

The neural origins of specific and general memory: the role of the fusiform cortex

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Abstract

Recognition of an object can be based on memory for specific details of a prior encounter with the object, or on a more general memory for the type of object previously encountered. Responding on the basis of general information alone can sometimes produce memory errors involving both distortion and forgetting, but little is known about the neural origins of general versus specific recognition. We extended the standard subsequent memory paradigm to examine whether neural activity at encoding predicts whether an object will subsequently elicit specific as compared to general memory. During event-related functional magnetic resonance imaging (fMRI), participants viewed objects and made size judgments about them. Later, they viewed *same*, *similar*, and *new* objects, labeling each as “same,” “similar,” or “new.” Specific recognition was indicated by a “same” response to a *same* object. By contrast, general, non-specific recognition was indicated by either a “same” response to a *similar* object (false memory) or a “similar” response to a *same* object (partial memory). As predicted, specific recognition, as compared to non-specific recognition, was associated with encoding-related activity in the right fusiform cortex, while non-specific recognition, as compared to forgetting, was associated with encoding-related activity in the left fusiform cortex. Furthermore, all successful recognition (specific and general), as compared to forgetting, was associated with encoding-related activity in bilateral fusiform cortex. These results suggest that the right fusiform cortex is associated with specific feature encoding, while the left fusiform cortex is involved in more general object encoding.

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1. Introduction

Memory can be expressed as specific or verbatim recognition of a previously encountered item, or as non-specific recognition of the general sense or gist of what was encountered (Brainerd & Reyna, 1995; Schacter, Norman, & Koutstaal, 1998). For example, after studying a picture of a car, on a later memory test people may show specific recognition of the exact car that they saw earlier, or they may have a non-specific memory that they saw a car. Such non-specific recognition can be associated with two types of errors: partial forgetting of the precise details of the studied item (e.g. remembering they saw a car, but failing to recognize the exact car they saw), or false recognition of a similar but not identical item (e.g. falsely remembering a different car based on

general familiarity) (Koutstaal, 2003; Koutstaal & Schacter, 1997).

Behavioral studies have begun to examine the cognitive properties of specific versus non-specific recognition, and it is increasingly accepted that non-specific forms of memory, such as false recognition, have important theoretical implications (Brainerd & Reyna, 1995; Koutstaal, 2003; Koutstaal & Schacter, 1997; Schacter et al., 1998). By contrast, neuroimaging research concerned with the neural basis of memory has focused on specific recognition, examining either the neural correlates of encoding processes that are associated with subsequent recognition judgments (e.g. Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Kirchoff, Wagner, Maril, & Stern, 2000; Otten, Henson, & Rugg, 2001; Wagner et al., 1998) or retrieval processes that occur during a recognition test (e.g. Buckner, Koutstaal, Schacter, Wagner, & Rosen, 1998; Eldridge, Knowlton, Furmanski,

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Bookheimer, & Engel, 2000; Rugg, Henson, & Robb, 2003; Wheeler & Buckner, 2003). Little is known about encoding-related neural activity associated with the two types of previously noted errors that are hallmarks of non-specific recognition: false recognition (when people incorrectly “remember” items that are similar but not identical to studied items) and partial recognition (when people forget specific item details). Studies exploring the neural basis of non-specific recognition do exist, but they have focused on the differential brain activity associated with true and false recognition at the time of memory retrieval (e.g. Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997; Schacter et al., 1996; Slotnick & Schacter, 2004; for review, see Schacter & Slotnick, 2004). Moreover, virtually nothing is known about encoding-related neural activity that is associated with subsequent non-specific recognition (i.e. partial or false recognition), as compared to specific recognition. An event-related potential (ERP) study, in which participants perceived or imagined objects, has investigated brain activity (as reflected by scalp voltage topography) associated with memorial encoding that resulted in subsequent confusions between objects that had been previously perceived or imagined (Gonsalves & Paller, 2000). However, there have been no studies delineating the precise neural substrates at encoding that support later false recognition of non-studied objects (i.e. objects that have been neither perceived nor imagined). Furthermore, no studies have explored the encoding-related activity associated with subsequent partial memory, where one claims that an item is only “similar” to a studied item when in fact it is identical to the studied item. In the present study, we extended the standard subsequent memory paradigm, where neural activity at encoding has been shown to predict subsequent veridical recognition memory performance (e.g. Brewer et al., 1998; Wagner et al., 1998), to examine whether neural activity associated with a particular item at encoding is predictive of subsequent specific or non-specific recognition.

Recent findings suggest that the right and left fusiform cortex are involved in encoding processes, but may play different roles during the encoding of visual objects associated with subsequent specific recognition compared with non-specific recognition. Much previous research has provided evidence that the fusiform cortex is essential for object perception (e.g. Haxby et al., 2001). Furthermore, several studies have reported activity increases in bilateral fusiform cortex during the successful encoding of faces (Bernstein, Beig, Siegenthaler, & Grady, 2002; Kuskowski & Pardo, 1999; Sperling et al., 2001, 2003), scenes (Kirchhoff et al., 2000), and words (Wagner et al., 1998), thereby indicating that fusiform activity at the time of encoding is associated with subsequent memory outcome. Relevant information is also provided by studies of repetition priming effects, where imaging studies have consistently revealed that priming of objects, words, and other material is accompanied by neural activity decreases in several cortical regions, including bilateral fusiform cortex (Schacter & Buckner, 1998). An

attenuated but significant repetition priming effect has also been observed for similar, but previously unseen, exemplars of previously seen objects (Koutstaal et al., 2001). Importantly, the right fusiform cortex shows a greater sensitivity to this exemplar change (a smaller repetition priming effect) than does the left fusiform cortex; this latter region is particularly sensitive to general/semantic manipulations but rather insensitive to minor perceptual changes (Simons, Koutstaal, Prince, Wagner, & Schacter, 2003). These findings suggest that right fusiform cortex activity is associated with specific visual feature processing, while left fusiform activity is associated with non-specific object processing. Similarly, in another fMRI study of repetition priming, left fusiform cortex showed reduced activity due to priming both when words were repeated in the identical visual form (i.e. same case) as well as when the same words were repeated in a new visual form (i.e. different case), while right extrastriate cortex (just posterior of right fusiform cortex) showed a priming effect only for words repeated in the identical visual form (i.e. same case) (Dehaene et al., 2001).

In addition to these findings within the fusiform cortex, other previous research supports the more general claim that the right hemisphere is associated with specific form processing, while the left hemisphere is associated with abstract, categorical processing. For instance, Marsolek and colleagues have reported a series of explicit and implicit memory studies where stimuli were presented directly to one cerebral hemisphere in order to detect hemispheric asymmetries in specific form versus abstract processing and encoding. Results suggest that the right hemisphere more efficiently distinguishes specific exemplars from a given category, while the left hemisphere is most effective at storing abstract information that does not vary across exemplars (Marsolek, 1995, 1999; Marsolek, Schacter, & Nichols, 1996; Marsolek, Squire, Kosslyn, & Lulenski, 1994). Furthermore, studies investigating memory in split brain patients show that when items are processed in the right rather than left cerebral hemisphere, patients are better able to distinguish between old items and similar (related but new) items on a subsequent recognition test (Metcalf, Funnell, & Gazzaniga, 1995; Phelps & Gazzaniga, 1992). Finally, patients with semantic dementia, who generally have severe atrophy in the left fusiform cortex but relatively little damage to the right fusiform cortex (Galton et al., 2001), are able to perform relatively normally on recognition tests in which the target is perceptually identical to the studied item, while they are impaired when the target item is a new exemplar of a studied item (Graham, Simons, Pratt, Patterson, & Hodges, 2000).

