



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 (Brodmann 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. © 2002 Elsevier Science Ltd. All rights reserved.

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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 recapitulation 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. \times 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 \times 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)

and T1-weighted spin echo structural images (co-localized to the functional slices) were collected. Head movement was minimized by using a bite-bar formed with each subject's dental impression; residual motion was corrected using an automated registration algorithm [34].

2.5. Data analysis

Data were analyzed using SPM99 (Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB (Version 5.2 Mathworks Inc., Sherborn, MA). Following reconstruction and motion correction, images were normalized into a standard space [28] by first normalizing each subject's 3D anatomical volume to a normalized template, smoothing the normalized 3D volume using a 8 mm full width at half-maximum Gaussian kernel, and then normalizing each subject's inplane anatomical and functional image volumes to their smoothed normalized 3D volume. Normalized functional images were interpolated to 2 mm × 2 mm × 2 mm cubic voxels and spatially smoothed using a 8 mm full width at half-maximum Gaussian kernel.

Data were analyzed according to a mixed-effects general linear model. First, low-frequency covariates were removed and activation maps were generated using linear contrasts comparing the three types of blocks in the encoding and retrieval scan separately, for each subject. Second, activation maps for each contrast were averaged across subjects by treating subjects as a random effect to allow population inference [8]. Group averages were generated to identify picture-specific regions activated during encoding (i.e. picture versus word) and retrieval (i.e. words encoded as pictures versus words encoded as words) scans using a voxel-level height threshold of $P < 0.005$ uncorrected and a cluster-level spatial extent threshold of $P < 0.05$ corrected for multiple comparisons (following [7]). Interpretation at the level of clusters rather than single voxels is more meaningful when inferring activation patterns for whole brain volumes and also when making a priori predictions about anatomic regions of activation (retrieval activations are predicted based upon encoding activations). Third, in order to determine common regions of activation between picture-specific regions activated during encoding (picture versus word) and recognition memory (words encoded as pictures versus words encoded as words), a conjunction analysis [25] was performed using a height threshold of $P < 0.001$ uncorrected (SPM99 does not allow specification of a corrected cluster threshold for conjunction

analysis; therefore, only voxels active at $P < 0.05$ corrected are considered significantly active).

3. Results

3.1. Behavioral performance

During the encoding scan, response times did not differ reliably for pictures ($M = 743$ ms, S.D. = 147 ms) and words ($M = 773$ ms, S.D. = 134 ms), $t(7) = 1.7$, $P = 0.13$. Error rates were identical for pictures and words ($M = 1.2\%$, S.D. = 2.2%). During the retrieval scan, percentage of hits ("yes" responses to old items) did not differ for words that were encoded as pictures ($M = 89.9\%$, S.D. = 9.0%) and for words that were encoded as words ($M = 93.4\%$, S.D. = 6.8%), $t(7) = 1.1$, $P = 0.30$. False alarms ("yes" responses to new items) were identical for the two types of blocks ($M = 6.2\%$, S.D. = 8.6%). Subjects were slower to make recognition memory decisions for words that were encoded as pictures ($M = 910$ ms, S.D. = 164 ms) than for words that were encoded as words ($M = 796$ ms, S.D. = 117 ms), $t(7) = 3.2$, $P = 0.01$. This latency difference is consistent with encoding specificity and transfer appropriate processing principles because memory was accessed more efficiently when retrieval-cues matched exactly the encoded stimuli.

3.2. Imaging

3.2.1. Encoding scan

Regions that were involved in picture encoding were identified by directly comparing picture and word blocks (Table 1 and Fig. 1). Semantic classification of pictures relative to words activated primarily ventral regions of extrastriate cortex, bilaterally. Specifically, significantly activated foci were located in fusiform, lingual, middle occipital gyri (Brodmann area (BA) 18, 19/37). Although the global maxima for the large posterior cluster was located in left medial fusiform gyrus, that cluster extended laterally (local maxima $-42, -62, -18$) and posteriorly to include the lingual gyrus (local maxima $6, -76, 4$). Activation in the fusiform gyrus was more extensive in the left than right hemisphere. Furthermore, a significantly activated cluster was observed in the middle occipital gyrus in the right hemisphere. Greater extrastriate activation during picture than word processing does not reflect differences in inspection time or effort of semantic classification for the two types of materials because

