well as after 7 days, regardless of whether or not the material was retrieved between encoding and test (Dewar et al., 2012). Similar effects have been demonstrated over short delays in amnesic patients (Dewar et al., 2009; 2012), lending further support to the notion that wakeful rest following an event is beneficial to memory consolidation and retention (Dewar et al., 2012).

The authors argued that the effects of wakeful rest could be due to reduced interference by other information (Dewar et al., 2012). More specifically it was proposed that wakeful rest allows for un-interrupted hippocampal replay following learning. Hippocampal replay is believed to be one of the neural substrates of memory consolidation (Carr et al., 2011; Craig et al., 2015) and has been shown to be facilitated in resting states such as slow-wave sleep (Wilson et al., 1994; Takashima et al., 2006; Buzsaki, 1998) and consummatory behaviour in rodents (Carr et al., 2011).

In the context of trauma memory, a window of consolidation might highlight an important period in which the newly acquired memories could potentially be altered to ameliorate trauma-related symptoms. It has been proposed that the amygdala enhances consolidation for emotional information via different influences such as stress hormones (for review, see McGaugh, 2004). Consistent with this idea, the use of β-adrenergic receptor antagonists (such as propranolol) as a possible drug to treat PTSD symptoms has been investigated. Propanolol is a non-selective beta-blocker, which blocks the actions of epinephrine and norepinephrine and with that, significant aspects of the stress response (Cahill, 1994). For example, in a pilot study, Pitman et al. (2002) found that propranolol administration within six hours after trauma reduced subsequent development of PTSD. Others have replicated these findings (Vaiva et al., 2003), indicating that post-encoding processing plays a role in PTSD development and that emotional processing in the aftermath of a traumatic event may contribute to PTSD pathogenesis.

Evidence from analogue trauma studies also appears to support the idea that intrusive memory experiences can be affected during this period. Indeed, of studies in which traumatic footage is viewed and intrusions are collected over the following week, a number have shown that playing the computer game Tetris 30 minutes after encoding can reduce the number of intrusions experienced (Holmes et al., 2009). This effect is also observed when performed 4 hours after encoding (Holmes et al., 2010) or when prior reactivation of the material is performed to trigger reconsolidation (James et al., 2016). Interestingly, these studies show that whilst intrusions were reduced by a task performed following traumatic material, deliberate memory was unaffected, suggesting that the task might selectively interfere with consolidation of negative imagery or reduce arousal to leave consolidation processes intact.

A recent proof-of-concept RCT with 71 patients investigated the effects of playing Tetris in the immediate aftermath of a motor vehicle accident (Iyadurai et al., 2017). Compared to a control group, people who played Tetris within 6 hours after the trauma showed an overall reduction in the occurrence of intrusive trauma memories and a faster decline in reported intrusions (Iyadurai et al., 2017). These findings were mirrored in a similar study conducted with women who underwent an emergency caesarean section (Horsch et al., 2017). These studies suggest that impairing post-encoding sensory processing of traumatic material by introducing a visuospatial task, which competes with trauma memory for visuo-spatial resources can reduce intrusive memories. More generally, these studies indicate that there is a window during the consolidation period, where trauma memories are malleable and can be subject to post-encoding processing that can ameliorate or exacerbate subsequent PTSD symptoms.

The aim of the studies in this chapter was complementary to studies aiming to impair consolidation of traumatic visuo-spatial material, instead aiming to improve consolidation of hippocampal-dependent contextual material. Thus we sought to investigate how a period of brief wakeful rest following encoding might affect the consolidation, subsequent deliberate memory and intrusion development from a set of traumatic videos. Investigating this will shed light on a potential role for rest following trauma as a means to ameliorate intrusive memories.

In addition, the study was developed in the context of predictions from two opposing accounts of intrusion development: the unitary account would predict that if a rest period facilitates any consolidation, this will result in both better retention of the trauma memory and a higher frequency of reported intrusions (Rubin et al., 2005; 2008a; 2008b). In contrast, the dual representation theory asserts that if wakeful rest enhances hippocampal consolidation of contextual representations concerning the traumatic stimuli, this would result in better deliberate memory performance for the trauma stimuli, whereas the number of reported intrusions would be reduced (Jacobs and Nadel, 1985; Brewin et al., 2010; Brewin, 2001; Bisby and Burgess, 2014; Schwabe and Wolf, 2013). In short, if both memory types are changed in the same direction, this would suggest that they are part of the same underlying memory system (supporting the unitary account). In contrast, if the interventions lead to changes in opposite directions where one memory type is increased while the other is reduced, this would suggest that different memory systems underlie the two forms of memory and such findings would therefore be in support of the DRT.

4.3 Experiment 4.1

To investigate the effects of wakeful rest on memory consolidation and subsequent memory for emotionally negative stimuli, an experimental trauma paradigm (James et al., 2015; Bourne et al., 2013; Holmes et al., 2004; 2009; Halligan et al., 2002; see Holmes and Bourne, 2008 and James et al., 2016 for reviews) was used in which participants are presented with a series of emotionally negative videos. One group of participants were assigned to a wakeful rest condition following encoding, while another was instructed to engage in a 0-back task (working memory (WM) task). This task was chosen as a control condition because it is known to engage working memory and neither uses verbal or visuospatial resources, which have previously been shown to exert opposite effects on intrusion development (Deeprose et al., 2012). In the week between encoding and follow-up, participants were instructed to record intrusive memories for the material. Deliberate memory for the footage was assessed via a surprise memory test completed after 1 week.

4.3.1 Methods

4.3.1.1 Sample size estimations

Based on an effect size from a previous study investigating post-encoding interventions and intrusions (Holmes et al., 2009) of $d=0.91$ a sample size estimation was calculated using the G*power 3.1 software (Faul et al., 2007). This analysis indicated a required sample size of $N=20$ in each group to achieve an 80% power level at $\alpha=0.05$.

4.3.1.2 Participants

A total of 40 healthy volunteers (29 females, mean age = 22.8 years, SD=3.36) were recruited for the experiment. The experimental protocol was approved by the University College London Research Ethics Committee and written informed consent was obtained from all participants prior to taking part in the experiment. All volunteers were recruited from the UCL research subject pool. Volunteers were informed about the nature of the study and were aware that they would be presented with traumatic video clips. Participants in the study were paid and participants with a history of psychiatric or neurological disorders were excluded from the study.

4.3.1.3 Materials

4.3.1.3.1 Video clips

Stimuli consisted of 20 audio-visual video clips, each with a duration of 30 seconds and included recordings of real life events collected from video sharing websites or from realistic film scenes (see Appendix, Table A3 for a content list). The videos were emotionally negative clips involved traumatic scenes of varying types such as accidents, surgeries, attacks etc., and these videos had a graphic content. The videos partially overlapped with videos from the previous experiment but were adjusted to a duration of 30 seconds (Table A3). The validity of using the videos for this purpose came from pilot studies where volunteers gave subjective ratings of the clips (indicating subjective valence and arousal measures for each video; see below), confirming that participants found the emotionally negative clips distressing and disturbing. Each video had a title that was shown on the screen above the video. The videos were presented in a pseudo-randomised order. The videos were presented on a black background in a dark room to optimise viewing conditions. The corresponding audio to the videos was presented through headphones.

4.3.1.3.2 Working memory task

The working memory (WM) task consisted of a visual n-back task in which participants are shown single numbers (1-9) on a screen in a pseudo-randomised order. In the typical n-back, participants are required to attend to each number and make a response when the number on the screen matches the number in n positions backwards. We utilised a 0-back version of the task in which the numbers are presented in black font and participants must respond via key press when the number on the screen appears in a different colour. Hence, this task required sustained attention and hence actively engages the participants in the task, not allowing time to ruminate, rest or think about other things. Each number was presented for 1500 ms followed by an inter-trial interval consisting of fixation for 1000 ms. Participant were instructed to respond to the target stimulus as quickly as possible with the total time of the task being 10minutes.

4.3.1.3.3 Questionnaires

Trait and state anxiety was measured using the State-Trait Anxiety Inventory (STAI; Spielberger et al., 1983). Each of the scales comprised 20 items for assessing trait or state anxiety and participants rated all items on a 4-point scale, yielding a total score in the range of 20-80. Higher scores indicated greater anxiety. Positive and negative affect was measured using the PANAS (Positive Affect and Negative Affect Scales) questionnaire, yielding separate scores for positive and negative affect (Watson et al., 1988). Participants also filled out the Dundee Stress State Questionnaire (DSSQ), which assesses subjective stress state symptoms related to mood, motivation and cognition as well as assessing trauma-related thoughts (Matthews et al., 1999). Hence, this measure reflects the degree to which participants thought about the experimental trauma videos during the subsequent intervention with either wakeful rest or WM task.

4.3.1.3.4 Intrusion diary

Spontaneous memories were recorded using a diary. Spontaneous memories were defined as memories that either occurred with no apparent reason or memories that were triggered by environmental stimuli. In Experiment 4.1, a pen-and-paper diary was used and participants were instructed to report all video-related spontaneous memories in the diaries, with a different entry for each memory specifying 1) what they spontaneously remembered 2) in what situation the memory occurred and 3) which video the memory was related to. If participants had days with no spontaneous memories, they were still required to make an entry in the diary with a notification that they had not experienced any video-related spontaneous memories on that day. This was done to ensure that participants were compliant in carrying out the task.

4.3.1.4 Experimental protocol

4.3.1.4.1 Encoding

On arrival, participants were randomly assigned to one of the two experimental conditions (wakeful rest or working memory task) and completed the first parts of the STAI and PANAS (see above). Prior to the start of the encoding session, participants were instructed to watch the presented videos carefully but without actively rehearsing the material (Figure 4.1). They were also instructed to imagine that they were at the scene, watching the events unfold (similar to procedure in James et al., 2015). During encoding, participants watched a sequence of 20 emotionally negative videos separated by an ISI of 2 seconds where a white fixation cross was presented in the middle of the screen. Immediately after watching the videos, participants either sat quietly for 10 minutes (wakeful rest condition) or carried out a 10-minute 0-back task (working memory task condition). At the end of the session, participants completed the second part of the state anxiety questionnaires (STAI and PANAS) and the Dundee Stress State Questionnaire.

4.3.1.4.2 Intrusion diary

Participants were given instructions on how to fill out the diary and over the next 7 days, participants recorded memory intrusions detailing any video-related spontaneous memories.

4.3.1.4.3 Memory test

One week after encoding, participants returned and completed a recognition memory test. To test memory at follow up, 3 images were taken from each video clip giving a total of 60 images. Each image was a cropped section of the full scene viewed during a clip (e.g., a person or object from a scene) to increase difficulty. In addition, 37 new images were taken from clips showing similar events and used as foils. On each trial, one image was presented on the screen and participants were instructed to respond OLD if they recognised the image from one of the previously seen clips or NEW if they thought the image was not from the viewed clips.

4.3.1.4.4 Subjective video ratings

To assess how distressing participants found the videos, as the last task on follow up, participants carried out a task where they were presented with one picture from each video to cue them with the specific video in question. Participants were instructed to make two ratings for each video, based on how they remembered feeling when they first watched the video the week earlier. Participants indicated subjective valence and arousal ratings on a 7-point Likert scale, where each number was associated with an icon indicating the meaning of each number.

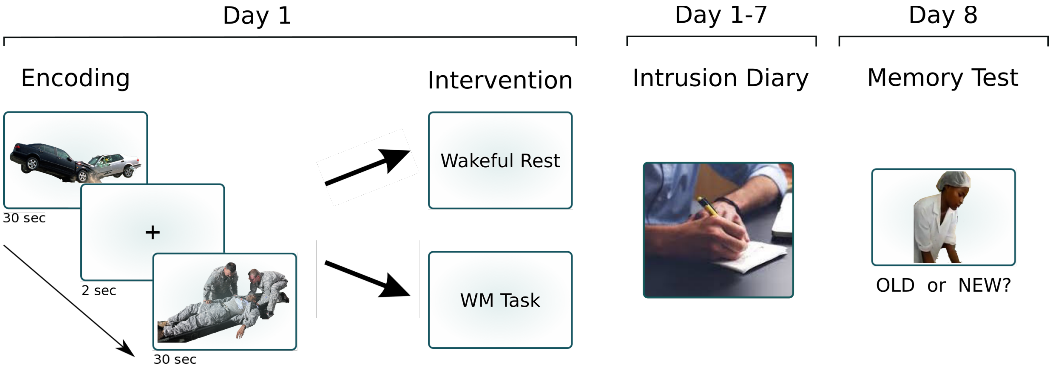

Figure 4.1. Experimental design for Experiment 4.1 and 4.2. During encoding, participants watched a sequence of videos and were assigned to either a wakeful rest group where participants rested for 10 minutes immediately following encoding, or to a working memory task (0-back task). Participants filled out diaries of memory intrusions related to the videos over the next week and returned for at memory test on Day 8.

4.3.1.4.5 Statistical analysis

Data from the trait anxiety questionnaire was analysed using an independent samples t-test to examine group differences. Self-report questionnaire data (STAI, PANAS) were analysed using mixed factorial ANOVAs with group as a between subjects factor and time as a within subjects factor. Similarly, intrusion data and recognition data were analysed with mixed factorial ANOVAs with memory test as a within-subject factor and group as a between-subject factor. Recognition performance was analysed by computing d’ values which takes both the number of hits (correctly recognised old videos) and false alarms (new videos identified as old) into account. All data were checked that they met assumptions of normality and where violated, a log transformation was performed prior to analyses. The alpha-level was set at 0.05.

4.3.2 Results

4.3.2.1 Subjective ratings

First, subjective ratings taken prior to and over the course of the experiment were analysed in order to compare the two groups (see Table 4.1 for a full breakdown of ratings). Analysis of trait anxiety scores showed no baseline differences between the wakeful rest and working memory group (t(38)=0.44, p=0.65, d=0.14, equal variances not assumed). Likewise, there were no differences between the two groups on global DSSQ scores (t(38)=0.41, p=0.69, d=0.13) or trauma-related component of the DSSQ (t(38)=0.35, p=0.73, d=0.11). State anxiety was analysed using a 2x2 mixed ANOVA with group as a between participants factor and time (pre-encoding, post-encoding) as a within participant factor. This showed main effect of time (F(1,38)=124.00, p<0.001, η^2=0.77) with an increase in state anxiety from before to after viewing the traumatic footage. Analysis showed no significant main effect of group (F(1,38)=2.04, p=0.16, η^2=0.05) or group x time interaction (F(1,38)=0.12, p=0.74, η^2<0.01).

PANAS scales measuring positive and negative affect before and after viewing the trauma videos were analysed using a 2x2 mixed ANOVAs with group as a between subject factor and time (pre-encoding, post-encoding) as a within subject factor. For the positive affect scale, this analysis showed a main effect of time (F(1,38)=44.83, p<0.001, η^2=0.54) with a decrease in positive affect scores after viewing the trauma videos compared to before viewing. There was no main effect of group (F(1,38)=0.31, p=0.58, η^2=0.01) or group x time interaction (F(1,38)=3.80, p=0.059, η^2=0.09. Analysis of negative affect also showed a main effect of time (F(1,38)=104.67, p<0.001, η^2=0.73), due to an increase in negative affect from before to after viewing the trauma film. The main effect of group was not significant (F(1,38)=1.10, p=0.30, $\eta^2=0.28$), nor was the group x time interaction (F(1,38)<0.001, p>0.99, $\eta^2<0.01$).

Table 4.1 Means (SD) of questionnaire measures of anxiety and affect during Experiment 4.1.

	Brief Wakeful Rest N=21		**Working Memory Task N=19**	
	Pre	**Post**	**Pre**	**Post**
Trait anxiety	41.0 (11.7)	n/a	39.5 (8.2)	n/a
DSSQ	n/a	18.50	n/a	18.10
State anxiety	30.4 (6.6	51.5 (12.9)	33.2 (6.1)	55.7 (11.9
Positive affect	29.4 (7.5)	25.2 (6.8)	29.9 (8.3)	22.3 (5.8)
Negative affect	11.8 (1.7)	22.4 (7.5)	13.2 (2.5)	23.8 (7.4)

4.3.2.2 Deliberate memory

Deliberate memory performance was assessed by calculating a d' value yielding a corrected score taking both hits and false alarms into account. An independent samples t-test showed no significant difference between wakeful rest and working memory task conditions on memory d' scores (t(36)=0.24, p=0.81, d=0.08. In addition, in the wakeful rest condition there was an increase in proportion of hits (t(36)=1.99, p=0.05, d=0.68) compared to the WM task. Interestingly, by visual inspection there was also a higher false alarm rate (t(36)=1.53, p=0.14, d=0.49 in the wakeful rest group but this effects did not reach significance.

Further, to directly assess differences between intrusive and deliberate memory, a mixed 2x2 ANOVA with memory test (intrusions, recognition memory) as a within-subject factor and group intervention (wakeful rest, working memory task) as a between subject factor revealed a significant test x condition interaction, F(1,36)=5.10, p=0.03, $\eta^2=0.124$, suggesting that the two interventions (wakeful rest and working memory task) had different effects on intrusive thoughts and recognition memory. The main effect of group was also significant, F(1,36)=4.39, p=0.04, $\eta^2=0.53$.

4.3.2.3 Memory intrusions

Firstly, the proportion of intrusions that could be matched to a specific video was 90%. The remaining intrusions were omitted from analysis, however intrusions that could not be matched to a specific video but were clearly associated with trauma films were still included as the study used a between-group design. The number of intrusive memories recorded over one week was compared for the two groups using a non-parametric test, as intrusions were not normally distributed. A Shapiro-Wilk test ($p<0.001$) revealed that the data was not normally distributed with skewness of 1.64 (SE=0.37) and kurtosis of 3.84 (SE=0.73). Hence, a log-transformation was carried out prior to further analysis. Analysis of intrusions showed a significant difference between groups ($t(37)=2.04$, $p<0.05$, $d=0.65$) with fewer intrusive memories reported in the brief wakeful rest group compared to the working memory task (Figure 4.2).

