

Opposing patterns of neural priming in same-exemplar vs. different-exemplar repetition predict subsequent memory

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ABSTRACT

The present neuroimaging study examines how repetition-related neural attenuation effects differ as a function of the perceptual similarity of the repetition and subsequent memory. One previous study (Turk-Browne et al., 2006) reported greater attenuation effects for subsequent hits than for misses. Another study (Wagner et al., 2000) found that neural attenuation is negatively correlated with subsequent memory. These opposing results suggest that repetition-related neural attenuation for subsequent hits and misses may be driven by different factors. In order to investigate the factors that affect the degree of neural attenuation, we varied perceptual similarity between repetitions in a scanned encoding phase that was followed by a subsequent memory test outside the scanner. We demonstrated that the degree of neural attenuation in the object processing regions depends on the interaction between perceptual similarity across repeated presentations and the quality their encodings. Specifically, the same areas that decreased neural signal for repetitions of same exemplars that were subsequently recognized with confidence that the repetitions were identical showed a decrease in neural signal for different-exemplar *misses* but not for the corresponding subsequently recognized *hits*. Our results imply that repetition-related neural attenuation should be related to the more efficient processing of perceptual properties of the stimuli only if subjects are able to subsequently remember the stimuli. Otherwise, the cause of attenuation may be in the failure to encode the stimuli on the second presentation as shown by the pattern of neural attenuation for the different-exemplar misses.

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Introduction

Repeated presentation of a stimulus often facilitates behavioral performance (e.g., decrease in response time) and decreases activation in task-specific brain regions (Buckner and Koutstaal, 1998; Grill-Spector et al., 1999; Henson, 2003; Schacter and Buckner, 1998; Wig et al., 2005; Wiggs and Martin, 1998). Recent studies have established that the magnitude of neural attenuation in the task-specific brain regions (e.g., inferior temporal, fusiform and inferior frontal cortices) depends on the perceptual similarity between the two stimulus presentations (e.g., Eddy et al., 2007; Koutstaal et al., 2001; Simons et al., 2003). Koutstaal et al. (2001) found larger attenuation in occipito-temporal and prefrontal cortices when repetitions involved perceptually identical stimuli (i.e., same-exemplar priming) than when they involved different exemplars of the same category (i.e., different-exemplar priming). Further investigation of the differences in neural attenuation

between same- and different-exemplar repetition found greater perceptual specificity in right fusiform cortex than in left fusiform cortex and greater “cross-exemplar” generalization in left fusiform cortex than in right (Simons et al., 2003). These results supported earlier behavioral findings of hemispheric dissociation underlying abstract and specific object recognition (e.g., Marsolek, 1999).

Previous studies have also shown that the degree of neural attenuation for repeated stimuli depends on the encoding effort in terms of subjects' attention to the stimuli. Vuilleumier et al. (2005) presented subjects with pictures of two overlapping objects and specified which of the two stimuli should be attended. Neural attenuation effects were observed in the left inferior frontal, fusiform and lateral occipital cortices, but only for attended stimuli. These results were consistent with Eger et al. (2004) who presented subjects with two lateralized images and cued subjects to attend to either a left or a right image. Repetition-related decreases were observed in bilateral fusiform and lateral occipital regions for this study, but only when subjects had been cued to attend to the stimulus. Yi and Chun (2005) presented subjects with overlapping scene and face images and found significant neural attenuation in the parahippocampal place area for scenes, but only when the scenes were attended to on both the first and second presentations.

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Subjects' encoding effort not only increases the magnitude of neural priming (Eger et al., 2004; Vuilleumier et al., 2005; Yi and Chun, 2005), it also enhances subsequent recognition (e.g., Block, 2009). In Turk-Browne et al.'s (2006) recent fMRI study, subjects encountered each picture of a scene twice while performing an indoor/outdoor classification task. A recognition task administered after the classification task indicated that the subsequently recognized scenes were associated with greater repetition-related neural attenuation in the parahippocampal place area and in the fusiform regions as compared to scenes that were not recognized at test. This difference in neural attenuation was driven by a stronger BOLD response on the first stimulus presentation for hits relative to misses. These results were, however, inconsistent with the results of Wagner et al. (2000), who reported that the magnitudes of neural and behavioral priming were both negatively correlated with subsequent recognition. This paper explores possible factors that might account for this discrepancy. For example, neural attenuation may result from facilitation of stimulus processing (e.g., Henson, 2003; Grill-Spector et al., 2006; Schacter and Buckner, 1998; Wiggs and Martin, 1998). However, another explanation for the decrease in neural activity results from a failure to encode the stimulus on the second presentation.

We tested this hypothesis in an event-related fMRI study in which we varied perceptual similarity between repetitions (identical pictures vs. different exemplars of a concept) in a scanned encoding phase. The subsequent recognition test, outside the scanner, involved test probes that were words, rather than pictures. This allowed us to ask for a second memory judgment. When subjects responded "old" to a word, they then had to indicate whether the two stimulus presentations corresponding to the probe word were identical or different exemplars of the same concept. Detecting the difference between the two exemplars requires that the subject recollect details of both preparations. This design allowed us to examine neural attenuation when it seems likely that perceptual details are retained from both presentations (when confident that the two presentations were identical or different), compared to trials in which memory for such details seems weak. The inclusion of identical vs. different exemplars of a concept also allowed us to explore the neural activation patterns for perceptual repetitions and for repetitions that are conceptually the same but not visually identical.

Recognition memory can be based on a familiarity process or a recollective process (Jacoby and Dallas, 1981; Joordens and Hockley, 2000; Mandler, 1980; Reder et al., 2000; Yonelinas, 1994, 2002). When subjects are confident (and correct) about whether the two presentations were same or different exemplars, it is likely that the comparison involved recollection of the two exemplars. Such *recollective* judgments should require hippocampal processes (e.g., Daselaar et al., 2006; Eldridge et al., 2000; Wheeler and Buckner, 2004). In order to facilitate recollective processes, we used stimuli of objects because they are easily labeled. We believe that object stimuli that are easily labeled are more easily bound to episodic context (Reder et al., 2006, 2007) and, with a consistent discriminative label, the episodic trace is more easily retrieved.

It seems reasonable that we will replicate the Turk-Browne et al. results of greater neural attenuation for hits than misses for conditions involving same-exemplar repetition; however, we may find a different pattern of activation for hits vs. misses when the repetition involves different exemplars of the concept. Specifically, we may not find significant neural attenuation in the object processing areas for different-exemplar repetition hits. When the two presentations are identical, there is no discrepancy to notice and the second repetition should facilitate both perceptual and conceptual processing. However, when the two presentations are different, more visual processing is required to detect this difference, which in turn should decrease neural attenuation on the second presentation. Of particular interest is how these processing regions behave when subjects both recognize the item

and can recall that the two presentations were different. In summary, we predict that we should see neural attenuation for confident hits of same-exemplar repetitions but not different-exemplar repetitions. Like Turk-Browne et al., we also predict poor encoding of the first and second presentation for misses, regardless of the type of repetition.