Based on the encoding-related increases in the bilateral fusiform cortex associated with successful recognition (Bernstein et al., 2002; Kirchhoff et al., 2000; Kuskowski & Pardo, 1999; Sperling et al., 2001, 2003) and the above-noted hemisphere-specific explicit and implicit memory effects (Dehaene et al., 2001; Graham et al., 2000; Koutstaal et al., 2001; Marsolek, 1995, 1999; Marsolek et al., 1994, 1996; Metcalfe et al., 1995; Phelps & Gazzaniga, 1992; Simons

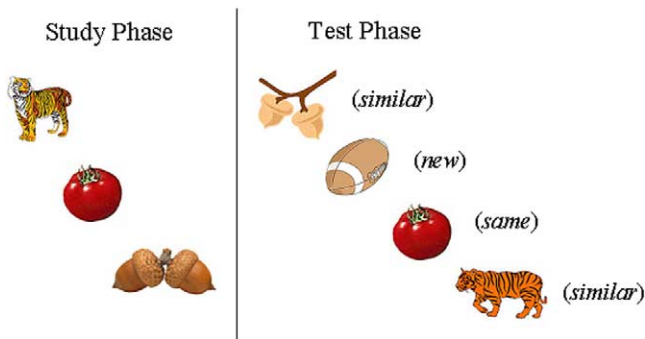


Fig. 1. Left panel: examples of objects seen during the study phase. Right panel: examples of objects shown at recognition and the condition in which each item is shown.

et al., 2003), we hypothesized that activity within the right fusiform cortex during encoding would be predictive of subsequent specific as compared to non-specific object recognition. Because specific recognition may result from memory encoding of both the specific and the general features of an object, we did not predict that encoding-related activity within the left fusiform cortex would be associated with subsequent non-specific object recognition when compared with specific object recognition. However, since non-specific recognition should result from the successful encoding of general object features while forgetting should result from a failure to encode these features, we did expect that left fusiform activity during encoding would predict subsequent non-specific recognition as compared to forgetting. Similarly, we predicted that both right and left fusiform cortex activity during encoding would be predictive of subsequent recognition of all types (specific, partial, and false) as compared to forgetting, since forgetting should result from a failure to encode both the specific and the general features of the studied object.

To test our hypotheses, we conducted an event-related functional magnetic resonance imaging (fMRI) study (see Section 2). At encoding, fMRI scans were acquired while participants made size judgments about colored objects (Fig. 1). During a subsequent recognition test conducted outside of the scanner, participants viewed three types of objects: (i) *same*—objects identical to those seen at encoding; (ii) *similar*—objects similar but not identical to objects seen at encoding (i.e. different exemplars of objects with the same name); and (iii) *new*—non-studied, unrelated objects. For each object at test, participants made a “same,” “similar,” or “new” judgment (see Fig. 2 for a description of the cognitive process associated with each object type–response type pairing), followed by a confidence judgment (“high” or “low”). According to our hypotheses, there should be greater right fusiform cortex activity associated with the encoding of objects that subsequently elicit specific recognition (“same”/*same*), as compared to the encoding of objects subsequently associated with non-specific recognition (including false recognition—“same”/*similar*, as well as

| | | Item Type | | |
|----------------------|-----------|----------------------|---------------------------------|----------------------------|
| | | <i>same</i> | <i>similar</i> | <i>new</i> |
| Participant Response | “same” | specific recognition | false recognition | baseline false recognition |
| | “similar” | partial recognition | specific OR partial recognition | partial false recognition |
| | “new” | complete miss | partial miss | correct rejection |

Fig. 2. Memory processes associated with item types and behavioral responses in the current paradigm.

partial recognition—“similar”/*same*). Furthermore, there should be greater left fusiform cortex activity associated with the encoding of objects that subsequently elicit non-specific recognition (“same”/*similar* or “similar”/*same*), as compared to forgetting (“new”/*same* or *similar*). Moreover, “same” or “similar” responses to any previously viewed object (*same* or *similar*), as compared to “new” responses to those objects, are indicative of some degree of successful object encoding (as opposed to forgetting). Such responses should therefore be associated with bilateral fusiform cortex activity, which would elicit both specific and non-specific subsequent recognition. Given that the fusiform cortex is the target of the hypotheses in the present investigation, our description of findings will focus on this region.

2. Methods

2.1. Participants

Thirteen participants took part in this study (11 females; mean age 23.9 years, range 20–30 years; right handed, native English speakers, with normal or corrected to normal vision and no history of neurological trauma). Informed consent was obtained from all participants before both the behavioral and imaging portions of the study. The Harvard University Institutional Review Board approved the behavioral protocol and the Massachusetts General Hospital Institutional Review Board approved the imaging protocol.

2.2. Task and procedure

During fMRI, participants were presented with 360 nameable, colored objects (Fig. 1) in three 12 min sessions of 120 objects each. Objects appeared in the center of the screen for 1 s followed by a varying inter-trial-interval ranging from 3 to 15 s. A unique stimulus order and time sequence was created for each participant. The stimulus order was pseudo-random with the following constraints: (i) no more than three objects in any given broad category (e.g. *animals*) were shown in a row; (ii) no more than four objects in any given condition

at recognition (*same* or *similar*) were shown sequentially at encoding; and (iii) the same number of objects in each condition at recognition (*same* or *similar*) were shown in each study session. Such item sequences and “jittered” time sequences were used in order to optimize estimation of the event-related fMRI signal (Dale, 1999). Participants were instructed to respond as to whether each object, in the real world, would fit inside a 13 in. square box. A button-box was used to record participants’ responses in the scanner. Prior to the scanning session, participants practiced the task while being shown an actual 13 in. square box to aid in their decisions. Participants were not instructed that there would be a later test of memory.

One day later, an object recognition test was administered outside of the scanner. At this time, participants viewed three types of objects: (i) objects that were identical to studied objects (*same* objects); (ii) objects that were similar but not identical to studied objects (*similar* objects); and (iii) new, unrelated objects (*new* objects). Similar objects varied from the originally studied objects in several perceptual aspects like color, shape, orientation, or surface pattern (Fig. 1); however, both the original and the similar exemplar in each object pair had the same verbal label (e.g. “umbrella” given as the name for both a solid green and a red and blue striped umbrella). Each object appeared in the center of the screen for 2.5 s followed by a screen prompting a confidence decision (see below), which was shown for 2 s. Finally, a fixation cross was shown for 0.5 s before the next object appeared. Stimulus order was constant, and the same object within the object pair was tested across all participants, while the condition of each object (*same*, *similar*, or *new*) was counterbalanced across participants. Thus, those objects that were assigned to the *similar* condition for a particular participant were shown at encoding as the non-tested object in that object pair. The recognition test consisted of 450 objects (180 *same*, 180 *similar*, and 90 *new*). *Same*, *similar*, and *new* objects were equally distributed across each third of the recognition test. Furthermore, no more than four objects in any given condition (*same*, *similar*, or *new*) and no more than two objects from the same broad category (e.g. *animals*) appeared in a row. Participants were asked to respond as to whether each object was: (i) the “same”—identical to a studied object; (ii) “similar”—similar but not identical to a studied object; or (iii) “new”—an unstudied, unrelated object. Then, participants were asked to decide whether they had “high confidence” or “low confidence” in the decision they had just made. After the test data were scored, the scans at encoding were conditionalized (or ‘binned’) based on the subsequent response to each object during the recognition test (i.e. whether the object was tested in the *same* or *similar* form and whether the participant responded “same,” “similar,” or “new” to the object). The nine possible cognitive states that result from this stimulus-response protocol are illustrated in Fig. 2. It is important to note that new items were shown only at recognition, and since we are studying neural activity at encoding, only responses to *same* and *similar* items were used in fMRI data analysis.

