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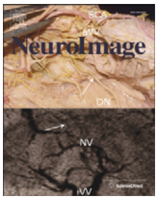

Reactivation of visual cortex during memory retrieval: Content specificity and emotional modulation

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ABSTRACT

Studies on memory retrieval suggest a reactivation of cortical regions engaged during encoding, such that visual or auditory areas reactivate for visual or auditory memories. The content specificity and any emotion dependency of such reactivations are still unclear. Because distinct visual areas are specialized in processing distinct stimulus categories, we tested for face and word specific reactivations during a memory task using functional magnetic resonance imaging (fMRI). Furthermore, because visual processing and memory are both modulated by emotion, we compared reactivation for stimuli encoded in a neutral or emotionally significant context. In the learning phase, participants studied pairs of stimuli that consisted of either a scene and a face, or a scene and a word. Scenes were either neutral or negative, but did not contain faces or words. In the test phase scenes were presented alone (one in turn), and participants indicated whether it was previously paired with a face, a word, or was new. Results from the test phase showed activation in a functionally defined face-responsive region in the right fusiform gyrus, as well as in a word-responsive region in the left inferior temporal gyrus, for scenes previously paired with faces and words, respectively. Reactivation tended to be larger in both the face- and word-responsive regions when the associated scene was negative as compared to neutral. However, relative to neutral context, the recall of faces and words paired with a negative context produced smaller activations in brain regions associated with social and semantic processing, respectively, as well as poorer memory performance overall. Taken together, these results support the idea of cortical memory reactivations, even at a content-specific level, and further suggest that emotional context may produce opposite effects on reactivations in early sensory areas and more elaborate processing in higher-level cortical areas.

Introduction

Neuroscience research suggests that remembering an episodic memory might entail the reactivation of some of the same brain regions that were engaged when encoding the corresponding information. For instance, it has been shown that recalling a visual memory activates visual cortices, and likewise the retrieval of an auditory memory activates auditory cortices (Nyberg et al., 2000; Wheeler et al., 2000). However, less is known about whether these reactivations indeed code for the specific content of retrieved memories, or reflect more general top-down modulation of sensory areas due to memory search similar to the “baseline shifts” in activity produced by endogenous attention (Kastner et al., 1999).

Only a few studies have examined content-specific reactivations in the visual modality (Polyn et al., 2005; Skinner et al., 2010; Woodruff et al., 2005). In a pioneer study by Polyn et al. (2005), subjects freely recalled a list of previously seen pictures of famous places, famous faces, and familiar objects, while their brain activity during retrieval was classified according to a multi-voxel pattern analysis trained on brain responses to these different categories. The classifier was able to categorize brain activation several seconds prior to the successful verbal recall of memorized items. This effect was attributed to internal cueing signals that serve to focus memory search on previously learned material and thus guide the retrieval of specific items (Polyn and Kahana, 2008), consistent with the fact that recall tended to occur in a blocked manner (i.e. faces, places, or objects were retrieved in series of about 3–6 successive items from the same category). However, the classification maps included several brain regions, and the univariate analysis of content-specific regions of interest (ROIs) showed no significant increase in activity for faces in fusiform

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Abbreviations: FFA, fusiform face area; VWFA, visual word form area; MTL, medial temporal lobe; DLPFC, dorsolateral prefrontal cortex; OFC, orbitofrontal cortex; RSC, retrosplenial cortex; IFG, inferior frontal gyrus.

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gyrus during recall. In another study (Woodruff et al., 2005), volunteers encoded either pictures or names of objects, and were later presented with test names that had to be judged as corresponding or not to a studied item (using a remember-know procedure). The authors observed activation in the lateral fusiform for the contrast of recollecting words vs pictures, but in the anterior fusiform for the reverse contrast, suggesting a regionally specific reinstatement of cortical activity during the retrieval of words vs objects. However, there was no evidence that these subregions within the fusiform cortex were content-specific (i.e. showing discriminative responses to word or object). In a more recent study (Skinner et al., 2010), to-be-remembered nouns were seen with intact or scrambled faces, and subsequently presented alone for recollection testing. Correct recognition yielded some reactivation in a face-specific region of the fusiform cortex, when comparing the retrieval of nouns paired with faces vs those paired with scrambled faces. However, although these data again suggest that visual regions implicated during stimulus encoding are also recruited during retrieval, they do not provide direct evidence for content-specific reactivation since no comparison was made with the retrieval of memories with another visual content. Words alone may also activate fusiform regions nearby the face-selective area (Cohen and Dehaene, 2004). In addition, increases in fusiform cortex could potentially reflect top-down cueing signals or attentional effort during memory search (Kastner et al., 1999; Polyn and Kahana, 2008), rather than the actual content of retrieved information. Furthermore, other studies have reported that activation to faces and places in category-selective visual areas correlates with successful encoding (and subsequent memory success) but not with retrieval (Prince et al., 2009).

