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Evidence for cortical encoding specificity in episodic memory: memory-induced re-activation of picture processing areas

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Abstract

Functional magnetic resonance imaging (fMRI) was used to examine whether neural pathways used to encode pictures into memory were re-activated during retrieval of those memories. At encoding, subjects semantically classified common objects presented as pictures or words. At retrieval, subjects performed yes/no recognition memory judgments on words that had been encoded as pictures or as words. The retrieval test probed memory for the encoded item, but not memory for the modality of the encoded item (picture/word). Results revealed that a subset of the brain regions involved specifically in encoding of pictures were also engaged during recognition memory for the encoded pictures. Specifically, encoding of pictures relative to words engaged bilateral extrastriate visual cortex, namely fusiform, lingual, middle occipital, and inferior temporal gyri (Broadman area (BA) 18/19/37). Recognition memory judgments about words that were encoded as pictures relative to those that were encoded as words activated fusiform and inferior temporal gyri primarily in the left hemisphere. Thus, cortical areas originally involved in perception of a visual experience become part of the long-term memory trace for that experience. These findings suggest a neural basis for encoding specificity and transfer appropriate processing in human memory.

Keywords: fMRI; Declarative memory; Words; Pictures; Healthy adults; Explicit memory

1. Introduction

What is remembered depends upon how it was recorded into memory. This idea is central to two principles of memory that have broad behavioral support, encoding specificity and transfer appropriate processing. Encoding specificity states that encoding operations determine storage which in turn determines the effectiveness of retrieval-cues [29]. Transfer appropriate processing states that memory is enhanced to the extent that encoding operations are recapitulated at retrieval [19]. Thus, both principles predict an overlap between encoding and retrieval processes, psychologically, and by extension, in the brain. Specifically, both theories predict that brain regions activated during encoding ought to be re-activated during episodic retrieval.

Functional neuroimaging has visualized the overlap between brain regions underlying encoding and retrieval of the sensory modality of those encoding operations [22,33]. Subjects studied visual–auditory cue–target pairs and recalled the auditory information in response to the visual–cue at test. Regions in auditory cortex activated during encoding of auditory target stimuli were re-activated during visually cued recall. Functional imaging of cross-modality encoding and retrieval, therefore, provides evidence for the test-phase recapitualtion of modality-specific encoding operations.

Evidence for the neural overlap of encoding and retrieval operations *within* the same sensory modality remains inconclusive [18,20,21,23,31]. In these studies, study and test stimuli comprised the same materials (e.g. study-faces, test-faces) or evoked the same stimulus attributes (study-object location, test-objects in two locations). Thus, encoding operations (e.g. perception of faces and location) performed at study were performed again during the retrieval test. Therefore, encoding-related regions that were activated during the study-phase would also be activated during the test-phase. Indeed, activation patterns for non-studied words in a recognition memory test were the same as those observed for encoding words in the study-phase [2]. Thus, in within-modality encoding and retrieval tests, it is impossible to separate activation associated with encoding of test-phase stimuli from that associated with the recapitulation of encoding operations.

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One study that allowed for separation between activation due to encoding of test-phase stimuli and recapitulation of encoding operations failed to find conclusive evidence for overlap in brain regions underlying encoding and retrieval [13]. Subjects studied words and pictures and performed a recognition memory task using four types of retrieval-cues, study-phase words, pictures corresponding to study-phase words, study-phase pictures, and words corresponding to study-phase pictures. Visual materials presented at study differed from those at test in two retrieval conditions, pictures corresponding to study-phase words and words corresponding to study-phase pictures. These retrieval conditions, therefore, allow examination of the extent to which brain regions involved in material-specific encoding operations were re-activated during retrieval. Results revealed that brain regions associated with material-specific encoding were not activated significantly during retrieval. Studies of within-modality encoding and retrieval, therefore, have not visualized successfully the overlap in brain activation between encoding and retrieval.

We used functional magnetic resonance imaging (fMRI) to examine the extent to which picture-specific encoding regions were re-activated during episodic retrieval. At study, subjects encoded objects presented as pictures or words. At test, recognition memory was tested only with *words* that had been encoded as pictures or as words, or were novel. Thus, all test-phase stimuli were words and differed only in how they had been encoded. Therefore, observed activation differences between words that had been encoded as pictures and those that had been encoded as words could only be attributed to their material-specific mnemonic history rather than ongoing perception at test.

2. Methods

2.1. Participants

Eight (three men and five women) right-handed Stanford University students ranging in ages 19–29 years ($M = 22.6$) participated in the experiment for payment. All subjects were right-handed native English speakers without a history of substance abuse and neurological or psychiatric illness.

2.2. Stimulus materials

Stimulus materials consisted of 96 line drawings from Snodgrass and Vanderwart [27] and their verbal labels. Half of the stimuli were drawn from semantic categories of manufactured items (e.g. furniture, musical instruments) and the remaining half were drawn from semantic categories of natural items (e.g. animals, body parts). All stimuli were presented centrally within a 2.5 in. × 2.5 in. square border.

2.3. Task procedure

Stimuli were generated by a Macintosh G3 (Apple, Cupertino, CA) computer and back-projected via a magnet-compatible projector onto a screen that could be viewed through a mirror mounted above the participant's head. Subjects responded with an optical button held in their right hand and responses were recorded by a computer interfaced with the optical switch using the PsyScope button box [4].

Each subject performed three functional scans, encoding, repeated encoding, and recognition memory, each lasting 5 min and 42 s. Each scan consisted of six cycles with 19 trials per cycle. For the encoding scan, each cycle consisted of three blocks: pictures, words, and fixation. The picture and word blocks consisted of seven trials each, and the fixation block consisted of five trials of plus signs. Picture blocks consisted of line drawings of common objects. Word blocks consisted of names of common objects. Each trial lasted for 3 s and consisted of the stimulus item appearing for 2.5 s followed by a 0.5 s lag. Subjects were told to press the button in response to plus signs and to words and pictures that referred to a manufactured entity. In order to boost subsequent recognition memory, the encoding scan was repeated, and therefore, subjects encoded each picture and word stimuli twice. For the recognition memory scan, each cycle consisted of three blocks, words corresponding to encoded pictures, words encoded as words, and fixation. Each block of words consisted of seven trials, six old items and one new item, and the fixation block consisted of five trials of plus signs. Inclusion of only one novel item in each block ensured that the bulk of the activation measured at retrieval was due to previously presented stimuli. Subjects were told to press the button for plus signs and for items that they remembered from the previous scan regardless of whether they had seen them as pictures or words. For both the encoding and retrieval scans, the order of the three blocks in each cycle was varied in a latin-squares design in order to prevent subjects from predicting the nature of upcoming trials.

2.4. Imaging procedure

Magnetic resonance imaging was performed on a 1.5TGE whole-body scanner with a receive-only whole head coil for signal amplification. Twenty-nine coronal slices (6 mm, 0 mm skip, 3.43 mm inplane resolution) angled 90 degrees perpendicular to the AC-PC line covering the whole brain were imaged. Functional images were acquired every 3 s using a T2*-sensitive gradient echo spiral pulse sequence [9] with parameters of TR = 3000 ms, TE = 40 ms, FOV = 22 cm, 64 × 64 matrix, flip angle = 89°, and one spiral interleave. A total of 114 image volumes were acquired during each scan. Two dummy images (6 s) were collected and stimulus presentation began only after that period in order to allow for dissipation of gradient-induced auditory cortical activation [1]. A 3D SPGR T1-weighted volume (min full TE, flip angle = 15°, FOV = 24 cm, 0.94 mm resolution)