4.3.2.4 Relationship between subjective ratings and intrusions

We conducted an analysis where a correlation coefficient between subjective ratings (valence or arousal) and intrusions was calculated for each participant. These within-subject correlations were then converted into Z-scores using a Fisher's r-to-z transformation. A one-sample t-test carried out on the converted scores for all participants (groups collapsed) revealed that across participants, there was a very small but significant positive correlation ($r=0.09$) between the arousal ratings and the number of reported intrusions ($t(33)= 2.07$, $p=0.05$, $d=0.35$). The average correlation for valence ratings ($r=-0.63$) was not significantly different from zero ($t(33)=1.47$, $p=0.15$, $d=0.25$).

Another way of examining the relationship between subjective ratings and intrusions was to calculate, for each participant, a mean valence and arousal value for videos that intruded and for videos that did not intrude. A mixed 2x2 ANOVA with intruded/not intruded as a within-subject factor and group (wakeful rest or 0-back) as a between-subjects factor was then performed on these values. For the valence data, this analysis revealed a main effect of group, F(1,32)=4.62, p=0.04, η^2=0.12, reflecting that the wakeful rest group gave higher valence ratings than the 0-back group. The main effect of intrusion (F(1,32)=0.50, p=0.48, η^2=0.02) and the intrusion x group interaction (F(1,32)=0.29, p=0.61, η^2<0.01) were both non-significant. For arousal, the ANOVA analysis showed no significant main effect of group (F(1,32)=2.16, p=0.15, η^2=0.06). The main effect of intrusions was also non-significant (F(1.32)=3.83, p=0.06, η^2=0.11). The intrusion x group interaction was non-significant (F(1,32)=0.08, p=0.78, η^2<0.01).

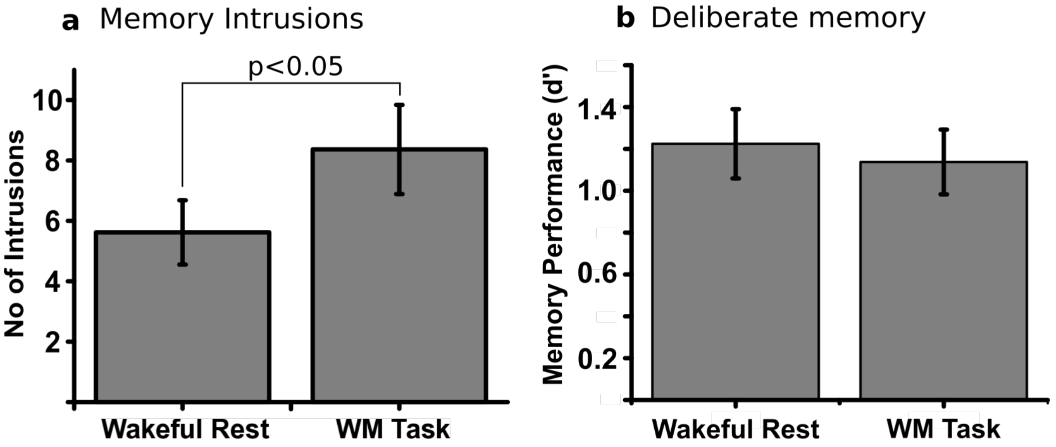

Figure 4.2. Mean number of intrusions and mean memory performance in Experiment 4.1. Mean (a) number of intrusions reported over 1 week and (b) memory performance (expressed as d') during the deliberate memory task at follow up across brief wakeful rest and working memory task groups. Bars represent standard error.

4.3.2.5 Relationship between intrusions and recognition memory

The relationship between intrusions and recognition memory was assessed with a bi-serial correlation and across the two groups, there was no significant correlation between the number of reported intrusions and performance on the recognition memory test (d'), r=0.20, p=0.28. This relationship was also assessed for the two groups individually but there was no significant correlation between memory intrusions and recognition memory for neither the wakeful rest group (r=-0.14, p=0.62) nor the 0-back group, r=0.41, p=0.10.

4.3.3 Discussion

The present study investigated intrusive and deliberate memory development following exposure to traumatic footage and specifically whether brief wakeful rest during the immediate aftermath of the footage would increase or decrease the number of intrusions experienced.

The main finding in this study was the effect of wakeful rest on memory intrusions. It was demonstrated that compared to the 0-back task, wakeful rest reduced reported frequencies of memory intrusions over the week following encoding. This finding is in line with other studies showing that trauma memory is malleable in a period following encoding, offering a potential window of intervention.

The finding suggesting a beneficial effect of wakeful rest on intrusion development highlight the critical importance of the specific nature of tasks used to modulate memory intrusions and argue against a ‘distraction’ hypothesis suggesting that any task that competes with the trauma memory for attention will reduce intrusions (Bourne et al., 2010). All things being equal, distraction should be greater in the 0-back task group than in the wakeful rest group, where participants in principle have time to ruminate over the trauma videos. According to the distraction hypothesis, the 0-back task should therefore produce fewer intrusions than wakeful rest but the current study shows the opposite pattern. In the study by Bourne et al. (2010), it was argued that the observed reduction of intrusions in the Tetris group was due to the nature of this visuospatial task, which would compete with trauma memory for sensory (visual) resources. From the viewpoint of the dual representation theory, our results are consistent with these findings: the DRT proposes that an imbalance in sensory and contextual representations will lead to intrusion development and both the Bourne (2010) study and the current study ameliorate this imbalance in different ways; in the case of Bourne et al. (2010) intrusions can be said to be reduced due to impairment of the sensory representation, leading to fewer intrusions whereas in the current study, intrusions might be reduced due to facilitation of contextual representations.

In contrast to our hypothesis, wakeful rest was not found to affect deliberate memory performance on a recognition memory test one week following encoding. This finding contrasts previous findings showing that rest following encoding of neutral stimuli is beneficial to subsequent memory retrieval (Dewar et al., 2009; 2012; Cowan et al., 2004; Müller and Pilzecker, 1900 in Lechner, 1999). Speculatively, the reason for this lack of statistical significance could be related to the pattern noticed by visual inspection, of numerically higher false alarm rates (and also higher hit rate) in the wakeful rest group compared to the working memory task group.

As this study showed that wakeful rest reduced intrusion development while deliberate memory performance was not affected, the results are to some extent consistent with the DRT, showing different effects of wakeful rest on deliberate memory and memory intrusions and demonstrating that these types of memory can be differentially modulated (Brewin et al., 2010). In contrast, the results contradict a unitary account proposing that increased consolidation would lead to facilitation of both deliberate memory performance and a higher number of reported intrusions (Rubin et al., 2008a; 2008b).

4.4 Experiment 4.2

Results from experiment 4.1 suggest that brief wakeful rest during the immediate aftermath of traumatic footage could reduce memory intrusions and had differential effects on intrusion development and deliberate memory. That is, individuals given 10 minutes of brief wakeful rest after watching the aversive clips reported fewer intrusive memories compared to those individuals given a simple working memory task to complete for 10 minutes. In contrast, deliberate memory for the footage tested 1 week later was not affected.

These findings provide initial evidence that brief wakeful rest could potentially benefit the consolidation processes and hence also contextual encoding in the aftermath of viewing traumatic footage to reduce intrusive memory experiences. Further, the finding that memory intrusions were reduced by wakeful rest while deliberate memory was not affected is in support of a dual representation view of intrusive memory development. Experiment 4.2 aimed to further explore these processes by adopting a within-participant design whereby participants performed both conditions (brief wakeful rest or 0-back (WM) task) on separate occasions. This was done to achieve a stronger design where the significance of individual differences was reduced.

4.4.1 Methods

For Experiment 4.2, all materials and procedure were the same as Experiment 4.1 except for the following additions or changes.

4.4.1.1 Sample size estimation

An effect size of d=0.65 in the intrusion analysis from Experiment 4.1 was used to estimate the required sample size in G*power 3.1 (Faul et al., 2007), yielding a required sample of 12 to enable an 80% power at $\alpha=0.05$. However a sample size estimation from the effect size of d=0.42 (transformed from $\eta^2=0.04$) from the analysis of deliberate memory indicated a required sample size of N=47 (80% power, $\alpha=0.05$).

4.4.1.2 Participants

A total of 42 healthy volunteers (35 females, mean age = 22.7 years, SD=4.38, range 18-35 years) took part. Participants gave written informed consent prior to taking part and were debriefed and paid at the end of the study.

4.4.1.3 Materials

4.4.1.3.1 Video clips

A total of 40 emotionally neutral and negative video clips were used as stimuli in Experiment 4.2. There was some overlap with previous experiment, see the Appendix, table A4 for a full list of videos, their duration and content.

4.4.1.3.2 Intrusion diary

Memory intrusions were recorded via a mobile phone app that participants downloaded when visiting the lab on day 1. This app was designed in house and incorporated the same elements as the paper and pen diary used in Experiment 4.1. That is, participants were instructed to report all video-related spontaneous memories in the diary with a different entry for each memory specifying the content of the memory and what video it was related to. Participants were instructed on how to use mobile dairy app on their phones were told to complete an entry whenever an intrusion occurred over following week. If participants had days with no spontaneous memories, they were still required to make an entry in the diary with a noting that they had not experienced any video-related spontaneous memories on that day. This was done to ensure that participants were compliant in carrying out the task. Each time a participant completes an intrusions entry, data from the app is automatically uploaded to an online database. For participants unable to download the app, a paper and pen diary was used.

4.4.1.3.3 Memory test

3-5 images from each video was prepared from each video clip yielding a total of approximately 80 test pictures (~40 neutral and ~40 negative) and ~40 foils (~20 negative, ~20 neutral; numbers vary slightly depending on the allocation of videos on the two sessions). Each image was a cropped section including a specific person or object from the entire scene, to increase difficulty. Foils were collected from other similar videos that were not included in the study.

4.4.1.3.4 Intrusion provocation task

In addition to recording intrusions through a diary, an intrusion provocation task was also used at follow up, equivalent to the task used in James et al. (2015). This task involves presenting participants with a blurred image taken from each video clip that was representative of that video (James et al., 2015). Images were blurred using a Gaussian Blur function (GIMP Software; Free Software Foundation, 2010) set at 40-70 pixels depending on the image, so that the features of the image could be vaguely distinguished. During the task, images were presented in a randomised order with each presented for 2sec. Immediately after viewing the blurred images, participants were instructed to sit quietly and relax for 2 minutes and, if they experienced any video-related spontaneous memories, were instructed to write down the memory on a sheet of paper.

4.4.1.4 Procedure

Participants were instructed to attend two full test sessions, with each session lasting 1 week.

4.4.1.4.1 Encoding

As this study used a within-subject design, each participant completed two encoding sessions with at least one-week interval arranged at a time convenient for the participant. For encoding, participants watched a total of 40 video clips over the course of two independent encoding sessions with 20 videos in each session. For each encoding session, participants watched 10 neutral and 10 negative video clips. In one session, the participant would have 10 minutes of wakeful rest following encoding and in the other session, participants would carry out a 0-back working memory task immediately following encoding. The order of the two sessions and which videos were presented with each condition was randomised. The procedure within the two sessions was the same as described in Experiment 4.1.

4.4.1.4.2 Intrusion diary

Participants downloaded the memory intrusion app at the end of the encoding session and used this to record memory intrusions. This part of the procedure was identical to Experiment 4.1.

4.4.1.4.3 Memory test

Participants completed two follow-up sessions. Each session comprised a recognition memory test where participants were presented with a randomised sequence of pictures on the screen and were instructed to respond with OLD or NEW, depending on whether they recognised the picture or not. There were approximately 60 trials in each test session.

4.4.2 Results

4.4.2.1 Questionnaires

First, changes in subjective ratings (see Table 4.2) elicited by viewing the traumatic footage were analysed. For the state anxiety measure (STAIS), a 2x2 repeated measures ANOVA with condition (brief wakeful rest, WM task) and time (pre-, post-encoding) as within participant factors showed a significant main effect of time ($F(1,28)=131.43$, $p<0.001$, $\eta^2=0.82$) with increase in anxiety from pre- to post-encoding. The main effect of condition, $F(1,28)=0.25$, $p=0.62$, $\eta^2<0.01$ and the time x condition interaction $F(1,28)=2.39$, $p=0.13$, $\eta^2=0.08$ were non-significant. A corresponding analysis on the positive PANAS scale also showed a main effect of time ($F(1,28)=18.73$, $p<0.001$, $\eta^2=0.40$), reflecting a decrease in positive affect from pre- to post-encoding. The main effect of condition was also significant ($F(1,28)=7.59$, $p=0.01$, $\eta^2=0.21$), which was due to higher positive affect scores in the wakeful rest condition compared to the 0-back condition. The condition x time interaction was non-significant ($F(1,28)=0.25$, $p=0.62$, $\eta^2<0.01$. For the negative PANAS scale, a corresponding 2x2 repeated measures ANOVA showed a main effect of time, $F(1,28)=46.57$, $p<0.001$, $\eta^2=0.63$, due to an increase in negative scores after encoding compared to before. The main effect of condition

(F(1,28)=0.08, p=0.78, $\eta^2<0.01$) and the condition x time interaction (F(1,28)=0.68, p=0.42, $\eta^2=0.02$) were both non-significant for the negative PANAS scale.

Table 4.2 Means for questionnaire measures of anxiety and affect during Experiment 4.2.

	Brief Wakeful Rest		Working Memory Task	
	N=47			
	Pre	Post	Pre	Post
Trait anxiety	39.90	n/a	n/a	n/a
DSSQ	n/a	15.76	n/a	14.16
State anxiety	30.58	49.63	35.07	49.78
Positive affect	30.36	26.81	28.29	23.97
Negative affect	13.83	20.27	13.65	21.44

4.4.2.2 Subjective ratings

As in Experiment 4.1, a mean subjective valence and arousal measure for intruding and non-intruding negative videos was calculated for each participant. Participants reported fewer intrusions in Experiment 4.2 compared to Experiment 4.1. Doing the appropriate test to assess these data – a 2x2 full factorial ANOVA with condition (wakeful rest or working memory task) and intrusive memory (intruded or non-intruded) as within-subject factors – would reduce the sample-size dramatically as most participants would report zero intrusions in at least one of the conditions.

Therefore, a mixed ANOVA was chosen to carry out analysis on the negative video data with intruded/not intruded as a within subject factor and treat the condition as a between group factor to enhance the sample size. For the valence data, this analysis revealed a main effect of intrusive memory, (F(1,39)=5.993, p=0.019, $\eta^2=0.133$), reflecting that participants rated the intruding videos as more sad than non-intruding videos. The main effect of group (F(1,39)=0.11, p=0.74, $\eta^2<0.01$) and the intrusion x group interaction (F(1,39)=0.19, p=0.66, $\eta^2=0.01$) were non-significant. Likewise, for the arousal data, there was a significant main effect of group (F(1,39)=4.247, p=0.046, η^2=0.098), due to participants giving higher arousal ratings for videos that intruded compared to those that did not intrude. The main effect of group (F(1,39)=0.003, p=0.954, η^2=0.003) and the Intrusion x Group interaction (F(1,39)=0.189, p=0.666, η^2=0.005) were both non-significant.

4.4.2.3 Deliberate memory

Deliberate memory performance (recognition) was first assessed using a 2x2 repeated measures ANOVA with emotion (neutral, negative) and condition (wakeful rest, working memory task) as within-subject factors. This analysis showed a significant main effect of emotion, F(1,39)=53.07, p<0.001, η^2=0.58, which was due to higher d' values for neutral videos compared to negative videos. The main effect of condition, F(1,39)=1.28, p=0.27, η^2=0.03 and the emotion x condition interaction F(1,39)=0.02, p=0.88, η^2=0.001 were not significant.

Further, a 2x2 repeated measures ANOVA with memory test for negative material (intrusions, recognition memory) and condition (wakeful rest, working memory task) as within-participant factors was carried out. This analysis revealed a significant test x condition interaction, F(1,35)=5.63, p=0.02, η^2=0.14, suggesting that the wakeful rest and working memory task interventions had different effects on intrusive memories and recognition memory.

An additional analysis of the false alarm (FA) data was conducted with a 2x2 repeated measures ANOVA with emotion (neutral, negative) and condition (wakeful rest, working memory task) as within-subject factors. This analysis showed a main effect of emotion, F(1,39)=44.26, p<0.001, η^2=0.53, reflecting that the FA rate was higher for negative items compared to neutral items. The main effect of condition, F(1,39)=0.14, p=0.71 η^2<0.01 and the emotion x condition interaction F(1,39)=0.12, p=0.73, η^2<0.01 were non-significant.

Likewise, a supplementary analysis of the hits (proportion correct) was conducted with a 2x2 repeated measures ANOVA identical to the one mentioned above. This analysis revealed a significant main effect of condition F(1,39)=4.20, p=0.05, $\eta^2=0.10$, which was due to a higher hit rate in the wakeful rest condition compared to the working memory task condition. The main effect of emotion F(1.39)=0.12, p=0.73, $\eta^2<0.01$ and the emotion x condition interaction F(1,39)=0.05, p=0.83, $\eta^2<0.01$ were non-significant.

