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Research report

Reinstatement of encoding context during recollection: Behavioural and neuroimaging evidence of a double dissociation

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HIGHLIGHTS

- Participants studied words paired with famous faces or places, or scrambled images.
- Brain activation compared during recollection of words presented alone.
- Recollection was higher for words studied with meaningful visual contexts.
- Double dissociation of brain activation found in the FFA and PPA.
- Results provide strong evidence of cortical reinstatement during recollection.

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ABSTRACT

In both a behavioural and neuroimaging study, we examined whether memory performance and the pattern of brain activation during a word recognition task differed depending on the type of visual context presented during encoding. Participants were presented with a list of words, paired with either a picture of famous face, a famous scene, or a scrambled image, to study for a later recognition test. During the recognition test, participants made 'remember', 'know', or 'new' responses to words presented alone. In the neuroimaging experiment, the retrieval phase was scanned using event-related fMRI and brain activation was compared for remember and know responses given to words studied with famous faces and famous scenes. Behaviourally, in both studies, memory was enhanced if initial encoding was accompanied by a meaningful image (famous face or famous scene) relative to a scrambled image which contained no semantic information. At the neural level, whole brain analysis showed a double dissociation during recollection: BOLD signal in the right fusiform gyrus (within the Fusiform Face Area) was higher for remember responses given to words studied with famous faces compared to famous scenes, and was higher in the left parahippocampus (within the Parahippocampal Place Area) for words studied with famous scenes relative to famous faces. No such differential activation was found for know responses. Results suggest that participants spontaneously integrate item and meaningful contexts at encoding, improving subsequent item recollection, and that context-specific brain regions implicated during encoding are recruited during retrieval for the recollective, but not familiarity, memory process.

Research on context-dependent memory and transfer appropriate processing have provided strong evidence for an overlap in memory processes engaged at encoding and retrieval (for examples see [26] and [39]). These ideas have been expanded to the biological level, articulated in the 'cortical reinstatement hypothesis'. According to popular forms of this model, cues provided at retrieval activate patterns of activity in the hippocampus, which in turn reinstate the pattern of activity produced at encoding (see, for example, [2]). This suggests that recollection involves both content-independent brain regions, including activation of the hippocampus, and content-specific brain regions that vary depending on the specific processes engaged during encoding [21,33]. Studies using functional neuroimaging have provided strong support for the reinstatement hypothesis, demonstrating overlap between the brain regions engaged at encoding and retrieval [18,27,28,42,47]. For example, [27] showed that the recognition of visual words,

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initially paired with sounds at encoding, activated primary and secondary auditory cortex at retrieval. These results suggest that context-information is stored in brain regions involved in the original processing of the context and that these cortical patterns of activity are reactivated at retrieval (for a review of such data see [5]). In the current study we tested this hypothesis, using both behavioural and neuroimaging data, by examining whether memory performance, and a priori predicted regions of brain activation during a word recognition task, differed depending on the type of visual context presented during encoding.

Related research has incorporated dual process theories of memory to determine whether the reinstatement of context-specific brain regions is found exclusively during recollection [20,45]. Dual process theories suggest that recognition may involve the retrieval of detailed contextual information about the learning episode, known as recollection, or a more nonspecific sense that an item has been previously encountered, known as familiarity [12,51]. At the behavioural level, research has shown that recollection and familiarity are differentially affected by divided attention at encoding, levels of processing, and speeded responding [51]. In addition, neuropsychological studies suggest that damage to the hippocampus impairs recollection and spares familiarity, whereas damage to the surrounding temporal lobe has been shown to impair familiarity and spare recollection [4,53]. Neuroimaging data provide converging evidence of this double dissociation [25] and additional research suggests that recollection and familiarity also differ in the frontal and parietal brain regions recruited [35,43].

