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Retrieved emotional context influences hippocampal involvement during recognition of neutral memories

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ABSTRACT

It is well documented that emotionally arousing experiences are better remembered than mundane events. This is thought to occur through hippocampus-amygdala crosstalk during encoding, consolidation, and retrieval. Here we investigated whether emotional events (context) also cause a memory benefit for simultaneously encoded non-arousing contents and whether this effect persists after a delay via recruitment of a similar hippocampus-amygdala network. Participants studied neutral pictures (content) encoded together with either an arousing or a neutral sound (that served as context) in two study sessions three days apart. Memory was tested in a functional magnetic resonance scanner directly after the second study session. Pictures recognised with high confidence were more often thought to have been associated with an arousing than with a neutral context, irrespective of the veridical source memory. If the retrieved context was arousing, an area in the hippocampus adjacent to the amygdala exhibited heightened activation and this area increased functional connectivity with the parahippocampal gyrus, an area known to process pictures of scenes. These findings suggest that memories can be shaped by the retrieval act. Memory structures may be recruited to a higher degree when an arousing context is retrieved, and this may give rise to confident judgments of recognition for neutral pictures even after a delay.

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1. Introduction

Memories for emotional or arousing events are remembered well and are often highly vivid even long after their occurrence (for reviews: Cahill and McGaugh (1998), Christianson (1992), Kensinger and Corkin (2004), LaBar and Cabeza (2006), Phelps (2006)). The hippocampus is a critical brain structure for encoding and retrieval of newly learned information (Alvarez and Squire, 1994; Moscovitch et al., 2005; Nadel and Moscovitch, 1997; Squire, 1992). The amygdala is considered to up-regulate hippocampal processing during encoding, consolidation (McGaugh, 2006; Richardson et al., 2004), and retrieval (Dolcos et al., 2005; Ritchey et al., 2008; Sharot et al., 2007; Smith et al., 2005, 2006, 2004; Sterpenich et al., 2009) leading to enhanced memory for arousing

Abbreviations: AAL, automated anatomical labelling; E-, encoding; FWE, family-wise error corrected; ITI, inter-trial interval; MNI, Montreal Neurological Institute; PPI, psycho-physiological interaction; R-, retrieval; ANOVA, analysis of variance; ROI, region of interest; SVC, small volume correction.

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events (LaBar and Phelps, 1998). However, the neural mechanisms via which emotion contributes to enhanced memory retrieval are unclear as they are difficult to isolate. First, emotional retrieval cues can inherently evoke online processing of sensory information that in turn evokes emotional responses and can influence retrieval. Second, mnemonic mechanisms may reinstate an emotional experience that occurred during encoding and influence retrieval. One way to isolate the neural mechanisms underlying the retrieval of emotion from perception evoked responses is to use neutral cues that have been associated with emotional context during encoding to test the emotional memory.

Memories for neutral content can be influenced by an arousing context at encoding. For instance, emotional context, such as emotional background pictures and emotional context sentences, can positively influence the recognition of neutral pictures/words embedded in these emotional contexts when tested in short succession (Maratos and Rugg, 2001; Smith et al., 2004). The previous studies also investigated the neural responses at retrieval shortly after encoding. They observed heightened involvement of the hippocampus and amygdala for retrieval of neutral contents embedded in emotional contexts, which is suggestive of enhanced memory and emotion processing at the time of retrieval for

neutral items arising from their study history. For a longer delay, memory persistence for neutral items encoded under a threat of shock has been shown (Dunsmoor et al., 2014, 2015), but less is known about the neural responses at the time of delayed retrieval.

Retrieved memories are not always veridical. Memories of emotionally arousing events are often vivid, detailed and accompanied by a high feeling of confidence, despite potential inaccuracy (Neisser and Harsch, 1992; Talarico and Rubin, 2003). Thus, if a retrieved memory is thought to have been encoded in an arousing context, this may enhance the subjective confidence for the retrieved memory, even though this may not result from a proper reconstruction of the past event. The hippocampus has been reported to show more activity when the retrieved memory is accompanied by a feeling of recollection compared to a feeling of familiarity (Diana et al., 2007a, 2007b; Weis et al., 2004). Moreover, item-emotion binding via the amygdala has been suggested to be the key for persistence of emotional memories (Yonelinas and Ritchey, 2015). This raises the question whether hippocampal and amygdala involvement at retrieval may be influenced by the retrieved emotional association independent of veridical accuracy.