4.4.2.4 Memory intrusions

Intrusion data from both the diary and provocation task was initially assessed and matched to videos presented at encoding, yielding a 90% match between intrusions and videos. The remaining videos were omitted from further analysis. As memory intrusions were recorded using the diary method over 1 week and at follow up using the provocation task (see Figure 4.3), intrusion data were analysed using a 2x2 repeated measures ANOVA with condition (brief wakeful rest, working memory task) and test (diary, provocation) entered as within participant factors. This analysis showed a significant main effect of condition (F(1,29)=5.68, p=0.02, $\eta^2=0.16$) due to significantly fewer intrusions in the brief wakeful rest condition compared to the working memory condition. There was no main effect of test (F(1,29)=2.69, p=0.11, $\eta^2=0.09$) and no condition x test interaction (F(1,29)=0.65, p=0.43, $\eta^2=0.02$).

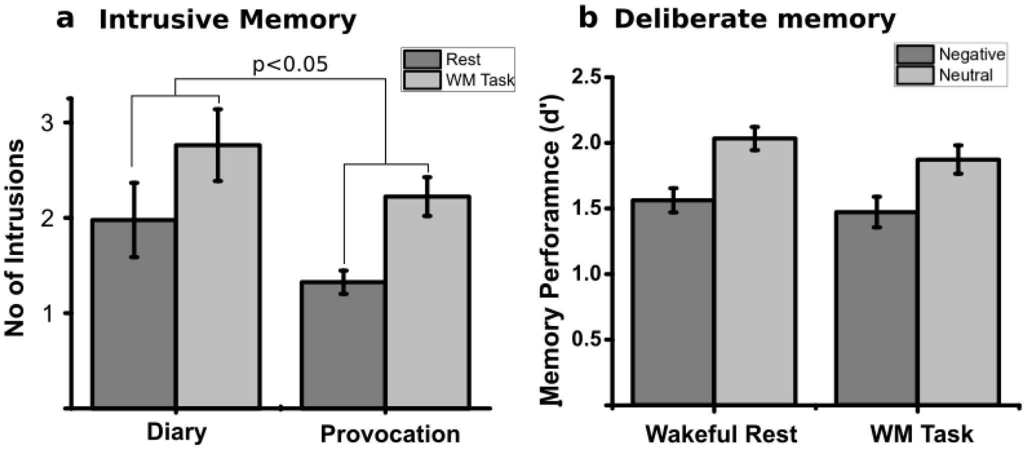

Figure 4.3. Intrusion and deliberate (recognition) memory results in Experiment 4.2. Mean (a) number of reported intrusions in the 7-week diary and the intrusion provocation task (Dark grey shows Wakeful rest and light grey shows working memory task) and (b) recognition memory performance (expressed as d') for neutral and negative items for each of the two task conditions of brief wakeful rest and working memory task. Error bars represent standard error. Dark grey shows Wakeful rest and light grey shows working memory task.

4.4.3 Discussion

This study used a within-subject design to study the effects of wakeful rest following encoding of negative and neutral video clips on intrusion development and deliberate memory performance.

For intrusions, wakeful rest resulted in a decrease in the number of reported intrusions in the week following encoding. Convincingly, the same pattern was present in the intrusion provocation task completed following encoding. The intrusion provocation task began with participants viewing blurred images from the videos, and the reduced frequency of intrusions in the wakeful rest condition could indicate that these intrusions are simply less likely to be triggered by environmental stimuli compared to those stemming from the session ending with a 0-back task. It is possible that stronger contextual encoding in the wakeful rest condition rendered intrusions from this condition less likely to be involuntarily retrieved. Taken together, the findings from the intrusion analyses confirm that there might be a window of opportunity for secondary prevention of cognitive PTSD symptoms in the early post-encoding phase following trauma.

Secondly, as in the previous experiment, wakeful rest was not shown to significantly affect deliberate memory performance compared to the 0-back condition. This finding is in contrast to previous accounts reporting facilitation of memory performance with wakeful rest (Dewar et al., 2009; 2012; Cowan et al., 2004). A higher hit rate was observed in the wakeful rest condition in this experiment compared to the 0-back task condition so this effect might be driven by subtle changes in the FA rate, but these differences did not reach significant so this relationship remains speculative.

Overall, participants showed better memory performance for neutral clips compared to negative clips. This finding stands in contrast to the wealth of studies demonstrating facilitated memory for emotionally negative or arousing stimuli (Hall and Berntsen, 2008; LaBar, 2007). However this finding is more consistent with studies proposing that certain types of memory may be impaired by negative emotion while others are enhanced (Anderson and Shimamura, 2005; Mather and Knight, 2008; Rimmelé et al., 2011; Madan et al., 2012).

Finally, the differential modulation of intrusions and deliberate memory performance support a dual representation account and speaks against a unitary account.

4.5 General discussion

The present study investigated intrusive and deliberate memory development following exposure to traumatic footage and specifically whether brief wakeful rest during the immediate aftermath of the footage would increase or decrease the number of intrusions experienced. Across two experiments, it was consistently shown that, compared to performing a working memory task, brief wakeful rest resulted in differential effects on intrusions and deliberate memory. That is, brief wakeful rest following viewing of aversive clips resulted in a reduction in the number of reported intrusive memories while deliberate memory was not affected and it was shown that the two interventions had different effects on intrusions and deliberate memory.

Across two studies, it was consistently shown that wakeful rest reduced the number of intrusions reported as part of the intrusion diary as well as those reported in an intrusion provocation task. Reduced intrusive memories following wakeful rest in combination with no impairments in deliberate memory suggests that consolidation of traumatic material might be beneficial to intrusive memory development. A potential mechanism underlying this effect could be that consolidation facilitates contextual representation encoding of the traumatic material, integrating the trauma with existing episodic memories in a flexible memory representation. Hence, consolidation would make the memory more alike other episodic memories and make the trauma memory less susceptible to being spontaneously triggered by emotional/environmental stimuli. Likewise, it is possible that the working memory task would block consolidation and contextual encoding of the traumatic material through retroactive interference (Dewar et al., 2007).

Interestingly, whilst it is shown that brief wakeful rest can influence consolidation to reduce memory intrusions compared to carrying out a task, other studies have demonstrated that performing a visuospatial task during this period can also *reduce* intrusions (Holmes et al., 2009; Deeprose et al., 2012). Our findings may seem at odds with these results given that we saw more intrusions when participants performed the working memory task after encoding. It is possible the visuospatial task introduced competition for perceptual resources, thereby reducing 'consolidation' of the perceptual representation of the traumatic material. We suggest that the 0-back task used in this study impaired consolidation of episodic memory through retroactive interference, thereby allowing relative strengthening of the emotional/perceptual representation. That is, the effect of wakeful rest vs. 0-back task on intrusion development does not appear to be due to distraction, where participants are prevented from consciously thinking about the video contents in the 0-back conditions. Rather, it appears that it is the specific lack of rest, thought to enhance processing of the memory outside conscious control (so-called offline processing).

To recap on the previous outlined hypotheses, if both types of memory had been enhanced by wakeful rest (that is, changed in the *same* direction), this would indicate that they are part of the *same* memory system and therefore increasing of one type of memory (e.g. intrusions) will also increase the other type of memory (e.g. deliberate memory). This hypothesis is consistent with the unitary account, suggesting that memory intrusions and deliberate memory are produced from the same memory system and therefore enhancing one will also enhance the other. In contrast, if an intervention such as wakeful rest would result in *opposite* effects on memory, that is, one memory type (deliberate memory) will being increased while the other (intrusions) would be decreased, this would suggest that the same manipulation would cause *different* effects on the two memory systems, indicating that the two forms of memory rely on *different* neural systems.

The observed differential effects of wakeful rest on memory intrusions and deliberate memory in the studies presented in this chapter are largely in line with a dual representation account of memory and contrasts a unitary account. The DRT proposes that intrusive re-experiencing of traumatic experiences arise as a result of an imbalance during encoding between the formation of contextual and affective/perceptual representations of the traumatic event. In this view, memories can be encoded in two different representational modes, where one supports ordinary episodic memory and provides a flexible, contextually based representation that can be consciously accessed and integrated with other memories and information. In contrast, the other type of memory representation comprises lower-level perceptual and emotional information about an experienced event that is poorly integrated with existing memories. As mentioned in the introduction, the DRT proposes that intrusive memories arise following a traumatic event because these memories to a higher extent will be encoded as the lower-level representation and hence lacks the contextual integration and deliberate control supported by the contextually based representation. This account predicts that deliberate memory and intrusive memory will be modulated in opposite directions. This was not found the current studies as deliberate memory was unaffected but nevertheless, it was found that interventions differentially affected memory intrusions and deliberate memory, which is consistent with previous findings (Krans et al., 2009).

In contrast, our results do not support a unitary account of memory formation proposing that deliberate memory and memory intrusions are based on the same memory representation and will therefore be modulated in the same direction by any intervention that modulate memory (Berntsen and Rubin, 2014).

In PTSD, patients experience vivid memory intrusions (flashbacks) that are characterised as being highly emotional, perceptually rich and patients report feelings of reliving the trauma in the present during flashbacks (DSM-V, Brewin et al., 1996). If these flashbacks arise as a result of a relative strengthening of emotional/perceptual representations compared to contextual representations, this could explain why these memories are easily triggered by perceptual or emotional cues, giving rise to the experience of flashbacks. Another result of the impaired contextual encoding is that deliberate recall for the traumatic event may be poor and fragmented, although this topic is the subject of continuous debate (Harvey and Bryant, 1999; Ehlers and Clark, 2000; Rubin et al., 2008a; 2008b; 2016; Brewin, 2016). Our results are largely consistent with this notion of cognitive symptomatology in PTSD, although the facilitation effect of wakeful rest on deliberate memory was absent when false alarm rates were taken into account (d').

The recommended first-line treatments in PTSD are psychotherapy interventions focusing on imaginal or *in vivo* exposure to the traumatic event and elaboration of the traumatic event (NICE). These interventions include trauma-focused therapy, prolonged exposure therapy and imagery re-scripting (Foa et al., 1998; Cooper and Clum, 1989). Hence, a critical component is to further process memory of the trauma and incorporate the traumatic event within episodic memory. This strategy is consistent with the dual representation theory and our results, as rest is known to strengthen memory consolidation and memory processing. Furthermore, a recent study has highlighted the critical role of the hippocampus in the treatment response, showing that PTSD patients with larger hippocampal volumes responded more positively to trauma-exposure treatment (Rubin et al., 2016). Although other factors may also interfere with these processes, our results suggest that strengthening episodic memory consolidation following trauma might be beneficial.

In conclusion, our results favour a dual representation account of emotional memory, demonstrating that episodic and intrusive memory systems can be manipulated independently. Furthermore, our results can contribute to furthering the mechanistic understanding of why psychotherapeutic interventions that enhance processing of the trauma successfully reduce memory intrusions.

5 THE ROLE OF NEURAL PERI-AND POST-ENCODING PROCESSING IN INTRUSION DEVELOPMENT AND DELIBERATE MEMORY RECALL

5.1 Overview

As shown in previous chapters, the period following a traumatic event seems, at least in some instances, to be an important window in predicting deliberate memory accuracy and the development of intrusive memories. As outlined in Chapter 1, studies also demonstrate that the period of encoding is influential in contributing to memory alterations in deliberate memory and memory intrusions (e.g. Holmes et al., 2004; Bourne et al., 2010). Recently, a small number of studies have examined changes in neural activity during encoding of traumatic scenes and retrieval of spontaneous imagery. However, it still remains unclear how specific brain regions might alter encoding and post-encoding processes of traumatic scenes to support subsequent intrusive memory re-experiences. The aim of this final experiment was to examine how changes in neural activity during both encoding and post-encoding processing of experimental traumatic events might contribute to intrusive memory development and changes in subsequent deliberate memory recall for the events.

5.2 Introduction

The period following a traumatic event is believed to play a role in PTSD symptoms over the long term. Accordingly, attempts to offer preventive interventions aimed to reduce development of PTSD are often offered following the traumatic experience. For example, psychological debriefing interventions in the immediate aftermath of a traumatic event have been used widely to help victims following trauma (McNally et al., 2003). Although studies have shown that these interventions might in fact exacerbate subsequent adverse reactions to the trauma (Mayou et al., 2000) this only demonstrates that processing in the immediate aftermath of a trauma is a crucial factor and is fragile to external influences.

Experimental studies have established that the time during encoding of emotionally negative events is important to subsequent memory intrusions. For instance, studies using the trauma paradigm (described in Chapter 1.2.5) generally demonstrate that a visuospatial task (such as the computer game Tetris, modelling clay or complex finger tapping) administered during encoding reduces the number of subsequent memory intrusions (Bourne et al., 2010; Krans et al., 2009; Holmes et al., 2004;

Logan and O'Kearney, 2012). In contrast, carrying out a verbal task (e.g. counting backwards in threes) during encoding has been shown to increase the number of subsequent intrusions (Bourne et al., 2010; Krans et al., 2009; Nixon et al., 2007). Likewise, studies investigating neutral deliberate memory have shown that carrying out a task during encoding can impair subsequent memory performance due to divided attention. For instance, Craik et al. (1996) showed that carrying out a distracting task while encoding information impaired subsequent recognition, cued recall and free recall memory performance. For emotionally negative material, deliberate memory have been assessed along with studies investigating memory intrusions. These studies showed more mixed results for deliberate memory, with some showing an effect of peri-traumatic manipulations (Bourne et al., 2010; Krans et al., 2009; Holmes et al., 2004) while others found no effect (Das et al., 2016; Krans et al., 2010). Taken together, these studies demonstrate that modulating processing during trauma film encoding plays an important role in how the 'event' is subsequently remembered.

Theories on memory consolidation also implicate the time *following* encoding of an event as critical in memory formation. In relation to memory intrusions, several studies have shown that manipulating processing after encoding of a trauma film can affect the subsequent number of reported intrusions (Deeprose et al., 2012; Holmes et al., 2009; Das et al., 2016). Many of these studies used designs similar to the studies investigating intrusions and the relationship with peri-traumatic processing and have shown that intrusion development can be affected by tasks carried out immediately after encoding (Deeprose et al., 2012) and 30 minutes post-encoding (Holmes et al., 2009; Deeprose et al., 2012; Green and Bavelier, 2003).

Furthermore, a recent study tested the use of a visuo-spatial task in preventing memory intrusions in people who had just been exposed to trauma (traffic accidents) and found that carrying out a visuospatial task in the aftermath of the traumatic experience did indeed reduce memory intrusions for real-life events (Iyadurai, et al., 2017).

These findings are consistent with studies showing that neural processing both during and after an event influences subsequent memory. For neutral information, studies have found that spontaneous post-encoding fluctuations in neural activity during rest are similar to activity patterns during encoding. It is believed that this reinstatement is comparable to the post-encoding replay processes observed in animals, which are believed to reflect memory consolidation (Bird et al., 2015; Staresina et al., 2013; Tambini et al., 2010; Tambini and Davachi, 2013, Foster and Wilson, 2006; Marr, 1971; McClelland et al., 1995, Ben-Yakov et al., 2011, 2013).

Staresina et al. (2013) investigated post-encoding offline processing of learned information in a study where participants were presented with object-scene pairs during encoding followed by an active delay period in which participants carried out an odd/even number judgement task. This period was immediately followed by a source memory test, in which participants were cued with either an object or a scene presented during encoding and were instructed to retrieve its paired associate. Findings from this study showed that spontaneous offline reinstatement of activity in the entorhinal cortex in the MTL and in the retrosplenial cortex that was present during encoding of an object-scene pair predicted whether or not the pair was subsequently retrieved in the memory test.

In a more recent study, Bird et al. (2015) demonstrated that the above findings could be extended to include naturalistic scenes. In this study, participants were presented with a series of short audio-visual video clips and were subsequently asked to actively rehearse silently most of these videos while still in the MRI scanner, while some were used as controls with no rehearsal. Analysis of these data showed that rehearsed videos were remembered better than videos that were not rehearsed and that the similarity in neural activity in the posterior cingulate cortex between encoding and rehearsal predicted subsequent memory performance on a free recall test (Bird et al., 2015). Similarly, Ben-Yakov et al. (2011) showed that hippocampal and caudate nucleus activity time-locked to the offset of an audiovisual video clip correlated with subsequent memory performance for gist in the scenes, suggesting that the offline activity might play a role in memory formation, perhaps by binding together the individual elements of the video clips over time (Ben-Yakov et al., 2011).

Taken together, these studies show that increases in pattern similarity between encoding and post-encoding phases as a result of either conscious rehearsal or offline processing predict subsequent memory performance for both object scene pairs and naturalistic information (Staresina et al., 2013; Bird et al., 2015; Tambini and Davachi, 2013)

Recently, studies have begun to elucidate the neural correlates of intrusion development. Bourne et al. (2013) conducted the first prospective study investigating the neural basis of intrusive memory formation. Here, participants encoded emotionally negative videos while in the MRI scanner and activity during encoding was subsequently matched with scenes that intruded, potential intruding scenes (scenes where others had intrusions but not the participants) and control scenes. This study found that intruding scenes were related to increased neural activity in a wide range of regions such as the amygdala and anterior cingulate cortex (ACC). Both of these regions are known to be involved in processing of negative emotion, including a critical role of the amygdala in fear memory (Davis, 1992) and a role of the ACC in self-regulation of emotion and threat perception qua the role of the ACC in error and conflict detection (Allman et al., 2001; Kalish et al., 2005; Carter et al., 1998). Furthermore, comparing encoding activity for intruding scenes and potential scenes showed an increase in activity in the left inferior frontal gyrus and in the bilateral middle temporal gyrus for intruding scenes (Bourne et al., 2013). In a more recent study by Clark and colleagues (2016) another imaging phase of the above study was added immediately after encoding where participants reported spontaneous memory intrusions for the scenes they had just encoded, allowing the investigation of neural signatures of both encoding and retrieval of intrusive scenes. Consistent with the study by Bourne et al. (2013), this replicated their finding of increased encoding activity in the left inferior frontal gyrus for subsequently intruding scenes. Moreover, this study showed that this structure is also involved in the involuntary retrieval of the traumatic scenes (Bourne et al., 2013). Hence, both of these studies indicate a role of activity in the inferior frontal gyrus (IFG) during encoding for subsequent intrusions, and more generally demonstrate the use of the experimental trauma paradigm in neuroimaging studies. The left IFG is involved in sentence comprehension and semantic processing, indicating a role for this structure in verbal and conceptual processing of information (Friederici et al., 2003). This finding is consistent with unitary accounts of trauma memory, proposing that memory intrusions arise as a result of particularly strong encoding and rehearsal (Rubin et al., 2008a; 2008b).