2.3. Stimuli

The majority of the object pairs used in this study have been used in previous research (Koutstaal et al., 2001; Simons et al., 2003). To sufficiently increase the number of objects to conduct the present study, we created additional object pairs that were indistinguishable from the original stimulus set with regard to size, image quality, and all other visual aspects. Care was taken to ensure that no added object pairs overlapped with existing object pairs (e.g. when a pair of baseball caps were included in the original stimulus set, a pair of cowboy hats were not added in order to avoid confusion with regard to categorical similarity).

2.4. Image acquisition and data analysis

All images were acquired on a 3 Tesla Siemens Allegra MRI scanner. Stimuli were back-projected onto a screen at the superior end of the scanner bore, and participants viewed the objects through an angled mirror attached to the head coil. Detailed anatomic data were acquired using a multiplanar rapidly acquired gradient echo (MP-RAGE) sequence (TR = 30 ms, TE = 3.3 ms, 128 slices, 1 mm × 1 mm × 1.33 mm voxels). Functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, 30 slices, 4.5 mm isotropic voxels).

SPM99 (Wellcome Department of Cognitive Neurology) was used to perform all pre-processing and data analysis. Standard pre-processing was performed on the functional data, including slice-time correction, motion correction, normalization to the SPM99 EPI template (re-sampling at 2 mm isotropic resolution using sinc interpolation), and spatial smoothing using a 6 mm full-width half maximum (FWHM) Gaussian kernel.

For each participant, on a voxel-by-voxel basis, an event-related analysis was first conducted where all instances of a particular event type were modeled through convolution with a canonical hemodynamic response function, and were then entered into a general linear model resulting in a beta-weight (i.e. model amplitude) associated with each event type. The difference in magnitude between beta-weights associated with two event types of interest were then computed, and these differences were entered into a random effects analysis, where one-sample *t*-tests were used to examine the consistency of activity at each voxel (using between participant variability to estimate variance). An individual voxel threshold of $p < 0.01$ with a cluster threshold of 46 contiguous voxels was used to yield results corrected for multiple comparisons to $p < 0.05$ (Forman et al., 1995; Slotnick, Moo, Segal, & Hart, 2003; Slotnick & Schacter, 2004). All activations are presented in neurological coordinates (i.e. activity in the right hemisphere is presented on the right side of the brain images). Voxel coordinates are reported in Talairach coordinates (Talairach & Tournoux, 1988) and reflect the most significant voxel proximal to the center of each uniquely active

region. In order to characterize the pattern of activity in the clusters defined by the random effects analysis, event-related time-courses were extracted from clusters of interest using custom written software in MATLAB. Linear trends were removed from all time-courses, and the timepoints from 0 to 4 s preceding stimulus onset were used to correct for baseline activity. Unless otherwise noted, statistics were conducted on event-related activity 4–8 s after stimulus onset. If a cluster of activity was too large to be considered a single area of activation, timecourses were extracted from a 9 mm sphere within the region of interest. (In the current study, this only occurred for the left fusiform gyrus in the subsequent any recognition versus forgetting contrast.) For contrasts where the random effects analysis revealed activity in the fusiform gyrus in only one hemisphere, a laterality test was used to directly compare activity in the right and left fusiform gyri. The difference in beta-weights associated with the event types of interest in each contrast was extracted from a 9 mm sphere within the active region defined by the random effects analysis (centered on reported coordinate x, y, z) as well as from the analogous 9 mm sphere in the opposite hemisphere (centered on coordinate $-x, y, z$). Statistics were then conducted on these beta-weight differences.

If a participant did not have at least 10 events in every condition used in a contrast, that participant's data were excluded from the analysis for that specific comparison. Under those criteria, if 12 or more participants had a sufficient number of high confidence response events in each necessary condition in a specific contrast, then that contrast was analyzed using only the high confidence response events in order to eliminate noise in the data due to guessing. As such, both the specific recognition versus non-specific recognition and the non-specific recognition versus specific recognition contrasts were analyzed using only high confidence response events—12 of the 13 participants had a sufficient number of high confidence responses in all relevant conditions to be included in these contrasts. Both the non-specific memory versus forgetting as well as the any memory versus forgetting contrasts were analyzed collapsing over high and low confidence responses due to a low number of high confidence "new" responses to *same* objects in a large number of participants. After collapsing over confidence, 12 of the 13 participants fit the criteria to be included in these non-specific versus forgetting and any memory versus forgetting analyses.

3. Results

3.1. Behavioral results

Participants were able to successfully distinguish between studied and non-studied objects on the recognition test (Fig. 3). Specifically, *same* items were called "same" significantly more often than they were called "similar" or "new" ($t=2.7, p<0.02$ and $t=6.4, p<0.001$, respectively, paired t -tests); *similar* items were called "similar" more of-

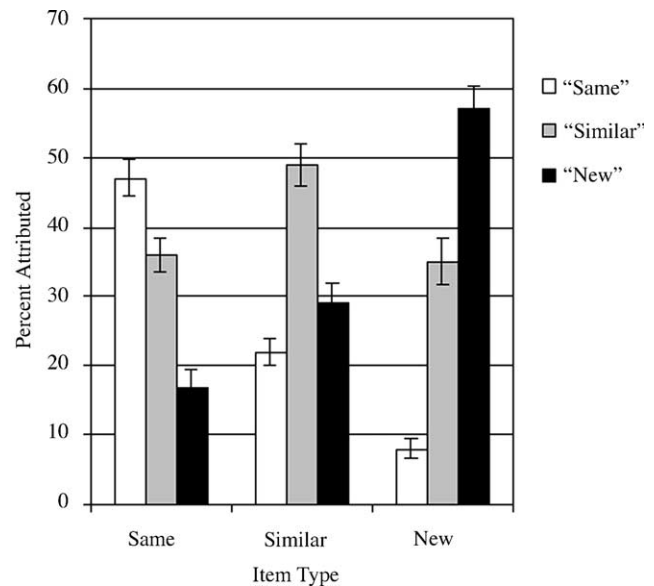


Fig. 3. Behavioral responses associated with same, similar, and new items at recognition (mean \pm 1 S.E.). The y-axis refers to the percentage of responses to a specific object type (*same, similar, or new*) that were associated with a specific response type ("same," "similar," or "new"). Thus, the sum of "same," "similar," and "new" response percentages to any single object type equals 100%.

