CORTEX 91 (2017) 142–156

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Special issue: Research report

Recapitulation of emotional source context during memory retrieval

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ARTICLE INFO

Article history:
Received 26 June 2016
Reviewed 17 August 2016
Revised 9 September 2016
Accepted 3 November 2016
Published online 16 November 2016

Keywords:
Recapitulation
Emotion
Memory
Source memory
Reactivation

ABSTRACT

Recapitulation involves the reactivation of cognitive and neural encoding processes at retrieval. In the current study, we investigated the effects of emotional valence on recapitulation processes. Participants encoded neutral words presented on a background face or scene that was negative, positive or neutral. During retrieval, studied and novel neutral words were presented alone (i.e., without the scene or face) and participants were asked to make a remember, know or new judgment. Both the encoding and retrieval tasks were completed in the fMRI scanner. Conjunction analyses were used to reveal the overlap between encoding and retrieval processing. These results revealed that, compared to positive or neutral contexts, words that were recollected and previously encoded in a negative context showed greater encoding-to-retrieval overlap, including in the ventral visual stream and amygdala. Interestingly, the visual stream recapitulation was not enhanced within regions that specifically process faces or scenes but rather extended broadly throughout visual cortices. These findings elucidate how memories for negative events can feel more vivid or detailed than positive or neutral memories.

1. Introduction

The hallmark of episodic memory is the ability to bring back to mind the contextual and source details associated with an event (Tulving, 1972). This ability to mentally travel back to the time of encoding during retrieval is a central feature of several memory theories (Morris, Bransford, & Franks, 1977; Moscovitch et al., 2005; Rolls, 2000; Tulving & Thomson, 1973) and supported by studies of reinstatement and recapitulation—reactivation of the cognitive and/or neural processes that were engaged at encoding at the time of retrieval (Buckner & Wheeler, 2001; Rugg, Johnson, Park, & Uncapher, 2008; Waldhauser, Braun, & Hanslmayr, 2016; Wheeler, Petersen, & Buckner, 2000)—sometimes referred to as ecphory (Tulving, 1976, 1983; also see; Bowen & Kark, 2016; Waldhauser et al., 2016).

Empirical studies of recapitulation have shown that when recalling a visual memory, visual cortices that were active during encoding become reactivated during retrieval and likewise retrieval of an auditory memory activates auditory cortices, even when that visual or auditory information is no longer present at retrieval (Gottfried, Smith, Rugg, & Dolan, 2004; Nyberg et al., 2000; Slotnick, 2004; Wheeler & Buckner, 2004; Wheeler et al., 2000). Several researchers have also

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http://dx.doi.org/10.1016/j.cortex.2016.11.004

established reactivation of content-specific brain regions. The fusiform gyrus contains a portion—often referred to as the fusiform face area (FFA)—that is consistently active during the perception of faces (Kanwisher & Yovel, 2006), and retrieval of words studied in the context of faces has been shown to reactivate that fusiform region, even when the words were presented alone at retrieval (Skinner, Grady, & Fernandes, 2010). Similarly, content-specific reactivation has been found for images previously paired with faces (in the FFA) and with words (in the left middle fusiform cortex, an area sensitive to word reading; Cohen & Dehaene, 2004) even when those images were not presented with the face or word at retrieval (Hofstetter, Achaibou, & Vuilleumier, 2012).

These findings of content-specific reactivation suggest that neural processes at retrieval involve similar neural processes to those that were engaged when the information was originally encoded. In fact, recapitulation may explain why, when we remember, it often feels as though we are re-experiencing the event. Indeed, some research has suggested that recapitulation during recognition may be greater when individuals have the subjective experience of recollection as compared to when their memories are based on feelings of familiarity with no retrieval of specific detail (Johnson & Rugg, 2007; Johnson, Minton, & Rugg, 2008; Johnson, Price, & Leiker, 2015; Waldhauser et al., 2016; Wheeler & Buckner, 2004). Just as the sensory processes implemented during mental imagery share overlap with those implemented during perception (e.g., Ishai, 2010), the processes that allow someone to bring to mind a prior event appear to overlap with the processes that were invoked during the original occurrence of that event.