Materials and methods

Subjects

Fourteen volunteers (age ranged between 20 and 35 years old, all right-handed, eight female) participated in this fMRI study. One subject was excluded from the study due to biased responses in the subsequent recognition test (always answered "old, confident"). Subjects were graduate students and post-doctoral fellows from the psychology department at Carnegie Mellon University with normal or corrected to normal vision. All subjects were fluent in English and were treated in accordance with the CMU and Pittsburgh University IRB guidelines. None of the subjects were aware of the specific design or hypotheses concerning the experiment prior to their participation. They were fully debriefed at the study's completion.

Design and procedure

Subjects viewed 336 pictures (168 different concepts) (randomly selected from a pool of 1016 pictures) presented one at a time in the center of a screen placed at the bore of the scanner. Subjects were asked to judge whether the object depicted by the picture was man-made or naturally occurring by pressing a key on the right or left response glove. Each man-made and natural object was presented twice. None of the repetitions occurred until all stimuli had been shown once.¹ Same-exemplar repetitions consisted of showing the identical picture of an object twice (84 pairs of pictures). Different-exemplar repetitions were defined as presenting two perceptually different exemplars of objects with the same label (e.g., a red apple and a green apple) (84 pairs of pictures). Assignment of items to condition (identical vs. different or new condition) as well as order of presentation of items during study and test was randomly determined for each subject. In this way any effects of materials became part of a given subject's error term. There were 42 pairs of each kind (man-made same-exemplar, natural different-exemplar, etc.) for a total of 336 trials. Stimuli were presented continuously, stayed on until the subject responded (the task was self-paced) and were separated with an inter-stimulus interval (ISI) of 1.5 s. Subjects were shown a fixation cross against gray background during ISI.

After completing the classification task (encoding phase) subjects were removed from the scanner and given a short break (10–15 min) before taking a surprise recognition test. During the recognition test, subjects were presented with words, one at a time and asked to make one or two judgments about each word (see Fig. 1). A reason for using words instead of pictures was to avoid a ceiling effect and to obtain enough hits and misses for the analysis of neuroimaging data. Subjects were asked to respond "old, confident," "old, maybe" or "new" depending on whether they thought they had seen a picture that corresponded to the label during the categorization task in the scanner. Following Turk-Browne et al. (2006), two-thirds of the test items were old and one-third were new, yielding 252 test words, 168 old and 84 new. When subjects responded "old" (confident or maybe), they were asked to indicate whether the two pictures represented by the word were identical or different (i.e., second-order

¹ This allowed us to analyze the effects of practice within the first and second half of the experiment separately. This will be explained in more detail in the results section.

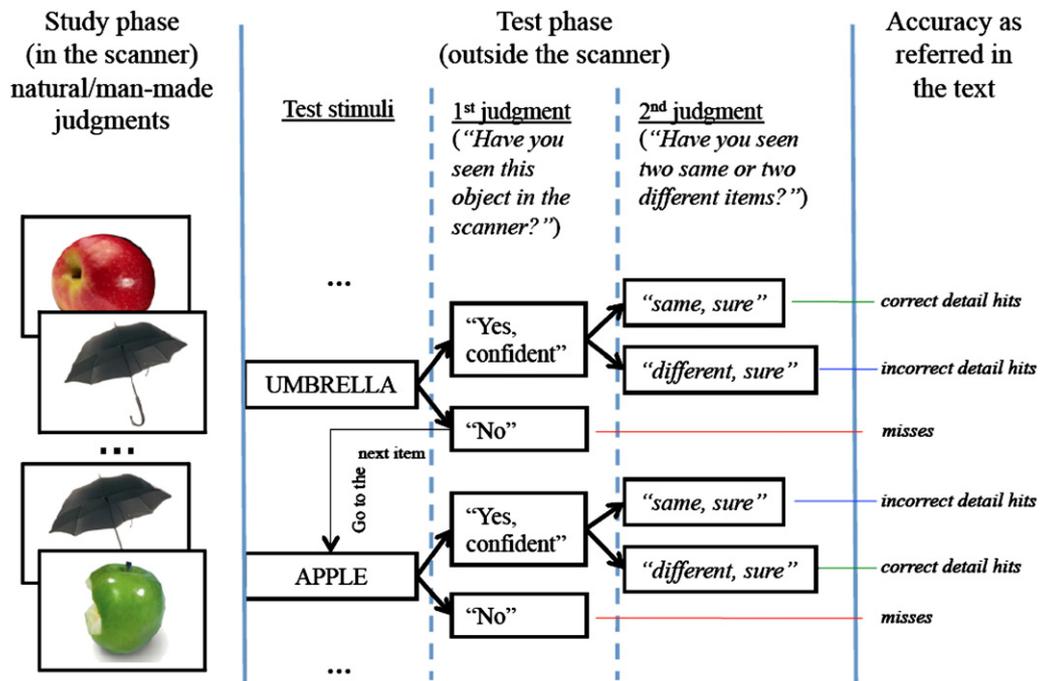


Fig. 1. A simplified description of the experimental design. For simplicity the figure omits the response choice “old, maybe” from the first judgment and the possible responses “same, unsure” and “different, unsure” from the second judgment. “Correct detail hits” refer to the high confidence hits (based on the 1st judgments) when subjects were correct and sure about seeing two identical or two different exemplars during encoding. “Incorrect detail hits” refer to the high confidence hits (based on the 1st judgments) when subjects were incorrect but sure about seeing two identical or two different exemplars during encoding. “Misses” refer to the “new” judgments when, in fact, the object was shown during encoding.

judgment). Subjects were told at test that there were always two pictures associated with each old word. If subjects remembered that the two presentations were identical pictures, they should respond “same, sure.” If they remembered that the two pictures were different, they should respond “different, sure.” If they were unsure whether the two pictures were identical or different, they were to respond either “same, unsure” or “different, unsure.” Assignment of concepts to condition (foil or a studied concept; identical or different exemplars for the studied) was randomly determined for each subject with the constraint that number of trials in each condition was balanced. In that way, any effects due to stimulus materials would become part of the subject’s error term.

The trials that were miscategorized (e.g., an ‘apple’ called man-made) and the trials that were longer than 6 s were removed from the behavioral and neuroimaging data analysis. Overall, less than 7% of all trials were discarded.