Table 1

Location (in gyral anatomy, BA, and standard coordinates), global maxima, and size of significantly activated clusters during semantic classification of pictures relative to words

Location	BA	Z	Voxels	X	Y	Z	P corrected
L Fusiform Gyrus	18/19/37	4.33	1030	-17	-66	-8	0.0001
R Fusiform Gyrus	19/37	3.81	366	25	-54	-7	0.0001
R Mid Occipital Gyrus	18/19	3.79	469	37	-85	17	0.0001

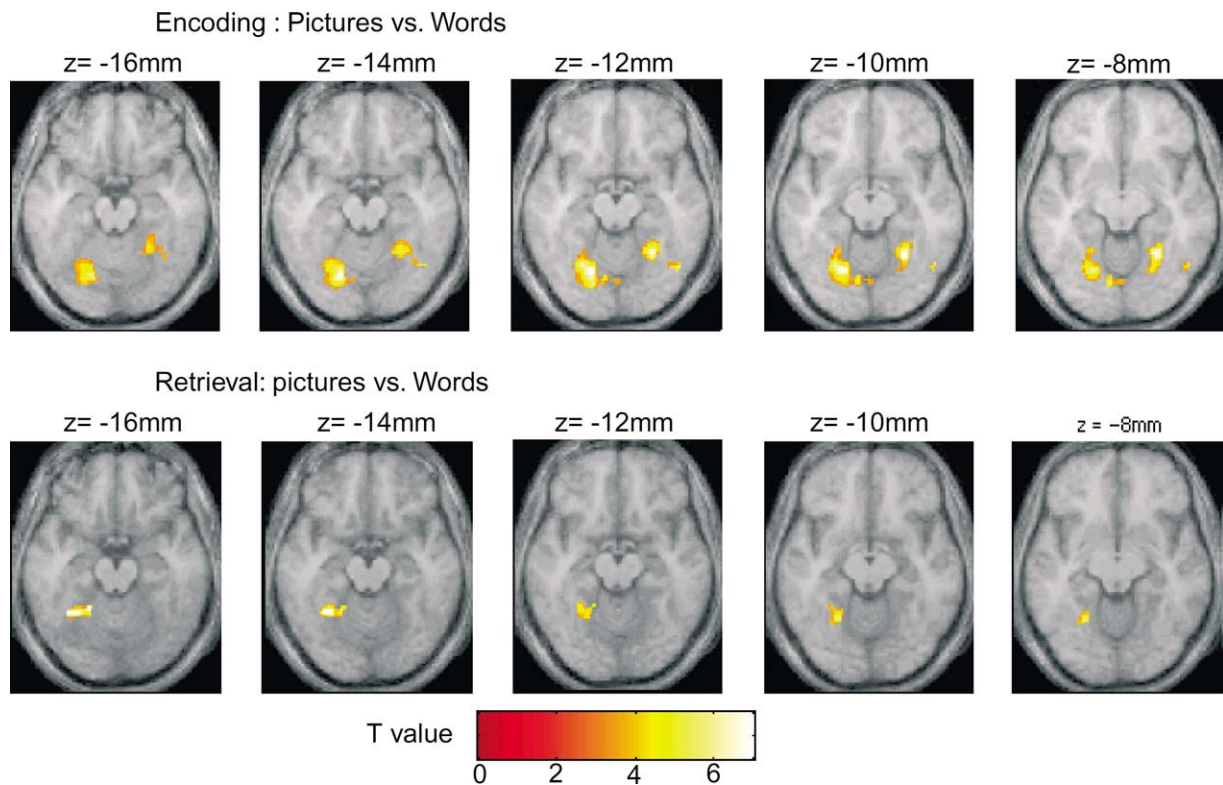


Fig. 1. Group average of activation overlaid upon axial slices of the group averaged brain (height threshold $P < 0.005$ uncorrected; cluster threshold $P < 0.05$ corrected) for encoding and retrieval scans.

reaction time and accuracy did not differ for pictures and words.

