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Neural mechanisms of visual object priming: evidence for perceptual and semantic distinctions in fusiform cortex

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Abstract

Previous functional imaging studies have shown that facilitated processing of a visual object on repeated, relative to initial, presentation (i.e., repetition priming) is associated with reductions in neural activity in multiple regions, including fusiform/lateral occipital cortex. Moreover, activity reductions have been found, at diminished levels, when a different exemplar of an object is presented on repetition. In one previous study, the magnitude of diminished priming across exemplars was greater in the right relative to the left fusiform, suggesting greater exemplar specificity in the right. Another previous study, however, observed fusiform lateralization modulated by object viewpoint, but not object exemplar. The present fMRI study sought to determine whether the result of differential fusiform responses for perceptually different exemplars could be replicated. Furthermore, the role of the left fusiform cortex in object recognition was investigated via the inclusion of a lexical/semantic manipulation. Right fusiform cortex showed a significantly greater effect of exemplar change than left fusiform, replicating the previous result of exemplar-specific fusiform lateralization. Right fusiform and lateral occipital cortex were not differentially engaged by the lexical/semantic manipulation, suggesting that their role in visual object recognition is predominantly in the visual discrimination of specific objects. Activation in left fusiform cortex, but not left lateral occipital cortex, was modulated by both exemplar change and lexical/semantic manipulation, with further analysis suggesting a posterior-to-anterior progression between regions involved in processing visuoperceptual and lexical/semantic information about objects. The results are consistent with the view that the right fusiform plays a greater role in processing specific visual form information about objects, whereas the left fusiform is also involved in lexical/semantic processing.
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Introduction

Repetition priming refers to the facilitated processing of a stimulus on repeated, relative to initial, presentation (Richardson-Klavehn and Bjork, 1988; Roediger, 1990; Schacter, 1987; Schacter and Buckner, 1998). This facilitation may be shown behaviorally as decreases in the amount of time taken to complete a task, and/or as increases in accuracy of performance on the task. Priming is characterized as an example of implicit memory (Graf and Schacter, 1985), whereby the influence of prior processing of a stimulus on subsequent performance can occur without conscious awareness, as contrasted with the explicit conscious remembering of events. The validity of such a distinction is supported by demonstrations of double dissociations between patients with medial temporal lobe amnesia, who have impaired explicit memory but exhibit relatively preserved priming (Warrington and Weiskrantz, 1974), and patients with more posterior cortical lesions, who perform well on explicit memory tasks but are impaired at implicit memory (Gabrieli et al., 1995; Vaidya et al., 1998; Wagner et al.,1998).

Cognitive studies of visual object priming in healthy

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individuals have demonstrated that priming effects may transfer across different exemplars of an object (e.g., two different umbrellas), but the degree of facilitation is attenuated compared with repeated presentation of the identical object (Biederman and Gerhardstein, 1993; Warren and Morton, 1982). Studies using divided visual-field methodology have shown that sensitivity to such alteration of the perceptual form of objects on repeated presentation may differ depending on the cerebral hemisphere to which the objects are preferentially presented (Marsolek, 1995, 1999). The right hemisphere has been reported to be more sensitive to stimulus alteration, suggesting that it is involved in processing specific visual form information about objects, while the left hemisphere, which displays a pattern of generalization across different exemplars, may process more abstract (Marsolek, 1999) and/or lexical/semantic (Koutstaal et al., 2001) information about objects. Consistent with this view, damage to posterior regions of the right hemisphere has been associated with impaired visual form-specific priming (Vaidya et al., 1998).

In recent years, functional neuroimaging studies have provided much further evidence on the brain regions associated with repetition priming phenomena (see Henson, in press; Schacter and Buckner, 1998, for recent reviews). These studies have demonstrated that behavioral priming effects can be mirrored in the levels of activation observed in brain regions involved in stimulus processing, showing reduced activity for previously processed stimuli (Buckner et al., 1995; Raichle et al., 1994; Squire et al., 1992). This reduced activity may reflect "response suppression" or reduction in the firing rate of neurons, as has been recorded in nonhuman primates (Desimone, 1996), diminished response of neurons coding features that are unnecessary for processing, which "sharpens" the representation (Wiggs and Martin, 1998), or shortened duration of neuronal/synaptic activity (Henson and Rugg, 2003). During visual object priming, for example, some of the regions exhibiting significant activation associated with initial visual processing of objects show reduced activation during repeated processing of the objects (Buckner et al., 1998; Henson et al., 2000; Wagner et al., 1997; Wiggs and Martin, 1998). These regions include fusiform and lateral occipital cortices associated with visual perception and lexical/semantic processing (Buckner et al., 1998, 2000; Grill-Spector et al., 1999; Henson et al., 2000; Martin and Chao, 2001; Simons et al., 2001; Thompson-Schill et al., 1999), as well as inferior prefrontal cortices thought to play a role in the controlled retrieval of lexical/semantic information (Dapretto and Bookheimer, 1999; Fiez, 1997; Gabrieli et al., 1996; Martin and Chao, 2001; Poldrack et al., 1999; Wagner et al., 2000, 2001).

Two recent studies (Koutstaal et al., 2001; Vuilleumier et al., 2002) extended these findings of priming-related activation reduction by examining the effects of perceptually manipulating stimuli between repeated presentations (see also Grill-Spector et al., 1999). Koutstaal et al. (2001) compared neural responses associated with the repeated processing of identical objects and perceptually different exemplars of objects. Activation in fusiform and inferior prefrontal regions reflected the pattern found on the behavioral index of priming; these regions showed significant neural priming for different exemplars, but priming was attenuated compared to that found for identical exemplars. Echoing the results of Marsolek's (1999) divided visual-field studies, the activation difference between identical and different exemplar processing was more pronounced in right than left fusiform, consistent with the idea that specific visual form processing occurs in the right hemisphere, but that more abstract or perhaps lexical/semantic processing—the precise nature of which is currently unclear—is supported by the left hemisphere. Similar fusiform lateralization was observed by Vuilleumier et al. (2002), who found greater sensitivity to changes in the viewpoint of perceived objects in right than left fusiform cortex. Unlike Koutstaal et al., however, Vuilleumier and colleagues did not find lateralization of activation in fusiform cortices associated with perceptually different exemplars.

The primary aim of the present study was to investigate in more detail the involvement of left fusiform cortex in visual object processing. As alluded to above, evidence exists consistent with roles for left fusiform in both abstract visual object representation and the processing of lexical/semantic information (Buckner et al., 1998; Koutstaal et al., 2001; Marsolek, 1995; Vuilleumier et al., 2002). To investigate this issue, a lexical/semantic manipulation was employed whereby, immediately prior to and concurrent with the onset of a pictured object, either the object's name or a nonsense word was auditorily presented. If left fusiform is involved exclusively in abstract visual form processing, as has been suggested (Marsolek, 1995), then no difference in activation would be expected for objects accompanied by their actual names relative to objects accompanied by nonsense words. If, however, left fusiform plays a role in the processing of lexical/semantic representations (e.g., Buckner et al., 2000), it might be predicted that activation in this region, and in others involved in semantic processing such as inferior prefrontal cortex, would be modulated by the name manipulation.

This study also attempted to ascertain whether it would be possible to replicate Koutstaal et al.'s (2001) finding of differential sensitivity to exemplar change in right versus left fusiform cortex when different stimuli, different participants, and a different fMRI scanner were used. Given Vuilleumier et al.'s (2002) failure to observe greater exemplar specificity in right than left fusiform cortex, it is important to seek confirmation that fusiform lateralization for processing of different exemplars is a reliable outcome, and can be reproduced in a new experiment. If right fusiform cortex is indeed involved more than left fusiform in processing object-specific visual form information that differentiates between exemplars, then it should be possible to replicate Koutstaal et al.'s observation of a significant in-

teraction between BOLD fMRI signal change in left and right fusiform, and the type of object presented (same or different exemplars). This would allow confirmation that the object recognition processes subserved by right and left fusiform are differentially sensitive to changes in exemplar (as well as perhaps in viewpoint; Vuilleumier et al., 2002).