ten than they were called "same" or "new" ($t=6.6, p<0.001$ and $t=3.5, p<0.005$, respectively, paired t -tests); and *new* items were called "new" more often than they were called "same" or "similar" ($t=12.3, p<0.001$ and $t=3.5, p<0.005$, respectively, paired t -tests). The false recognition rate to similar objects ("same"/*similar*) was significantly higher than the baseline false recognition rate to unrelated, new objects ("same"/*new*; $t=7.6, p<0.001$, paired t -test). Furthermore, although the partial recognition rate ("similar"/*same*) and partial false recognition rate ("similar"/*new*) were comparable, significantly more high confidence ratings were associated with partial recognition (63% high confidence) than with partial false recognition (42% high confidence; $t=4.9, p<0.001$, paired t -test). Assuming that high confidence responses, for the most part, reflected memory for some subset of specific and/or general information about the studied item while low confidence responses predominantly reflected a sense of familiarity or a guess, these results suggest that partial recognition most frequently occurred when the gist of the studied object or a subset of its features were remembered with high confidence (e.g. those features that overlapped between the studied and tested objects), whereas partial false recognition responses were more frequently based on a false feeling of familiarity for a new object.

Considering those conditions involved in imaging contrasts, the mean reaction time at encoding for objects that were later specifically remembered with high confidence ("same"/*same*) was no different than the mean reaction time for objects that were later non-specifically remembered with high confidence ("similar"/*same* and "same"/*similar*; $t=1.1$,

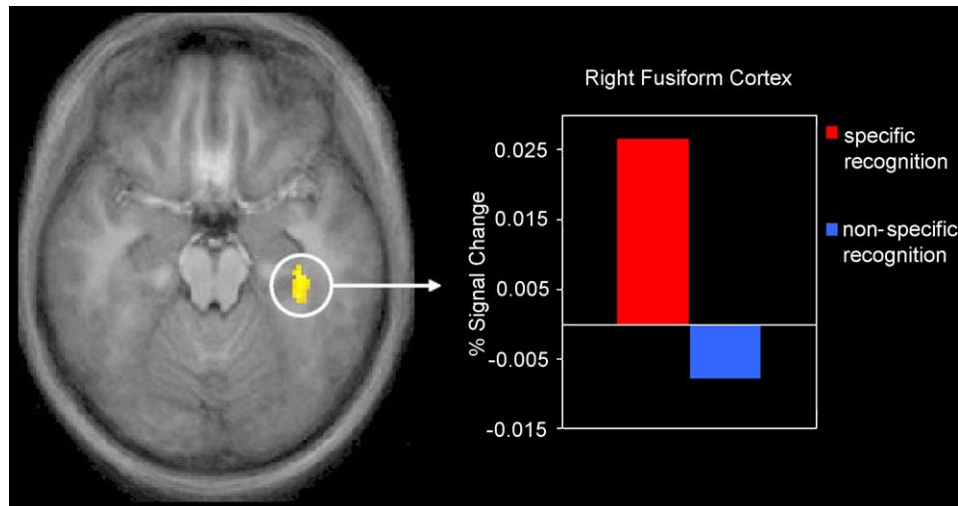


Fig. 4. Encoding-related activity associated with specific (“same”/same) as compared to non-specific (“same”/similar or “similar”/same) object recognition. To the left, neural activity is projected onto an axial slice of the group mean anatomic image ($Z = -20$, SPM99). The right fusiform cortex (extending into the right parahippocampal gyrus) is demarcated with a circle, and to the right, the magnitude of specific and non-specific event-related activity within this region is shown.

$p > 0.2$, paired t -test). Furthermore, the mean reaction time at encoding for objects that were later non-specifically remembered (“similar”/same and “same”/similar) was no different than the mean reaction time for objects that were later forgotten (“new”/same or similar; $t = 0.8$, $p > 0.2$, paired t -test). Consistent with several previous subsequent memory studies (Morcom, Good, Frackowiak, & Rugg, 2003; Wagner et al., 1998), the mean reaction time for objects that were later remembered either specifically or non-specifically (“same” or “similar”/same or similar) was longer than for objects that were later forgotten (“new”/same or similar; $t = 2.3$, $p < 0.05$, paired t -test).

3.2. Imaging results

As expected, object encoding (as compared to fixation) was associated with robust sensory activity in visual cortical processing regions. To test our hypotheses, we first examined the neural activity at encoding that was associated with subsequent, high-confidence specific recognition (“same”/same) as compared to high-confidence non-specific recognition (“same”/similar [false recognition] or “similar”/same [partial recognition]). In support of our hypothesis, activity in the right fusiform gyrus, extending into the parahippocampal gyrus, during encoding was preferentially associated with specific recognition (Table 1, top, and Fig. 4). Characterizing the nature of this result, encoding-related activity associated with specific recognition within this region (as assessed 4–8 s following stimulus onset) was significantly greater than baseline activity (as assessed 0–4 s before stimulus onset; see Section 2; $t = 2.0$, $p < 0.04$, one-tailed paired t -test), while there was no significant difference between encoding-related activity associated with non-specific recognition and baseline ($t < 1$, n.s., one-tailed paired

t -test). Furthermore, the direct contrast between the magnitude of event-related activity associated with specific versus non-specific recognition within this region was also significant ($t = 2.0$, $p < 0.04$, one-tailed paired t -test; Fig. 4). Supporting the appropriateness of combining high confidence false recognition and high confidence partial recognition to create the high confidence non-specific recognition condition, there was no difference between encoding-related activity associated with high confidence false recognition and high confidence partial recognition in this region of right fusiform cortex ($t < 1$, n.s., one-tailed paired t -test). The right fusiform cortex/parahippocampal gyrus region was the only active brain area observed in this contrast.

A laterality test was used to directly compare activity in the right fusiform cortex with activity in the analogous area of the left fusiform cortex during the encoding of items eliciting subsequent specific as compared to non-specific recognition (see Section 2). In the area of right fusiform gyrus, defined by the subsequent specific versus subsequent non-specific recognition contrast, there was a significant difference in beta-weights between items that were subsequently remembered specifically as compared to those subsequently remembered non-specifically ($t = 3.0$, $p < 0.01$, one-tailed paired t -test), while in the analogous area of left fusiform gyrus, there was no significant difference in beta-weights between these two event types ($t < 1$, n.s., one-tailed paired t -test). Furthermore, the interaction between hemisphere and change in beta-weight was marginally significant ($p = 0.07$). To further confirm this laterality test, we relaxed the cluster extent threshold to examine subthreshold activity in the random effects analysis. Even when the cluster extent threshold was reduced to the point where the random effects analysis was reflecting activity corrected for multiple comparisons to $p = 0.2$ (i.e. non-significant activity), there was no activation in the left