Image acquisition

The fMRI experiment was conducted using a Siemens 3T Allegra MR system. In the beginning of the experiment, a high-resolution structural image (TR = 1540 ms, TE = 3.04 ms, slice thickness = 1 mm, FOV = 205, FA = 8°, number of slices = 192, resolution 1 × 1 × 1 mm) was acquired using an MPRAGE (a magnetization-prepared rapid acquisition in gradient echo) sequence. Functional data (BOLD signal) were collected using a gradient echo, echo-planar sequence (TR = 2000 ms, TE = 30 ms, slice thickness = 3.2 mm, FOV = 205, FA = 79°, number of slices = 35, resolution = 3.2 × 3.2 × 3.2). Stimuli were presented in a self-paced manner, which resulted in a variable number of volumes in subjects’ fMRI data (ranged from 377 to 547 volumes).

fMRI data analysis

The images were processed and analyzed with FSL 4.1.5 (FMRIB’s Software Library, www.fmrib.ox.ac.uk/fsl) software. On each raw

BOLD dataset, nonlinear noise reduction (SUSAN (Smallest Univalve Segment Assimilating Nucleus)); motion correction (MCFLIRT (Jenkinson et al., 2002)); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Smith, 2002); spatial smoothing using a Gaussian kernel of FWHM 6 mm; multiplicative mean intensity normalization of the volume at each time point and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 25.0$ s) were applied. A hemodynamic response function (HRF) was modeled using a Gamma function. Registration to high-resolution structural (MPRAGE) and standard MNI (the Montreal Neurological Institute) space images was carried out using FLIRT (Jenkinson and Smith, 2001; Jenkinson et al., 2002).

The FEAT (fMRI Expert Analysis Tool) was used for the first- and higher-level analysis. The first-level analysis included the contrast between the first and second encoding presentations of the stimuli for trials collapsed across repetition types and recognition judgments to compute a main effect of presentation. To compute a main effect of memory we collapsed across repetition types and presentations, back-sorted trials based on subsequent recognition (Wagner et al., 1998) and contrasted correct detail hits with misses. We also collapsed across repetition types and memory judgments and contrasted the two stimulus presentations in order to examine whether there was a main effect of presentation. Task learning was assessed by contrasting the block 1 trials (first 84) with the block 2 trials (second 84). A mean task learning effect was calculated as a mean difference between block1 – block2 and block3 – block4.

The higher-level analyses were carried out using OLS (ordinary least square) mixed effects. Group means were computed for each of the first-level comparisons. Z-statistics images were thresholded at $p < 0.001$ (uncorrected) unless specified in the text. Functional localization was determined using the Harvard–Oxford cortical and subcortical structural atlases. The BOLD signal changes were extracted from the regions that revealed a main effect of presentation or a main effect of subsequent memory. The mean BOLD signal changes in each activation cluster were subjected to a 2 × 2 ANOVA (Presentation

(presentation 1/presentation 2) \times Repetition type (same-exemplar/different-exemplar) \times Memory (correct detail hits/misses). Given our particular interest in whether repetition-related neural attenuation (or enhancement) that is associated with subsequent recognition varies as a function of perceptual similarity of the repeated stimuli, our analyses place a special emphasis on the three-way interaction involving Presentation \times Repetition type \times Subsequent memory.

Behavioral data

Subsequent memory

The proportions of high confidence hits, low-confidence hits and misses for target words did not differ between same-exemplar and different-exemplar repetitions ($p > 0.1$ in all cases) and therefore, are presented collapsed on Fig. 2A. Fig. 2B and C shows the proportions of correct detail hits, incorrect detail hits and unsure responses for the second question regarding whether the two presentations were same or different. The data are presented only for high confidence hits. New items (foils) were correctly rejected 81% of the time; of the 19% false alarms, 8% were high confident old responses.

Response times

In this paper, we focus on correct detail hits and misses in order to compare neural priming for two extremes—the stimuli that are later recollected (or have the strongest memory trace) and stimuli that are later forgotten (or have the weakest memory trace). The behavioral and neuroimaging data for other responses (e.g., incorrect detail hits, low-confidence hits) will be reported in another paper. Subjects' RTs corresponded to each type of repetition for subsequent correct detail hits and misses are presented in Table 1.

A $2 \times 2 \times 2$ ANOVA (Presentation \times Repetition type \times Memory) conducted on response times (RT) revealed a main effect of presentation, $F(1,12) = 15.9$, $p < 0.01$, with longer responses for the first than for the second presentation. There was also a marginally significant main effect of subsequent memory, $F(1,12) = 3.7$, $p < 0.1$, with slower RT for hits compared to misses.

Behavioral priming was calculated as a difference in RT required to make natural/man-made judgments between the first and second stimulus presentation. Ignoring subsequent memory performance, both same-exemplar ($M = 99.6$ ms, $SE = 24.8$) and different-exemplar

Table 1
Response time as a function of presentation, repetition type and subsequent memory.

	Same-exemplar repetitions		Different-exemplar repetitions	
	Correct detail hits	Misses	Correct detail hits	Misses
Presentation 1	837.7 (42.8)	803.7 (52.0)	901.0 (60.3)	843.2 (72.4)
Presentation 2	732.3 (48.4)	734.28 (44.9)	761.2 (53.5)	706.6 (29.8)

Note. Standard errors of mean (SE) are in parentheses.

($M = 62.0$ ms, $SE = 33.0$) priming effects were significantly different from zero. The difference in the size of priming effects in the two types of repetition did not reach significance, $p > 0.1$. Fig. 2D illustrates behavioral priming for subsequent correct detail hits and misses for same- and different-exemplar repetitions. Priming was not different among these four categories of trials and was significantly above zero in all cases (same-example, hits: $t(12) = 4.0$, $p < 0.005$; same-exemplar, misses: $t(12) = 2.5$, $p < 0.05$; different-exemplar, hits: $t(12) = 2.8$, $p < 0.05$; different-exemplar, misses: $t(12) = 2.3$, $p < 0.05$).

Task learning effects

In repetition priming studies, the second presentation necessarily comes later in the task. Therefore it is useful to distinguish the neural changes associated with the facilitation of object processing and those associated with task learning. Given that all stimuli in our study were initially presented during the first 168 trials and then repeated during the second 168 trials (i.e., trials 169–336), the decrease in response time for the second presentation could occur due to the subjects' learning to perform the task (e.g., mapping between the response key and the natural/man-made judgment) as opposed to faster object processing on the second presentation.