The studies by Bourne et al. (2013) and Clark et al. (2016) investigated the role of neural activity during encoding in subsequent memory intrusions. However the relationship between post-encoding neural activity and subsequent memory intrusions is unknown. Hence, this chapter aimed to investigate the role and neural correlates of both peri- and post-encoding in relation to subsequent memory intrusions. Furthermore, this study builds on studies investigating the role of post-encoding processing to subsequent deliberate memory performance and investigates if previous findings generalise to include emotionally negative information.

For this study, the following analyses were planned: 1) GLM analyses of intruding versus non-intruding videos and also of remembered versus forgotten videos. 2) Fit finite impulse response models to the data to include a time series analysis which allows for more detailed analysis of neural responses to the presented stimuli and 3) an RSA analysis which allows the comparative analysis of the similarity of activity patterns in the encoding and subsequent 30 sec rest phases. The latter two analyses were planned but were not included in this thesis.

Hypotheses for the GLM analyses were formulated based on previous empirical studies investigating intrusion development and on theory-driven hypotheses in terms of the dual representation theory and on unitary accounts of intrusion development outlined in previous chapters. Based on the unitary account, it would be expected that intruding clips and remembered clips would both be associated with greater amygdala and hippocampal activity than non-intruding and forgotten clips as both memory types would depend on hippocampal processing and be facilitated by increased amygdala activity.

In contrast, from the dual representation theory it could be predicted that remembered video clips would be associated with greater hippocampal activity compared to forgotten clips, and this contrast was not expected to be significant for intruding versus non-intruding clips. Conversely, intruding clips would be associated with more amygdala activity than non-intruding clips and this contrast was not expected to be significant for remembered versus forgotten clips.

Also, based on previous experiments investigating intrusion development (Bourne et al., 2013; Clark et al., 2016), it was expected that intruding clips would be associated with greater activity in the amygdala and the ACC. The present study did not distinguish between intruding and potential scenes, but as a wide range of videos intruded across participants, it was also expected that intruding scenes would be associated with greater activity in the left inferior frontal gyrus and in the bilateral middle temporal gyrus.

5.3 Methods

5.3.1 Sample Size

The sample size for the current study was based on previous fMRI studies investigating neural mechanisms underlying intrusion development (Clark et al., 2016; Battaglini et al., 2016).

5.3.2 Participants

Forty volunteers (25 females) aged 20-45 years (M=25.1, SD=5.9) were recruited for the experiment. Six participants were excluded from fMRI analyses due to drop out or excess head movement, falling a sleep or closing their eyes during the experiment. The study took place at the Wellcome Trust Centre for Neuroimaging at University College London. The experimental protocol was approved by the University College London Research Ethics Committee and written informed consent was obtained from all participants prior to taking part in the experiment.

Volunteers were recruited from the UCL research subject pool and had no history of psychiatric or neurological disorders.

5.3.3 Materials

5.3.3.1 Stimuli

Thirty audio-visual video clips were used for the study with varying degrees of valence and arousal but with the majority of videos categorised a negative in content. Each video had a duration of 30 seconds. The videos were collected from video sharing web sites or taken from realistic film scenes, there was high overlap with videos from experiments presented in previous chapters, in particular Experiment 4.1 and 4.2 (but see Appendix table A5 for a full content list). Hence, the majority of videos were distressing in content and included scenes of serious injury and death in car accidents, attacks etc. The emotionally neutral videos included scenes of everyday events such as people shopping or meeting for a coffee. The validity of using these videos in an experimental trauma paradigm was based on my pilot studies where volunteers gave subjective ratings of the video clips, confirming the distressing and disturbing nature of the video clips.

5.3.3.2 Intrusion diary

The procedure for recording memory intrusions was the same as the second wakeful rest study where a mobile phone app was used to record memory intrusions. For each entry in the electronic diary, participants were able to write a description of the memory intrusion and gave ratings of how vivid and distressing the memory had felt. The electronic diary would give reminders to participants once a day to help them remember to fill in the diary. For a small number of participants it was not possible to download the app and therefore these participants used a pen and paper diary instead.

5.3.3.3 Memory test

4 pictures from each video were prepared for the recognition memory test. Each picture was a cropped section from a video scene, depicting a single object, person or detail from a video presented at encoding. Foil pictures included pictures taken from videos not presented at encoding. In total, there were 120 test pictures and 60 foil pictures.

5.3.3.4 Subjective Ratings

For the subjective ratings task, participants were presented with a picture on the screen depicting a central aspect of a given video. When the participant had retrieved which video the picture referred to, they pressed a key and were then presented with two ratings below the screen. The first rating was a subjective valence rating where participants indicated on a 7-point Likert scale ranging from 1 (very sad) to 7 (very happy) how the video in question had made them feel during encoding. Likewise, following the valence rating participants completed an arousal rating for the video, indicating on a 7-point Likert scale ranging from 1 (calm) to 7 (very excited) how they had felt during encoding of the video.

5.3.4 Procedure

5.3.4.1 Encoding

Participants were thoroughly instructed about the nature of the study prior to taking part in the study. In the scanner, participants watched the videos, which were projected onto a screen behind the participant and presented to the participant via a mirror placed on top of the head coil. Audio was delivered through fMRI-compatible headphones. The general viewing instructions was identical to those described in the video experiments in Chapter 2, 3 and 4. Each video was followed by a rest period of 30 seconds where participants would see a blank grey screen. Participants were instructed to rest with their eyes open and without manipulating what came to mind during this period of wakeful rest. Each rest period was followed by an ITI initiated with a beep tone and a black fixation cross was presented on the centre of the grey screen for a jittered duration of 2-8 seconds before the start of the next video.

5.3.4.2 Intrusion diary

At the end of the first session, participants were given instructions on how to use the memory intrusion app and downloaded the app on their mobile phones. Participants were instructed to report all video-related memory intrusions in the diary with a new entry for each memory. Participants specified the content of each memory and the video it was related to. If participants had days with no memory intrusions, they would make a diary entry noting that they had not experienced any intrusions on that day. This was done to ensure that participants were compliant in carrying out the task. Data from the memory intrusion app was automatically uploaded to an online database. Upon arrival for the second session, any disambiguous intrusions were discussed with the experimenter to ensure that the matching between intrusion and video was correct. This process was similar to the method used by Bourne et al. (2013).

5.3.4.3 Memory test

One week after encoding, participants returned to complete a memory test and subjective ratings of the videos. During the memory test, participants were presented with a randomised sequence of test and foil pictures on the screen and for each trial they judged whether they recognised the picture and responded with ‘Old’ or ‘New’. Following the memory test, participants also made subjective ratings of the videos they had seen the week before.

5.3.4.4 fMRI data acquisition

All MRI data was acquired using a 32-channel head coil on a 3T Trio Magnetom Siemens (Erlangen, Germany) scanner at the Wellcome Trust Centre for Neuroimaging. Participants initially had a high-resolution structural scan, where a T1-weighted 3D MDEFT structural image (1 mm^3) was acquired to co-register function data. Functional images were acquired using a T2*-weighted gradient-echo echo-planar imaging (EPI) sequence with the following parameters: repetition time (TR), 3360 ms; echo time (TE), 30 ms; slice thickness, 2 mm, inter-slice gap, 1 mm, in-plane resolution, 3 x 3 mm, field of view, 64 x 72 mm^2, 48 slices per volume. Slices were tilted 45° up at the front and acquired in an ascending order. A field-map using a double echo FLASH sequence was recorded for distortion correction of the acquired EPI (Weiskopf et al., 2006).

5.3.4.5 fMRI data analysis

Pre-processing and data analysis was carried out using SPM 8 (www.fil.ion.ucl.ac.uk/spm). The first 6 EPI volumes from each session were discarded to allow for T1 equilibration. EPI images were bias-corrected to adjust for local within-volume signal intensity differences. The EPI images were then unwarped, realigned to correct for head movement and slice time corrected. Both EPIs and MDEFT images were spatially normalized to MNI space by estimating a warping from each participant's structural image to a T1-weighted average template image and applying the resulting transformation to the EPIs. Finally, the normalised EPI images were spatially smoothed using an isotropic 8 mm FWHM Gaussian kernel.

BOLD responses were estimated using three separate general linear models (GLM) to examine subsequent intrusive memories and recognition memory. For each model, regressors were temporally convolved with the hemodynamic response function in SPM8. Six regressors corresponding to motion parameters obtained during the realignment procedure were included as regressors of no interest. Single subject parameter estimates from each condition taken from the first level were included in subsequent random effects analyses. For second level analyses, effects of interest were analysed using factorial analysis of variances (ANOVAs).

Encoding activity relating to subsequent recognition memory performance was first examined. As some participants did not fulfil all experiment conditions for this analysis (e.g., zero misses due to all clips being successfully remembered), they were omitted from the analysis (final analysis N=27). To analyse recognition memory performance, five regressors were created for (1) viewing clips that were subsequently recognised (videos with at least a score of 1), (2) rest periods following correctly recognised clips, (3) viewing clips that were subsequently forgotten, (4) rest periods following clips that were later forgotten and (5) ITI.

A second analysis of neural activity and recognition memory performance was carried out using parametric modulators for the videos' recognition scores (ranging from 1-4; N=32). Hence, five regressors were created for (1) viewing clips, (2) rest periods, (3) ITI, (4) parametric modulator for recognition memory scores for viewing and (5) parametric modulator for recognition memory scores for rest periods immediately following video clips.

Participants reporting zero intrusions during the week after encoding were omitted from the intrusive memory analysis (yielding N=29 for analysis). To assess intrusions, activity at encoding was examined by creating regressors for (1) viewing clips that later intruded, (2) rest periods immediately following clips that intruded, (3) viewing clips that subsequently did not intrude, (4) rest periods following clips that did not intrude and (5) ITI. Data from each model were analysed at the second level using a 2 x 2 ANOVA (memory, period). As videos used in the current experiment were quite short (30s) and generally only comprised a single central event, it was not relevant to match each intrusion to a specific time sequence within each video as it has been done in previous studies (e.g. Bourne et al., 2013).

5.4 Results

5.4.1 Behavioural results

5.4.1.1 Subjective ratings

Participants' subjective ratings for each video were recorded and participants gave an overall mean valence rating of 2.61 (SD=0.49). For arousal, participants gave a mean rating of 3.79 (SD=1.03). Hence, these results indicate that on average, participants found the videos sad and arousing.

5.4.1.2 Memory

Prior to analysis, each intrusion was matched to a video: this procedure yielded a match of 95% and the remaining 5% of intrusions were omitted from further statistical analysis. On average, participants reported 5.18 intrusions (SD=4.60, Md=5) over the seven days. For recognition memory, participants scored an average score of .57 (SD=0.13) reflecting the total proportion of recognised images out of the total number of old pictures. There were no relationship between recognition memory and intrusions, r=-0.10, p=0.57 or between recognition memory and subjective ratings for arousal (r=0.07, p=0.73) or valence (r=0.-16, p=0.42).

5.4.2 fMRI results

fMRI data were analysed by identifying regions where changes in activity were predictive of intrusion and recognition memory. For results outside the hippocampus, results are reported corrected for family-wise error (FWE) at $p < 0.05$ across the whole brain unless otherwise stated (Friston et al., 1994). Given the a priori hypotheses (that remembered items are associated with more hippocampal activity), separate masks were created for the bilateral hippocampus, amygdala and MTL using the WFU PickAtlas toolbox, with hippocampal and MTL regions defined from the Automated Anatomical Labelling atlas (AAL; REF).

5.4.2.1 Recognition memory

Recognition memory was analysed by contrasting periods during clip encoding (viewing) and post-encoding (rest) for clips subsequently recognised at test (that is, clips with a score of 1 or above) with the same periods of viewing and resting for clips later forgotten. A clip was scored as correctly recognised if a participant correctly recognised any one of the three recognition trials for that particular clip during test, whereas forgotten clips were categorised when a participant did not recognise any of the recognition trials. Looking for areas during encoding responsive to viewing clips (viewing > rest) irrespective of whether they were recognised or forgotten, showed greater activity in a broad range of areas along the ventral and dorsal visual streams, superior temporal gyrus (p<0.05 FWE) and bilateral amygdala ($p<0.05$ FWE SVC; see Figure 5.1A and the Appendix, Table A6). The reverse contrast of rest periods versus viewing periods revealed no regions of interest.

Next, encoding activity for clips subsequently recognised at test was contrasted with activity for clips forgotten, irrespective of viewing or rest periods. This analysis showed greater activity in the right entorhinal cortex (see Figure 5.1B and Supplementary table A7; $p<.05$ FWE SVC), left angular gyrus, vmPFC, left superior frontal gyrus and middle temporal gyrus ($p<.001$ uncorrected). The reverse contrast showed no regions of interest nor did the interaction analysis.

Given that the memory test comprised four questions for each viewed clip, a parametric modulator was created that reflected the score for each video, ranging from 0-4. A second analysis of the recognition memory data was then performed using a parametric modulator for recognition memory scores, rather than the remembered/forgot dichotomy. A one-sample t-test performed on these data across the whole brain showed greater activity in the bilateral hippocampus ($p<.05$, FWE) for higher scores (Figure 5.2. Other areas included the left ACC, left inferior frontal gyrus (pars triangularis) and the right precuneus (see also Supplementary table A8)

In summary, a large network along the ventral and dorsal streams showed greater activity during video presentation compared to rest. For remembered videos, there was greater activity in the right entorhinal cortex, left angular gyrus, left superior frontal gryus and middle temporal sulcus, compared to forgotten videos. Also, the analysis using a parametric modulator for recognition memory scores showed an effect in the bilateral hippocampus, left ACC and right precuneus.

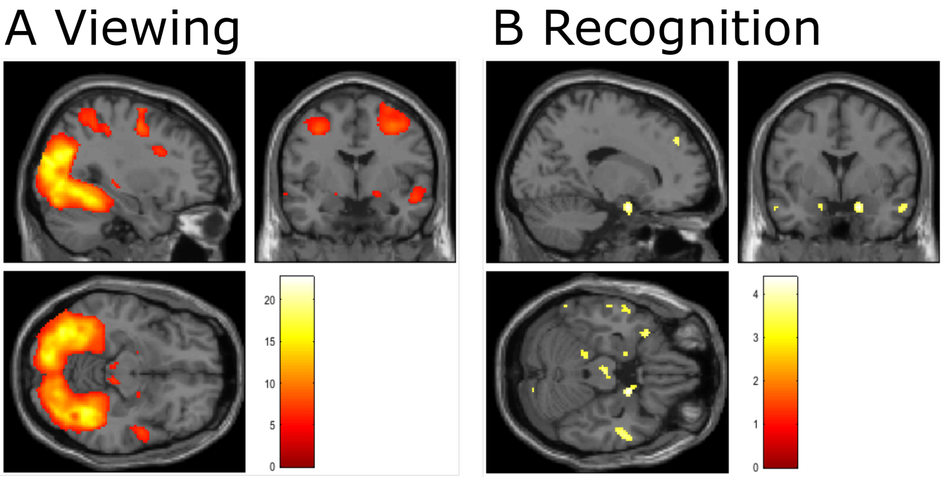

Figure 5.1. Encoding activity for viewing and recognition in Experiment 5. (A) Encoding activity for View > Rest, showing activity in visual areas at P<0.05 FWE. (B) Encoding activity showing subsequent memory effects for Remembered > Forgotten across view and rest in several areas including the entorhinal cortex at p<0.001 uncor.

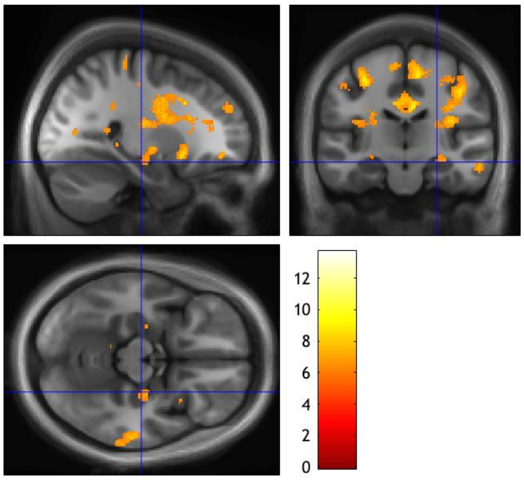

Figure 5.2 Encoding activity for recognition performance applied as a parametric modulator in Experiment 5. Encoding activity showing that greater activity in a large network including the bilateral hippocampus was associated with higher scores on the recognition memory test at P<0.05 FWE.

5.4.3 Memory intrusions

Assessing regions that showed more activity during clip encoding (viewing) compared to post-encoding (rest) periods irrespective of whether the clip later intruded or not (view > rest), greater activity was observed in a broad range of areas, similar to what is described above for recognition memory.