If the reactivation of context-specific brain regions during retrieval represents the reinstatement of encoding context, such activation should be found during recollection, but not familiarity, as only the former process is believed to involve the retrieval of rich contextual detail. To test this hypothesis, [45] employed the remember-know paradigm, originally developed by [41]. In this procedure, participants study a list of items and, during a recognition test, are asked to state whether they 'remember' the item (i.e., if they can recall specific details about it from the study episode), whether they 'know' an item (i.e., if it is familiar but lacks specific details from the study episode), or whether they deem the item to be 'new', and not from the study list. Remember responses are believed to align with recollective memory processes, whereas know responses support familiarity-based recognition [50]. In [45]Wheeler and Buckner's (2004) study, participants studied words (e.g., dog) with accompanying related pictures (a picture of a dog), and on a later scanned recognition test using event-related fMRI, made remember, know, or new responses to the words presented alone. They found that activity in a region of the left inferior temporal cortex, known to be activated during the perception of visual information based on a previous experiment, was higher for remember than know responses, supporting their prediction. Additional research suggests that such reinstatement effects can be differentiated from content-insensitive regions activated during recollection, known as the 'core recollection network', including the hippocampus, which are activated regardless of the encoding context [21].

In our recent work [38], we used a recognition paradigm examining how the meaningfulness of context information present at encoding affects subsequent memory performance to provide additional evidence that context-sensitive brain regions are selectively engaged during recollection. In this paradigm, participants view target words presented with visual context information rich in meaning (such as the picture of a face) or low in meaning (such as a scrambled face) and subsequently perform a remember-know recognition test. Our behavioural work has shown that memory is higher for words studied with pictures of intact faces than for words studied with pictures of scrambled or inverted faces, and that these effects are specific to remember, and not know, responses [37]. We have additionally found that while meaningful encoding contexts increase subsequent recollection in younger adults, older adults fail to show this recollection benefit unless instructed to make an arbitrary link between the context and study word [36]. We suggested that younger adults spontaneously use elaborative processes to bind item and meaningful contexts, creating rich memory traces later retrieved using recollective memory processes.

We used this paradigm in conjunction with fMRI to provide strong support of the cortical reinstatement hypothesis [38]. As the processing of face information is known to elicit activation in the fusiform gyrus, known as the fusiform face area (FFA; [23,29]), we were able to define, a priori, the specific region of the brain that should be activated during recollection. We found that activation in the right fusiform gyrus was higher for remember responses given to words studied with faces than remember responses given to words studied with scrambled faces, and further, a comparison of know responses showed no such activation. In addition, a regression analysis demonstrated that activation in the right fusiform gyrus increased as the relative recollection benefit for words studied with faces as compared to scrambled faces increased. These results further demonstrate that the brain regions used to process context information at encoding are recruited at retrieval and extend this theory by suggesting that the extent of activation in context-specific brain regions is related to recollection performance. They additionally bolster our suggestion that participants spontaneously bind meaningful context information with study words at encoding and that this context information is exclusively retrieved during recollection.

In the current experiments, we extended this paradigm to investigate recollection benefits associated with the reactivation of context-specific brain regions. In both a companion behavioural and event-related fMRI study, participants studied words paired with either famous faces, famous scenes, or scrambled images and made remember, know, or new judgments to words presented alone. Famous face and famous scene contextual stimuli were chosen for two reasons. First, by choosing two different classes of stimuli that activate well-defined brain regions we can extend our previous work, which showed only a single dissociation. Such double dissociations of context reactivation have been shown in previous work. For example, [20] found that the brain activation at retrieval was higher in left occipital and anterior fusiform regions when study words were integrated with scene information at encoding whereas activation was higher in the ventromedial frontal cortex when study words were integrated into a sentence [21]. Similarly, Woodruff and colleagues [47] showed a double dissociation in the lateral and anterior fusiform regions depending on whether recognized words were studied with visual word or picture information. However, by using very specific contextual stimuli, pictures of famous faces and famous scenes, we can show a double dissociation using extremely well-defined context-specific brain regions. Research suggests that face and scene information are processed by distinct neural regions, known as the fusiform face area (FFA) and parahippocampal place area (PPA; [29]). In addition, the visual imagery of famous face and scene information is known to elicit activation in these distinct neural regions, suggesting that such stimuli are particularly apt to demonstrate a powerful double dissociation of reinstatement effects. [19] have used face and scene stimuli to demonstrate that stimuli-specific temporal and frontal lobe activation at encoding is related to subsequent memory performance. However, this study did not look at activation at retrieval. Following this approach, we believe that by using context-specific brain regions identified a-priori, we can make specific inferences regarding the nature of observed context-specific reactivation *at retrieval* which will augment the findings of studies examining more global patterns of brain activation (as in [21]).