Materials and methods

Participants

Sixteen right-handed native speakers of English (10 male, 6 female), with normal or corrected-to-normal vision, took part in the experiment. The volunteers (mean age = 21.4 years, range 18–30) were recruited through sign-up sheets and received $50 for their participation. Data from two additional participants were excluded due to technical problems with the scanner or peripheral equipment. Participants were screened using a comprehensive medical questionnaire and informed consent was obtained in a manner approved by the Human Studies Committee of the Massachusetts General Hospital.

Design and materials

There were six conditions in the experiment, which manipulated object type (novel items, repeated same, repeated different) and the concurrent presentation of lexical/semantic information (name, nonsense word). The stimuli consisted of 288 color picture pairs and corresponding auditory word pairs. The picture pairs depicted single man-made or living objects (e.g., umbrella, octopus), with the items in each pair representing perceptually different exemplars of objects with the same name, as in our previous study (Koutstaal et al., 2001). Behavioral pilot testing, involving 12 young adults from the same population as those who took part in the imaging study, confirmed that name agreement for the exemplar pairs was high, with 95% of items on average (SD = 8%) given the same or a minor variant (e.g., "television" vs "TV") of the same name. The auditory word stimuli were digital recordings of the name (e.g., "umbrella") and a phonologically matched nonsense word (e.g., "wa-su-to") for each of the 288 items. The nonsense words were created by pseudo-randomly combining phonemes into nonwords that were each matched with their corresponding object name for syllable length. The nonsense words were independently screened by three of the authors (S.P., W.K., and J.S.S.), with nonwords being replaced if any semantic associations were elicited. Although it is not possible to rule out the possibility that some meaning-related processing occurred for a few of the nonsense words, it is unlikely that the meaning was systematically related to the pictured objects with which the nonsense words were paired. The stimuli were divided into 36 sets of eight items, with the sets systematically counterbalanced between subjects across the six conditions.

Procedure

Across 16 scans, eight study-test cycles were administered to subjects. The study and test phases were very similar; indeed, on debriefing after the experiment, none of the subjects reported being aware of a difference between consecutive phases. In both tasks, a picture was presented for 1 s and participants were asked to judge whether the object depicted was, in real life, larger or not larger than a 13-inch box. As part of the test instructions before scanning, subjects were shown an actual 13-inch box to aid them with this judgment. They indicated their decision by pressing one of two buttons on a button box. Beginning 50 ms prior to the onset of each picture, when a central fixation cross was displayed on the screen, an auditory word or nonword was presented to the subjects through headphones. For half the items, the word was the item's name (e.g., "umbrella") whereas for the other half, the word was a nonsense word (e.g., "wa-su-to"). Participants were instructed to listen attentively to the auditorily presented stimulus (word or nonword), but to base their size judgment on the picture they were viewing. In order to optimize the efficiency of the imaging-analysis design matrix, the order of the conditions in each scan was determined using an optimal sequencing program, with additional periods of baseline fixation lasting between 2 and 10 s pseudo-randomly interspersed between trials (Dale, 1999).

The study and test phases differed in that, in the study phase, the same set of 32 items was repeated three times, whereas in the test phase, 64 items were presented once each. The test items consisted of three item types: 32 *novel* items (objects not previously presented; 16 accompanied by a name, 16 by a nonsense word), 16 *repeated same* items (the identical picture to one presented in the preceding study phase; 8 name and 8 nonsense word items), and 16 *repeated different* items (the different exemplar of an item presented in the preceding study phase; 8 name and 8 nonsense word items). Although the precise picture presented in the study and test phases might differ (in the repeated different condition), the auditory word that was associated with a particular item for a given subject (either the item's name or a nonsense word) was always the same across the study and test phases. Within the study phase, the 32 items were presented in a different pseudo-random order for each of the three repetitions; within the test phase, the 64 items were pseudo-randomly intermixed in accord with the algorithm for optimizing the event-related fMRI design matrix (Dale, 1999).

Imaging acquisition and data analysis

A 3T Siemens Allegra system was used to acquire high-resolution T1-weighted anatomical images (MP-RAGE)

and T2*-weighted gradient-echo echo-planar functional images (TR = 2000 ms, TE = 30 ms, 21 sequential axial slices aligned parallel to the AC-PC transverse plane, 5 mm thickness, 1 mm interslice skip, 200 mm FOV, 64 × 64 matrix, 126 volume acquisitions per study phase run, 96 acquisitions per test phase run). Four additional volumes were collected and discarded at the beginning of each run to allow for T1 equilibration.

Data were preprocessed using SPM99 (Wellcome Department of Cognitive Neurology, London). Images were first corrected for differences in slice acquisition timing by resampling all slices in time to match the first slice, followed by motion correction across runs (using sinc interpolation). Data were then spatially normalized to an EPI template based upon the MNI305 stereotactic space (Cocosco et al., 1997). Images were resampled into 3-mm cubic voxels and then spatially smoothed with an 8-mm FWHM isotropic Gaussian kernel.

Statistical analysis was performed using the general linear model in SPM99. Scanning was undertaken during both study and test phases, although only data from the test phases are described here. Trials were excluded if participants made no behavioral response, or if the response occurred within 250 ms of the onset of the picture. The remaining test trials were categorized according to condition, and each of the six conditions was modeled using a canonical hemodynamic response. These effects were estimated using a subject-specific fixed-effects model, with session-specific effects and low-frequency signal components treated as confounds. Movement parameters in the 3 directions of motion and 3 degrees of rotation were entered as covariates of no interest.

Linear contrasts were used to obtain subject-specific estimates for each of the effects of interest. These estimates were entered into a second-level analysis treating subjects as a random effect, using a one-sample t test against a contrast value of zero at each voxel. Statistical parametric maps were created for each contrast of interest, and were subsequently characterized using, at the voxel level, an uncorrected height threshold of $P < 0.001$ and, at the cluster level, an extent threshold of $P < 0.05$, corrected for the entire imaged volume. The brain regions and Brodmann areas of significant cluster maxima were estimated from the Talairach and Tournoux (1988) atlas, after adjusting coordinates to allow for differences between the MNI and Talairach templates (Brett et al., 2001).

To further explore the nature of the activation associated with each condition, regions of interest (ROIs) were identified from clusters that survived the thresholding criteria in the linear contrast between all novel items and all repeated items, a contrast providing the most unbiased index of priming. The maximal voxel of each cluster was used to define the center of a sphere of radius 8 mm, with the signal of each voxel within this sphere extracted on a subject-by-subject basis. The mean percentage signal change for each condition relative to the fixation baseline was calculated over the hemodynamic response window, and these responses subjected to repeated-measures analyses that included condition and, where specified, region, as repeated factors and peak magnitude percentage signal change as the dependent variable.