Table 1

Neural regions differentially associated with specific recognition (labeling a *same* object “same”) and non-specific recognition (false recognition—labeling a *similar* object “same”—or partial recognition—labeling a *same* object “similar”)

| Region | BA | (x, y, z) |
|---|----|--------------|
| Specific recognition > non-specific recognition | | |
| Right fusiform gyrus | 20 | 40, -30, -15 |
| Right parahippocampal gyrus | 36 | 38, -32, -14 |
| Non-specific recognition > specific recognition | | |
| Left superior frontal gyrus | 10 | -35, 56, -1 |
| Right superior frontal gyrus | 10 | 28, 53, 14 |
| Left middle frontal gyrus | 10 | -31, 56, 3 |
| Left superior frontal gyrus | 11 | -28, 50, -16 |
| Right superior frontal gyrus | 6 | 22, 14, 55 |
| Right medial frontal gyrus | 6 | 8, 15, 44 |
| Right precentral gyrus | 6 | 60, -12, 40 |
| Left inferior frontal gyrus | 44 | -54, 4, 15 |
| Right precentral gyrus | 44 | 44, 13, 7 |
| Left inferior frontal gyrus | 9 | -60, 12, 22 |
| Right inferior frontal gyrus | 47 | 39, 15, -14 |
| Right postcentral gyrus | 3 | 63, -18, 33 |
| Right anterior cingulate gyrus | 32 | 10, 32, 23 |
| Left cingulate gyrus | 24 | -2, 11, 28 |
| Left cingulate gyrus | 23 | -10, -23, 30 |
| Left insula | 13 | -37, 14, 10 |
| Left inferior parietal lobule | 40 | -52, -25, 33 |
| Right superior parietal lobule | 7 | 22, -56, 61 |
| Left precuneus | 7 | -13, -55, 43 |
| Left cuneus | 7 | -14, -72, 31 |
| Right precuneus | 31 | 13, -72, 29 |
| Left lingual gyrus | 19 | -8, -63, 1 |
| Left cuneus | 19 | -7, -78, 36 |
| Right cuneus | 18 | 2, -71, 22 |
| Right cuneus | 30 | 6, -63, 9 |
| Left superior temporal gyrus | 42 | -57, -29, 16 |
| Left middle temporal gyrus | 37 | -53, -53, 2 |
| Right thalamus | - | 11, -23, 4 |
| Left thalamus | - | -19, -26, 6 |
| Right substantia nigra | - | 15, -21, -5 |
| Right putamen | - | 22, 15, -7 |
| Left cerebellum | - | -3, -51, -14 |

BA refers to Brodmann area, and coordinates (x, y, z) are reported in Talairach space.

fusiform or parahippocampal gyri.

We also explored the encoding-related activity differentially associated with subsequent high-confidence non-specific as compared to high-confidence specific recognition (the inverse of the above comparison). This contrast was associated with activity in areas including the left inferior frontal gyrus, bilateral prefrontal cortex, bilateral parietal cortex, cuneus, precuneus, and anterior cingulate (Table 1, bottom, and Fig. 5). Of note, the left inferior prefrontal cortex finding has been previously associated with both encoding and retrieval of semantic information (Demb et al., 1995; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001) (see Section 4). The encoding-related activity associated with subsequent non-specific recognition in the left inferior frontal gyrus was significantly greater than baseline ($t = 2.4, p < 0.02$, one-tailed paired t -test). By contrast, there was no significant difference between baseline and subsequent specific recognition-related

Table 2

Neural regions differentially associated with non-specific recognition (false recognition—labeling a *similar* object “same”—or partial recognition—labeling a *same* object “similar”) as compared to forgetting (labeling a *same* or *similar* object “new”)

| Region | BA | (x, y, z) |
|---------------------------------------|----|---------------|
| Non-specific recognition > forgetting | | |
| Left superior frontal gyrus | 8 | -9, 47, 42 |
| Left middle frontal gyrus | 8 | -18, 33, 36 |
| Right middle frontal gyrus | 9 | 52, 7, 37 |
| Right precentral gyrus | 4 | 42, -15, 55 |
| Right precentral gyrus | 6 | 32, -10, 65 |
| Right precentral gyrus | 6 | 53, 2, 27 |
| Left inferior frontal gyrus | 45 | -58, 14, 20 |
| Left inferior frontal gyrus | 47 | -25, 10, -12 |
| Left superior parietal lobule | 7 | -21, -56, 60 |
| Left inferior parietal lobule | 40 | -48, -39, 54 |
| Left superior parietal lobule | 7 | -27, -56, 43 |
| Left inferior parietal lobule | 40 | -50, -29, 44 |
| Right precuneus | 7 | 27, -56, 49 |
| Left cuneus | 17 | -4, -89, 5 |
| Right posterior cingulate | 23 | 7, -26, 28 |
| Right subcallosal gyrus | 34 | 27, 7, -11 |
| Left lingual gyrus | 18 | -9, -78, 5 |
| Right lingual gyrus | 18 | 4, -65, 4 |
| Left lingual gyrus | 19 | -27, -73, -1 |
| Right lingual gyrus | 19 | 28, -70, -2 |
| Left parahippocampal gyrus | 36 | -33, -33, -21 |
| Left fusiform gyrus | 20 | -34, -36, -23 |
| Left fusiform gyrus | 37 | -38, -51, -18 |
| Left middle temporal gyrus | 37 | -58, -44, -8 |
| Right middle temporal gyrus | 37 | 54, -53, -10 |
| Right medial globus pallidus | - | 11, -3, -5 |
| Right brainstem (pons) | - | 11, -30, -27 |
| Right cerebellum | - | 8, -78, -15 |
| Right cerebellum | - | 39, -67, -40 |

BA refers to Brodmann area, and coordinates (x, y, z) are reported in Talairach space.

activity within this region ($t < 1$, n.s., one-tailed paired t -test). Moreover, activity in this region was significantly greater for encoding trials eliciting subsequent non-specific rather than specific recognition ($t = 3.3, p < 0.005$, one-tailed paired t -test; Fig. 5).

To further test our hypotheses, we contrasted encoding-related activity associated with subsequent non-specific recognition (“same”/*similar* [false recognition] or “similar”/*same* [partial recognition]) with encoding-related activity associated with subsequent forgetting (“new”/*same* or *similar*). In this contrast, it was necessary to collapse across high- and low-confidence responses to ensure there were a sufficient number of responses to conduct the analysis (see Section 2). In support of our predictions, activity in the left fusiform gyrus was preferentially associated with subsequent non-specific recognition (Table 2 and Fig. 6). In this region of left fusiform cortex, encoding-related activity associated with subsequent non-specific recognition was significantly greater than encoding-related activity associated with subsequent forgetting ($t = 3.0, p < 0.01$, one-tailed paired t -test; Fig. 6), while encoding-related activity associated with both non-specific recognition and forgetting was