To examine memory intrusions, activity when viewing each clip and during the rest period immediately after each clip were analysed by contrasting clips that intruded with those that did not later intrude. For clips that later intruded (intruded > non-intruded; irrespective of viewing or resting periods), analysis showed greater activity in an area of the left amygdala ($p<0.05$ FWE SVC) and also in the right amygdala at a more lenient threshold ($p<0.005$ uncorrected; see Figure 5.3 and the Appendix Table A9). The reverse contrast (non-intruded > intruded) showed no areas of interest.

Finally, this analysis revealed an interaction (view vs rest x intruded vs non intruded) with greater activity in the right insula, right inferior parietal lobule and dorsal medial prefrontal cortex when viewing clips that intruded (view: intruded > non-intruded), a difference that was greater than during the rest period (rest: intruded > non-intruded; $p<0.001$ uncorrected).

In summary, a broad range of areas along the ventral and dorsal visual streams showed greater activity when viewing clips compared to rest periods following each clip. For clips that later intruded, analysis found greater activity in bilateral amygdala irrespective of viewing or rest periods associated with each clip. Further, dmPFC, insula and parietal areas were found to correlate with intrusions specifically during viewing clips.

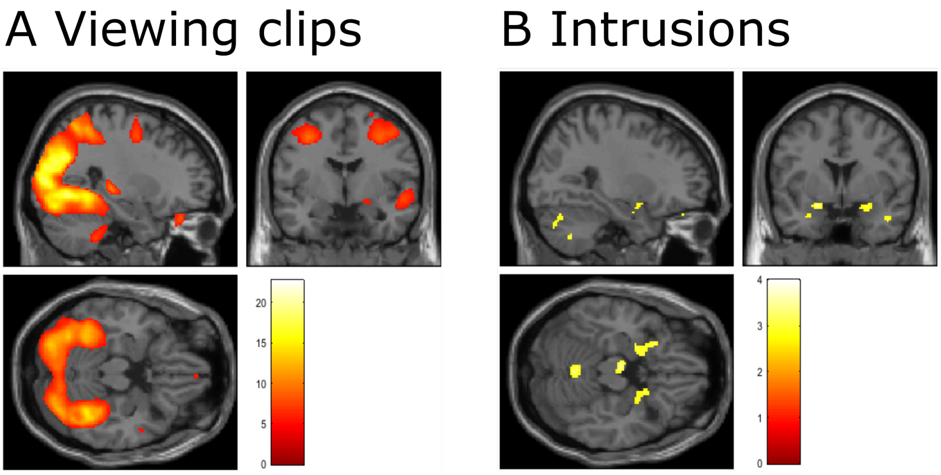

Figure 5.3. Encoding activity for viewing and intruding videos in Experiment 5. Encoding activity showing view > rest (A) and subsequent effects on intrusions across view and rest (B). (A) showed enhanced activity in occipital areas and along ventral and dorsal streams at P<0.05 FWE across the whole brain. (B) showed greater activity in the left amygdala for intrused > non-intruded.

5.5 Discussion

Understanding the role of encoding and post-encoding processing in trauma memory and the neural structures that might contribute to these processes is important to developing new interventions for PTSD, in particular for those targeting secondary prevention of cognitive PTSD symptoms. The current study investigated the neural mechanisms underpinning peri- and post-encoding processing in relation to subsequent memory intrusion development and recognition memory performance.

It was found that across view and rest, there was greater activity in the bilateral amygdala for videos that later intruded compared to those that did not subsequently intrude. For the view condition only, subsequently intruding videos were associated with activity in the dmPFC, insula and parietal areas. For recognition memory, there was greater activity in the right entorhinal cortex, left angular gyrus, left superior frontal gyrus and middle temporal sulcus for remembered videos compared to forgotten videos. Furthermore, an analysis investigating the relationship between memory scores and neural activity using a parametric modulator for video scores showed greater activity in the bilateral hippocampus.

These results suggest that our paradigm is sensitive to variation in neural activity in the medial temporal lobes relating to subsequent deliberate and involuntary memory. Further analysis will examine the locations and timing of activity specifically contributing to these two forms of memory, and attempt to resolve the extent of overlap or differences, and whether these support a unitary or dual representation account.

5.5.1 Recognition

The current study identified greater activity in the entorhinal cortex across encoding and subsequent rest period for videos that were later remembered compared to those that were forgotten. Also, there was greater activity in the bilateral hippocampus and several other areas for videos with higher scores (see Supplementary Table S8). Thus we found activity in the medial temporal lobes predicting subsequent memory for the videos, following many related studies (Wagner, Schacter et al., 1998). However, the precise locations of this activity are harder to interpret.

It is well established that the MTL plays a critical role in episodic memory formation and consolidation (Byrne, Becker, Burgess, 2007), and MTL activity during encoding and post-encoding has been associated with enhanced memory performance. For instance, it has been shown that hippocampal activity during encoding correlates with subsequent memory performance (Kirwan and Stark, 2004; Jackson and Schacter, 2004). The hippocampus is known to play a critical role in episodic memory formation and previous studies have demonstrated that hippocampal activity during encoding is related to better subsequent performance on associative memory tasks. In turn, the entorhinal cortex is the major source of neocortical input to the hippocampus (e.g. Van Strien, Cappaert, Witter, 2009).

The finding presented here is consistent with the study by Staresina et al. (2013) who reported greater entorhinal activity during encoding for object-scene asssociations that were later successfully retrieved compared to those that were forgotten. The study by Staresina used an associative memory task placing demands on the hippocampal-entorhinal system whereas the current study used a recognition memory task. Recognition memory is thought to be supported by familiarity-related processing which may to rely on structures outside the hippocampal formation such as the perirhinal cortex (Aggleton and Brown 1999). However, recognition can also be performed on the basis of deliberate memory for the item, and the two processes can occur in parallel (e.g. Yonelinas, 2002). Indeed, the recognition memory test used in this study also places demands on associative processes to some extent, as the pictures shown were cropped pictures only depicting a single element or object from the scene, hence requiring recollection of the entire scene in order to judge of the object is familiar or not. This process of 'filling in' the surroundings would be expected to rely on hippocampal-entorhinal regions, consistent with the findings presented here. In addition, our finding that hippocampal activity across encoding and post-encoding processing is related to subsequent memory performance is consistent with the findings of Ben-Yakov et al. (2011) who found that post-encoding hippocampal and dorsal striatum activity correlated with subsequent memory performance. Hence, these neural processes appear to consolidation processes.

Finally, increased activity in the left inferior frontal gyrus (pars triangularis) was found. This area is part of Broca's area and it has been suggested that this area is involved in the conversion of a subjective experience into a speech (Rauch et al., 1995 in Kolk and Fisler). Hence, activity in this region associated with deliberate memory performance could indicate stronger narrative representations for videos that were subsequently remembered.

5.5.2 Intrusions

The findings presented here demonstrate that intruding videos were related to greater activity in the amygdala across view and rest periods compared to videos that did not intrude, and related to greater activity in the dmPFC, insula and parietal areas during encoding compared to videos that did not intrude. The finding that subsequently intruding videos were associated with greater amygdala activity during encoding is consistent with the established role for the amygdala in emotional processing and with the previous study by Bourne et al., (2013) which also identified increased amygdala activation for intruding versus non-intruding stimuli.

Hence these results indicate that the amygdala enhances memory representations that are prone to involuntarily entering consciousness. Several have proposed that the amygdala might up-regulate sensory and affective representations of an emotional event (Hamann, 2001; Hamann et al., 1999; Phelps and LeDoux, 2005), which is consistent with the enhanced insula and parietal activity. For instance, studies have consistently shown increased amygdala involvement and its interaction with visual areas during processing and memory for negative stimuli (Vuilleumier et al., 2001, 2004; Phelps and LeDoux, 2005). Therefore, the amygdala might contribute to strong item representations for negative stimuli that are later involuntarily re-experienced.

Like the amygdala, the insula is also implicated in emotional processing; it is believed to play a role in the subjective emotional experience, such as the feeling of sadness and anger based on interoceptive information from bodily afferents (Craig, 2003, Phan et al., 2002, Damasio et al., 2000) as well as signalling of salience. In turn, the insula projects to other structures involved in emotional processing including the amygdala (Stein et al., 2007). Hence, it is possible that a network involving the amygdala, insula and parietal areas enhance egocentric, affective and sensory representations of a negative event. Indeed, it has been shown that the insula and parietal cortex both play a role in sensory binding between visual and auditive information (Calvert et al., 2001; Bushara et al., 2001, 2003). Another possibility would be that the amygdala facilitated memory processing via the hippocampus but the current results do not support this idea, as there was no enhanced activity in the hippocampus for intruding videos.

Finally, it has been shown that enhanced activity in the dorsomedial PFC was related to subsequent memory intrusions. The medial PFC plays a role in emotional processing and it has been suggested that the dorso-medial PFC is specifically involved in fear conditioning and appraisal of negative emotion (Etkin et al., 2011).

Hence, these findings point to the involvement of a large network for emotional processing associated with subsequent memory intrusions, which may enhance emotional representations of the traumatic event and render these representations more likely to be triggered by subsequent internal or external cues.

The study by Bourne et al. (2013) also highlighted a role for a large network associated with subsequent memory intrusions rather than a single region, including structures associated with emotional and visual processing. There was some overlap between regions identified in the Bourne (et al., 2013) study and the current study, as both studies identified increased activity in the amygdala for intruding versus non-intruding scenes.

Consistent with the studies by Bourne et al. (2013) and Clark et al. (2016), results from this study demonstrates that subsequent development of memory intrusions is related to different encoding and post-encoding processing compared to videos that did not intrude showing increased activity in regions associated with affective and sensory processing for intruding event.

Overall, this study emphasizes a role for amygdala processing during encoding and post-encoding in the subsequent development of memory intrusions. These findings are consistent with previous studies and empirical evidence from the clinical literature showing increased amygdala activation during symptom provocation in PTSD patients. For example, studies on PTSD patients have found that amygdala reactivity is positively correlated with severity of symptoms (Yehuda and LeDoux, 2007; Shin et al., 2006). Furthermore, it has been suggested that increased amygdala reactivity is a causal factor in the disorder rather than a result PTSD as a study showed that combat veterans who had suffered amygdala damage were less likely to develop subsequent PTSD than veterans without amygdala damage (Koenigs et al., 2008). Hence, it is possible that people prone to developing memory intrusions have higher amygdala reactivity to emotional stimuli. If, as suggested in the current study, amygdala activity during encoding and post-encoding up-regulates sensory and affective representations of an negative event, the heightened amygdala reactivity seen in PTSD patients could be a vulnerability factor in developing memory intrusions.

By contrast, for deliberate memory, we found that greater hippocampal and entorhinal activity during encoding predicted higher subsequent memory performance on a memory recognition test, requiring retrieval of the scene from which the presented object was taken. These findings are consistent with other studies showing that greater hippocampal activity during and after encoding is associated with better memory performance on associative memory tests. However, further analysis is required to see if there is a significant dissociation in the activity supporting deliberate and involuntary memory (i.e. a significant interaction of region x subsequent memory type). Further analysis is also required to fully identify the locations and time courses of activity correlating with subsequent deliberate memory and involuntary intrusions. Nonetheless, the findings so far suggest a partial dissociation between amygdala processing supporting intrusive memory and hippocampal processing of deliberate memory.

6 GENERAL DISCUSSION

6.1 Overview

This thesis used a combination of behavioural and fMRI techniques to investigate the role of post-encoding processing in subsequent intrusion development and deliberate memory. The theoretical background, of opposing unitary or dual representation theories, concerning the processing underlying intrusive or deliberate memory provided one of the motivations for looking at the contributions of post-encoding processing to these different aspects of memory.

In Chapter 2, different techniques to study intrusion development were investigated and it was found that using short video clips was more appropriate to elicit memory intrusions than static images. Chapter 3 investigated retroactive interference effects on memory for a stimulus when that stimulus is immediately followed by another stimulus. Combining data from the experiments in this chapter in a collective analysis showed that the immediate presentation of a second stimulus impaired memory for the first stimulus, most likely due to disrupted post-encoding processing. Building on these findings, Chapter 4 contrasted the effects of wakeful rest and a 0-back working memory task following encoding of a series of videos. Here, it was shown that wakeful rest following encoding resulted in fewer intrusions and that interventions had different effects on memory intrusions and deliberate memory. In contrast, no direct effects of wakeful rest versus a WM task on deliberate memory was found. Overall, findings from these experiments indicated that post-encoding processing does play a significant role in subsequent trauma memory. More specifically, facilitating post-encoding memory processing and consolidation by having a period of rest following encoding can be beneficial in reducing the number of memory intrusions, while disrupting post-encoding processing can increase the number of memory intrusions. These results provide some support for a dual representation view, in suggesting that the effects of post-encoding processing can reduce intrusions while deliberate memory is not affected. However, the video study in Chapter 2 found a positive correlation between deliberate and involuntary memory, indicating the presence of some common processes too.

Finally, Chapter 5 investigated the neural correlates of encoding and post-encoding processing of traumatic material and how they might support intrusions. Results showed that, across periods during which participants viewed clips and rest periods immediately following the clip, intruding videos were associated with greater amygdala activity compared to non-intruding videos. By contrast, remembered videos showed greater activity in the entorhinal cortex and hippocampus compared to forgotten videos. Thus, these results suggest a partial dissociation in the metabolic correlates of the two types of subsequent memory, but further work will be required to show the extent and nature of these differences in activity.

In the following, I conclude by briefly discussing the general theoretical and clinical implications of the findings presented in previous chapters.

6.2 Is the period following a traumatic experience important?

In accordance with a number of previous studies (e.g. Holmes et al., 2009; Deeprose et al., 2012), results from this thesis further highlight the way in which the period post-encoding is an important factor in predicting how memory is affected. That is, over a number of experiments it was shown that manipulations during periods following encoding of traumatic material could affect both deliberate memory reports for the information (Chapter 3) and the number of intrusive memories reported over a one-week period (Chapter 4).

The experiments from this thesis demonstrated that simple tasks performed after encoding a number of traumatic clips could alter memory. For instance, the experiments in Chapter 4 showed that participants given a simple working memory task reported more intrusive memories compared to participants given a short wakeful rest during the same period and for the same duration. In contrast to what was expected, the experiments in Chapter 4 did not show beneficial effects of wakeful rest on deliberate memory when the rate of false alarms was taken into account in the memory performance. However when data from the studies in Chapter 3 were combined, it was found that a short rest period following encoding could enhance memory performance compared to when a second event would immediately follow the first. These latter results are consistent with previous studies using rest to improve memory. For instance, Dewar et al. (2012) showed that wakeful rest following encoding improved subsequent memory for a story the participants had learned at encoding compared to when participants carried out a spot-the-difference task. Another study showed that a 9-minute delay interference of learned material showed better memory performance in amnesic patients compared to when interference was presented closer to encoding (Dewar et al., 2009). Presumably, such disruptions or improvements to memory accuracy via post-encoding manipulations could be due to impaired or enhanced consolidation, in accordance with consolidation theory (McGaugh, 2000; Dudai, 2004) and related studies in highlighting this period as an important time in which memory is fragile (e.g. Müller and Pilzecker in Lechner, 1999; Ben-Yakov et al., 2013; Dewar et al., 2012).

By visual inspection, the pattern of results from Chapter 3 was consistent with results in Chapter 4 in that there was a distinct pattern of numerically fewer intrusions for videos where participants had a short rest following encoding, compared to when a video was followed immediately by another video. However, findings from these experiments were weaker than in Experiment 4 and did not reach significance. The two studies were similar in that they both involved a short rest period compared to a task or presentation of a second stimulus. But whereas the rest periods in Chapter 3 were short periods of 30 seconds following a single trial, participants watched the full sequence of videos in Chapter 4 before having a longer rest period of 10 minutes. As effects of wakeful rest on deliberate memory performance did not reach significance in Chapter 4, it is possible that a short rest after each event was sufficient and superior compared to when rest was given after the entire encoding session in terms of facilitation of deliberate memory. Alternatively, the numerically (but non-significant) higher proportion of false alarms in the wakeful rest condition compared to the WM task condition might explain absence of a memory facilitation effect, as discussed earlier.

In chapter 5, it was demonstrated that videos that intruded were associated with greater amygdala activity during encoding and subsequent 30 seconds rest period compared to videos that did not intrude, while deliberate memory was related to enhanced activity in MTL structures. As the activity for remembered and intruded videos was significantly different from videos that did not intrude or were forgotten, these results suggest that neural processing during and immediately after encoding modulates subsequent memory intrusions and deliberate memory, supporting the behavioural findings in previous chapters.

Taken together, the experimental findings described in this thesis support the view that processing in the period following encoding is important in stable memory formation (Dudai, 2004). Further, this thesis extends this view with a framework of processing traumatic events, showing that short rest periods following each event also enhanced deliberate memory (Chapter 3). In contrast, these short rest periods did not affect intrusion development but intrusions were reduced by a period of wakeful rest following encoding (Chapter 4), which is also a more clinically relevant finding in terms of preventing post-traumatic stress reactions. These findings are also consistent with previous studies demonstrating that manipulating post-encoding processing of experimental trauma could induce or prevent development of memory intrusions (Deeprose et al., 2012; Holmes et al., 2009). Importantly, these results also indicate that the period following a traumatic event could be a target for secondary preventive interventions.