Table 1
Behavioral responses in the test phases

	Nonsense condition			Name condition		
	Novel	Same	Different	Novel	Same	Different
Reaction time						
Mean	816.7	705.5	761.5	799.8	691.0	724.4
SD	124.6	104.2	118.9	119.6	83.7	93.7
Accuracy						
Mean	0.85	0.90	0.88	0.85	0.88	0.88
SD	0.05	0.04	0.04	0.06	0.06	0.05

Results

Behavioral data

Behavioral data from the test phase are presented in Table 1. There were significant main effects on reaction time of object type, F (2, 30) = 102.4, $P < 0.0001$, and lexical/semantic condition, F (1, 15) = 14.4, $P < 0.005$, with a trend toward an interaction between the two, F (2, 30) = 3.1, $P = 0.06$. In both lexical/semantic conditions, paired t tests revealed significant behavioral priming, as measured by diminished reaction times, for both repeated same and repeated different items, compared with novel items, all t (15) > 6, $P < 0.0001$ (corrected for multiple comparisons). Importantly, these priming effects were significantly greater for same than different items, both t (15) > 5, $P < 0.0001$. The lexical/semantic manipulation did not significantly affect priming of repeated same items, t (15) = 1.8, n.s., but provision of items' names rather than nonsense words led to significantly faster responses to novel items, t (15) = 2.9, $P < 0.05$, and repeated different items, t(15) = 3.5, $P < 0.005$.

Examination of size judgment accuracy scores for each condition revealed a significant main effect of object type only, F (1.5, 21.9) = 6.9, $P < 0.01$ (noninteger degrees of freedom indicate Huynh-Feldt adjustment for nonsphericity). Paired t tests indicated that novel items were classified significantly less accurately than repeated same and repeated different items in the nonsense condition, both t (15) > 3, $P < 0.005$, but that there were no accuracy differences when the item's name was provided, all t(15) < 2.5, n.s.

Imaging data

We first examined activation patterns that differentiated between novel and repeated items, combining across lexi-

Table 2
Regions demonstrating greater activation for novel than for repeated objects (combining across lexical/semantic and same/different manipulations)

Brain region	Coordinates			Z	Voxels
	x	y	z		
Left hemisphere					
Fusiform/lateral occipital cortex (BA 37, 19, 18)	−45	−54	−24	5.57	1585
Anterior and posterior inferior prefrontal cortex (BA 44, 45, 47)	−36	30	−9	5.00	1003
Lingual gyrus (BA 18)	−18	−69	0	4.63	91
Anterior fusiform gyrus (BA 20)	−36	−3	−45	3.97	43
Right hemisphere					
Fusiform/lateral occipital cortex (BA 37, 19, 18)	48	−66	−15	5.38	1208
Posterior inferior prefrontal cortex (BA 44)	51	6	27	4.27	122
Middle temporal gyrus (BA 21)	57	−30	0	4.26	56
Anterior inferior prefrontal cortex (BA 45)	54	33	6	4.23	83
Anterior inferior prefrontal cortex (BA 47)	51	21	−12	3.60	60
Midline					
Anterior cingulate cortex (BA 32)	0	24	45	4.72	96

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas.

cal/semantic and same/different manipulations. This contrast was associated with significant reductions in neural activity in large regions of bilateral fusiform, lateral occipital, and lingual cortex (Brodmann areas [BA] 37, 19, 18), as well as areas that included bilateral inferior prefrontal (BA 47, 45, 44) and medial anterior cingulate cortices (BA 32) (see Table 2 and top row of Fig. 1). Separate comparison of novel and repeated same items revealed reduced activation for the repeated items in many of the regions identified in the previous contrast (see second row of Fig. 1). Separate comparison of novel and repeated different items showed activity reductions in left fusiform (BA 37) and lateral occipital cortex (BA 18), as well as left (BA 44, 6) and right (BA 47) inferior prefrontal cortex (see third row of Fig. 1). A direct comparison of the repeated same and repeated different conditions revealed reduced activation for the same compared to different items (indicating greater priming) in bilateral fusiform/lateral occipital cortex (BA 37, 19, 18) and inferior prefrontal cortex (BA 44) (see Table 3 and bottom row of Fig. 1).

Combining across semantic conditions once more, the time courses of signal change in regions exceeding threshold in the all novel > all repeated contrast revealed several areas in which levels of activation for different items were significantly greater than those for same items. This pattern, which echoed the behavioral result of less priming for different than same items, was observed particularly in left and right fusiform and lateral occipital cortices (see Fig. 2), all $F(1, 15) > 43$, $P < 0.0001$. As noted above, the voxel-based analysis comparing novel and repeated different items revealed significant priming-related reductions of neural activity in left but not right fusiform cortex, suggesting greater generalization between repeated exemplars in the left fusiform. Inspection of signal change in the left and right fusiform regions derived from the general priming (all novel > all repeated) contrast (see top row of Fig. 2) supported this view, yielding a significant interaction between region (left and right fusiform) and item type (novel and different exemplars), $F(1, 15) = 5.9$, $P < 0.05$. Further evidence of less exemplar generalization in right than left

Table 3
Regions demonstrating greater activation for repeated different than for repeated same objects (combining across lexical/semantic manipulations)

Brain region	Coordinates			Z	Voxels
	x	y	z		
Left hemisphere					
Fusiform/lateral occipital cortex (BA 37, 19)	−48	−60	−18	5.13	505
Inferior parietal lobe (BA 39, 19)	−27	−81	39	4.58	151
Posterior inferior prefrontal cortex (BA 44)	−42	9	33	4.26	187
Lateral occipital cortex (BA 18)	−33	−93	9	4.25	46
Right hemisphere					
Fusiform/lateral occipital cortex (BA 37, 19, 18)	54	−63	−15	5.03	755
Posterior inferior prefrontal cortex (BA 44, 45)	48	12	24	4.39	265
Inferior parietal lobe (BA 40)	45	−45	54	4.07	50

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas.