3.2.2. Retrieval scan

Regions involved in episodic retrieval of items that differed in their material-specific mnemonic history (e.g. how they had been encoded), the condition pertinent to

the present hypothesis, were identified by comparing directly blocks of words that were encoded as pictures with blocks of words that were encoded as words (Table 2 and Fig. 1). Recognition memory judgments to words encoded as pictures relative to those encoded as words activated significantly a large cluster in left ventrolateral extrastriate cortex. Ventral extrastriate activation was in the fusiform

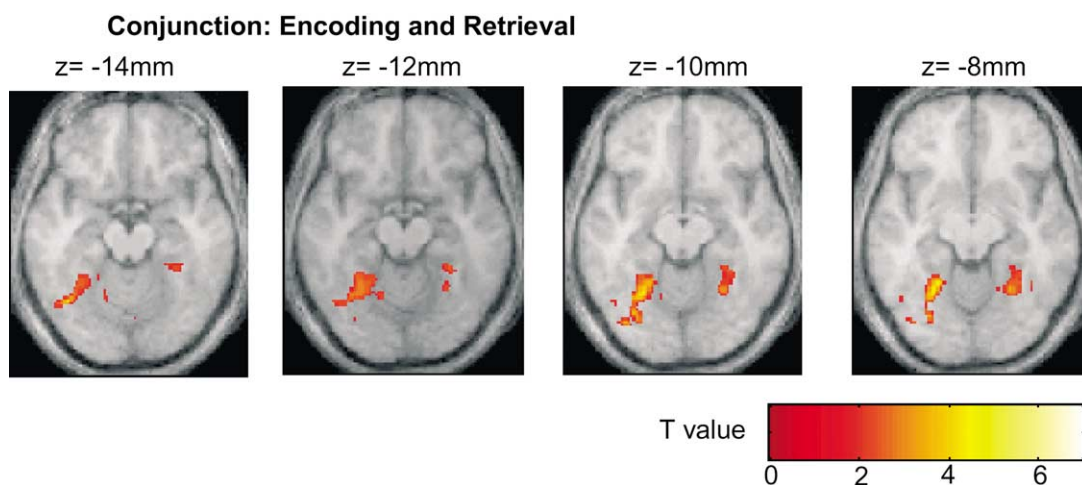


Fig. 2. Group average of conjunction analysis of the pictures vs. words contrast at encoding and the words that were encoded as pictures vs. words that were encoded as words contrast at retrieval ($P < 0.001$ corrected).

Table 2

Location (in gyral anatomy, BA, and standard coordinates), global maxima and size of significantly activated clusters during recognition memory judgments for words encoded as pictures relative to words encoded as words

Location	BA	Z	Voxels	X	Y	Z	<i>P</i> corrected
L Fusiform Gyrus	19/37	4.26	195	−35	−51	−13	0.03

Table 3

Location (in gyral anatomy, BA, and standard coordinates), global maxima, and size of significantly activated clusters activated in a conjunction analysis of picture relative to word conditions during encoding and episodic retrieval

Location	BA	Z	Voxels	X	Y	Z	<i>P</i> corrected ^a
L Fusiform Gyrus	19/37	5.85	498	−41	−58	−13	0.001
R Mid Occipital Gyrus	18/19	5.05	116	42	−73	12	0.026

^a Voxel-level corrected *P*-values; SPM99 does not allow specification of corrected cluster thresholds for conjunction analyses.

gyrus (19/37) extending laterally to the inferior temporal gyrus and included the junction of middle occipital and middle temporal gyri.

3.2.3. Encoding and retrieval

A conjunction analysis was performed to determine precisely voxels that were activated in the picture conditions during both encoding (i.e. pictures relative to words) and retrieval (i.e. words encoded as pictures relative to words encoded as words) in each subject [25] (see Table 3 and Fig. 2). This analysis revealed one large ventral extrastriate cluster in the left fusiform gyrus (BA 19/37) that extended laterally to the inferior temporal gyrus, and a lateral cluster in the right middle occipital gyrus (BA 19).