6.3 Post-encoding manipulation and intrusions

Manipulations to post-encoding processing were able to alter the frequency of intrusive memories reported by participants. Interestingly, manipulations performed during the post-encoding period were typically disruptive in that people seemed to report more intrusions. As observed in Chapter 4, people given short wakeful rest actually showed fewer intrusive memories in the week following encoding. This finding suggests that lack of offline processing of information immediately after a traumatic might make intrusive memory occurrences worse and could potentially increase PTSD rates.

In a similar way, an equivalent numerical pattern was evident from Chapter 3, showing that a short break after each trial numerically reduced subsequent memory intrusions, although this should be taken with caution given that the result did not reach significance. Taken together, these findings indicate that having a period of rest after encoding can be helpful in reducing memory intrusions compared to processing further information either by carrying out another task (0-back) or by viewing a further traumatic clip after encoding. Previous studies have established that different post-encoding interventions can reduce or increase subsequent memory intrusions (Deeprose et al., 2012; Holmes et al., 2009; James et al., 2015). More specifically, a number of studies have suggested that carrying out a visuospatial task post-encoding reduces the number of reported memory intrusions over the following week, whereas carrying out a verbal task increases memory intrusions (Bourne et al., 2010; Deeprose et al., 2012). It has been suggested that these findings reflect the fact that various tasks demand different cognitive resources (Bourne et al., 2010). Hence visuospatial tasks will reduce intrusions as they compete with trauma memory for visual processing, thereby making the memory intrusions less vivid, whereas verbal tasks might compete with conceptual processing of the trauma memory, preventing conceptual processing of the trauma that might contribute to processing, desensitising and integrating the trauma with other information (Holmes et al., 2009; Bourne et al., 2010).

At a first glance, these findings may seem at odds with the current findings, as it was shown in the current experiments that introducing a task post-encoding increased intrusive memories. Hence, in terms of a distraction hypothesis, any task interfering with post-encoding processing would affect memory. However, based on the idea that memory intrusions can be reduced or facilitated depending on specific modality processing, the critical point is what kind of processing or representation of the trauma memory is facilitated and which are impaired (Bisby and Burgess, 2017). Within this framework, memory intrusions can be reduced by either facilitating conceptual and contextual processing, by reducing sensory processing or by reducing emotional aspects of the trauma memory. Hence, engaging in a visuospatial task would compete with the trauma memory for visuo-spatial resources, perhaps making the traumatic event less visually salient. In turn, wakeful rest and the proposed resulting memory consolidation would increase contextual representations of the event (Dewar et al., 2012; Brewin et al., 2010).

The conditions used in the current studies were immediate post-stimulus encoding (presentation of a second stimulus immediately following presentation of a previous stimulus) versus short rest (post-trial 30-second interval; Chapter 3) and longer period of rest (10 min) versus a 0-back working memory task (Chapter 4). In both cases, rest reduced the number of intrusions reported in the week following encoding (although the difference was non-significant in Chapter 3). Hence, these findings indicate that rest following a trauma is beneficial and might prevent involuntary memory intrusions and result in better deliberate memory of the event (although see Porcheret et al., 2015). Rest is believed to facilitate hippocampal memory consolidation processes (Ben-Yakov et al., 2013; Dewar et al., 2013) and hence might facilitate the conceptual processing of the emotional event and its integration with other information and thereby reduce memory intrusions, as proposed in social-cognitive theories of PTSD (Janoff-Bulman, 2010).

6.4 How is deliberate memory affected by post-encoding manipulations?

Chapter 3 demonstrated that *interfering* with post-encoding processing of an event by introducing a second event immediately following the first event impaired memory performance for both neutral and negative material. In contrast, no effect of wakeful rest on deliberate memory was found in Chapter 4 when false alarm rates were taken into account in the memory score (although when assessing proportion hits alone, there was a facilitative effect of wakeful rest). Taken together, results from this thesis tentatively suggest that having peace to consolidate material after encoding benefits memory performance compared to carrying out interfering tasks or perceiving new stimuli.

The observed negative effects of immediate presentation of a second stimulus following the first on deliberate memory performance could be explained by less rehearsal of stimuli during post-encoding. However, participants were not instructed to think about the videos during breaks and, anecdotally, many participants reported that they thought of other things during rest. Hence, better memory was not necessarily due to conscious processing of the videos. Evidence suggests that both conscious rehearsal as well as consolidation through offline processing can enhance memory performance. For example, studies have demonstrated that facilitating offline post-encoding processing by introducing a period of wakeful rest following encoding resulted in better memory performance (Cowan et al., 2004; Dewar et al., 2007; Dewar et al., 2009) while a study by Bird et al. (2015) showed that conscious rehearsal also facilitated subsequent memory performance.

What appears to be a common mechanism between studies finding an effect of conscious rehearsal and studies investigating offline processing is the subsequent reinstatement of the activity pattern that was present during encoding (Ben-Yakov et al., 2011; Tambini et al., 2010). The study by Ben-Yakov et al. (2011) showed this effect in the hippocampus and dorsal striatum. In Chapter 5, the neural correlates of post-encoding processes were investigated. Although specific analyses of reinstatement was not performed in this study, results demonstrated that hippocampal activity across view and rest conditions correlated with deliberate memory performance, consistent with existing literature.

In sum, Chapters 3 and 5 demonstrated that facilitation of post-encoding processing benefits subsequent memory performance and indicates that this facilitation is mediated by enhanced hippocampus activation.

6.5 Contrasting effects on memory

6.5.1 Deliberate memory for neutral versus negative stimuli

In the studies presented in this thesis, several effects of emotion on subsequent deliberate memory performance were observed. In Chapter 2, participants showed better memory performance for negative pictures compared to neutral pictures on a recognition memory test. Consistent with this result, Experiment 3.2 also showed that memory performance for negative videos was superior to memory for neutral videos. However, in Experiment 4.2, the opposite pattern was observed, showing better memory for neutral compared to negative videos. How might these different findings be explained? The findings from Chapter 2 and 3 are consistent with the modulation hypothesis stating that negative emotion facilitates memory. This facilitation effect is well known and numerous empirical studies support this view (see e.g. LaBar and Cabeza, 2006 for a review).

The memory test in Experiment 2.1 was a recognition memory test, not requiring recollection or contextual retrieval to answer correctly. Evidence suggests that recognition memory (familiarity, item memory) and recollection (contextual memory) can be dependent on different underlying memory systems where item/recognition memory may be facilitated by negative emotion while recollection/contextual memory is impaired. The findings in Experiment 2.1 are consistent with this idea. However the memory test in Chapter 3 was a cued recall test where participants answered questions related to the videos. This type of memory test it thought to be dependent on retrieval of a scene as a whole, providing context and binding of the single elements of the memory. Hence, at a first glance, these findings appear to be inconsistent with the idea that negative emotion primarily facilitates item memory and impair memory for context.

However, many of the questions in the cued recall test in Chapter 3 were related to gist of the videos, rather than detail or context. Studies have showed that emotion facilitates memory specifically for gist (Burke et al., 1992; Touryan et al., 2007; Rimmelé et al., 2011; Adolphs et al., 2005; Bisby and Burgess, 2014) For instance, a neuropsychological study by Adolphs (et al., 2005) showed that damage to the amygdala was associated with impaired emotional memory for gist but not for details, suggesting that negative emotion selectively facilitates memory for gist. Also, a study by Burke et al. (1992) showed that whereas negative emotion enhanced memory for gist and details associated with the event's centre, whereas memory for other details was impaired. Hence, it is possible that the facilitation of memory for negative items in Experiment 3.2 was due to enhanced memory for gist, similar to recognition/item memory and contrasting recollection/contextual memory.

In contrast to these findings, in the second wakeful rest experiment (Experiment 4.2), participants showed enhanced memory performance for neutral videos compared to negative items. Here, the memory test was a form of recognition memory test so based on the above, facilitated memory for negative items would be expected. However this memory test comprised recognition memory for single details from the videos, hence requiring retrieval of the surroundings of the item rendering this task more dependent on contextual/associative memory. For this type of information, facilitation of neutral information over negative information would be expected.

Taken together, results from experiments presented in this thesis show partial support for a modulation hypothesis. It is possible that the diverging findings across experiments reflect differences in the resources required to carry out the different memory tasks, where tasks that require contextual processing might be impaired while memory for single items might be enhanced.

6.5.2 Are intrusions and deliberate memory affected in opposing ways?

There is ongoing dispute as to whether or not memory intrusions and deliberate memory is affected in the same or in different ways by manipulations during and after encoding. As mentioned, similar effects of these manipulations would support a unitary account (Rubin et al., 2008; Talarico et al., 2004), while different effects would support a dual representation account (Brewin et al., 2010; Bisby and Burgess, 2017).

The experiments in this thesis did not provide clear evidence of whether deliberate memory and intrusions are affected in opposing ways by post-encoding interventions, as several studies did not yield significant results. However, in Chapter 4, it was shown in two studies that the chosen interventions affected memory intrusions and deliberate memory differently. This was supported by repeated findings showing an effect of intervention of one type of memory but not the other (Chapter 3 and 4). Further, visual inspection of the results showed systematically that intrusions and deliberate memory was affected in opposite directions, although these effects were non-significant (Chapter 2, 3 and 4). Taken together, the results presented in this thesis offer tentative support of the DRT in this regard. However, other findings presented in this thesis directly support a unitary account, such as the positive correlation between deliberate memory performance and intrusions in the video experiment in Chapter 2.

6.6 Neural structures supporting trauma memory

6.6.1 Encoding versus post-encoding

In chapter 5, neural activity underlying encoding and post-encoding processing was examined. Here, it was found that there was greater activity for encoding compared to post-encoding (rest) across a large network including the occipital cortex and dorsal and ventral visual streams. The dorsal stream is known to be involved in visuo-motor coordination and the processing of egocentric spatial locations and actions, whereas the ventral stream is involved in the conscious perception and categorisation of objects and scenes (Mishkin et al., 1983). Hence, the greater activity in these visual streams during video presentation is not unexpected.

6.6.2 Deliberate memory

Chapter 5 demonstrated that subsequent deliberate memory performance for emotional stimuli was related to greater activation across encoding and rest in a large network including the right entorhinal cortex and the bilateral hippocampus. These findings are consistent with evidence proposing a role for these structures in episodic memory encoding and consolidation (Bird and Burgess, 2008). In Chapter 3, evidence was presented that short rest periods following encoding increased memory performance and it has been suggested that allowing some form of post-encoding rest of an event enhances memory performance by increasing hippocampal processing of the event (Dewar et al., 2012; Ben-Yakov et al., 2013), which would be consistent with the findings presented in Chapter 5. Together the behavioural and neuroimaging results are consistent with other studies showing enhanced memory performance when post-encoding processing is facilitated

(Dewar et al., 2007; 2012) and impaired memory performance when post-encoding processing is interrupted (Ben-Yakov et al., 2013).

6.6.3 Memory intrusions

Theories of intrusive memories have often emphasized the emotional and sensory rich nature of these memories (Ehlers and Clark, 2000; Brewin et al., 2001; 2010). Results from the fMRI experiment presented in Chapter 5 is consistent with this view, as it was reported here that activation in the bilateral amygdala across presentation and rest, and in the insula, dmPFC and parietal areas during presentation only, was related to subsequent memory intrusions. The amygdala is known to modulate processing of emotional memory formation and insula activity is associated with visceral reactions to negative stimuli, such as disgust (Craig, 2009). Furthermore, parietal areas are known to be involved in integration of sensory processing. In sum, the fMRI results presented in Chapter 5 are consistent with what is known about intrusions as being highly emotional and sensory memory representations (Holmes et al., 2010).

6.7 Use of the trauma film paradigm to study consolidation and intrusions

Building on previous studies, the studies in this thesis confirm and extend the usefulness of the experimental trauma paradigm to investigate encoding and post-encoding factors related to subsequent trauma memory alterations. The experimental trauma paradigm allows prospective and controlled investigation of intrusion development and not least allows manipulation of processing during and after encoding. However, studying memory intrusions and deliberate memory in the lab is a sensitive and complex process that relies on compliance of participants to fill in the diary when experiencing memory intrusions. Also, in order for the use of this paradigm to be successful, the presented video stimuli must be distressing to the participants. It was established in Chapter 2 that this requirement was better satisfied by using naturalistic video clips compared to still images. However, using complex multimodal stimuli comes at a cost of having less clear cut boundaries between different deliberate memory types including associative and recognition memory.

6.8 What are the theoretical implications of this research?

Two opposing accounts of trauma memory and intrusion formation have been influential. The unitary account (Rubin et al., 2008a; 2008b; Berntsen and Hall, 2004) proposes that trauma memories are merely particularly strong episodic memories, which are more strongly encoded and more rehearsed than other memories. Because of the salience and importance of trauma memories, these memories tend to intrude more than other memories, but are inherently the same as other episodic memories.

In contrast, a dual representation account (Brewin et al., 2010; Jacobs and Nadel, 1985) builds on the episodic memory model by Byrne, Becker and Burgess (2007) and suggests that two complementary representations are formed of episodic events. One is an allocentric representation, which is dependent on the hippocampus and encodes the context and integration of single elements of the memory into a coherent whole. The other representation encodes sensory and affective details from the event and is egocentric. During trauma, hippocampal processing and hence contextual representations are down-regulated while sensory representations are facilitated via the amygdala, resulting in vivid and emotional memories with poor contextual binding, which are more prone to being triggered involuntarily.

In the following, the results presented in this thesis will be discussed in terms of these two accounts.

6.8.1 Can a unitary account of trauma memory explain the results?

Some results presented in this thesis support a unitary account of intrusion development. In Chapter 2, a study using video stimuli was conducted, with follow-up memory tests either immediately following encoding (Immediate group) or after one week (Delay group). For the Delay group, a positive correlation was reported between memory intrusions and memory performance on a cued recall memory test. This finding indicates that memory intrusions and deliberate memory are modulated in the same direction and so are likely to rely on some shared underlying mechanisms. Hence, this finding supports a unitary account.

However, the other studies presented in this thesis did not find similar correlations between intrusions and deliberate memory. Furthermore, Chapter 3 found that the presentation of a second video immediately following another video showed a retroactive interference effect on deliberate memory for the first video, while there were no significant effects of this intervention on memory intrusions. The opposite pattern was evident from Chapter 4, where wakeful rest reduced intrusions but did not affect deliberate memory. However these findings do not necessarily reflect a dissociation but could be due to insufficient statistical power to detect an effect. It should be noted however that by visual inspection, patterns of deliberate memory and intrusions were generally opposite each other rather than similar, making it reasonable to assume that with higher statistical power, results would at the very least not have shown that the two memory forms were modulated in the same direction by interventions. Taken together, findings showing that intrusions and deliberate memory can be manipulated independently of each other speak against a unitary account where intrusions and deliberate memory are considered different manifestations of the same emotional memories.

Chapter 5 examined the peri- and post-encoding processes influencing subsequent memory intrusions and deliberate memory at a neural level. Again, there appeared to be a dissociation between neural activity related to videos that were subsequently remembered and videos that subsequently intruded. However, further analyses are required to determine if these findings do in fact reflect a dissociation or if they reflect that some effects did not meet threshold. Deliberate memory performance was associated with greater activity in the hippocampus and entorhinal cortex while intruding videos were related to greater amygdala activation. The hippocampus and entorhinal cortex are both part of the MTL memory system and are known to be involved in episodic memory formation (Eichenbaum and Cohen, 1988; Scoville and Milner, 1957; Byrne, Becker and Burgess, 2007). The unitary account would predict that both videos that intruded and videos that were subsequently remembered would be associated with greater MTL activity, but our findings do not support this view.

Taken together, although some results in Chapter 2 supports a unitary account, the overall results from experiments presented in the preceding chapters do not favour a unitary account of trauma memory.

6.8.2 Do the findings support a dual representation account?

The dual representation theory (DRT) proposes that intrusions and deliberate memory performance can be modulated in opposing directions as each of these memory types rely on different underlying memory representations (of course a given manipulation might also have the same effect on both). Thus, finding a manipulation that facilitates or impairs one representation compared to the other is evidence for a dual representation account. In Experiment 3 it was demonstrated that when data from two experiments were collapsed to increase statistical power, presentation of two videos in close succession produced significant retroactive interference effects for the first video on deliberate memory performance, but non-significant opposite effects on memory intrusions. Also, in Chapter 4 it was shown that a period of wakeful rest following encoding reduced memory intrusions one week later but did not significantly affect deliberate memory. These findings suggest that the two forms of memory are not modulated in the same way by the presentation of a second stimulus, which supports the DRT at a general level. Deeprose et al. (2012) reported similar results as it was demonstrated that while carrying out a verbal and a visuospatial task had differential effect on memory intrusions, these interventions did not affect deliberate memory.

In terms of neural mechanisms, the DRT predicts that memory intrusions arise from memory representations with a weak contextual/hippocampal encoding and strong sensory/affective encoding in parietal regions facilitated by the amygdala, insula and early sensory cortices (Brewin, et al., 2010). This prediction was the motivation for using wakeful rest, as this is generally thought to boost hippocampal-dependent consolidation of deliberate memory. Consistent with this hypothesis, the findings in Experiment 5 revealed greater activity in the amygdala across encoding and rest for videos that intruded compared to those that did not intrude. Furthermore, looking at encoding only, videos that subsequently gave rise to memory intrusions showed greater activity in the insula, vmPFC and the right inferior parietal lobule. It has been proposed that the insula is part of the egocentric/sensory memory representation, as this structure is involved with interpreting interoceptive signals and the resulting subjective emotional experience (Brewin et al., 2010; Bisby and Burgess, 2017).

Overall, the majority of behavioural findings and imaging results presented in this thesis are broadly consistent with the dual representation account, at least at a general level.