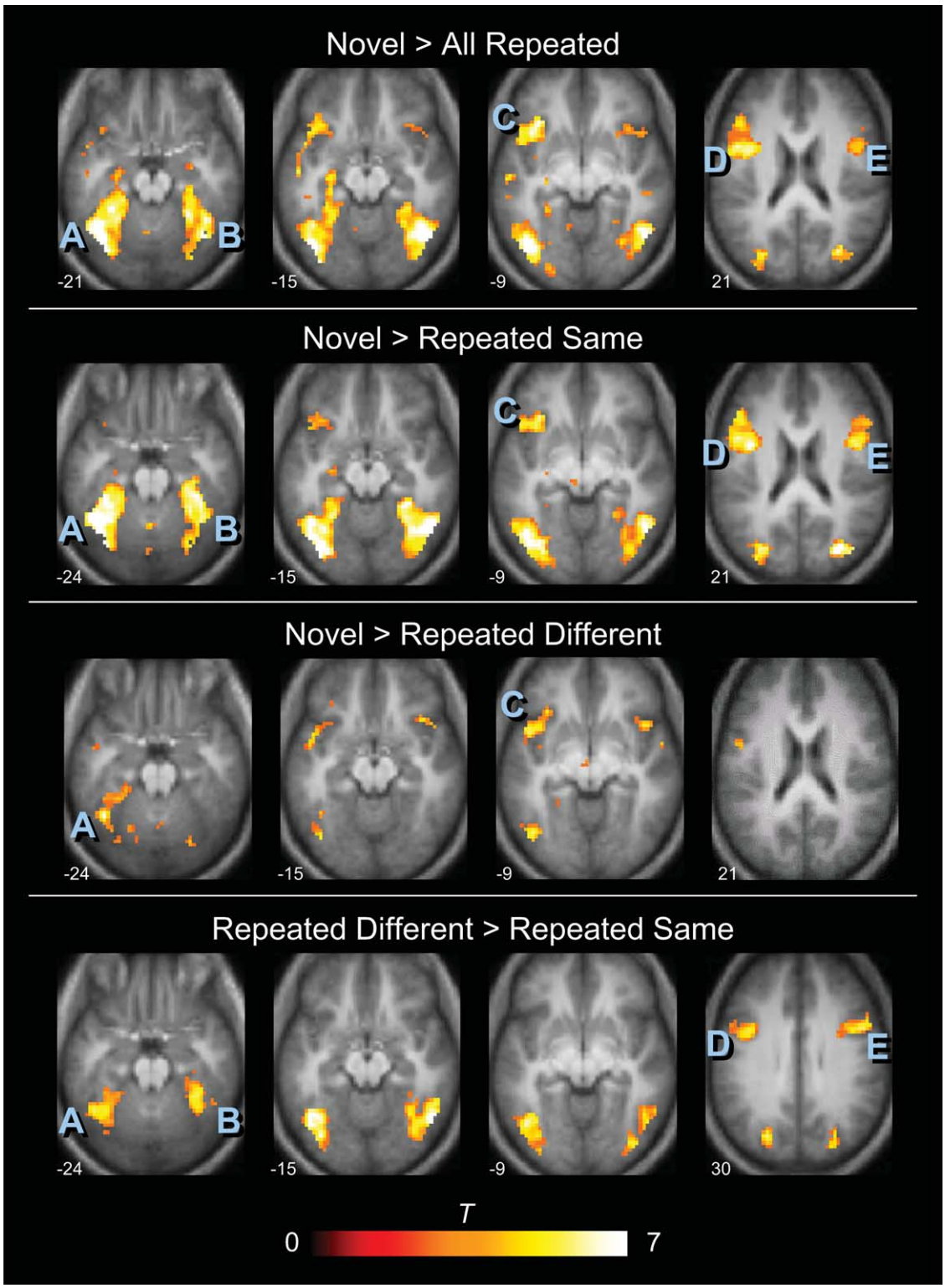
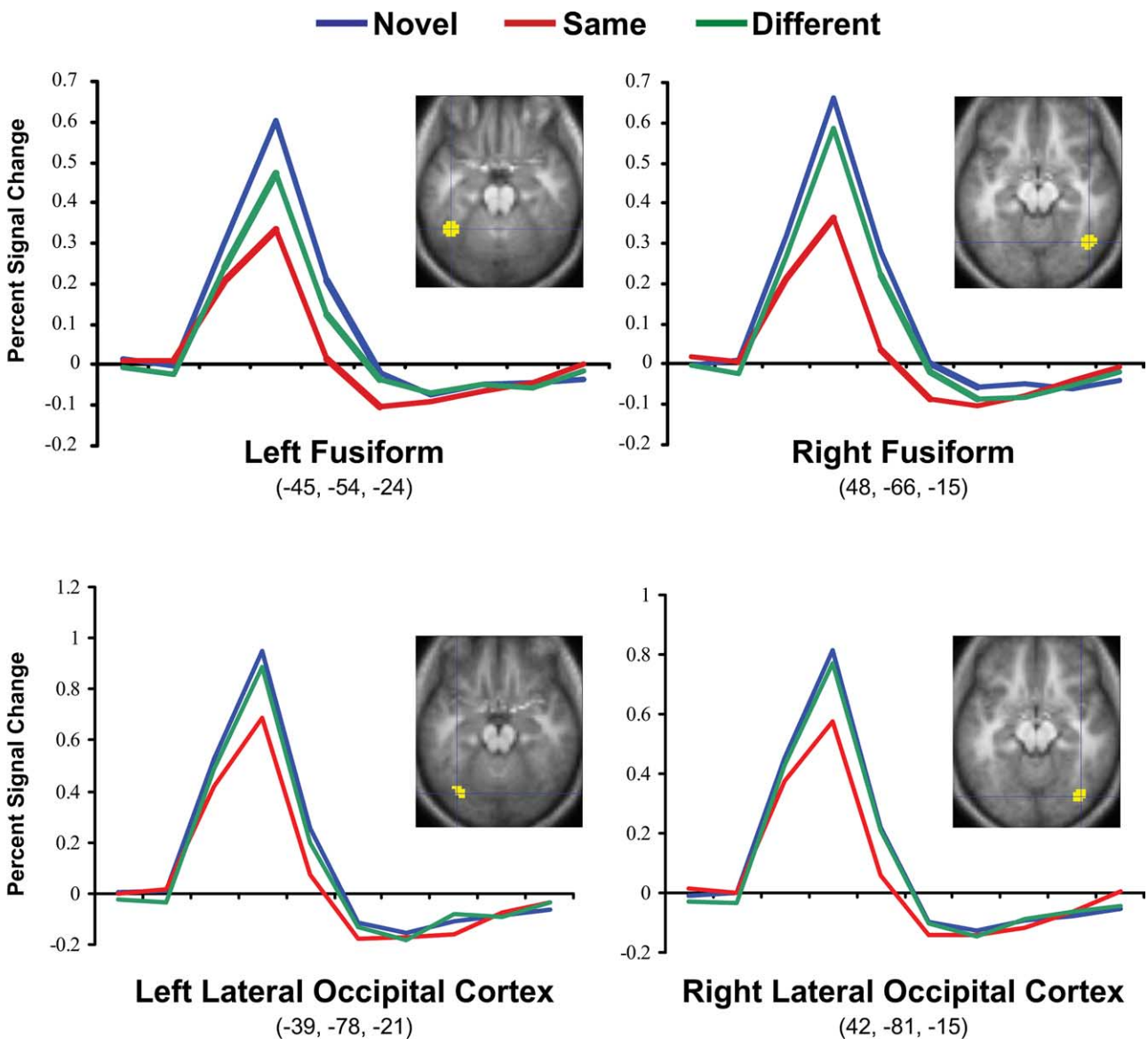
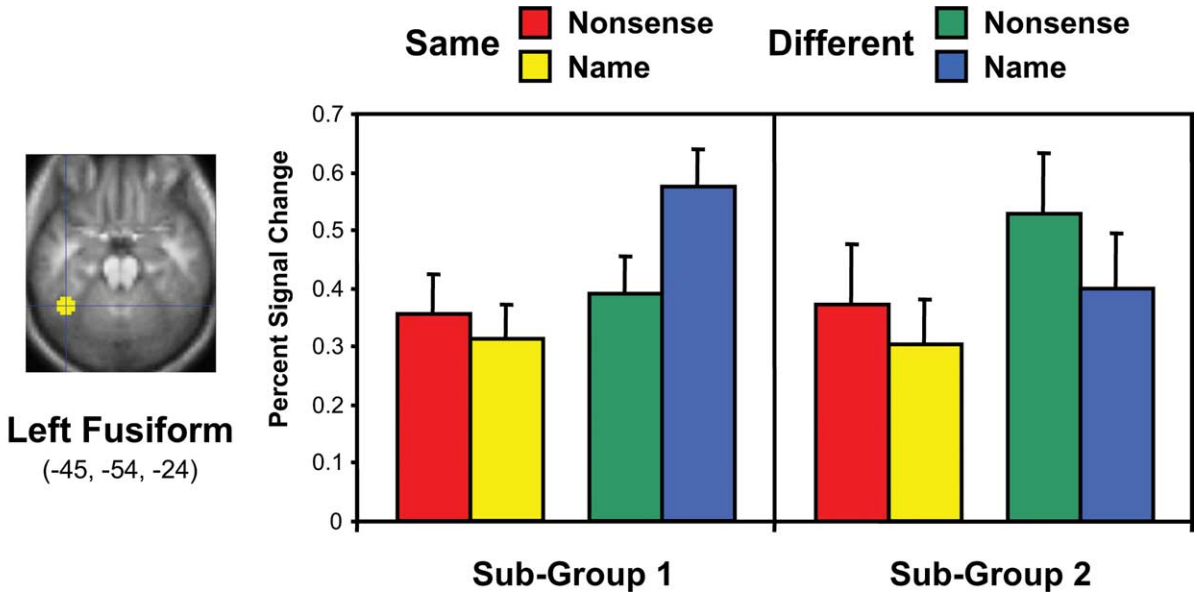


