

Biased Competition during Long-term Memory Formation

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Abstract

■ A key task for the brain is to determine which pieces of information are worth storing in memory. To build a more complete representation of the environment, memory systems may prioritize new information that has not already been stored. Here, we propose a mechanism that supports this preferential encoding of new information, whereby prior experience attenuates neural activity for old information that is competing for processing. We evaluated this hypothesis with fMRI by presenting a series of novel stimuli concurrently with repeated stimuli

at different spatial locations in Experiment 1 and from different visual categories (i.e., faces and scenes) in Experiment 2. Subsequent memory for the novel stimuli could be predicted from the reduction in activity in ventral temporal cortex for the accompanying repeated stimuli. This relationship was eliminated in control conditions where the competition during encoding came from another novel stimulus. These findings reveal how prior experience adaptively guides learning toward new aspects of the environment. ■

INTRODUCTION

The external world constantly bombards sensory systems with information, and thus, a fundamental task for our brains is to determine which pieces of this information should be retained in memory. Studies of attention have examined how stimulus properties and task goals influence memory encoding (e.g., Turk-Browne, Golomb, & Chun, 2013; Uncapher, Hutchinson, & Wagner, 2011; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996), but less is known about the role of memory itself in guiding selection (Awh, Belopolsky, & Theeuwes, 2012; Hutchinson & Turk-Browne, 2012). Memory allows the brain to distinguish between old information with which it has prior experience and new information that could help form a more complete representation of the environment. Accordingly, in situations where old and new information are both present, memory for old information may bias processing toward and enhance encoding of new information.

This prediction is complicated by the fact that memory is reflected in multiple brain systems (Squire & Wixted, 2011; Turk-Browne, Yi, & Chun, 2006; Ranganath & Rainer, 2003; Gabrieli, 1998; Willingham, 1997; Tulving, 1985) and its influence might vary depending on which system is involved (e.g., Stokes, Atherton, Patai, & Nobre, 2012; Soto, Humphreys, & Rotshtein, 2007). Here, we focus on perhaps the simplest signal of memory, repetition attenuation—the reduced neural response for repeated versus novel stimuli in sensory areas that code for these stimuli (also known as repetition suppression or fMRI adaptation; Turk-Browne, Scholl, & Chun, 2008; Schacter, Wig, & Stevens, 2007; Grill-Spector, Henson, & Martin, 2006).

The effect of repetition attenuation on competitive processing has been considered in neurophysiological studies of attention (Desimone, 1996). Specifically, biased competition theory predicts that, when old and new information are presented concurrently, the weaker neural activity for old information biases processing toward other (in this case, new) information with stronger activity. Here, we extend this theory to investigate its consequences for long-term memory: Insofar as biased processing enhances encoding into memory, then greater repetition attenuation for old information should be associated with a higher probability of later remembering new information.

To test this hypothesis, we ran two fMRI experiments that linked repetition attenuation for old items during incidental encoding of new items to subsequent memory for the new items. Experiment 1 examined space-based competition—that is, how attenuation for a repeated stimulus at one location in space influences the encoding of a novel stimulus at a different location. Experiment 2 sought to more cleanly disentangle the neural responses for the repeated and novel stimuli by examining category-based competition—that is, how attenuation for a repeated stimulus from one category influences the encoding of a novel stimulus from a different category.

METHODS

Experiment 1

Overview

This experiment consisted of three phases: incidental encoding, memory test, and functional localizer. In the incidental encoding phase, participants were presented with

scene stimuli while performing a cover task of detecting inverted scenes that appeared infrequently. Each trial consisted of three sequential events (Figure 1): The first two events each contained one scene at fixation, and the third event contained two scenes in the periphery on either side of fixation. In the critical same-repeated (SR) condition, the same scene was presented in the first two events, and then it was repeated again in the third event alongside a novel scene. There were two additional conditions to control for different aspects of this sequence. In the same-novel (SN) condition, the same scene was presented in the first two events, but two novel scenes were presented in the third event. In the different-novel (DN) condition, two different scenes were presented in the first two events, followed by two other novel scenes in the third event. In the memory test phase, subsequent recognition memory was tested for the previously novel scenes from the third event of all conditions. The functional localizer phase served to define ROIs for analyzing repetition attenuation. The results of a behavioral pilot study are also reported.

This experimental design permitted assessments of (1) preferential encoding of new items in competition with old items, by testing whether subsequent memory was better for novel scenes paired with repeated scenes (SR) than with other novel scenes (SN, DN); (2) repetition attenuation in stimulus-selective visual cortex, by comparing evoked responses for repeated scenes (second event for SR and SN; third event for SR) versus novel scenes (all DN events; third event for SN); and critically, (3) the rela-

tionship between repetition attenuation and encoding of new items, by logistic regression analysis of the two aforementioned measures.

Participants

Sixty-nine adults in total (49 women, mean age = 21.1 years) participated in the behavioral pilot study (36 participants) and first fMRI experiment (33 participants). Three participants were excluded from the fMRI experiment because of excessive head motion, resulting in a sample of 30 participants. All participants had normal or corrected-to-normal visual acuity, received course credit (behavioral pilot) or monetary compensation (fMRI experiment), and provided informed consent to a protocol approved by the Princeton University institutional review board.