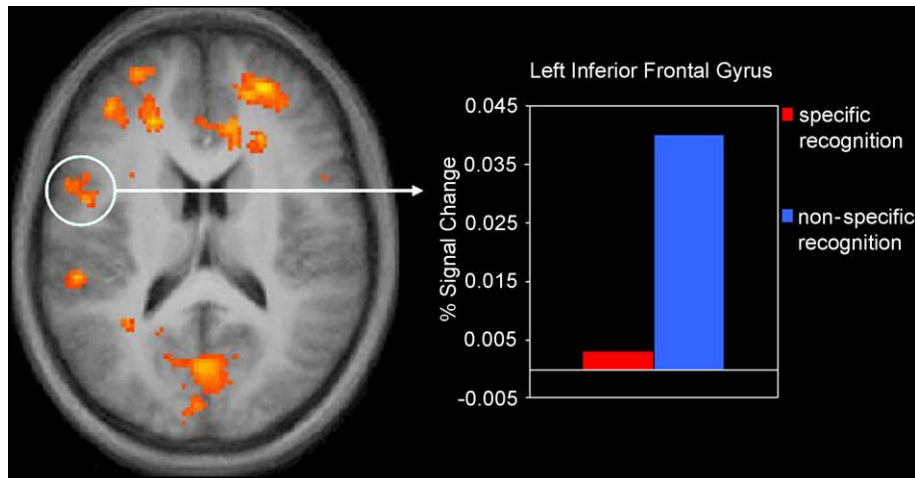


Fig. 5. Encoding-related activity associated with non-specific (“same”/similar or “similar”/same) as compared to specific (“same”/same) recognition. To the left, a circle demarcates activity in the left inferior frontal gyrus, projected onto an axial slice of the group mean anatomic image ($Z = 18$, SPM99), and to the right, the magnitude of event-related activity within this region is shown.

significantly greater than baseline (non-specific recognition, $t = 6.7$, $p < 0.0001$, one-tailed paired t -test; forgetting, $t = 4.5$, $p < 0.001$, one-tailed paired t -test). This non-specific recognition versus forgetting contrast revealed additional activity in multiple other brain regions including bilateral prefrontal gyrus, left inferior frontal gyrus, left parietal cortex, bilateral middle temporal gyrus, right precentral gyrus, and bilateral lingual gyrus (Table 2), with the notable absence of activity in the right fusiform or parahippocampal gyri.

A laterality test showed that, in the left fusiform gyrus, there was a significant difference in beta-weights associated with objects that were subsequently remembered non-specifically as compared to objects that were forgotten ($t = 3.4$, $p < 0.005$, one-tailed paired t -test), while in the anal-

ogous area of right fusiform cortex, there was no difference in beta-weights associated with these two event types ($t < 1$, n.s., one-tailed paired t -test). Moreover, there was a significant interaction between hemisphere and beta-weight difference ($p < 0.005$). Again, we confirmed this laterality test by relaxing the cluster extent threshold (to correct for multiple comparisons at $p = 0.2$) to examine subthreshold activity in the random effects analysis; no activity was found in the right fusiform or parahippocampal gyri.

In further support of our hypothesis, the comparison between subsequent memory of any type (“same” or “similar”/same or similar) and forgetting (“new”/same or similar) revealed bilateral fusiform cortex activity (Table 3 and Fig. 7a). Again, we collapsed across high- and low-

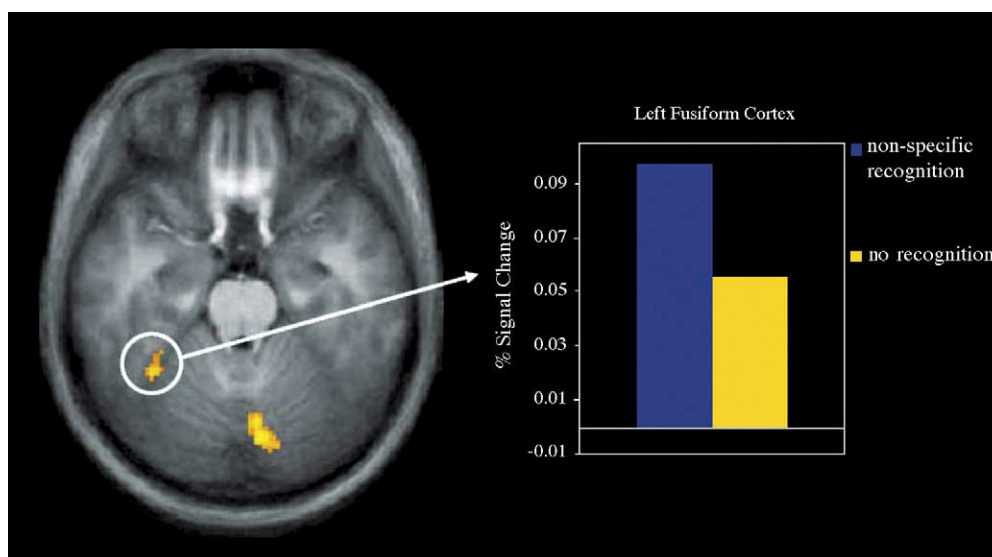


Fig. 6. Encoding-related activity associated with non-specific object recognition (“same”/similar or “similar”/same) as compared to forgetting (“new”/same or similar). To the left, a circle demarcates activity in the left fusiform gyrus, projected onto an axial slice of the group mean anatomic image ($Z = -24$, SPM99), and to the right, the magnitude of event-related activity within this region is shown.

Table 3

Neural regions differentially associated with any memory (labeling a *same* or *similar* object “same” or “similar”) as compared to forgetting (labeling a *same* or *similar* object “new”)

| Region | BA | (x, y, z) |
|--------------------------------|------|---------------|
| Any memory > forgetting | | |
| Left middle frontal gyrus | 11 | −41, 41, −16 |
| Right middle frontal gyrus | 6 | 30, 15, 53 |
| Left superior frontal gyrus | 8 | −10, 47, 42 |
| Right middle frontal gyrus | 8 | 53, 8, 38 |
| Left middle frontal gyrus | 46 | −47, 20, 23 |
| Left inferior frontal gyrus | 45/9 | −60, 15, 20 |
| Right inferior frontal gyrus | 9 | 52, 3, 25 |
| Left inferior frontal gyrus | 46 | −54, 36, 7 |
| Right inferior frontal gyrus | 47 | 26, 9, −11 |
| Left inferior frontal gyrus | 13 | −26, 11, −11 |
| Left cingulate gyrus | 32 | −8, 24, 42 |
| Right caudate | – | 6, 13, 3 |
| Left caudate | – | −11, 16, 6 |
| Left inferior parietal lobule | 40 | −49, −39, 53 |
| Right superior parietal lobule | 7 | 26, −58, 47 |
| Left superior parietal lobule | 7 | −37, −54, 54 |
| Right cuneus | 19 | 32, −78, 32 |
| Right middle occipital gyrus | 19 | 35, −87, 9 |
| Left inferior occipital gyrus | 19 | −33, −77, −7 |
| Left cuneus | 17 | −12, −94, 5 |
| Right middle occipital gyrus | 18 | 28, −92, 5 |
| Right lingual gyrus | 18 | 26, −74, −3 |
| Left lingual gyrus | 18 | −28, −68, −1 |
| Left parahippocampal gyrus | 36 | −28, −16, −24 |
| Right parahippocampal gyrus | 34 | 14, −12, −16 |
| Left fusiform gyrus | 20 | −37, −42, −20 |
| Right fusiform gyrus | 20 | 38, −18, −23 |
| Right inferior temporal gyrus | 20 | 39, −13, −29 |
| Right middle temporal gyrus | 37 | 55, −54, −11 |
| Left middle temporal gyrus | 37 | −59, −46, −9 |
| Right putamen | – | 26, 10, −12 |
| Left putamen | – | −26, 12, −13 |
| Right cerebral peduncle | – | 10, −3, −7 |
| Right midbrain | – | 1, −25, −12 |
| Left cerebellum | – | −1, −58, −2 |
| Left cerebellum | – | −10, −81, −16 |
| Right cerebellum | – | 11, −82, −19 |