Fig. 1. Group functional activation maps from the comparisons of novel and repeated items (combining across lexical/semantic conditions) superimposed upon axial slices of an averaged anatomical MR image. For each image, the left side corresponds to the left side of the brain, and the distance in mm superior to the AC-PC transverse plane is noted at the bottom left of the image. Top row: in the novel > all repeated contrast, regions of significant activation (reflecting greater priming for repeated items) included left (A) and right (B) fusiform/lateral occipital cortex (BA 37, 19, 18), left anterior inferior prefrontal cortex (C; BA 45, 47), and bilateral posterior inferior prefrontal cortex (D and E; BA 44). Second row: the novel > repeated same contrast resulted in significant activation in many of the same regions as in the previous contrast. Third row: regions activated in the novel > repeated different contrast included left fusiform/lateral occipital cortex (A) and anterior inferior prefrontal cortex (C). Bottom row: in the repeated different > repeated same contrast, significant activation (indicating greater priming for repeated same items) was observed in left (A) and right (B) fusiform/lateral occipital cortex and in left (D) and right (E) posterior inferior prefrontal cortex.


Novel
Same
Different
Percent Signal Change
Left Fusiform
(-45, -54, -24)
Right Fusiform
(48, -66, -15)
Left Lateral Occipital Cortex
(-39, -78, -21)
Right Lateral Occipital Cortex
(42, -81, -15)

2


Same
Nonsense
Name
Different
Nonsense
Name
Percent Signal Change
Left Fusiform
(-45, -54, -24)
Sub-Group 1
Sub-Group 2

3

fusiform comes from direct comparison between neural responses associated with repeated same and different items. Comparison of time courses suggested that different items were treated less like same items (indicating greater perceptual specificity for different exemplars) in right than in left fusiform, resulting in a significant interaction between region and item type (same and different items), F (1, 15) = 13.5, $P < 0.005$, replicating the result of Koutstaal et al. (2001). When activation levels in the right and left lateral occipital cortex were compared, no such interactions between region and item type (novel, same, and different) were observed, suggesting that both lateral occipital cortices differentiated to a similar extent between items, both F (1, 15) < 0.4, n.s.

Turning to examination of the effects of the lexical/semantic manipulation, inspection of the time courses from the right fusiform and lateral occipital cortices did not suggest that repetition-related responses in these regions were modulated by lexical/semantic condition, with no interactions being evident between item type and lexical/semantic condition, both F (1, 15) < 0.3, n.s. Examination of left fusiform and lateral occipital cortex revealed that left fusiform cortex showed a nonsignificant interaction between item type and lexical/semantic condition, F (1, 15) = 2.04, $P = 0.17$, while left lateral occipital cortex was as unaffected by the lexical/semantic manipulation as the right hemisphere regions, F (1, 15) = 0.4, n.s. Inspection of the individual subject time courses in the left fusiform cortex suggested substantial variability between subjects in neural responses to repeated different items as a function of whether accompanying object-relevant lexical/semantic information was or was not provided. This factor might go some way to explaining the weakness of the interaction between item type and lexical/semantic condition in this left fusiform region. When the group was mean split into subgroups of 8 subjects each by difference in signal change between the two repeated different conditions, significant interactions were observed, both between subgroup and lexical/semantic condition, F (1, 14) = 15.6, $P < 0.001$, and between subgroup, lexical/semantic condition, and item type (same and different), F (1, 14) = 10.0, $P < 0.01$. This suggests that the subgroups of subjects differed significantly in their neural responses depending on the provision of the item's name or a nonsense word, and that this effect was significantly greater for repeated different than same items (see Fig. 3). In other words, the left fusiform cortex consistently exhibited sensitivity to the lexical/semantic manipulation, but this sensitivity appeared to be manifested differently in individual subjects. Importantly, there was no main effect of subgroup on signal change overall, $F = 0.0$, indicating that the lexical/semantic interactions were not attributable to global signal differences between subjects.

To confirm the apparent picture of sensitivity only to item type in right fusiform and bilateral lateral occipital cortex, but additional modulation by the availability of lexical/semantic information in left fusiform, the time courses were examined from every discrete cluster of at least 5 contiguous voxels in these areas that survived an uncorrected height threshold of $P < 0.001$ in the all novel > all repeated contrast. In Fig. 4, those clusters exhibiting differential engagement for item type but not for lexical/semantic condition are colored green, while those showing additional sensitivity to the lexical/semantic manipulation are colored red. It is clear that regions in the right hemisphere only responded differently to item type. Consistent with the above evidence that left fusiform, but not left occipital cortex, exhibited sensitivity to lexical/semantic condition, inspection of supra-threshold clusters in the left fusiform/lateral occipital cortex suggests a posterior-to-anterior progression from clusters modulated only by item type, to clusters showing additional differentiation between lexical/semantic conditions. This suggestion of progression within the left fusiform/lateral occipital cortex is supported by a comparison of distances from the anterior commissure of the maxima of clusters exhibiting the two patterns, which revealed that those modulated only by item type were, on average, significantly more posteriorly located in the left hemisphere than those additionally sensitive to lexical/semantic condition, F (1, 13) = 4.9, $P < 0.05$.

Beyond occipitotemporal cortex, priming-related reductions in neural activity were also observed in bilateral inferior prefrontal and anterior cingulate cortices (see Table 2). Examination of the time courses of activation in these areas revealed that an anterior region of left inferior prefrontal cortex, which was activated in the novel > all repeated contrast, differentiated between novel and repeated items, both F (1, 15) > 27, $P < 0.0001$, but generalized across repeated same and different items, F (1, 15) = 3.3, n.s. (see top left panel of Fig. 5). This region was also sensitive to the lexical/semantic manipulation, with a strong trend toward a main effect of lexical/semantic condition, F (1, 15) = 4.3, $P = 0.06$ (see top right panel of Fig. 5). Provision of the

Fig. 2. Selectively averaged percentage signal change (relative to fixation) for novel, repeated same, and repeated different items (combining across lexical/semantic conditions) in left and right fusiform cortex (top row) and left and right lateral occipital cortex (bottom row). Regions of interest, which were derived from the all novel > all repeated linear contrast, are displayed on axial slices of an averaged anatomical MR image. All regions showed a pattern of significantly greater activation for repeated different than repeated same items. Within fusiform cortex, a significant interaction emerged between hemispheres, with exemplar generalization in the left, and exemplar specificity in the right. No such lateralization was observed in lateral occipital cortex.
Fig. 3. Selectively averaged (and standard error) peak magnitude percentage signal change (relative to fixation) for repeated same and repeated different objects, shown separately as a function of the lexical/semantic manipulation. Object's name provided in "Name" condition, phonologically matched nonsense word provided in "Nonsense" condition. Results show responses in left fusiform cortex for subgroups of subjects mean split by signal change difference between the two repeated different conditions. Significant interactions were observed between subgroup and lexical/semantic condition, and among subgroup, lexical semantic condition, and item type.

names of items led to significantly greater priming for repeated same items, t (15) = 2.5, $P < 0.05$, but not for repeated different items, t(15) = 0.65, n.s., although the interaction between item type and lexical/semantic condition was not significant, F (1, 15) = 1.7, n.s. A more posterior region of left inferior prefrontal cortex was activated in the repeated different > repeated same contrast (see Table 3), as was an analogous right inferior prefrontal cortex region identified in the novel > all repeated contrast (see Table 2). These regions both exhibited similar patterns of perceptual exemplar specificity to that observed in occipitotemporal cortex, showing significantly greater activation for repeated different than same items, both F (1, 15) > 21, $P < 0.0001$ (see bottom panels of Fig. 5). A dissociation was evident, therefore, within the left inferior frontal gyrus, between exemplar generalization in anterior, and exemplar specificity in posterior, inferior prefrontal cortex, as reflected in a significant region by item-type interaction, F (1, 15) = 12.9, $P < 0.005$. All other regions to exhibit significant activation in the novel > all repeated contrast (including anterior cingulate cortex) generalized across repeated exemplars in a similar fashion to the anterior left inferior prefrontal cortex cluster, all F (1, 15) < 2, n.s., but were not differentially engaged by the lexical/semantic manipulation, all F (2, 30) < 1.2, n.s.