4. Discussion

The present findings revealed that material-specific activation associated with encoding was evident during recognition memory. Specifically, encoding pictures of objects relative to encoding names of objects (termed picture-specific encoding) engaged bilateral ventrolateral and medial extrastriate visual cortices. A subset of these regions in left ventral extrastriate cortex and right middle occipital gyrus were also engaged during recognition memory judgments to object-names that were encoded as pictures relative to those encoded as words (termed picture-specific retrieval). Our discussion focuses on the left ventral extrastriate re-activation during retrieval because that region was activated consistently in statistical tests of differing sensitivity, group average at retrieval and conjunction of encoding and retrieval.

Episodic retrieval was cued by words (object-names) which differed only in their encoded form (pictures/words). Therefore, picture-specific activation could be attributed to material-specific mnemonic history (i.e. how a stimulus was encoded) rather than ongoing perception at test. Word-specific activation at retrieval (i.e. words encoded as

words relative to those encoded as pictures), however, could not be attributed to mnemonic processes alone because of contributions from test-phase re-encoding of words. Thus, our findings indicate that left ventral extrastriate cortex is involved in picture-specific encoding operations that are recapitulated during episodic retrieval.

The present finding indicates that qualitatively distinct experiences remain distinct during their recollection. Recognition accuracy did not differ significantly for pictures and words, and therefore, retrieval-cues were equally effective in supporting recollection of both types of stored information. Distinct psychological processes underlied the recovery of pictures and words, however, because subjects were about 100 ms slower to make yes/no recognition memory judgments to words encoded as pictures relative to those encoded as words. The recollection of pictures and words was distinguished by the involvement of left ventral extrastriate cortex. Previous findings of material-specific activations within the visual modality, verbal versus non-verbal, have focused on the inferior frontal gyrus [12,18,32]. The extent to which observed differences, however, were driven solely by material-specific memories remains unclear because contributions of test-phase re-encoding of to-be-retrieved stimuli could not be discounted.

Other studies indicate that retrieval of experiences from distinct processing modalities can be distinguished in the brain. Auditory cortex was re-activated during retrieval of previously studied sounds (e.g. “dog barking”) in response to their paired visual cue-words [22,33]. In one study, auditory re-activation depended upon extensive study-phase training on the pairings and on intentional recall of the modality of initial experience [33]. In another study, however, re-activation of auditory cortex during retrieval was obtained under conditions that rendered the modality of past experience incidental rather than explicit to episodic retrieval [22]. Thus, together these studies show that the modality of past experiences (auditory/visual) is recovered during intentional or incidental episodic retrieval. Our findings differ from those studies because they show that symbolically

distinct experiences (e.g. picture or word) within the same modality (visual) can be distinguished in the brain under conditions that rendered the symbolic status of past experience incidental to episodic retrieval.

Wheeler et al.'s findings raise the possibility that re-activation of picture-specific regions observed in our study could have been due to intentional recollection of source information. Such recollection could occur during or after item retrieval, or as an artifact of our blocked fMRI design that may have induced subjects to adopt a set to recall pictures or words. While these possibilities cannot be fully ruled out, they appear unlikely for two reasons. First, instructions required "yes" responses to old items regardless of whether they had appeared as pictures or words. Performance levels were similar to those reported elsewhere for recognition memory following semantic encoding tasks similar to ours [10,30]. Source performance is often lower than recognition performance [11], and therefore, it is unlikely subjects were performing source rather than recognition judgments. Second, retrieval-cues did not occur in a predictable order. Blocks were ordered in a latin-squares fashion, such that blocks of words associated with pictures and words sometimes appeared in long runs. Therefore, subjects would not be able to distinguish them as blocks unless they were aware that blocks comprised seven items.

4.1. What processes are represented by the memory-induced re-activation of extrastriate cortex?

Re-activation of picture-specific regions during recognition memory could reflect at least two possible processes. First, subjects may be generating visual images of previously viewed objects. Imagery-related activation occurs in brain regions involved in perception such as bilateral visual cortex [14]. It is not possible to fully discount this explanation based on the present findings. However, the nature of the present re-activation differs from studies of visual imagery in two ways: (1) imagery-related activation was greater than perception in some studies [14], whereas our re-activated region was markedly smaller than that activated during perception; and (2) imagery-related visual activation in past studies extended bilaterally whereas our re-activation was strongly left-sided.