In the current study, we asked whether an arousing context at encoding influences the retrieval of memory for associated neutral content, and whether this potential influence changes as a function of time. Furthermore, we asked whether the memory of neutral content is modulated by the encoded and retrieved context. To address these questions, participants studied two sets of neutral pictures (content) experienced together with either an unpleasant arousing or a neutral non-arousing sound (context) at two occasions three days apart. To observe neural correlates of retrieval and the possible changes with time, we tested recognition memory for the pictures (content memory) and cued-recall of the associated sounds (context memory) for both recently (same day) and remotely (three days earlier) studied stimulus sets. Neural responses were recorded using functional magnetic resonance imaging (fMRI) during the retrieval session. We predicted enhanced memory for neutral content encoded within an arousing context over a non-arousing context, and possible influences of the encoded and retrieved context on the neural mechanisms associated with retrieval of neutral content.

2. Materials and methods

2.1. Participants

Twenty-four healthy, right-handed, male participants ($M=22.1$ years, $SD=2.8$, range: 18–28 years) with no neurological or psychiatric history were recruited from the university campus in Nijmegen. We restricted our participant population to males to avoid potential gender lateralisation (Cahill, 2010) and possible effects of the menstrual cycle in women (Toffoletto et al., 2014). All participants provided written informed consent and were compensated with either money or study credits. The study was approved by the institutional ethics committee (CMO Region Arnhem-Nijmegen, the Netherlands). Due to too few trials (less than 5) in one or more of the critical conditions of interest, data of four participants were excluded from the fMRI analyses.

2.2. Procedure

2.2.1. Day 1: remote memory encoding and sound rating

Upon arrival, participants were given an overview of the experiment. Next, participants intentionally encoded a set of picture-sound associations. The neutral pictures were delivered together with either an unpleasant arousing or a neutral non-arousing sound by a computer in a sound attenuated room. Participants

were instructed to remember the picture-sound associations and were explicitly told that their memory would be tested later, on Day 1 and again on Day 4. The sounds were presented through a headphone and the volume was adjusted individually to a comfortable volume level for each participant. Twenty pictures of landscapes were with- and 20 were without buildings. Each of these pictures were paired with one of the 10 unpleasant arousing sounds (resulting in each sound being associated to four different pictures). Another set of 40 pictures (20 pictures with- and 20 without buildings) were paired with one of 10 the neutral non-arousing sounds. Thus there were a total of 80 picture-sound pairs for the Day 1 encoding session (see Section 2.3 below). Prior to the encoding session, a practice session of six trials was given to acquaint the participant with the task using additional stimuli not used in the actual experiment.

The encoding session consisted of two runs and each pair appeared once in each run (Fig. 1A and B). For every trial, after an inter-trial interval (ITI) of 1 s, a picture appeared on screen for 3 s, of which the last 1 s overlapped with the sound stimulus, similar to what is done in delay conditioning paradigms (Knight et al., 2004). At the offset of the sound, participants were prompted to provide a response within a time limit of 2 s. During the first run, participants were asked to indicate whether the picture included a building (yes=left control key, no=right control key), and during the second run, they were asked to rate whether the sound was arousing or not (yes=left, no=right). The response to this question during the second run was used to categorise Encoded context as either Arousing or Neutral. To avoid rapid switching from arousing to neutral context, the trials were presented in a pseudo-random order such that three to five trials with the same sound category (Arousing/Neutral) were blocked together. Between blocks, an extra inter-block interval of 4 s was inserted. There was a break of 5 min between the first and the second run. We opted to have two encoding sessions to reinforce learning of the picture-sound pairs as to ensure memory retention after a 72 h delay. Furthermore, by probing the orientation question to both the picture (building/landscape) and the sound (arousing/neutral), we hoped that participants would pay attention to both the visual and the auditory information of the studied material.

In order to validate whether our choice of sound context was according to the experimental manipulation, participants rated each sound presented during the encoding session again during the sound rating session, but this time on two dimensions in two runs. In the first run, participants rated on 6-point Likert scales the pleasantness of the sounds (1=pleasant, 6=unpleasant), and in the second run the arousal level of the sounds (1=calm, 6=arousing). Participants responded at their own pace during this session.

2.2.2. Day 4: recent memory encoding, sound rating, and retrieval test

Three days after the remote memory encoding session, participants returned to the laboratory for a recent encoding session following the same routine as on Day 1. First, subjects studied a second set of 80 novel picture-sound associations (different pictures from the remote set, but the same sounds as the remote set). Next, they rated the sounds again identical to the procedure on Day 1.

After a 15-min break, subjects entered the magnetic resonance imaging (MRI) scanner for a recognition test (Fig. 1C). All pictures from the remote ($N=80$, encoded on Day 1) and recent ($N=80$, encoded on Day 4) sets, and another set of pictures (new, $N=80$) were presented once each in random order. Each trial started with a picture appearing on the screen for 2 s. To assess content memory, participants were prompted to indicate via a button press whether they thought the picture was old (studied in one of the

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