To examine task learning, we collapsed across repetition types as well as subsequent memory and examined all 336 trials as four blocks of 84 trials (blocks 1 and 2 correspond to the presentation 1 and blocks 3 and 4 correspond to the presentation 2). Table 2 presents the mean RT and SE for each of four blocks. We calculated the rate of learning during the first 168 trials by comparing blocks 1 and 2. We also computed the mean task learning by calculating the average between the rate of learning during the first 168 trials and the rate

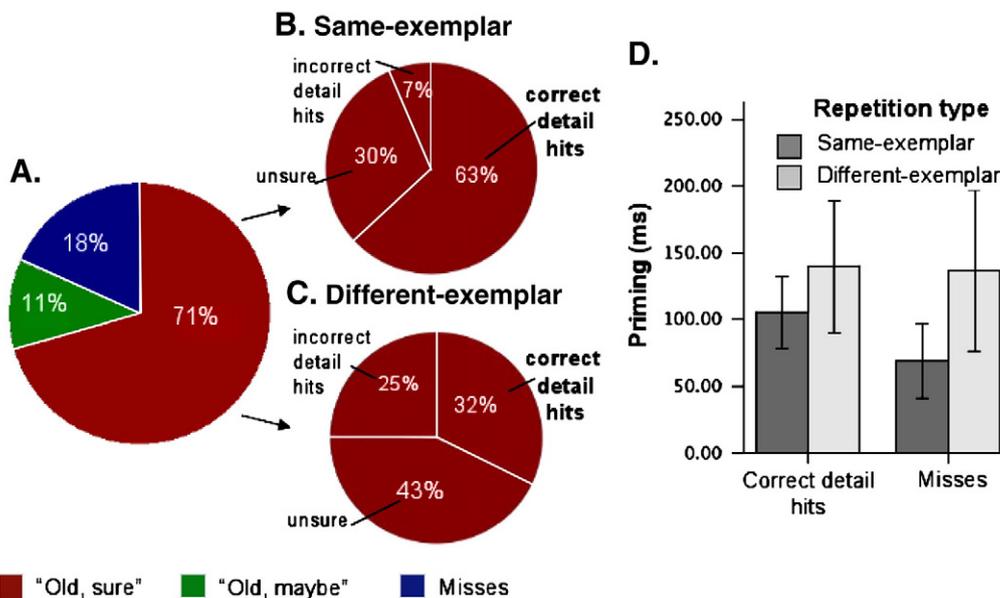


Fig. 2. A. Proportion of "old, sure" (i.e., high confidence hits), "old, maybe" (i.e., low-confidence hits) and "new" (i.e., misses) responses in the subsequent recognition task. B and C. Proportion of correct detail hits, incorrect detail hits and unsure responses in high confidence hits for same-exemplar (B) and different-exemplar (C) repetitions. D. Behavioral priming effects as a function of repetition type and subsequent memory (correct detail hits vs. misses).

Table 2

Mean RT as a function of a trial number in the study task.

	Presentation 1		Presentation 2	
	Block 1 1–84 trials	Block 2 85–168 trials	Block 3 169–252 trials	Block 4 253–336 trials
RT	851.3 (53.9)	798.7 (41.1)	753.2 (45.50)	715.5 (35.5)

Note. Standard errors of mean (SE) are in parentheses. Same- and different-exemplar repetitions as well as subsequent memory categories are collapsed together.

of learning during the second 168 trials $[((\text{block1} - \text{block2}) + (\text{block3} - \text{block4})/2)]$. The mean task learning effect was 45.2 ms (SE = 15.5), which was significantly above zero, $t(12) = 2.9$, $p < 0.05$. It is noteworthy that the rate of learning was significantly different from zero on both presentations (block1 – block2: $M = 52.6$ ms, SE = 20.6, $t(12) = 2.6$, $p < 0.05$; block3 – block4: $M = 37.7$ ms, SE = 13.8, $t(12) = 2.7$, $p < 0.05$).

While the RT speed up on the second presentation is not a linear combination of the task learning rate and the object processing facilitation, we subtracted the mean task learning from the mean behavioral facilitation and analyzed the residuals using a one-sample t -test (one-tailed) to examine whether the residuals are still greater than zero. We found that the residuals for subsequent hits in both repetition conditions were significantly above zero (same-exemplar repetitions: $M = 60.2$ ms, SE = 32.7, $t(12) = 1.8$, $p < 0.05$; different-exemplar repetitions: $M = 94.7$ ms, SE = 50.0, $t(12) = 1.9$, $p < 0.05$). The residuals for subsequent misses in both repetition conditions were also above zero, but the statistics did not reach the significance level (same-exemplar repetitions: $M = 24.3$ ms, SE = 32.4, $t(12) = 0.8$, $p = 0.23$; different-exemplar repetitions: $M = 91.4$ ms, SE = 53.7, $t(12) = 1.7$, $p = 0.06$).

Imaging data

Main effect of presentation: Presentation 1 vs. Presentation 2

The analysis of a main effect of presentation identified changes in fMRI activity between the first and second presentations. For this analysis, we collapsed across same- and different-exemplar repetitions and across correct detail hits and misses. The regions sensitive to stimulus repetition identified in this analysis were used as the functional ROIs in further analyses.

As expected, greater activity for the first presentation compared to the second presentation was found in the left inferior temporal gyrus (ITG) and left occipital fusiform gyrus (oFFG) (Table 3). The first presentation also elicited greater activity in left insular and temporal fusiform cortices, in left supramarginal, precentral and postcentral gyri, in right putamen, amygdala, hippocampus (HPC), precuneus and ITG. Greater activity for the second presentation relative to the first one was found in bilateral frontal pole and superior frontal gyrus, in left caudate and right posterior cingulate cortex (PCC).

Main effect of subsequent memory: Correct detail hits vs. Misses

To identify voxels associated with subsequent memory performance, and to generate ROIs for further investigation, we collapsed across same- and different-exemplar repetitions and across first and second presentations and compared correct detail hits (often referred to as “hits” in the text) and misses.

Greater activity for correct detail hits compared to misses was found in bilateral inferior frontal gyri (IFG), HPC, lateral occipital cortex, in left temporal occipital fusiform cortex (toFFC), ITG, and in right posterior temporal fusiform cortex, superior parietal lobule (SPL) and oFFG (Table 4). Greater activity for misses than for correct detail hits was found in bilateral posterior cingulate gyrus (PCC), right frontal pole, superior frontal gyrus, frontal orbital cortex and angular gyrus.

Table 3

Regions showing the repetition-related decreases (Presentation 1 > Presentation 2) and the repetition-related increases (Presentation 2 > Presentation 1), $p < 0.001$ (uncorrected), 10 voxels extent threshold.