The first goal of the current study was therefore to test for content-specific cortical reactivation using two different classes of visual stimuli known to recruit distinct areas in human visual cortex, namely faces and words (Kleinschmidt and Cohen, 2006). Abundant neuroimaging work has shown that perception of faces differentially activates a region in the (mostly right) lateral fusiform, hence termed the "fusiform face area" (FFA: Kanwisher and Yovel, 2006), whereas word reading activates a distinct region in the (mostly left) middle fusiform cortex, often called the "visual word form area" (VWFA: Cohen and Dehaene, 2004). In addition, memory for word and face stimuli are known to be associated with a preferential lateralization in medial temporal lobe structures (e.g. hippocampus) of the left and right hemisphere, respectively (for retrieval: Eldridge et al., 2000; see also Henson, 2005 for review; for encoding: Kelley et al., 1998), such that content-specific reactivation might lead not only to regionally-selective but also hemispheric-selective increases during retrieval. Furthermore, while previous memory studies used either spontaneous recall (Polyn et al., 2005) or cued recall with word prompts (Skinner et al., 2010; Wheeler et al., 2000; Woodruff et al., 2005), here we employed photographs of scenes with mixed content (but without people or text) as memory cues, in order to explore if a reactivation would still be observed even when complex and meaningful visual information is concomitantly processed by the visual system. During encoding, our participants saw scenes paired with either a face or a word that was irrelevant to the scene content; recall was later probed by presenting the scenes alone and asking participants to report whether these were previously seen with a face or word. We hypothesized that successful recall would be associated with selective increases in face- or word-responsive visual areas as a function of the stimulus previously paired with the scene.

In addition, our second goal was to test whether visual reactivations would be modulated by the affective context associated with the to-be-remembered information. Hence, half of the scenes were neutral (e.g. mug on a table, street with vehicles), and half were negative (e.g. mouldy food, car crash). Memory is known to be boosted for emotionally significant material (Dolan, 2002; Talmi et al., 2007b) or for neutral stimuli seen in emotional contexts (Adolphs et al., 2005; Cahill and McGaugh, 1995), with a tendency to be more richly experienced during subsequent recollection, particularly when negative (Kensinger and Corkin, 2003; Ochsner, 2000). A vivid recollection of the sensory features of life-threatening events is also characteristically present in memories associated post-traumatic stress disorder (Hackmann and Holmes, 2004). These effects are thought to reflect a strengthening of memory traces under the influence of emotional signals from amygdala and other neuro-hormonal pathways, which can modulate both hippocampal systems and sensory cortical areas (Buchanan, 2007; LaBar and Cabeza, 2006). Accordingly, emotional stimuli are known to lead to enhanced activation of extrastriate visual areas (Sabatinelli et al., 2007), an effect dependent on amygdala inputs and presumably leading to greater attention and greater memory for these stimuli (Dolan, 2002; Vuilleumier et al., 2004). On the other hand, some studies found that emotion can increase memory for central emotional information but at the expense of more peripheral background information (Kensinger et al., 2007), or even reduce memory for specific details while enhancing the general gist of the original emotional events (Adolphs et al., 2005).

Here we therefore investigated how memory recall and any corresponding cortical reactivation in visual areas would be modulated for stimuli that were previously paired with an emotional scene context, relative to a neutral context. Specifically, we tested for differential increases or decreases in face-selective (FFA) or word-selective regions (VWFA) during recall when the faces or words, respectively, had previously been seen with a negative scene. Note that in our paradigm, content-specific reactivation could be measured in response to the scene cue presented alone during recall, without actually seeing a face or word. Moreover, because faces and words themselves were always neutral, any differential increase in FFA or VWFA could not be explained by differences in stimulus distinctiveness or familiarity. To our knowledge, only a single study reported emotional effects on visual responses evoked by words previously associated with faces. In this study (Fenker et al., 2005), participants first encoded face–word pairs, where faces were either neutral or fearful, and then were tested on remember/know judgments in response to word cues. Greater activation was seen in the fusiform cortex when recalling words previously paired with fearful faces compared to neutral faces. Unlike this study, however, here we examined explicit recall of face vs word items associated with scenes, and tested whether content-specific visual reactivation would be modulated even when emotional information is not in the to-be-remembered, but in the associated context (i.e. the scenes).

Material and methods

Participants

18 healthy native French speakers (2 left-handed, 9 females, age range 20–37 mean: 25 years) participated in our experiment and gave written informed consent.

Stimuli

120 neutral and 120 negative scene pictures were compiled from various sources (including IAPS (Lang et al., 2008) and our own dataset). These scenes had various contents (objects, streets, houses, landscapes, etc.) but importantly were devoid of faces, humans, and text. All scenes (together with a group of more positive scenes, not used in our imaging study) were rated for emotional parameters (valence, arousal and dominance, each on a scale from 0 to 100; (see Bradley and Lang, 1994)), by an independent group of 10 subjects (not included in the imaging session). Based on these ratings, the 90 most neutral (mean valence: 58, arousal: 45) and the 90 most