BA refers to Brodmann area, and coordinates (x, y, z) are reported in Talairach space.

confidence responses in order to include a sufficient number of trials in the analysis (see Section 2). In the left fusiform cortex, although encoding-related activity (4–8 s following stimulus onset) associated with both subsequent memory of any type and subsequent forgetting was significantly greater than the baseline level of activity (0–4 s preceding stimulus onset) (any memory, $t = 6.9$, $p < 0.0001$, one-tailed paired t -test; forgetting, $t = 4.8$, $p < 0.001$, one-tailed paired t -test), the magnitude of this increase was significantly greater for any memory as compared to forgetting ($t = 3.7$, $p < 0.002$, one-tailed paired t -test; Fig. 7a). In the right fusiform cortex, only encoding-related activity associated with any memory was significantly greater than baseline ($t = 4.9$, $p < 0.001$, one-tailed paired t -test), while encoding-related activity associated with forgetting was similar to baseline ($t < 1$, n.s., one-tailed paired t -test). Furthermore, right fusiform cortex

activity associated with subsequent memory of any type was significantly greater than activity associated with subsequent forgetting ($t = 2.8$, $p < 0.01$, one-tailed paired t -test; Fig. 7a). The any memory versus forgetting contrast was also associated with activity in multiple other brain regions, including the left inferior frontal gyrus, a region previously associated with subsequent memory success (Kirchhoff et al., 2000; Otten et al., 2001; Sperling et al., 2003; Wagner et al., 1998) (Fig. 7b and Table 3).

4. Discussion

The results from the current study support our hypothesis regarding the roles of the right and left fusiform cortex during memorial encoding of visual objects. Activity increases in the right fusiform cortex at encoding were preferentially associated with subsequent specific recognition, as compared to non-specific recognition. This observation compliments previous repetition priming results that have suggested that the right fusiform cortex may be involved with processing specific features of visual objects (Koutstaal et al., 2001; Simons et al., 2003), and extends these findings by suggesting that the right fusiform cortex is associated with successful encoding of specific visual features which supports later episodic recognition. These results also imply that non-specific recognition for objects (including false recognition and partial recognition) can result from less specific feature processing at encoding, as reflected by relatively lower activity in the right fusiform cortex.

Furthermore, in support of our hypothesis, left fusiform activity that occurred during encoding predicted subsequent non-specific memory as compared to forgetting, and encoding-related activity in bilateral fusiform cortex was associated with subsequent memory of any type (specific or non-specific) as compared to subsequent forgetting. This pattern of results suggests that although the left fusiform cortex may not be associated with specific visual feature processing, it appears to be associated with non-specific object processing, thus aiding in subsequent general object memory (i.e. supporting subsequent false and partial recognition). The exact role of the left fusiform cortex cannot be determined in the current study, since activity in this area may reflect the coding of associations that are semantic in nature (e.g. the object's name, or a broader category of objects to which it belongs) or the successful encoding of relatively crude visual features; both possibilities would aid in successful non-specific recognition. Relevant previous work has reported an association between successful memory for words and left lateralized activity in the fusiform cortex during encoding (Wagner et al., 1998), which supports the notion that the left fusiform cortex may be involved in encoding general verbal information about the studied item (e.g. an object's verbal label). However, further research is necessary to delineate the precise role of the left fusiform cortex in general object encoding.

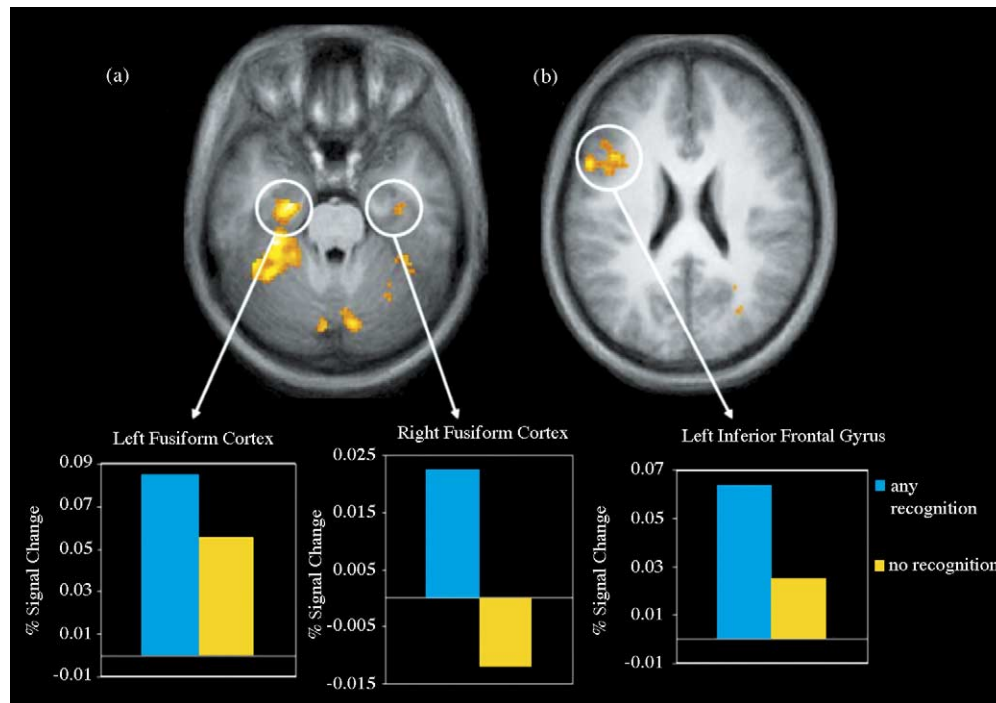


Fig. 7. Activity associated with successful object encoding of any type (“same” or “similar”/same or similar) as compared to unsuccessful object encoding (i.e. forgetting; “new”/same or similar). (a) Circles demarcate activity in the right and left fusiform cortex projected onto an axial slice of the group mean anatomic image ($Z = -28$, SPM99), with the magnitude of event-related activity associated with each of these regions shown below. (b) A circle demarcates the left inferior frontal gyrus (axial slice, $Z = 24$, SPM99), with the magnitude of event-related activity within this region shown below.

The contrast between subsequent non-specific recognition and subsequent forgetting, as well as the contrast between subsequent recognition of any type and subsequent forgetting, revealed activity in several regions such as the inferior prefrontal cortex and parahippocampal cortex, both of which have been shown to be predictive of subsequent specific memory (e.g. Wagner et al., 1998), thus extending the functional nature of activity within these regions to also support non-specific memory (i.e. general memory). While the contrast between subsequent non-specific recognition and subsequent forgetting revealed left but not right fusiform activity, the contrast between subsequent memory of any type versus forgetting was associated with bilateral fusiform activity. This encoding-related activity in right fusiform cortex revealed in the latter contrast was presumably due to the large subset of specific recognition items entering into the any subsequent memory versus subsequent forgetting comparison.