Several regions showed evidence of priming-related activation *increases* in an all repeated > all novel contrast. These included left frontopolar (BA 10; peak at −30, 60, 0; $Z = 4.05$; 17 voxels) and dorsolateral prefrontal cortex (BA 9; peak −42, 21, 45; $Z = 3.89$; 23 voxels), as well as medial parietal/precuneus (BA 31; peak 0, −54, 36; $Z = 4.84$; 520 voxels) and left inferior parietal (BA 40; peak −42, −63, 42; $Z = 4.31$; 34 voxels) cortices. Examination of the time courses of activation in these areas disclosed that all showed deactivation for the size judgment task relative to fixation (similar results were reported by Koutstaal et al., 2001). The extent of deactivation was significantly greater for novel items than for repeated items in each of the regions, all F (1, 15) > 7, $P < 0.05$. Only the precuneus region differentiated between repeated same and repeated different objects, F (1, 15) = 6.7, $P < 0.05$, perhaps consistent with the proposed role for this region in visual imagery (Fletcher et al., 1995). None of the regions exhibited responses that were modulated by the lexical/semantic manipulation.

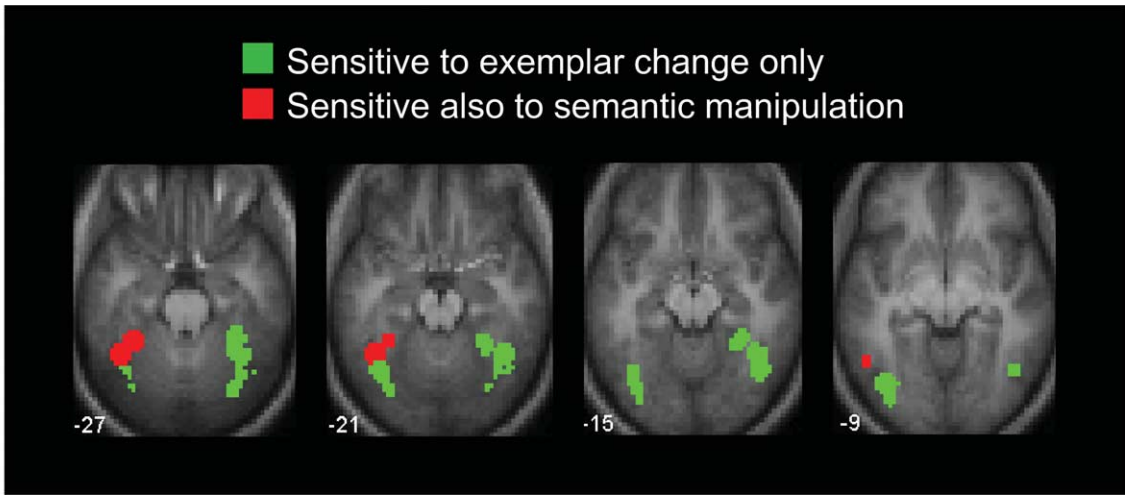
Discussion

The present fMRI study examined the influence of perceptual and lexical/semantic manipulations on visual object priming and its neural representation in fusiform/lateral occipital cortex. Significantly decreased brain activity for repeated, relative to novel, objects was observed in bilateral fusiform/lateral occipital cortex, as well as in frontal and anterior cingulate regions. Right fusiform cortex showed significantly greater perceptual specificity than left fusiform (replicating the result of Koutstaal et al., 2001), differentiating to a greater degree between identical repeated pictures versus perceptually different exemplars of repeated objects. Right fusiform and lateral occipital regions were not modulated by the lexical/semantic manipulation (providing the auditory name of the object or a nonsense word), suggesting that their role in visual object recognition is principally in the visual discrimination of specific object exemplars. Differential roles for regions of left occipitotemporal cortex were identified, with activation in left fusiform cortex, but not left lateral occipital cortex, showing modulation in response to both perceptual exemplar change and the lexical/semantic manipulation. Further analysis suggested a posterior-to-anterior progression within the left occipitotemporal area, between regions involved in processing visuoperceptual, and lexical/semantic, information about objects.

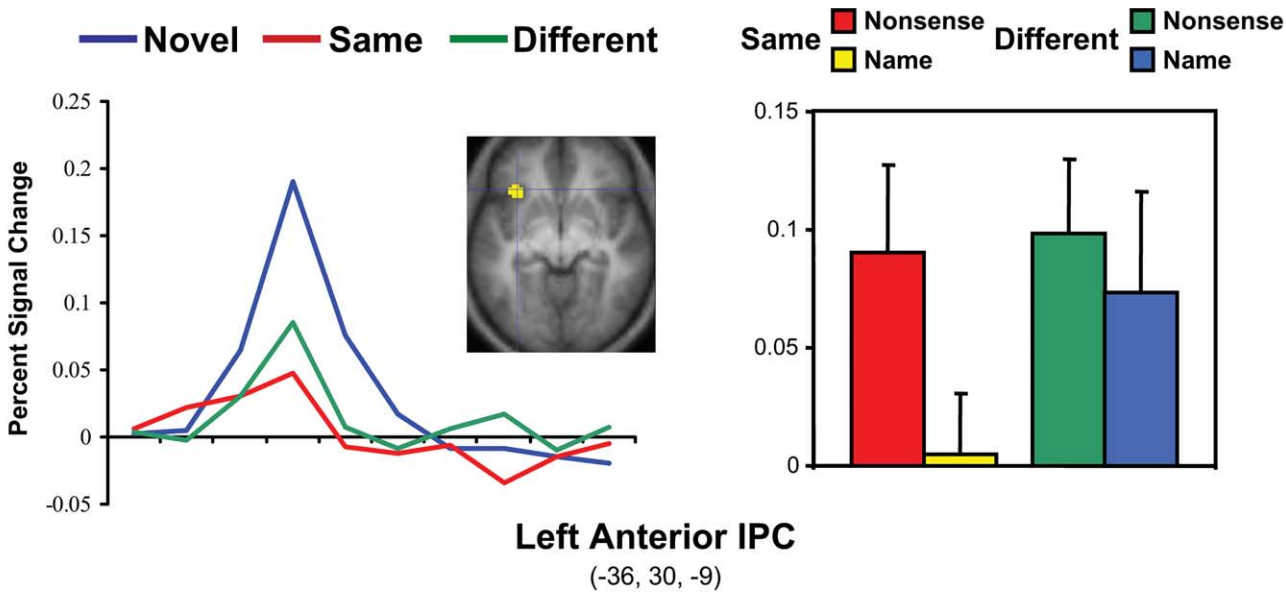
The regions exhibiting diminished activation for repeated over novel objects are consistent with those reported by a number of previous studies (Buckner et al., 1998; Grill-Spector et al., 1999; Henson et al., 2000; Koutstaal et al., 2001; Vuilleumier et al., 2002). Reduced neural activity for repeated stimuli was observed in fusiform and lateral occipital regions that have been associated principally with visual perceptual (Buckner et al., 1998; Henson et al., 2000; Wiggs and Martin, 1998) and lexical/semantic (Buckner et al., 2000; Martin and Chao, 2001; Mummery et al., 1999; Simons et al., 2001; Thompson-Schill et al., 1999) processing, as well as in inferior prefrontal regions that are thought to be involved in the controlled selection and/or retrieval of lexical and semantic information (Dapretto and Bookheimer, 1999; Fletcher and Henson, 2001; Gabrieli et al., 1996; Martin and Chao, 2001; Poldrack et al., 1999; Thompson-Schill et al., 1997; Wagner et al., 2001).