Region	N voxels	Z-Max	MNI coordinates		
			x	y	z
<i>Presentation 1 > Presentation 2</i>					
L Insular cortex	44	3.57	–30	12	6
R Putamen	167	3.8	24	8	12
R Amygdala	11	3.51	30	–6	–18
R Hippocampus	17	3.58	30	–26	–4
L Supramarginal gyrus, anterior division	15	3.81	–66	–30	30
L Postcentral gyrus	32	3.78	–32	–32	44
L Precentral gyrus/postcentral gyrus	13	3.43	–16	–34	46
L Temporal fusiform cortex, posterior division/parahippocampal gyrus, posterior division	36	4.15	–26	–38	–18
R Inferior temporal gyrus, temporo-occipital part	94	3.72	50	–60	–4
R Precuneus cortex	28	3.93	14	–68	44
L Inferior temporal gyrus, temporo-occipital part	16	3.33	–50	–68	–10
L Occipital fusiform gyrus	15	4.01	–20	–72	–12
L Occipital fusiform gyrus	68	4.03	–32	–84	–18
<i>Presentation 2 > Presentation 1</i>					
R Cingulate gyrus, posterior division	21	3.44	6	–40	28
B Superior frontal gyrus	20	3.52	0	36	44
L Frontal pole	20	4.02	–22	68	8
B Frontal pole	14	3.45	0	62	22
L Frontal pole	14	3.4	–4	60	–20
L Planum temporale	13	3.69	–54	–20	2
L Caudate	10	3.51	–6	12	0

Note. The regions that demonstrated a Presentation \times Repetition type \times Memory interaction are in **bold**.

Presentation \times type of repetition \times memory interaction

We next addressed the question of how repetition-related neural attenuation (or enhancement) depended on the perceptual similarity of repeated stimuli and on the quality of encoding and, consequently, subsequent memory. This relationship is revealed in a three-way interaction between Presentation \times Repetition type \times Memory. We performed a three-way repeated measures ANOVA (Presentation (presentation1 vs. presentation2) \times Repetition type (same- vs. different-exemplar) \times Memory (correct detail hits vs. misses) on the activation data in each of the functional ROIs determined in previous analyses, which were unbiased with respect to this interaction. For ROI analyses, activity was averaged over all voxels in the ROI.

Among the regions showing the repetition-related attenuation of the BOLD signal (i.e., a main effect of presentation), a three-way interaction was found in left ITG (Fig. 3A), $F(1,12) = 13.8$, $p < 0.005$, left oFFG (Fig. 3B), $F(1,12) = 5.9$, $p < 0.05$, and right amygdala, $F(1,12) = 6.4$, $p < 0.05$. All these regions demonstrated greater decreases for same-exemplar than different-exemplar repetitions when they were subsequent hits, but greater decreases for different-exemplar than same-exemplar repetitions when they were subsequent misses. Of note, there was also a main effect of memory in the left ITG, $F(1,12) = 14.0$, $p < 0.005$, and left oFFG, $F(1,12) = 20.5$, $p < 0.005$.

Contrasts between the first and second presentations for each repetition type \times memory condition revealed that the neural attenuation between two presentations was significant for the same-exemplar hits (left ITG, $t(12) = 6.0$, $p < 0.001$, left oFFG, $t(12) = 4.6$, $p < 0.001$, right amygdala, $t(12) = 3.5$, $p < 0.005$) and for the different-exemplar misses (left ITG, $t(12) = 3.5$, $p < 0.005$, left oFFG, $t(12) = 2.5$, $p < 0.05$, right amygdala, $t(12) = 4.6$, $p < 0.001$). On the other hand these contrasts were not significant for different-exemplar hits or same-exemplar misses.

Table 4
Regions showing effects of subsequent memory (Hits>Misses or Misses>Hits), $p < 0.001$ (uncorrected), 10 voxels extent threshold.

Region	N voxels	Z-Max	MNI coordinates		
			x	y	z
<i>Hits>Misses</i>					
L Inferior frontal gyrus, pars triangularis	99	4.36	-50	32	14
R Inferior frontal gyrus, pars triangularis	25	3.67	56	26	10
L Precentral gyrus/inferior frontal gyrus, pars opercularis	141	3.83	-52	10	32
R Insular cortex	10	3.31	36	-4	10
L Thalamus	13	3.45	-24	-32	-2
R Hippocampus	13	3.33	28	-36	-8
R Temporal fusiform cortex, posterior division	33	3.67	26	-36	-24
R Temporal fusiform cortex, posterior division	13	3.43	38	-38	-20
L Temporal occipital fusiform cortex	725	5.51	-34	-48	-20
R Superior parietal lobule	85	4.89	28	-56	48
R Inferior temporal gyrus, temporo-occipital part	87	4.58	48	-56	-16
L Inferior temporal gyrus, temporo-occipital part	12	3.95	-60	-58	-22
L Lateral occipital cortex, superior division	22	3.5	-36	-62	38
R Occipital fusiform gyrus	13	3.52	32	-66	-16
R Lateral occipital cortex, superior division	63	4.5	30	-74	28
L Lateral occipital cortex, superior division	231	4.28	-26	-76	20
<i>Misses>Hits</i>					
R Frontal pole	14	3.46	24	60	28
R Frontal pole	186	4.1	12	52	26
R Frontal pole/middle frontal gyrus	18	3.45	38	36	30
R Superior frontal gyrus	65	3.8	20	20	52
R Frontal orbital cortex	21	3.89	30	16	-18
B Cingulate gyrus, posterior division	242	4.75	-4	-28	44
R Cingulate gyrus, posterior division	27	3.64	10	-46	30
R Angular gyrus	13	3.93	60	-50	36

Note. The regions that demonstrated a Presentation \times Repetition type \times Memory interaction are in **bold**.

As illustrated in Fig. 3, the first presentation of the same- vs. different-exemplar hits did not differ. However, the first presentations of the same-exemplar misses were often lower than those of the different-exemplar misses. Moreover, the differences between hits and misses on the first presentation appeared greater in the same-exemplar condition than in the different-exemplar condition. Paired t -tests were conducted to evaluate the statistical significance of these differences. In the left ITG, activation for hits was significantly higher than for misses in the same-exemplar condition, $t(12) = 3.8$, $p < 0.005$, but not in the different-exemplar condition. The differences between hits and misses on the first presentation were significantly greater for the same-exemplar repetition than for the different-exemplar repetition in the left ITG, ($M = 0.26$, $SE = 0.09$, $t(12) = 2.9$, $p < 0.05$). Moreover, neural activity in this region was significantly lower for the same-exemplar misses than for the different-exemplar misses, $t(12) = 3.9$, $p < 0.005$. In the left oFFG, the same-exemplar hits were greater than misses, $t(12) = 3.6$, $p < 0.005$, and the different-exemplar hits were marginally greater than misses, $t(12) = 2.1$, $p < 0.1$, on the first presentation.

Among the regions showing repetition-related enhancement, bilateral frontal pole was the only region in which the three-way interaction was significant, $F(1,12) = 11.9$, $p < 0.005$. This region was also sensitive to repetitions of same-exemplar hits and different-exemplar misses, but in contrast to the regions described above, activity increased for the second presentation (same-exemplar hits, $t(12) = -2.4$, $p < 0.05$; different-exemplar misses, $t(12) = -3.6$, $p < 0.005$). The difference between the two presentations of different-exemplar hits and the same-exemplar misses was not significant.