The encoding-related activity associated with subsequent non-specific recognition as compared to specific recognition resembles patterns of activation that have been associated with semantic (Demb et al., 1995; Wagner et al., 2001) and episodic retrieval (Buckner et al., 1998; Slotnick et al., 2003; Wheeler & Buckner, 2003), including activity in the inferior prefrontal cortex, bilateral frontal cortex, and parietal cortex. We propose that this activity reflects elaborative retrieval-based processes during memorial encoding, which might include object–object associations (e.g. tiger–lion) and/or other information about the object (e.g. the object’s use or the last

time the object was encountered in the real world). In the current paradigm, additional retrieval-like, elaborative processing at encoding would enhance the amount of general information available at recognition; however, limitations in cognitive resources may result in an associated reduction in the amount of specific visual information encoded, thus decreasing the probability of specific recognition and increasing the probability of non-specific (false or partial) recognition. A more systematic manipulation of the encoding task would be necessary to confirm our suggestion that the retrieval-like activity we see in the current study is attributable to elaborative processing at encoding.

Interestingly, since previous studies have shown an association between inferior prefrontal cortex activity during encoding and subsequent successful verbatim recognition (as compared to forgetting; e.g. Wagner et al., 1998), one may have predicted that more activity would be seen in this area during the encoding of specifically remembered rather than non-specifically remembered items. The fact that the inferior prefrontal cortex is instead more active during the encoding of subsequently non-specifically remembered as compared to specifically remembered events (see Fig. 5) suggests the possibility that activity in this region assumed to be associated with subsequent verbatim recognition in previous studies is actually reflecting successful general or gist encoding rather than specific encoding (both of which would lead to successful memory as compared to forgetting). In addition to finding that left inferior prefrontal cortex activity was preferentially involved

in encoding subsequent non-specifically rather than specifically remembered items, we also found that activity in this region is associated with subsequent non-specific recognition as compared to forgetting, which further supports the notion that this activity may reflect successful non-specific rather than specific encoding.

The fact that that we did not see fusiform cortex activity in the non-specific recognition versus specific recognition contrast should not be surprising because specific recognition would presumably be associated with both specific feature encoding (right fusiform activity) as well as non-specific processing (left fusiform activity). Thus, since the left fusiform cortex was presumably active in both the subsequent specific and subsequent non-specific recognition conditions, it was not expected to appear in any contrasts comparing subsequent specific and non-specific recognition.

An important and as yet unresolved question concerns the qualitative nature of specific recognition effects that are preceded by increased right fusiform activity during encoding. On the one hand, we have stressed that right fusiform activity has been associated with form-specific priming effects (Koutstaal et al., 2001; Simons et al., 2003). Thus, it is possible that subsequent specific recognition reflects the influence of priming-like processes (implicit memory). On the other hand, memory for specific details of previously studied items is often associated with recollective processes at retrieval (e.g. Gardiner & Richardson-Klavehn, 2000). Thus, it is likewise possible that specific recognition reflects the operation of conscious recollection (explicit memory). Although our data do not speak directly to this issue, a recollection view might lead us to expect that hippocampal activity at the time of encoding would be associated with subsequent specific recognition; we failed to observe any such effects. However, we would not want to make too much of a negative finding, and we view this question as an important unresolved matter to be explored by future research.

Overall, our findings support and extend results from previous studies suggesting a right hemisphere advantage in successfully processing the exemplar-specific details of a studied item along with a left hemisphere specialization in processing general, categorical features of an item (Graham et al., 2000; Koutstaal et al., 2001; Marsolek, 1995, 1999; Marsolek et al., 1994, 1996; Metcalfe et al., 1995; Phelps & Gazzaniga, 1992). In contrast, several studies have reported form-specific priming in both the right hemisphere and the left hemisphere, suggesting that the left hemisphere may also be capable of specific feature processing (e.g. Kroll, Rocha, Yonelinas, Baynes, & Frederick, 2001; Kroll et al., 2003), although these studies have generally utilized verbal stimuli rather than visual objects or scenes (for further discussion of these and other neuropsychological studies of specificity effects in priming, see Schacter, Dobbins, & Schnyer, 2004). Other studies that have used verbal stimuli, however, have reported exemplar-specific processing in the right hemisphere and general/categorical processing in the left hemisphere (Dehaene et al., 2001; Marsolek et al., 1994, 1996; Metcalfe

et al., 1995). Thus, the specific and non-specific processing distinction appears to be somewhat mixed for verbal stimulus processing, while it seems to be more ubiquitous with regard to visual object or scene processing (Graham et al., 2000; Koutstaal et al., 2001; Marsolek, 1995, 1999; Phelps & Gazzaniga, 1992; Simons et al., 2003).

Moreover, the present pattern of results complements a model of visuospatial hemispheric specialization proposed by Kosslyn and colleagues (e.g. Kosslyn, 1987; Kosslyn et al., 1989; Laeng, 1994; Slotnick, Moo, Tesoro, & Hart, 2001), where between-object coordinate-based visuospatial processing preferentially occurs in the right hemisphere while between-object categorical visuospatial processing preferentially occurs in the left hemisphere. Such visuospatial processing can also be considered for a single object, where coordinate-based processing includes the spatial relationships between an object's features (i.e. specific processing) while categorical processing refers to non-specific encoding. Our pattern of fusiform cortex results fit well within such a single object rendition of the whole-brain categorical versus coordinate visuospatial processing framework, with the right fusiform cortex performing more precise object encoding while the left fusiform cortex subserves less specific object encoding.

While the analyses in the present study focused on the encoding activity associated with specific versus general memory, the results also have implications for the encoding origins of false recognition. Previous behavioral work has shown that successfully encoding the 'gist' of an item (i.e. non-specific features) can increase the likelihood that a novel item with many overlapping features will be falsely recognized as a result of heightened familiarity for such items (Koutstaal & Schacter, 1997). Our results suggest that increased left fusiform cortex activity during object processing may be associated with increased gist encoding, and thus would promote subsequent false recognition. However, additional right fusiform activity at encoding would be expected to increase the amount of specific information available at recognition, and may serve to counteract such gist-based false recognition, in line with cognitive analyses of processes involved in reducing gist-based false recognition (e.g. Koutstaal, Schacter, Galluccio, & Stofer, 1999; Schacter, Israel, & Racine, 1999). Further research will be needed to determine whether our hypotheses about the differential role of right and left fusiform cortex activity in specific and general encoding are indeed also predictive of subsequent false recognition. For instance, if left fusiform activity at encoding (in the absence of right fusiform activity) does indeed prove to be predictive of subsequent high confidence false recognition, these results, in combination with our current finding that right fusiform activity at encoding is predictive of subsequent high confidence specific (true) recognition, would provide strong support for the fuzzy-trace theory (FTT) of memory. FTT posits that true recollection results from retrieval of verbatim traces of the exact item studied while false (or phantom) recollection results from strong gist-based traces (Brainerd & Reyna, 2001).

If, however, right fusiform activity at encoding is predictive of subsequent high confidence false recognition, these results would provide support for cognitive theories suggesting both true and false recognition are rooted in the same type of memory trace.

Previous neuroimaging studies of encoding processes have only considered whether studied items were remembered or forgotten (i.e. specific memory). In the present study, we provide the first evidence delineating the specific neural substrates associated with encoding of both specific and general information. Moreover, we have linked results from repetition priming studies to the domain of memory encoding, illustrating that the right fusiform cortex is preferentially associated with successful encoding of specific features of visual objects, while the left fusiform cortex is preferentially involved in successful encoding of more general aspects of visual objects.

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