6.8.3 Reconciling different accounts

In this thesis, some findings, such as the different effects of wakeful rest on intrusions and deliberate memory in Chapter 3 and 4, support a dual representation theory, while other findings, such as the positive correlation between memory intrusions and deliberate memory in Chapter 2 favours a unitary account. These mixed results correspond to findings in the literature where different studies support each of the two accounts.

The unitary account suggests that memory intrusions arise from trauma memories, which are central to the individual's life story and have particularly strong memory traces, rendering these memories more likely to be triggered involuntarily (Rubin et al., 2008a; 2008b). In turn the dual representation theory proposes that intrusions arise as a result of an imbalance in sensory and contextual representations of a negative event, creating emotionally and perceptually salient memory representations with poor contextual and conceptual encoding, rendering these representations more likely to be triggered by external or internal stimuli.

Hence, the two accounts do not disagree as to whether or not negative emotion is able to enhance memory traces. Both accounts accept that negative emotion can be a strong facilitator of emotion and this has been shown in numerous studies and is indicated by for instance the item memory results presented in Experiment 2.1. Rather, the difference consists of a dispute between whether it is the whole memory trace that is enhanced by negative emotion, or alternatively, that only some aspects or representations are enhanced by memory, while others are impaired. More specifically, it has been suggested that emotion may differentially affect memory for items, which are believed to rely on the amygdala and perirhinal cortex and input from the ventral visual stream, and associative or contextual memory, which relies on the hippocampus. (Eichenbaum et al., 2007; Farovik, et al., 2011; Bisby et al., 2016).

In terms of the two accounts, it appears that item memory might be enhanced by negative emotion and therefore be regulated in the same manner and direction as memory intrusions (more intrusions for more traumatic events), which is consistent with the unitary theory. In turn, it may be that contextual processing is modulated in a different manner to item and intrusive memories, supporting the DRT. This conceptualisation uses aspects from both accounts to explain the relationship between memory intrusions and deliberate memory for negative events.

Another possibility is that the way in which deliberate memory and memory intrusions are modulated by negative emotion depends on the intensity of the emotional experience. Evidence suggests that the relationship between stress and learning or memory follows an inverted U-shape pattern where learning is impaired at very low or high cortisol levels but facilitated at medium cortisol levels (Lupien and McEwen, 1997; Schilling et al., 2013). From this follows that an emotionally negative and salient stimulus might enhance hippocampal processing and subsequent memory for the stimulus if the stimulus does not elicit a very strong stress response. This might be positively correlated with involuntary memories understood as normal memories that are more often triggered if the remembered event is salient and therefore associated with more triggers in the environment. Hence, this conceptualisation of moderate stress would be consistent with the unitary theory. In turn, if an event is highly traumatic, this might impair hippocampal processing leading to poor contextual encoding, allowing the relative strengthening of sensory/affective representations and thereby lead to more memory intrusions, consistent with the dual representation theory (Brewin et al., 2010).

Another point is that it is difficult to separate memory intrusions and deliberate memory completely. For instance, if in the current experiments, some videos elicited intrusions, they would also be more likely to be the ones that participants remembered upon their return a week later, because they have been rehearsed more.

In sum, emphasizing different aspects of deliberate memory or different stress levels associated with trauma offers ways to reconcile the two accounts.

6.9 What are the clinical implications of this research?

The findings reported in the previous chapters carries several clinical implications for treatment and secondary prevention of memory alterations in PTSD. These implications are discussed in the following.

6.9.1 Could the period following trauma be targeted to improve memory?

The experiments presented in this thesis, in particular findings from Chapter 4 (and to some extent Chapter 3), indicate that ensuring post-encoding processing of traumatic experiences in trauma victims could reduce subsequent memory intrusions and adverse alterations in deliberate memory, such as reduced recall for aspects of the trauma and fragmented deliberate memories of the trauma. These findings are consistent with views emphasizing the early aftermath following a traumatic event as significant for subsequent symptom development (Vaiva et al., 2003; Rose et al., 2002).

In general, it appears that the mechanism underlying amelioration of symptoms due to post-encoding interventions relate to either enhanced contextual processing of the trauma, relating the trauma to other knowledge and episodic memory, down-regulation of the sensory aspects of the trauma or desensitisation to the emotional aspects of the trauma. Hence, making the trauma memory more contextually based and less emotion- and sensory-based appears to reduce subsequent development of PTSD symptoms such as intrusive memories.

From this follows that there are several ways to prevent development of memory intrusions which all either enhance hippocampal processing or reduce sensory or emotive processing. This would also explain why such different interventions as playing Tetris and having a rest after encoding could both be beneficial while carrying out other tasks (such as verbal tasks) might be harmful. The findings presented here suggest that having time to process and consolidate a traumatic experience through wakeful rest following encoding might be beneficial.

Previous experimental studies using the trauma paradigm have been tested in trauma victims (Iyadurai et al., 2017) and women undergoing emergency caesarean sections (Horsch et al., 2017) and have been found to successfully reduce memory intrusions; these two studies showed that previous findings showing that playing the computer game Tetris following encoding of traumatic material can reduce intrusions could be extended to real-life situations. Here, people who had been involved in a motor vehicle accident or who had undergone an emergency caesarean section a few hours before played Tetris and subsequently showed fewer involuntary memory intrusions of the trauma compared to people who did not play Tetris (treatment as usual). Hence, these studies demonstrate the clinical application of findings from experimental trauma studies in healthy subjects, showing that findings from these studies may be extended to a clinical population. Furthermore, intervention forms as those outlined here comprise a group of potential psychological treatments that are directly based on neuroscientific research on the mechanisms underlying observed effects and which may have few side effects. Hence, such approaches may be fruitful future avenues for the development of new effective interventions to treat psychiatric disorders (Holmes et al., 2014).

The idea that more contextually based and less emotional representations of a traumatic event in memory are beneficial is also consistent with successful current treatments for PTSD. The recommended first-line treatment is cognitive therapy with exposure. Both the exposure component and cognitive component will often involve imagery; in imagery rescripting, trauma images are re-experienced and altered through imagery. This process desensitises trauma memories and make them more coherent and verbalised as they are processed (Holmes et al., 2007). In prolonged exposure therapy, the trauma is put into context and processed with trauma-related cognitions and emotions, thereby facilitating a better understanding of the memory in its proper context, among other things (Goncalves et al., 2012). A number of studies have also shown that exposure to the trauma using detailed virtual reality (VR) reconstructions of the trauma can ameliorate PTSD symptoms (Difede et al., 2007; Rizzo et al., 2013; Rothbaum et al., 2001; see Goncalves et al., 2012 for a review). This virtual reality exposure therapy (VRET) provides a rich source of external trauma-related stimuli and aids further reprocessing of the trauma memory (Rizzo et al., 2013). Taken together, although these techniques may partly work by desensitising trauma memories and making them less emotional, it is likely that another effective component in these treatments is the more elaborate contextual processing through the treatment, rendering the trauma memories less emotional and more contextually based and integrated with other information.

6.9.2 Difficulties in helping in the immediate aftermath

In the immediate aftermath of trauma, it may not be possible to target neural processing of the traumatic event. Often, people will require medical care and may not be fit to engage with psychological tasks. Also, it might prove difficult giving trauma-victims a period of wakeful rest while preventing them from ruminating about the trauma during the rest period (however see box 6.1 for translational aspects of the wakeful rest results.

Box 6.1: Translational perspectives of wakeful rest. Potential instructions to clinicians

Wakeful rest may be beneficial in preventing the occurrence of memory flashbacks following trauma.

In this context, wakeful rest refers to a period of rest where the person sits quietly without talking or engaging in any activities and with their eyes closed.

This means that when a person is exposed to a traumatic event such as a car accident, then if circumstances allow and medical treatment is not otherwise required, it is better to let the victim rest with their eyes closed in a tranquil space rather than immediately talking about the event or engage in other activities.

The person should be instructed to neither rehearse nor try to suppress thoughts related to the trauma, but simply try to relax and let their mind wander.

This would be best accomplished in a quiet room where there is a minimum of external stimuli and disruptions.

One way to address this problem could be through the use of reconsolidation in secondary prevention of intrusive symptoms. Reconsolidation describes the phenomenon that previously encoded memory traces can become malleable again following reactivation (Misanin et al., 1968; Nader et al., 2000). This method has already investigated in other studies using the experimental trauma paradigm; James et al. (2015) tested the effects of reactivating memories of experimental trauma and subsequently instructing participants to play Tetris, which has previously been shown to reduce subsequent intrusion development (Deeprose et al., 2012). This study found that this intervention did indeed reduce subsequent memory intrusions, indicating that interventions that reduce memory intrusions when employed in the immediate aftermath of encoding might also prove useful after reactivation of the trauma memory at a later time. Hence, in terms of the current findings, it would be interesting to investigate whether engaging in wakeful rest immediately following reactivation could reduce memory intrusions.

6.10 Future directions

Based on the findings presented in this thesis as well as previous findings, it would be interesting to investigate the use of interventions meant to enhance hippocampal memory consolidation in the aftermath of a traumatic event. Studies applying findings from experimental trauma to clinical settings are beginning to emerge but are still in their infancy. As mentioned previously, two studies have investigated the effects of playing Tetris following trauma or emergency surgery and found that this intervention reduced intrusions (Iyadurai et al., 2017; Horsch et al., 2017). Our studies suggest that enhancing memory consolidation through a period of wakeful rest in the aftermath of trauma could also prove beneficial to people who have been exposed to a traumatic experience. Also, as described above, it would be interesting to test effects of wakeful rest on intrusion development when applied following reactivation of the trauma memory trace.

6.11 Conclusion

In this thesis, a series of behavioural studies and one fMRI study has investigated the relationship between memory intrusions and deliberate memory and the role of post-encoding processing in this context. Here, it is demonstrated that 1) enhancing memory consolidation by facilitation of post-encoding processing shows the same benefit for deliberate memory for negative information as has previously been observed for neutral information (Chapter 3), while 2) wakeful rest following encoding of experimental trauma material reduces memory intrusions and enhances memory performance (Chapter 4). The fMRI experiment began to examine the neural activity during and immediately following encoding that supports subsequent deliberate memory and subsequent intrusions, with preliminary indications of differential dependence on the hippocampus and amygdala respectively. The potential clinical applications of these findings for interventions targeting secondary prevention of memory intrusions were discussed.

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8 APPENDIX

Table A1. List of videos in used Experiments 2.2 and 3.1

No	Video	Duration	Narrative	Origin	Emotion
1	Supermarket	41s	A woman and her son are shopping at a supermarket. They ask a shop assistant for help and the woman's phone rings.	Clip from the TV series 'Lost'	Neutral
2	Café	51s	A woman enters a café where a man is on the phone with someone. The woman orders a coffee and listens to the man's conversation	Clip from the movie 'Meet Joe Black'	Neutral
3	Barbeque	46s	A family is having a barbeque in their garden with some friends. They are preparing the food while the children are playing with their dog. Later, they sit down and eat.	Clip from the movie 'K-PAX'	Neutral
4	Baking bread	52s	The video shows a large bakery in the Middle East. It is shown how pita bread is prepared, baked, transported to the market by bike and sold.	Real life clip from liveleak.com	Neutral
5	After school	41s	Two teenagers, a boy and a girl, exit their school. The girl is picked up and the parent greets her friend	Clip from movie	Neutral
6	Buying breakfast	56s	A bus driver enters a café where he meets a friend. They buy coffee, leave the café and wave	Clip from the movie 'Speed'	Neutral

			goodbye outside		
7	Choosing wine	50s	A man and a woman are talking about which wine to choose	Clip from the movie ‘Sideways’	Neutral
8	Swim Test	52s	A group of people are about to take a swim test. When they are told to jump in, a few of them don’t jump in and laugh at the rest.	Clip from movie	Neutral
9	Visit	54s	A pregnant girl pays a visit to a man. They go to the kitchen, he offers her some juice and they talk about his work	Clip from the movie ‘Juno’	Neutral
10	Market	52s	A journalist visits an Asian market where people are gambling and playing different games. Some think it’s fun to be filmed while others try to avoid the camera.	Real life clip from liveleak.com	Neutral
11	Ambulance	49s	A woman is in an ambulance and medical staff are intubating her	Real life clip	Negative
12	Woman attacked	53s	A woman is raped and beaten in an underpass	Clip from the movie ‘Irreversible’	Negative
13	Bangkok bomb	49s	The aftermath after a bomb has gone off. A man has lost his legs and is lying in the street	Real life clip from liveleak.com	Negative
14	Electrocuted man	48s	A man walks on top of a train and is electrocuted	Real life clip	Negative
15	Traffic accident Ghana	49s	Aftermath of a traffic accident in Ghana. A father is holding his dead son and people are carrying away the dead	Real life clip	Negative
16	Lion attack	51s	A man is being mauled by a lion. The lion pulls the man further away and some people arrive and shoot the lion	Real life clip	Negative

17	Nightclub fight	57s	Two men get into a violent fight in a nightclub. Others are cheering as one man is hit in the head with a fire extinguisher	Clip from the movie ‘Irreversible’	Negative
18	Shark	53s	A woman is attacked by a shark and sustains severe injuries to her leg. She is brought to the beach and medics arrive.	Real life clip	Negative
19	Moped accident	50s	A car crashes into a moped. The driver is in shock and calls for help. A policeman arrives	Real life clip	Negative
20	Skiing accident	53s	A man is in a bloody accident as he is hit in the head while skiing. His son finds him and help arrives	Real life clip	Negative

Table A2. List of videos used in Experiment 3.2

No	Name	Duration	Narrative	Origin	Valence
1	01_Neg_16s	16s	Train hits truck	Acquired from www.liveleak.com	Negative
2	02_Neg_16s	16s	Ambulance intubation	Original trauma film	Negative
3	03_Neg_16s	16s	Rollercoaster accident	www.liveleak.com	Negative
4	04_Neg_16s	16s	Man kicks woman in face	From the film 'Irreversible'	Negative
5	05_Neg_16s	16s	Man with no legs		Negative
6	06_Neg_16s	16s	Person under car fire	www.liveleak.com	Negative
7	07_Neg_16s	16s	Explosion in street	From movie	Negative
8	08_Neg_16s	16s	Circus Lions attack	www.liveleak.com	Negative
9	09_Neg_16s	16s	Cyclist hit by car	www.liveleak.com	Negative
10	10_Neg_16s	16s	Car flys through air	www.liveleak.com	Negative
11	11_Neg_16s	16s	Electric shock on train	Original trauma film study	Negative
12	12_Neg_16s	16s	Ferris wheel boy falling	Original trauma film study	Negative
13	13_Neg_16s	16s	Ghana accident	Original trauma film study	Negative
14	14_Neg_16s	16s	Woman sets on fire	liveleak.com	Negative
15	15_Neg_16s	16s	Shark and	Internet	Negative

			diver		
16	16_Neg_16s	16s	Woman hit by car	Internet	Negative
17	17_Neg_16s	16s	Lion biting man	Original trauma film study	Negative
18	18_Neg_16s	16s	Lorry crash victim	Original trauma films	Negative
19	19_Neg_16s	16s	Scooter hit by car	Internet	Negative
20	20_Neg_16s	16s	Man hits man with fire extinguisher	From the movie 'Irreversible'	Negative
21	21_Neg_16s	16s	Polar Bear at zoo	liveleak.com	Negative
22	22_Neg_16s	16s	Plane crash	liveleak.com	Negative
23	23_Neg_16s	16s	Man shot by police	liveleak.com	Negative
24	24_Neg_16s	16s	Bitten by shark	liveleak.com	Negative
25	25_Neg_16s	16s	Ski accident	liveleak.com	Negative
26	26_Neg_16s	16s	Man jumps in front of train	liveleak.com	Negative
27	27_Neg_16s	16s	Tiger at Delhi zoo	liveleak.com	Negative
28	28_Neg_16s	16s	Car spins and rolls	liveleak.com	Negative
29	29_Neg_16s	16s	Car hits cyclists	Internet	Negative
30	30_Neg_16s	16s	Niagara falls suicide	Internet	Negative
31	01_Neut_16s	16s	Man gets out	Internet	Neutral

			of car and opens boot		
32	02_Neut_16s	16s	Man gets Nerf gun from drawer	Internet	Neutral
33	03_Neut_16s	16s	Restaurant in the sky	Internet	Neutral
34	04_Neut_16s	16s	Elephants in pool	Internet	Neutral
35	05_Neut_16s	16s	Man puts hand in photocopied black hole	Internet	Neutral
36	06_Neut_16s	16s	Cycling - man in Mask costume	Internet	Neutral
37	07_Neut_16s	16s	Man get woman's legs out of drawer	Internet	Neutral
38	08_Neut_16s	16s	Making a table	youtube.com	Neutral
39	09_Neut_16s	16s	Fishing	youtube.com	Neutral
40	10_Neut_16s	16s	Cooking steak	youtube.com	Neutral
41	11_Neut_16s	16s	Swimming in sea	Internet	Neutral
42	12_Neut_16s	16s	Guys drinking shots	Internet	Neutral
43	13_Neut_16s	16s	Break dancers	liveleak.com	Neutral
44	14_Neut_16s	16s	Man in cafe	Internet	Neutral
45	15_Neut_16s	16s	Cricket game	Internet	Neutral