Among the regions that activated more for hits than for misses (i.e., a main effect of memory), a three-way interaction was found in left temporal occipital fusiform cortex (Fig. 3C), $F(1,12) = 16.9$,

$p = 0.001$, right ITG, temporo-occipital part (Fig. 3E), $F(1,12) = 4.8$, $p < 0.05$, and right superior parietal lobule, $F(1,12) = 7.0$, $p < 0.05$. A three-way interaction was marginally significant in the left IFG, pars triangularis (Fig. 3D), $F(1,12) = 4.1$, $p < 0.1$. Both left toFFC and left IFG demonstrated greater decreases for same-exemplar than different-exemplar repetitions when they were subsequent hits, but greater decreases for the different-exemplar than same-exemplar repetitions when they were subsequent misses. Activity on the second presentation was significantly lower for the same-exemplar hits, left toFFC, $t(12) = 5.2$, $p < 0.001$, and left IFG, $t(12) = 2.9$, $p < 0.05$. It was also significantly lower for the different-exemplar misses in the left IFG, $t(12) = 2.6$, $p < 0.05$, and marginally lower in the left toFFC, $t(12) = 1.9$, $p < 0.1$. Of note, right ITG also decreased activity for the second presentation of same-exemplar hits, $t(12) = 2.2$, $p < 0.05$, but did not change significantly for the second presentation of different-exemplar misses. Instead, activity in ITG increased for the second presentation of different-exemplar hits (the increase was marginally significant, $t(12) = -2.0$, $p < 0.1$).

In the left toFFC, hits vs. misses decreases were significantly greater for same-exemplar repetitions than for different-exemplar repetitions ($M = 0.1$, $SE = 0.04$, $t(12) = 2.6$, $p < 0.05$). However, hits were greater than misses in both encoding conditions, same-exemplar: $t(12) = 6.8$, $p < 0.001$, different-exemplar: $t(12) = 4.2$, $p < 0.001$. In addition, the same-exemplar misses were lower than the different-exemplar misses, $t(12) = 2.14$, $p = 0.05$, on the first presentation. In the left IFG and right ITG, hits were greater than misses in both encoding conditions (all p -values < 0.05), but the hits vs. misses difference did not differ between same- and different-exemplar conditions.

Among the regions that activated more for misses than for hits, the only significant three-way interaction was revealed in the bilateral PCC, $F(1,12) = 5.2$, $p < 0.05$. In addition, there was a presentation \times memory interaction in the left thalamus/HPC, $F(1,12) = 11.7$, $p = 0.005$, with the greater repetition-related decreases for hits than for misses.

Task learning

As we pointed out earlier, neural attenuation on the second stimulus presentation may occur as a result of practice at making artificial/natural judgments rather than the facilitation of object processing. An effect of task learning would be revealed if there was neural attenuation between blocks one and two (see methods), but no or a less pronounced effect of repetition. The priming effect would be revealed if there was an effect of repetition, but no or a less pronounced difference between blocks one and two.

To examine this possibility we explored the task learning effect in ROIs associated with either a main effect of presentation (right amygdala, left ITG, left oFFG, bilateral frontal pole) or a main effect of memory (right SPL, right ITG, left toFFC, bilateral PCC) and that demonstrated a three-way Presentation \times Repetition type \times Memory interaction. This analysis identified a decrease in neural activity in block 2 relative to block 1 in the left ITG, $t(12) = 2.7$, $p < 0.05$, right ITG, $t(12) = 2.9$, $p < 0.05$, and left toFFC, $t(12) = 2.9$, $p < 0.05$. In contrast, neural activity increased on the block 2 relative to the block 1 in the bilateral frontal pole, $t(12) = -3.8$, $p < 0.005$ (Fig. 4). There was no difference in activity between blocks 1 and 2 in the right amygdala, $t(12) = 1.5$, left oFFG, $t(12) = 1.0$, right SPL, $t(12) = 1.8$, and bilateral PCC, $t(12) = 1.9$ (Table 7). No differences between blocks 3 and 4 or mean task learning were revealed in either of the regions showing the Presentation \times Repetition type \times Memory interaction.

Table 5 presents the mean BOLD signal changes between blocks 1 and 2 and between presentations 1 and 2. Neural attenuation between the first and second presentation was significant in left ITG, oFFG, right amygdala (see Table 3) and marginally significant in left to FFC ($F(1,12) = 3.5$, $p < 0.1$). Importantly, these effects were greater