A more plausible interpretation is that re-activated regions reflect recapitulation of prototypical semantic information about objects. This interpretation is rooted in two features of encoding specificity and transfer appropriate processing principles. First, these principles state that the nature of the retrieval-cue determines what sort of encoding-related processes are recapitulated during retrieval. Thus, what is recollected is strongly influenced by what is accessible to the retrieval-cue. In the present study, the verbal nature of the retrieval-cues predicts that properties of encoded stimuli that were compatible with verbal representations will be recapitulated. Dual-coding theories of memory suggest that

pictures are associated with two mnemonic representations, pictorial and verbal [24]. Thus, the verbal retrieval-cue may guide recollection of the verbal representation for both pictures and words. The pictorial representation that is associated specifically with encoded pictures, however, is likely to be recollected to the extent that it contains information that is compatible with the verbal retrieval-cue. A verbal label as a cue represents inherently prototypical and visually non-specific information about objects. Therefore, it is likely that the pictorial information that is recapitulated is prototypical nature. This view is further supported by the strong left-lateralization of the re-activated region. By one view of hemispheric specialization, the left hemisphere processes more effectively prototypes or categories of visual information (e.g. generic "dog"; see review [16]). Categorical processing is thought to be language-related, and therefore, localized to the left hemisphere. In contrast, the right hemisphere processes more effectively memories for specific visual information (e.g. the color or shape of a particular dog). Left-lateralized re-activation indicates that recapitulated object information was of a prototypical rather than specific nature. We propose that prototypical representations of encoded pictures were recapitulated because of the verbal nature of the retrieval-cues.

Second, transfer appropriate processing theories conceptualize episodic memory tests as drawing upon semantic processing [19,26]. Evidence in support comes from levels of processing effects in episodic memory that show superior performance following semantic relative to perceptual encoding [5]. The extent of semantic encoding did not differ for pictures or words because both symbolic formats yielded comparable recognition memory. Semantic information is conveyed by different stimulus properties for words and pictures. Neuropsychological studies of category-specific visual object agnosias [6] and neuroimaging studies of category-specific activation in visual cortex [17] indicate that semantic information about objects is mediated by visual features. Re-activated ventral extrastriate areas in our study included regions that have been associated with analysis of the shape of visual objects (e.g. lateral occipital complex; [15]) and with storage of semantic information about objects (e.g. medial and lateral fusiform gyrus; [3]). Thus, the re-activated region in our study may represent re-capitulation of prototypical semantic information that is conveyed by object shape.

The present study found picture-specific recruitment of ventral extrastriate cortex, but in a prior study portions of this region were activated by both pictures of objects and their verbal labels [3]. This apparent paradox may be reconciled by consideration of differences in the encoding questions used in the two studies. In the Chao et al. [3] study, subjects named pictures of objects or answered category-specific questions (e.g. forest animal?) about words. Both object naming and categorization of the type used in that study require knowledge of the identity of objects. This similarity in the type of knowledge evoked by the encoding task

may have led to similar extrastriate activation for pictures and words. In contrast, our encoding question (e.g. manufactured/natural?) may be answered based upon different stimulus properties for pictures and words. For pictures, deciding whether they are manufactured or natural can be performed based solely on a visual feature (e.g. eyes or tail) without knowledge of object identity. For words, in contrast, that decision is necessarily based on knowledge of object identity. In our study, therefore, visual shape information was invoked to a greater extent for pictures than words, and therefore, resulted in more extensive ventral extrastriate activation.

Functional neuromaging studies of episodic memory have focused largely upon mediators of memory, i.e. the systems that record and retrieve experience such as prefrontal and medial temporal cortex. Little attention, however, has been paid to the contents of memory, i.e. the systems that determine the nature of what is recorded and retrieved. The current findings take a step in that direction.

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