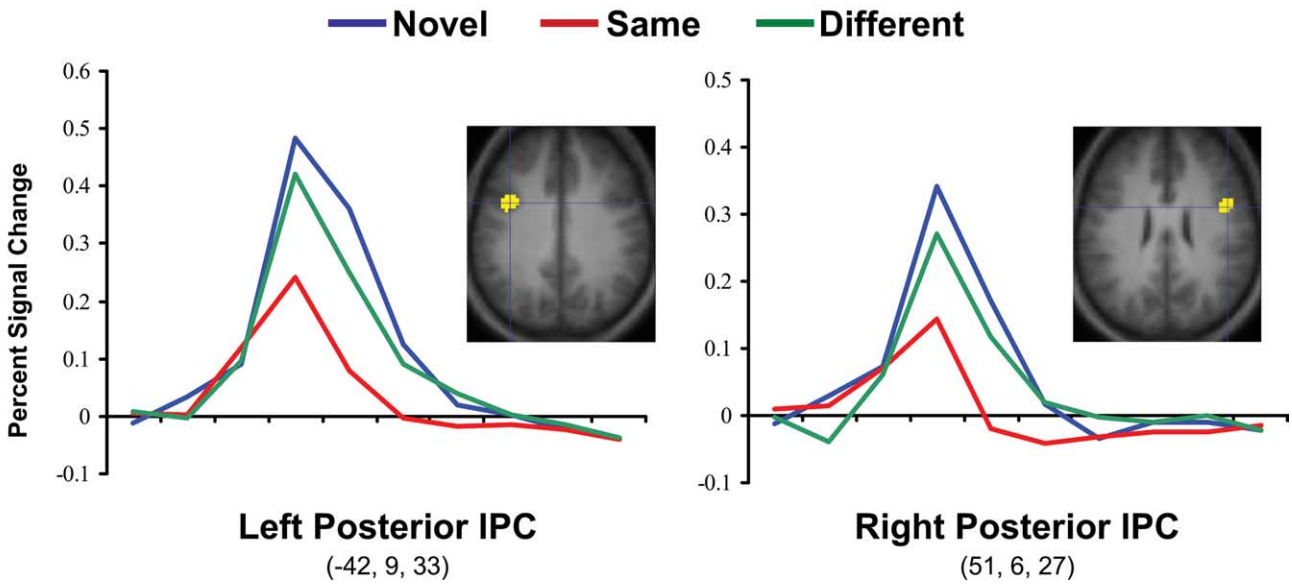
Effects of perceptual exemplar manipulation on visual object priming

The present results converge with and extend those of previous studies (Grill-Spector et al., 1999; Koutstaal et al., 2001; Vuilleumier et al., 2002) in finding that visual manipulation of objects appearing as prime and target items resulted in response modulation in posterior regions of occipito-temporal cortex, such as fusiform and lateral occipital cortices. Grill-Spector and colleagues (1999), who employed an "fMR adaptation" approach, identified regions of lateral occipital cortex which responded more to objects and faces than to textures and visual noise patterns, and which were sensitive to the illumination and viewpoint of the object. Activation in those experiments (see also Kourtzi and Kanwisher, 2000) was not correlated with behavioral priming, however, and occurred in the context of immediate, short-lag repetition (suggesting the possible involvement of a visual iconic store) rather than the longer-lag repetition typically used in priming experiments (Henson, in press). The results of the present study (see also Vuilleumier et al., 2002, discussed below) provide confirmation that


Sensitive to exemplar change only
Sensitive also to semantic manipulation
-27
-21
-15
-9

4


Novel
Same
Different
Percent Signal Change
0.25
0.2
0.15
0.1
0.05
0
-0.05
Same
Nonsense
Name
Different
Nonsense
Name
0.15
0.1
0.05
0
Left Anterior IPC
(-36, 30, -9)


Novel
Same
Different
Percent Signal Change
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
0.5
0.4
0.3
0.2
0.1
0
-0.1
Left Posterior IPC
(-42, 9, 33)
Right Posterior IPC
(51, 6, 27)

5

lateral occipital and fusiform cortices are sensitive to perceptual manipulations such as viewpoint and exemplar change, and that these differential neural responses are manifested behaviorally as priming, reflected in reaction times that are faster for repeated same than repeated different items, which are both faster than reaction times for novel items.

Consistent with the results of Koutstaal et al. (2001), a fusiform laterality effect was observed, whereby region (right and left fusiform) interacted significantly with item type (repeated same and different object), indicating greater perceptual specificity in responsiveness to repeated items in right than left fusiform cortex. This replication was extended by additionally demonstrating that a significant interaction also existed between fusiform region and item type when comparing novel and repeated different objects. This interaction disclosed that left fusiform differentiated more between novel and repeated different objects than did right fusiform, suggesting greater generalization in the left (that is, greater across-exemplar priming in left than right fusiform). These lateralization results were observed only in fusiform cortex, with no such hemispheric interactions being evident in other posterior regions, such as lateral occipital cortex. This is consistent with a view that lateral occipital cortex is involved in processing nonretinotopic, featural representations of perceived objects necessary for shape extraction (Grill-Spector et al., 1999; Malach et al., 1995), whereas fusiform cortex supports higher level processes of object recognition and identification (Martin and Chao, 2001; Ungerleider, 1995; see below for further discussion). The fusiform laterality results mesh well with predictions derived from split visual-field behavioral experiments (Marsolek, 1995, 1999), according to which dissociable object recognition systems exist in the brain, with a specific visual form system operating principally in the right hemisphere and an abstract visual form system operating predominantly in the left hemisphere.

Further support for the hemispheric asymmetry view comes from a recent study which found greater sensitivity to alterations in the viewpoint of repeated objects in right than left fusiform cortex (Vuilleumier et al., 2002). This result converges with those from the present study and from Koutstaal et al. (2001) in suggesting that the right fusiform retains object representations that are specific to the particular featural properties apparent in perceived objects, while the representations processed in left fusiform generalize to a greater extent across alterations of these features. Where the results of these fMRI studies differ, however, is that while Vuilleumier et al. observed fusiform lateralization differences according to the viewpoint of objects, they did not find such lateralization between perceptual exemplars of objects (as reported in our earlier study and confirmed in the present experiment). There may be several reasons for this discrepancy. First, as suggested by Vuilleumier and colleagues, it is possible that the different exemplars employed by Koutstaal et al. (and, presumably, the present study) were more visually similar to one another than those used in Vuilleumier et al.'s study. However, another possible explanation is that Vuilleumier et al. reported nonsignificant behavioral priming for repeated different, over novel, exemplars. It is possible that if subjects in that study had exhibited significant behavioral priming for repeated different exemplar objects, as in the present study and that by Koutstaal et al. (and also in the split visual-field behavioral experiments of Marsolek, 1999), they would also have exhibited some neural response generalization across exemplars in left fusiform cortex.

Effects of lexical/semantic manipulation on visual object priming

Although the predominant activation pattern in the present experiment was of sensitivity to perceptual exemplars, the left fusiform cortex, but not the left lateral occipital cortex, additionally exhibited responses that were modulated by the manipulation of lexical/semantic information as a result of the concurrent auditory presentation of either the object's name or a nonsense word. This apparent specificity of lexical/semantic sensitivity to left fusiform, as opposed to lateral occipital, cortex is consistent with the finding (Vuilleumier et al., 2002) that the latter region exhibited priming-related signal changes for both real and nonreal objects, but that fusiform cortex responses were specific to real objects (for which, presumably, more lexical/semantic information is available).