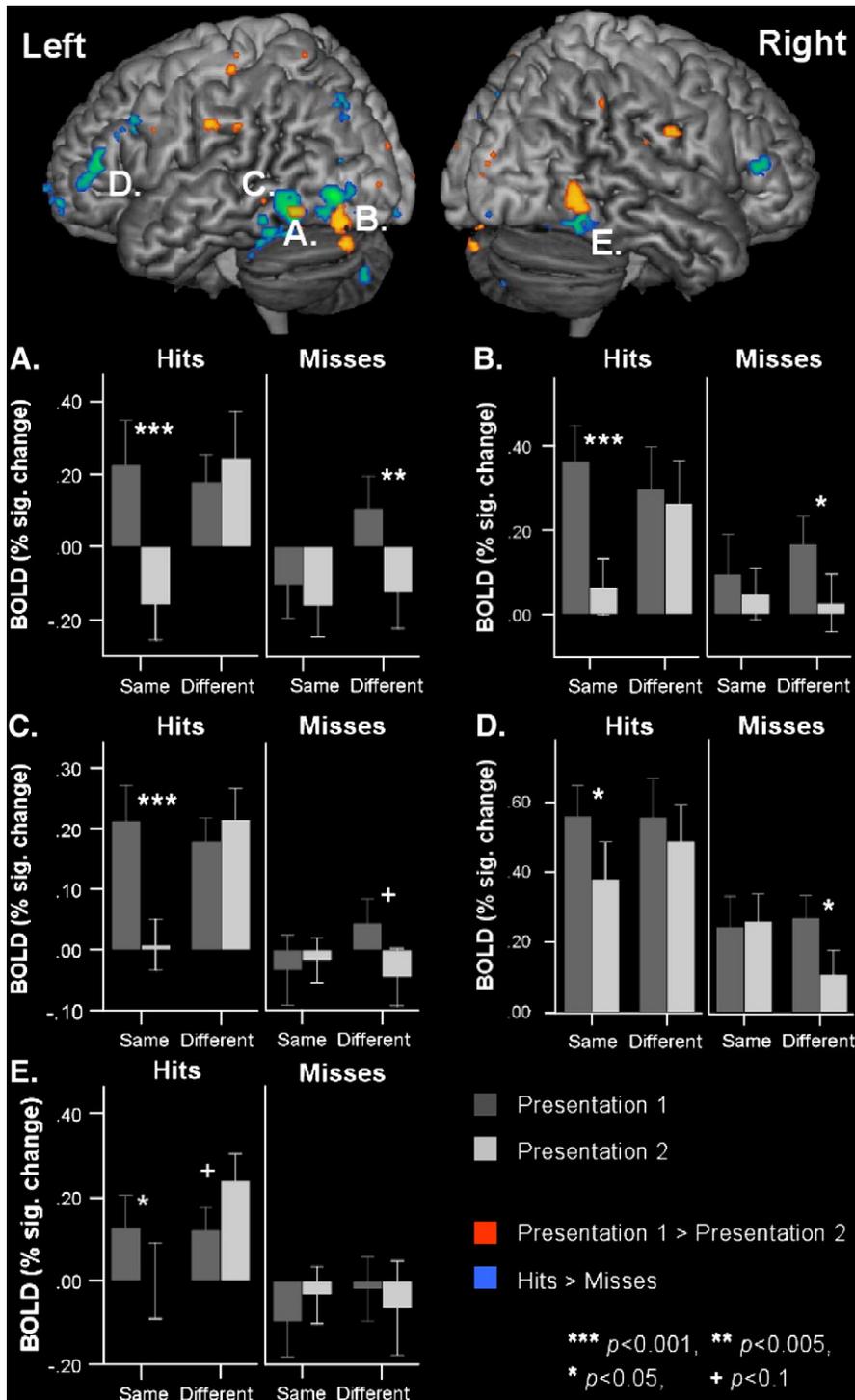


Fig. 3. Presentation × Repetition type × Memory interaction effects. A. Left inferior temporal gyrus. B. Left occipital fusiform gyrus. C. Left temporal occipital fusiform cortex. D. Left inferior frontal gyrus. E. Right inferior temporal gyrus. Red–yellow color depicts the Presentation 1>Presentation 2 contrast. Blue color depicts Hits>Misses contrast. Please note that the voxels from the 12 voxels are projected on the brain surface. The stars above the bars represent the results of a paired *t*-test on the presentation 1 vs. presentation 2.

than the difference between the blocks 1 and 2, and there was no difference between blocks 3 and 4. This pattern of data indicates that a repetition priming account explains the neural attenuation effects in these regions better than task learning. In contrast, in right ITG, right SPL and bilateral PCC the differences between blocks 1 and 2 were greater than presentations 1 and 2, and there was no main effect of presentation in these regions. This pattern of data indicates that a task

learning account explains the neural attenuation/increases in these regions better than a repetition priming account.

Discussion

This study investigated how neural attenuation from first to second presentation of a stimulus in a classification task varies as a joint

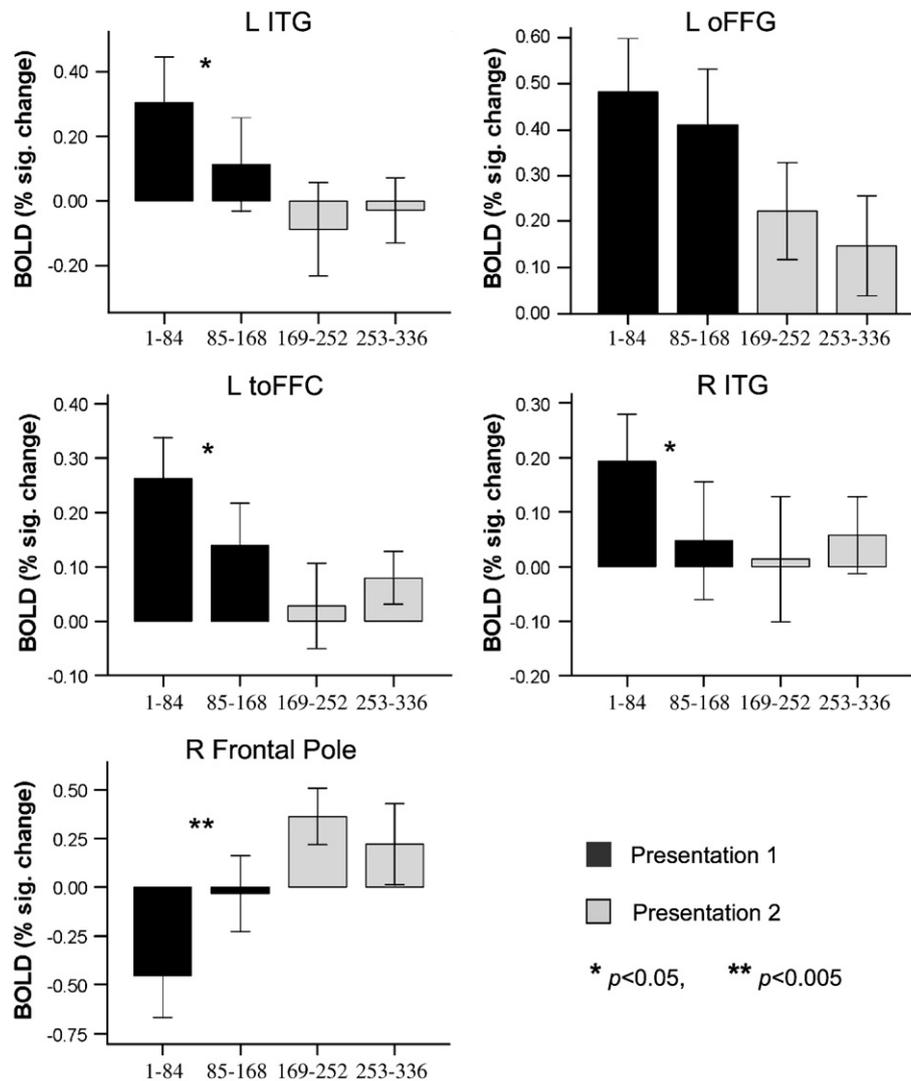


Fig. 4. Bold signal change as a function of a presentation and a trial number. The trial numbers are along the x-axis.

function of subsequent memory and the nature of the stimulus repetition. We examined whether neural attenuation would be larger for confident hits than misses, as shown by Turk-Browne et al. (2006), not just for identical repetitions but for stimuli that represent different exemplars of the same concept. The memory test required that the subject judge whether a test word corresponds to previously presented

Table 5

Comparison of the block effect and the presentation effect.

	Block 1 – Block 2		Presentation 1 – Presentation 2	
	Mean	SE	Mean	SE
R amygdala	0.09	0.06	0.16	0.03
L ITG	0.16	0.07	0.27	0.05
L oFFG	0.07	0.07	0.26	0.05
B frontal pole	-0.4	0.1	-0.54	0.1
L toFFC	0.12	0.04	0.15	0.03
R ITG	0.15	0.05	0.09	0.04
R SPL	0.12	0.07	0.1	0.05
B PCC	0.1	0.05	0.06	0.04

Note. A main effect of presentation in right amygdala, left ITG, left oFFG and bilateral frontal pole was highly significant ($p < 0.001$). These regions are presented in **bold** in the table. A main effect of presentation did not reach significance in right ITG, right SPL and bilateral PCC.

pictures and then, for “old” responses, judge whether the two presentations were of identical images or were different exemplars.