46	16_Neut_16s	16s	Man leaves office	Internet	Neutral
47	17_Neut_16s	16s	Kids in street	Internet	Neutral
48	18_Neut_16s	16s	Football in park	Clip from youtube.com	Neutral
49	19_Neut_16s	16s	Woman washing dishes	Internet	Neutral
50	20_Neut_16s	16s	Man busking in covent garden	Internet	Neutral
51	21_Neut_16s	16s	Couple in office	Internet	Neutral
52	22_Neut_16s	16s	Skiing lesson	Internet	Neutral
53	23_Neut_16s	16s	Dance lesson	Internet	Neutral
54	24_Neut_16s	16s	Divers	Internet	Neutral
55	25_Neut_16s	16s	Buying trainers	Internet	Neutral
56	26_Neut_16s	16s	Driving lesson	Internet	Neutral
57	27_Neut_16s	16s	Golfing	Internet	Neutral
58	28_Neut_16s	16s	Campus tour	Internet	Neutral
59	29_Neut_16s	16s	Horses	Internet	Neutral
60	30_Neut_16s	16s	Class	Internet	Neutral

Table A3. List of videos used in Experiment 4.1

No	Video	Duration	Narrative	Origin	Emotion
1	Traffic accident Ghana	30s	Aftermath of a traffic accident in Ghana. A father is holding his dead son and people are carrying away the dead	Real life clip taken from the internet	Negative
2	Ambulance	30s	A woman is in an ambulance and medical staff are intubating her	From original trauma film study	Negative
3	Bangkok bomb	30s	The aftermath after a bomb has gone off. A man has lost his legs and is lying in the street	Real life clip from liveleak.com	Negative
4	Injured youths in bike accident	30s	Two teenagers have been injured in a traffic accident. One boy's leg is caught in motorbike and the other boy's leg has been run over by truck	Real life clip from liveleak.com	Negative
5	Victim arrives at hospital	30s	Man involved in motorbike accident arrives at hospital. Staff is working on him. His arm is mangled and foot has been torn off	Real life clip from the internet/Discorvery Channel	Negative
6	Eye surgery	30s	Details of eye surgery such as stiches shown	Real life clip from the internet	Negative
7	Face reconstruction	29s	Person is having nose reconstructed with cartilage taken from elsewhere on their body	Real life clip from the internet	Negative
8	Ferris wheel	30s	Child screams as he falls from top of ferris wheel	Real life clip	Negative
9	Ice hockey Accident	28s	Ice hockey player tackled and blood pours from throat	Real life clip from www.liveleak.com	Negative
10	Lion	30s	A man is being mauled by a lion. The lion pulls the man further away	Real life clip from www.liveleak.com	Negative
11	Lorry Crash	30s	Lorry crash in motorway. People are watching as rescue crew is carrying away the dead	From original trauma study	Negative
12	Leg surgery	30s	Detailed footage of leg	From the	Negative

			surgery	internet	
13	Military Hospital	30s	Man is screaming as medical staff works on his injured leg where metal has been used to stabilise the leg	From the internet	Negative
14	Nightclub fight	30s	Two men are in a violent fight at nightclub while other men are watching. One man is hit repeatedly with fire extinguisher	Scene from the movie 'Irreversible'	Negative
15	Scooter accident	30s	A man on a scooter is hit by a car in a traffic light. The driver gets out of the car and calls for help	From the internet	Negative
16	Woman attacked	30s	A woman is raped in an underpass	Scene from the movie 'Irreversible'	Negative
17	Electrocuted man	30s	Man stands on top of the train, reaches for wires and is electrocuted. Body burns	Scene found at www.liveleak.com	Negative
18	Scaffold accident	30s	Two men have been impaled by a pole. Medics arrive to help	Scene found at www.liveleak.com	Negative
19	Motorway crash	30s	Aftermath of large traffic accident in motorway. Bodies are put in silver containers and carried away	Real life scene, from previous trauma study	Negative
20	Subway	30s	Man stands on platform while train is approaching and falls/jumps onto tracks. Two men try to signal to incoming train	Scene found at www.liveleak.com	Negative

Table A4. List of videos used in Experiment 4.2

No	Video	Duration	Narrative	Origin	Valence
1	Choosing wine	31s	A man and a woman are talking about which wine to choose	Clip from the movie 'Sideways'	Neutral
2	Visit	30s	A pregnant girl pays a visit to a man. They go to the kitchen, he offers her some juice and they talk about his work	Clip from the movie 'Juno'	Neutral
3	Travelling	29s	A family drives to the airport and walks through the terminal	Clip from Youtube	Neutral
4	Swim Test	30s	A group of people are about to take a swim test. They talk about whether or not it is fair to have to do it as adults	Clip from movie	Neutral
5	Shirt shopping	30s	A man is looking for shirts in a shop and the shop assistant helps him	Clip from Youtube	Neutral
6	After school	29s	Two teenagers, a boy and a girl, exit their school. The girl is picked up and the parent greets her friend	Clip from movie	Neutral
7	Restaurant	29s	A man is sitting in a chinese restaurant waiting for his food and observing the staff	Clip from the movie 'Kinamand'	Neutral
8	Picnic table	29s	Two men are building a picnic table and then have a picnic	Clip from Youtube	Neutral
9	Party	30s	A woman says hello to friends at party	Clip from the movie 'Irreversible'	Neutral
10	Market	30s	A journalist visits an Asian market where people are gambling and playing different games. Some think it's fun to be filmed while others try to avoid the camera.	Real life clip from liveleak.com	Neutral
11	Ice cream man	30s	A man sells ice cream from a cart on the beach	Clip from liveleak.com	Neutral
12	Dog	33s	Man playing with his dog at	Clip from	Neutral

			his home	Youtube	
13	Classroom	30s	A teacher is asking children questions about a teddy bear	Clip from Youtube	Neutral
14	Cafe	30s	A woman is sitting in a café and listens to a man's conversation with someone on the phone	Clip from the movie 'Meet Joe Black'	Neutral
15	Buying breakfast	30s	A bus driver enters a café where he meets a friend. They buy coffee and leave the café	Clip from the movie 'Speed'	Neutral
16	Barbeque	29s	A family is having a barbeque in their garden with some friends. They are preparing the food while the children are playing with their dog.	Clip from the movie 'K-PAX'	Neutral
17	Baking bread	30s	The video shows a large bakery in the Middle East. It is shown how pita bread is baked and transported to the market by bike where it is sold.	Real life clip from liveleak.com	Neutral
18	Supermarket	29s	A woman and her son are shopping at a supermarket. They ask a shop assistant for help and the woman's phone rings.	Clip from the TV series 'Lost'	Neutral
19	House	31s	A man arrives at a house and is invited in where he says hello to other guests	Clip from the movie 'Sideways'	Neutral
20	School class	30s	A man who has just given a talk to a school class talks to a teacher	Clip from the series 'Ed'	Neutral
21	Traffic accident Ghana	30s	Aftermath of a traffic accident in Ghana. A father is holding his dead son and people are carrying away the dead	Real life clip	Negative
22	Nightclub fight	30s	Two men are in a violent fight at nightclub while other men are watching. One man is hit repeatedly with fire extinguisher	Scene from the movie 'Irreversible'	Negative
23	Lorry Crash	30s	Lorry crash in motorway. People are watching as rescue crew is carrying away the dead	From original trauma study	Negative

24	Ferris wheel	30s	Child screams as he falls from top of ferris wheel	Real life clip	Negative
25	Scooter accident	30s	A man on a scooter is hit by a car in a traffic light. The driver gets out of the car and calls for help	From the internet	Negative
26	Woman attacked	30s	A woman is raped in an underpass	Scene from the movie 'Irreversible'	Negative
27	Lion	30s	A man is being mauled by a lion. The lion pulls the man further away	Real life clip from liveleak.com	Negative
28	Ambulance	30s	A woman is in an ambulance and medical staff are intubating her	From original trauma film study	Negative
29	Bangkok bomb	30s	The aftermath after a bomb has gone off. A man has lost his legs and is lying in the street	Real life clip from liveleak.com	Negative
30	Electrocuted man	30s	Man stands on top of the train, reaches for wires and is electrocuted. Body burns	Scene found at liveleak.com	Negative
31	Scaffold accident	30s	Two men have been impaled by a pole. Medics arrive to help	Scene found at liveleak.com	Negative
32	Face reconstruction	29s	Person is having nose reconstructed with cartilage taken from elsewhere on their body	Real life clip from the internet	Negative
33	Leg surgery	30s	Detailed footage of leg surgery	From the internet	Negative
34	Military Hospital	30s	Man is screaming as medical staff works on his injured leg where metal has been used to stabilise the leg	From the internet	Negative
35	Injured youths in bike accident	30s	Two teenagers have been injured in a traffic accident. One boy's leg is caught in motorbike and the other boy's leg has been run over by truck	Real life clip from liveleak.com	Negative
36	Victim arrives at hospital	30s	Man involved in motorbike accident arrives at hospital. Staff is working on him. His arm is mangled and foot has been torn off	Real life clip from the internet/Discorvery Channel	Negative
37	Eye surgery	30s	Details of eye surgery such as stiches shown	Real life clip from the internet	Negative

38	Ice hockey Accident	28s	Ice hockey player tackled and blood pours from throat	Real life clip from liveleak.com	Negative
39	Motorway crash	30s	Aftermath of large traffic accident in motorway. Bodies are put in silver containers and carried away	Real life scene, from previous trauma study	Negative
40	Subway	30s	Man stands on platform while train is approaching and falls/jumps onto tracks. Two men try to signal to incoming train	Scene found at liveleak.com	Negative

Table A5. List of videos used in Experiment 5.1

No	Video	Duration	Narrative	Origin	Emotion
1	Traffic accident Ghana	30s	Aftermath of a traffic accident in Ghana. A father is holding his dead son and people are carrying away the dead	Real life clip taken from the internet	Negative
2	Ambulance	30s	A woman is in an ambulance and medical staff are intubating her	From original trauma film study	Negative
3	Bangkok bomb	30s	The aftermath after a bomb has gone off. A man has lost his legs and is lying in the street	Real life clip from liveleak.com	Negative
4	Injured youths in bike accident	30s	Two teenagers have been injured in a traffic accident. One boy's leg is caught in motorbike and the other boy's leg has been run over by truck	Real life clip from liveleak.com	Negative
5	Victim arrives at hospital	30s	Man involved in motorbike accident arrives at hospital. Staff is working on him. His arm is mangled and foot has been torn off	Real life clip from the internet/Discorvery Channel	Negative
6	Eye surgery	30s	Details of eye surgery such as stiches shown	Real life clip from the internet	Negative
7	Face reconstruction	29s	Person is having nose reconstructed with cartilage taken from elsewhere on their body	Real life clip from the internet	Negative
8	Ferris wheel	30s	Child screams as he falls from top of ferris wheel	Real life clip	Negative
9	Ice hockey Accident	28s	Ice hockey player tackled and blood pours from throat	Real life clip from www.liveleak.com	Negative
10	Lion	30s	A man is being	Real life clip	Negative

			mauled by a lion. The lion pulls the man further away	from www.liveleak.com	
11	Lorry Crash	30s	Lorry crash in motorway. People are watching as rescue crew is carrying away the dead	From original trauma study	Negative
12	Leg surgery	30s	Detailed footage of leg surgery	From the internet	Negative
13	Military Hospital	30s	Man is screaming as medical staff works on his injured leg where metal has been used to stabilise the leg	From the internet	Negative
14	Nightclub fight	30s	Two men are in a violent fight at nightclub while other men are watching. One man is hit repeatedly with fire extinguisher	Scene from the movie 'Irreversible'	Negative
15	Scooter accident	30s	A man on a scooter is hit by a car in a traffic light. The driver gets out of the car and calls for help	From the internet	Negative
16	Woman attacked	30s	A woman is raped in an underpass	Scene from the movie 'Irreversible'	Negative
17	Electrocuted man	30s	Man stands on top of the train, reaches for wires and is electrocuted. Body burns	Scene found at www.liveleak.com	Negative
18	Scaffold accident	30s	Two men have been impaled by a pole. Medics arrive to help	Scene found at www.liveleak.com	Negative
19	Motorway crash	30s	Aftermath of large traffic accident in motorway. Bodies are put in silver containers and carried away	Real life scene, from previous trauma study	Negative
20	Subway	30s	Man stands on platform while train is approaching and	Scene found at liveleak.com	Negative

			falls/jumps onto tracks. Two men try to signal to incoming train		
21	Boston Marathon	30s	Video from Boston marathon bombing, bomb goes off and people lie injured	Scene found at liveleak.com	Negative
22	Shark	30s	A woman is attacked by a shark and sustains severe injuries to her leg. She is brought to the beach and medics arrive.	Real life clip	Negative
23	Stabbing	30s	Two men are fighting in an underground station and one stabs the other while people watch	Real life clip from liveleak.com	Negative
24	Soldier shot	30s	Combat scene from Afghanistan. A helmet cam films a fellow soldier getting shot and the man with the camera shouts and runs to help him	Real life clip from liveleak.com	Negative
25	Supermarket	29s	A woman and her son are shopping at a supermarket. They ask a shop assistant for help and the woman's phone rings.	Clip from the TV series 'Lost'	Neutral
26	Picnic table	29s	Two men are building a picnic table and then have a picnic	Clip from Youtube	Neutral
27	Market	30s	A journalist visits an Asian market where people are gambling and playing different games. Some think it's fun to be filmed while others try to avoid the camera.	Real life clip from liveleak.com	Neutral
28	**Restaurant**	**29s**	**A man is sitting in a chinese restaurant waiting for his food**	**Clip from the movie 'Kinamand'**	**Neutral**

			and observing the staff		
29	Woman burning	30s	A couple sits in a restaurant and the woman catches fire from a flame/oil used for cooking. The man runs away in horror	Real life clip from liveleak.com	Negative
30	Hit and run	30s	A car who hits a person and drives off is caught on CCTV	Real life clip from liveleak.com /The Guardian	Negative

Table A6. Summary of imaging findings for view and rest

Region	Laterality	MNI coordinates x	y	z	z-score
Condition (view, rest)					
Effect of view > rest					
Middle occipital gyrus	R	44	-74	4	Inf
Inferior frontal gyrus (IFG)	R	42	14	26	Inf
Medial cingulate cortex (MCC)	L	-34	-4	48	7.81
Precuneus	R	22	-52	18	6.98
Rectal gyrus	R	2	54	-18	6.04
Basal forebrain		20	-4	-10	5.24
Supramarginal gyrus	L	-58	-26	36	4.89
Inferior parietal lobe	L	-46	-26	38	4.76
Amygdala†	R	22	-4	-12	5.04
	L	-20	-6	-12	4.52

$p<0.05$ FWE across whole brain unless stated; †$p<0.05$ FWE SVC

Table A7. Summary of imaging findings for recognition memory across encoding and post-encoding rest I.

Region	Laterality	MNI coordinates x	y	z	z-score
Memory (remembered, forgotten) x condition (view x rest)					
Main effect of remembered items (remembered > forgotten)					
Parahippocampal gyrus	R	18	0	-22	4.13
	L	-16	0	-22	3.28
Superior medial gyrus	R	4	64	10	4.04
Angular gyrus	L	-44	-56	34	4.02
Mid orbital gyrus	L	-10	56	-6	3.99
Superior frontal gyrus	L	-22	36	46	3.83
	R	16	44	38	3.52
Temporal pole	L	-30	12	-30	3.73
Middle temporal gyrus	R	54	-2	-24	3.63
	L	-54	-40	-4	3.31
Medial temporal pole	L	-50	14	-28	3.53
	R	34	16	-34	3.31
Cerebellum	L	-12	-38	-12	3.53
	R	42	-58	-42	3.33
IFG (p. orbitalis)	L	-36	18	-20	3.53
	R	46	30	-20	3.49
IFG (p. triangularis)	R	54	38	-2	3.19
Superior medial gyrus	L	-4	64	12	3.49
Middle frontal gyrus	L	-40	14	52	3.48
Precuneus	L	-2	-50	34	3.43
Inferior temporal gyrus	L	-58	-24	-18	3.34
Anterior cingulate cortex	R	10	50	12	3.31
Amygdala	L	-22	-4	-26	3.20
Middle orbital gyrus	L	-36	56	-8	3.19

$p<0.05$ FWE across whole brain unless stated; $^{+}p<0.05$ FWE SVC

Table A8. Summary of imaging findings for recognition memory across encoding and post-encoding rest II.

		MNI coordinates			
Region	Laterality	x	y	z	z-score
Positive effect of parametric modulator for recognised scenes					
Anterior cingulate cortex	L	-3	33	21	7.72
Medial cingulate cortex	L	-3	-8	48	
Posterior medial frontal lobe	R	10	-16	54	6.91
Precentral gyrus	L	-30	-20	50	
Postcentral gyrus	L	30	-27	48	
Inferior parietal lobule	R	46	-51	45	
Angular gyrus	L	-40	-58	42	
Hippocampus	R	30	-26	-9	4.88
	R	33	-27	-9	
Precuneus	L	-6	-63	32	
	R	16	-56	39	
Cerebellum	R	40	-56	-36	
Cerebellar vermis		-2	-44	-18	
Middle orbital gyrus	L	-38	45	9	
Inferior temporal gyrus	L	-56	24	-20	4.99
	L	-52	-24	-18	4.97
Middle temporal gyrus	L	-64	-26	-6	
	L	-57	-24	-16	
	L	-42	3	-30	
Inferior frontal gyrus	L	-38	27	28	
Middle frontal gyrus	L	-33	22	45	
Superior frontal gyrus	R	22	40	39	

$p<0.05$ FWE across whole brain unless stated

Table A9. Summary of imaging findings for intruding vs non-intruding videos

Region	Laterality	MNI coordinates x	y	z	z-score
Intrusions (intruded, non-intruded) x condition (view, rest)					
Main effect of intruding items (intruded > non-intruded)					
Amygdala†	L	-20	2	-16	3.21
Amygdala†					

$p<0.05$ FWE across whole brain unless stated; †$p<0.05$ FWE SVC