The primary region in the present study to exhibit sensitivity to the lexical/semantic manipulation (centered on −45, −54, −24) is close to a region of fusiform/inferior temporal gyrus (BA 37; peak at −50, −58, −12) localized as playing a role in conceptual priming, independent of modality (Buckner et al., 2000). It is also near a region of inferior temporal cortex (BA 37; maximum at −51, −59,

Fig. 4. Fusiform/lateral occipital cortex clusters of significant activation in the group novel > all repeated contrast superimposed upon axial slices of an averaged anatomical MR image. Green clusters are those exhibiting differential engagement for item type but not for lexical/semantic condition, while those showing additional sensitivity to the lexical/semantic manipulation are colored red. In the right hemisphere, differential responses were observed only for item type. Within the left hemisphere, there was posterior-anterior progression from clusters modulated only by item type, to clusters showing additional differentiation between lexical/semantic conditions.

Fig. 5. Selectively averaged percentage signal change for novel, repeated same, and repeated different items (combining across lexical/semantic conditions) in left anterior inferior prefrontal cortex (IPC), left posterior IPC, and right posterior IPC. Left anterior IPC exhibited a pattern of exemplar generalization (top left panel) but sensitivity to lexical/semantic condition (top right panel). Both posterior IPC regions showed exemplar specific patterns of activation (bottom panels). The interaction within left IPC between anterior/posterior region and item type (compare left panels) was significant.

−11) activated when recognition memory decisions were made about different exemplars of studied everyday objects, a task thought to require processing of lexical/semantic information to support the decision about prior occurrence of the object type (Simons et al., 2001). On the basis of evidence such as this, it has been suggested that this region of inferior temporal cortex may play an important role in the processing of conceptual lexical/semantic representations that are involved in task performance. This is consistent with evidence from patients who have damage to this region, and who typically exhibit impairment at tasks requiring lexical/semantic comprehension and/or production, such as picture naming, selecting a picture from an array that goes with a given name, and matching pictures or words based on their semantic association (Foundas et al., 1998; Mummery et al., 1999; Patterson and Hodges, 2000; Simons et al., 2002).

The apparent role of left fusiform cortex in processing lexical/semantic representations may provide another possible explanation for the lack of generalization between perceptually different exemplars observed in left fusiform by Vuilleumier and colleagues (2002). As noted above, Vuilleumier et al. suggested that the object exemplars in their study may have been more visually dissimilar to one another than those in Koutstaal et al. (2001). Visual similarity is likely to covary to some extent with name agreement, suggesting that the larger perceptual differences between Vuilleumier et al.'s stimuli may have led to lower name agreement across the exemplars. Pilot experiments conducted as part of the present study, and that by Koutstaal et al. (2001), confirmed high levels of name agreement between the different exemplar pictures employed (95% in the present study, 91% in Koutstaal et al.'s study), but data on name agreement were not reported by Vuilleumier et al. If it was the case that name agreement across different exemplars was lower in that study, then it is possible that variation in the lexical/semantic representations activated by the different exemplars may have been sufficient to increase the neural signal in left fusiform above that associated with repeated same exemplars. Such lexical or semantically-related activation might explain the lack of exemplar-specific lateralization observed in fusiform cortex by Vuilleumier and colleagues.

The suggestion of posterior-anterior progression of object representations within left occipitotemporal cortex corresponds with previous results from human functional neuroimaging and nonhuman primate studies. Ungerleider (1995) reviewed a number of findings from both areas of research that converged toward the view that a hierarchical processing scheme exists within occipitotemporal cortex characterized by an "increase in the complexity of processing as activity proceeds anteriorly through the ventral stream into the temporal lobe" (p. 770). Accordingly, single-cell recording has demonstrated progression from sensitivity to basic visual features around the occipital pole (Hubel and Wiesel, 1962) to differential engagement by particular categories of objects in fusiform and inferior temporal cortex (Perrett et al., 1982). Evidence from functional neuroimaging studies in humans argues for similar progression from visual and perceptual representations in posterior occipitotemporal, to high-level, lexical/semantic representations in anterior fusiform cortex (Grill-Spector et al., 1999; Kanwisher et al., 1997; Lee et al., 2002; Malach et al., 1995; Martin and Chao, 2001; Schacter and Buckner, 1998; Simons et al., 2001; Wiggs and Martin, 1998).

Priming effects beyond occipitotemporal cortex

Significant response suppression for repeated, relative to novel, objects was additionally observed in regions other than fusiform/lateral occipital cortex, such as bilateral inferior prefrontal cortex and the anterior cingulate (Buckner et al., 1998; Koutstaal et al., 2001; Wagner et al., 1997). An anterior region of left inferior prefrontal cortex exhibited a pattern of generalization across perceptual exemplars but sensitivity to the lexical/semantic manipulation. This region is close to a frontal opercular cluster observed by Vuilleumier et al. (2002), which also exhibited generalization across perceptual exemplars. Another, more posterior, region of left inferior prefrontal cortex emerged in the present study in the repeated different > repeated same contrast, thus exhibiting an exemplar specific pattern in an almost identical location to a region showing similar behavior in the study by Koutstaal et al. (2001). This dissociation within the left inferior prefrontal cortex, confirmed by the observation of a significant item type interaction between anterior and posterior regions, corresponds with previous evidence that these areas may play distinct roles in semantic and phonological control processes, respectively (Dapretto and Bookheimer, 1999; Fiez, 1997; Otten and Rugg, 2001; Poldrack et al., 1999; Price et al., 1997; Wagner et al., 2000). The exemplar specificity exhibited by posterior left inferior prefrontal cortex suggests that this region mediates the top-down control of access to phonological codes, becoming more active when stimulus-driven phonological retrieval processes are not immediately successful, as might be expected when presentation of a perceptually different exemplar (in the test phase) follows repeated exposure to an identical exemplar (in the study phase).

Other regions exhibiting response suppression for repeated, over novel, items were characterized by patterns of generalization between exemplars. These regions included the right inferior prefrontal cortex, which has been suggested to play a role in visuospatial working memory (Awh and Jonides, 1998; D'Esposito et al., 1998), and the anterior cingulate, which has been identified as part of a semantic cognitive control network that also includes left inferior prefrontal cortex (MacDonald et al., 2000; Maril et al., 2001; Wagner et al., 2001).

Conclusions

In summary, the present fMRI study has confirmed that fusiform cortex exhibits asymmetric patterns of responses during a visual object priming task when the same or different exemplars of objects are repeatedly presented. Replicating the result of Koutstaal et al. (2001), there was significantly greater priming-related "neural discrimination" between different exemplars in right than left fusiform cortex, manifested in a significant interaction between region (right and left fusiform) and item type (same or different exemplars). Additional sensitivity to a lexical/semantic manipulation was observed in left fusiform cortex (as well as in left inferior prefrontal cortex), with further analysis suggesting posterior-to-anterior progression within the left occipitotemporal cortex between regions involved in processing visuoperceptual and lexical/semantic information about objects. The present results are, therefore, consistent with the view that dissociable object recognition subsystems operate in right and left fusiform/lateral occipital cortex (e.g., Marsolek, 1999). The right hemisphere appears to be principally involved in processing specific visual form representations about objects, while the left hemisphere additionally plays a role in processing lexical/semantic information. Together, these subsystems contribute to the ability, which is critical to survival, to rapidly perceive and identify objects in the world around us.

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