While we replicated the pattern of neural activity in the temporoparietal regions for hits and misses reported by Turk-Browne et al., we only did so for identical repetitions. We found a decidedly different pattern of changes in neural activity when the repetitions involved different exemplars. Specifically, there was a reliable attenuation in the BOLD response on the second presentation when it was physically identical to the first, and was later recognized as a correct detail hit but not when subjects failed to subsequently recognize it (miss). Conversely, there was no attenuation from the first to second presentation when subjects were confident (and correct) that they were different exemplars, yet there was attenuation from the first to second presentation of different exemplars when subjects failed to recognize the probe (miss).

We also found greater activation for correct detail hits than misses in the right posterior HPC, a region not reported in previous priming studies that involve subsequent recognition. Earlier work has identified HPC as a key region for recollecting previous experiences (e.g., Eldridge et al., 2000; Henson, 2005; Schacter and Wagner, 1999; Wheeler and Buckner, 2004). In many situations, subsequent correct recognition can be based on a familiarity process or a recollective process (e.g., Joordens and Hockley, 2000; Reder et al., 2000); however, we reasoned that for subjects to be able to judge confidently and correctly whether the two

presentations were different, they would have to recollect and compare the two presentations involved.

Facilitation of object processing

One explanation for repetition-related neural attenuation in object processing regions is a facilitation of stimulus processing over repetitions (e.g., Henson, 2003; Grill-Spector et al., 2006; Schacter and Buckner, 1998; Wiggs and Martin, 1998). This explanation fits well with our results pertaining to same-exemplar and different-exemplar hits. The levels of neural activity for the first presentations were not different between the two repetition conditions (given that they are remembered later). The processing of the second presentation, when the stimulus was exactly the same, was more efficient than the first presentation. On the other hand, when the second presentation was of a different exemplar (from the same category), the amount of neural activity involved in processing the stimulus was the same as for the first presentation. In other words, the difference in repetition-related neural attenuation for the same- vs. different-exemplar hits was driven by a change in stimulus processing on the second presentation.

Retrieval at encoding and failure to encode

While no previous study has examined the effect of neural attenuation for subsequent hits vs. misses when the repetitions involve different exemplars, the pattern of neural responses we obtained is reminiscent of the findings reported by Wagner et al. (2000). In their study, subjects classified words as abstract or concrete while in the scanner. Some of those words had also been classified on the previous day. Subjects were given a subsequent memory test after the scanning session. The authors were interested in the relationship between subsequent memory and neural attenuation for words that were seen just once (the first time was in the scanner) and words that had also been classified the day before. A correlation calculated over subjects showed a negative relationship between the hit rate difference for repeated vs. single presentation and the difference in the BOLD response between single and these repeated words such that subjects who showed more neural priming for repeated words showed less facilitation in subsequent memory.

Our study differed from Wagner et al. in many respects, but we also found that in some conditions better memory was associated with less neural attenuation. In particular, when subjects were confident that they had seen two different exemplars that correspond to the word, they showed less neural attenuation than when they failed to recognize the word. One explanation for the inverse pattern of neural attenuation is that it reflects poor encoding on the second presentation for misses.

Many previous studies have reported that the stimuli that are later remembered evoke stronger fMRI signals at encoding than the stimuli that are later forgotten (e.g., Brewer et al., 1998; Garoff et al., 2005; Wagner et al., 1998). Therefore, if a stimulus is well encoded on the first presentation but poorly encoded on the second, there should be a decrease in the neural signal from the first to the second presentation, but this drop should not be attributed to repetition priming. This might explain why we observed repetition-related decreases for different-exemplar misses in left ITG and toFFC. Those trials had higher levels of neural activity on the first presentation relative to the second presentation. The trace from the first encoding was not sufficiently strong to be subsequently recognized on its own and the second presentation was clearly too poorly encoded to aid recognition.

Same-exemplar misses did not produce the same pattern of neural response observed for different-exemplar misses (see Fig. 3). For same repetitions to be missed, both presentations had to be poorly encoded. We believe that this is because a poor encoding on the second presentation of an identical image would still reactivate the

same perceptual representation, thereby reinforcing a previously encoded representation. With this reinforced perceptual representation, the memory traces would be sufficiently strong to enable a low-confidence hit. If subjects do not pay attention to a stimulus on either the first or second presentation (indexed by a low level of activation on both presentations) they miss the trial (there is nothing to strengthen if nothing is encoded).

Task learning and response learning

One factor that may affect the magnitude of neural attenuation is task learning. We compared neural attenuation related to task learning and repetition priming and found that the repetition-related neural attenuation in the left temporo-occipital cortex was better explained by priming than task learning. Conversely, neural attenuation in the left inferior frontal and the right inferior temporal regions was better explained by task learning than priming.

Another factor that affects the magnitude of neural attenuation is strengthening a particular classification response to a stimulus item. It has been demonstrated that practicing a particular (classification) response to a stimulus reduces the need to engage the classification processes invoked on the first trial and that this savings in classification processes may underlie the neural attenuation effects (e.g., Dobbins et al., 2004; Schnyer et al., 2006; Schnyer et al., 2007).

While our study was not designed to disentangle repetition priming and response learning, a recent study by Horner and Henson (2008) investigated the locus of neural attenuation effects, specifically whether they should be attributed to repetition priming or response learning. In their study, subjects saw the stimuli only once before the classification task was repeated or changed. Horner and Henson found that visual processing regions (e.g., fusiform cortex) were more sensitive to repetition priming than response learning, while prefrontal regions were more sensitive to response learning than repetition priming. As in Horner and Henson's study, our stimuli were repeated only once, leading us to conjecture that the effects observed in the temporo-occipital regions should be attributed to repetition priming.

Conclusion

This study demonstrated a novel result that the degree of neural attenuation in object processing regions depends on the interaction between perceptual similarity across repeated presentations, and the quality of encoding. More specifically, the same areas that decreased neural signal for repetitions of same-exemplar correct detail hits, but not misses, decreased neural signal for different-exemplar misses but not correct detail hits. This pattern suggests that separate mechanisms may produce neural attenuation for items that are later recognized as opposed to items that are later missed. The neural attenuation observed for items that are later remembered is probably due to increased efficiency in processing the perceptual properties of the stimuli. It is only reasonable to expect increased efficiency in perceptual processing on the second occurrence when the perceptual properties of the stimuli remain the same from the first to second encoding and that is why the neural attenuation for correct detail hits occurred only for same exemplars. The neural attenuation from first to second presentation observed for different-exemplar misses we believe is due to poorer encoding on the second, relative to the first, presentation. Even a weakly encoded second presentation of an identical image is likely to boost the strength enough to elicit a low-confidence hit.

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