What is relatively unknown is how emotional valence influences recapitulation. Extensive research has suggested that compared to neutral, emotional memories—negative memories in particular—tend to be remembered vividly, with greater feelings of re-experiencing and with an overall emotional memory enhancement (see Phelps & Sharot, 2008 for a review). Most theories of emotional memory have explained this enhancement via processes engaged at encoding or consolidation (Mather & Sutherland, 2011; McGaugh, 2000, 2004; Yonelinas & Ritchey, 2015), yet there is also evidence that emotion can influence retrieval processes. For instance, even when retrieval cues are neutral, fMRI studies have demonstrated that when the studied content associated with those retrieval cues is emotional, there is greater activity in regions including the amygdala (Daselaar et al., 2008; Smith, Henson, Dolan, & Rugg, 2004) and the hippocampus (Ford, Morris, & Kensinger, 2014), and there is enhanced connectivity between those two regions (Smith, Stephan, Rugg, & Dolan, 2006) compared to when the memory target is neutral. These results demonstrate that the emotion present during an encoded episode can influence the processes that arise in response to a neutral cue at retrieval (see also ERP evidence from Jaeger, Johnson, Corona, & Rugg, 2009; Maratos, Allan, & Rugg, 2000; Smith, Dolan, & Rugg, 2004).

Additional research has suggested that emotional valence may also be of importance. Negative events are sometimes remembered more vividly than positive (see Kensinger, 2009 for a review) and, relatedly, negative events (e.g., financial loss) outweigh the impact of a relatively equivalent positive event (e.g., financial gain) suggesting that "bad is stronger than good" (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; see also; Tversky & Kahneman, 1991). Patients with amygdala damage tend to show greater deficits retrieving negative emotional memories than positive (Buchanan, Tranel, & Adolphs, 2006), although the reason for that asymmetry is unknown. There is also an increasing literature demonstrating that negative and positive stimuli engage different brain processes at encoding, and that this may lead to differences in the type of information available at retrieval. For example, retrieval of positive events engages frontal areas, and retrieval of negative events engages more posterior sensory regions (Markowitsch, Vandekerckhove, Lanfermann, & Russ, 2003) which is in line with evidence that frontal and sensory regions are engaged during encoding of emotionally positive and negative stimuli, respectively (Mickley & Kensinger, 2008).

What is clear from these studies is that emotional valence can affect the processes engaged at encoding *or* retrieval, but the likelihood that an emotional experience comes to mind, the accompanying subjective vividness, and the memory for contextual source details, may be influenced by the *overlap* of processes engaged at encoding and retrieval. We hypothesize that negative stimuli are associated with greater recapitulation in sensory cortices and this leads to subjective memory enhancement. However, only a handful of studies have examined emotion-modulated recapitulation. Fenker and colleagues (Fenker, Schott, Richardson-Klavehn, Heinze, & Düzel, 2005) examined recapitulation during retrieval of neutral words previously paired with a fearful or neutral face at encoding. Using a region of interest approach, they found that bilateral FFA activation was stronger for emotional compared to neutral trials that were accompanied with a remember response, but amygdala and hippocampus did not show this same distinction. Smith, Henson, Dolan and Rugg (2004) studied recapitulation during retrieval of neutral objects previously superimposed on a negative, positive or neutral background at encoding. Compared to positive or neutral, successful recognition of stimuli associated with a negative background was correlated with reactivation of visual processing regions. Ritchey, Wing, LaBar and Cabeza (2013) also provided evidence that encoding-to-retrieval similarity correlated with amygdala activity specifically during the successful retrieval of negative items, although valence differences were not the focus of the study.

We are aware of only one study that has directly compared the recapitulation (i.e., encoding-to-retrieval overlap) associated with successful retrieval of negative and positive memories. In this study (Kark & Kensinger, 2015), participants encoded black and white degraded line-drawing versions of International Affective Picture System (IAPS; Lang, Bradley, & Cuthburt, 2008) images, which were followed by the full colored photograph. After a short delay (20 min), participants were given the line-drawings as retrieval cues and asked to make an old or new judgment. Correctly remembered positive and negative images engaged posterior regions of the ventral occipital-temporal cortex more than correctly remembered neutral images, reflecting recapitulation of the emotional aspects of the stimulus. Furthermore, negative stimuli in