Stimuli

Colorful photographs of indoor and outdoor scenes subtending $\sim 7^\circ \times 7^\circ$ were shown on a monitor (behavioral pilot) or on a screen behind the scanner bore (fMRI experiment).

Procedure

During the encoding phase, participants completed 150 trials, each divided into three events. The first two events contained one scene at fixation, which was either the same across both events (66% of trials) or different (33%). The third event contained two scenes assigned randomly to the left or right of fixation (5.5° from fixation to image center).

When the initial two scenes were the same, the third event contained with equal probability either one novel scene and the scene from the preceding two events (SR) or two novel scenes (SN). When the initial items differed, the third event always contained two novel scenes (DN). The comparison between SR and SN conditions was the primary test of how repetition attenuation affected encoding. The comparison of both SR and SN with DN conditions provided a way to assess whether repetition attenuation occurred on the second event. We combined data from two versions of the behavioral pilot study, one with only the critical SR and SN conditions (12 participants) and the other with all three conditions (24 participants).

The task for the encoding phase involved detecting with a button press whether the scenes in any of the three events of a trial were inverted (20% of trials). One participant in the fMRI experiment used the wrong button in the encoding phase, and thus, their target detection performance was not available. Participants were also instructed to maintain fixation on a small central dot throughout encoding. During fMRI, gaze position was monitored with an iViewX MRI-LR eye tracker (60-Hz sampling frequency) (SMI, Teltow, Germany). Because of

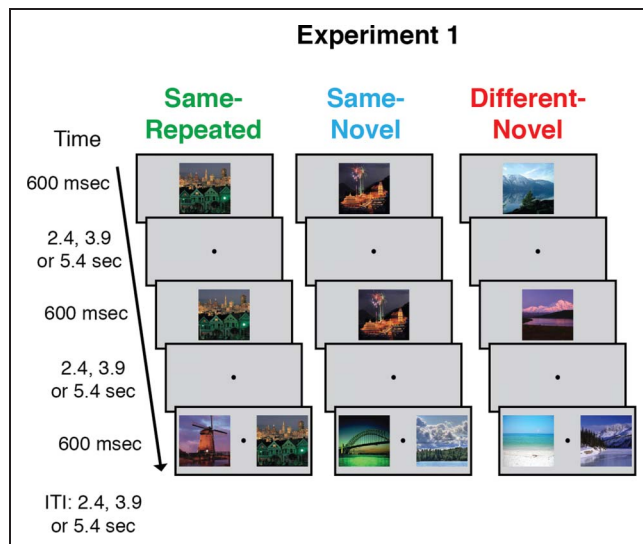


Figure 1. Trial structure of the incidental encoding phase for the behavioral pilot study and Experiment 1. Participants viewed a series of images while performing a cover task (detecting inverted images). A single image was presented at fixation for the first two events (the same image for SR and SN conditions; different images for the DN condition). The third event contained two images in the periphery: a novel scene alongside the same repeated scene for the SR condition and two novel scenes for the SN and DN conditions. Afterward, participants were given a surprise memory test for the novel scenes from the third event.

technical difficulties, eye-tracking data could not be collected from four participants.

All stimuli appeared for 600 msec, and the delay between events within and between trials was jittered pseudorandomly as 2.4, 3.9, or 5.4 sec. The 150 trials (30 inverted targets and 40 trials each for SR, SN, and DN conditions) were distributed across five fMRI runs (each lasting 6 min 57 sec). The sequence of trials was pseudorandom, with the order determined by an algorithm designed to minimize collinearity between onset regressors convolved with a hemodynamic response function.

During the test phase, participants were presented with (formerly) novel scenes from the third event of encoding trials (excluding inverted trials) or previously unseen novel lures. For SR encoding trials, there was only one novel scene to choose from. As these novel scenes were always presented alongside repeated scenes, we took subsequent memory performance on these items to reflect the degree to which processing was biased toward new information by the presence of old information. For SN and DN encoding trials, we randomly selected one of the two novel scenes (with equal number of left and right stimuli across trials) to serve as test items. We used subsequent memory performance on these items as a baseline for the processing of new information in competitive displays that lack old information. Contrasting SR and SN/DN trials thus isolates the influence of a repeated scene on the processing of a novel scene.

At test, items appeared one at a time, and participants were instructed to respond “old,” “unsure,” or “new.” There were 180 trials, 120 old items, and 60 lures. No more than three old items or lures could appear consecutively; otherwise, trial order was random. Trials ended when the participant responded or 3 sec expired, followed by a 1-sec delay.

After the test phase, participants completed two functional localizer runs, one to identify voxels selective for the scene stimuli and the other to identify voxels selective for the peripheral location where stimuli were presented. The category localizer contained 18 blocks: 6 face blocks and 12 scene blocks. Twice as many scene blocks were used for a purpose unrelated to the current study (to compare processing of “open” and “closed” scenes). Six blocks is sufficient for defining category-selective ROIs in ventral temporal cortex (Turk-Browne, Simon, & Sederberg, 2012). Participants judged whether faces were male or female and whether scenes contained primarily manmade or natural elements. Each image was presented for 500 msec, followed by a 1000-msec blank. There were 12 images per block, resulting in a block duration of 18 sec, followed by 12 sec of fixation (total duration = 9 min 6 sec). The peripheral localizer employed identical timing and block/trial structure. However, instead of containing faces and scenes, all events contained two scenes presented at the same locations as the images in the third event of encoding trials. Participants were instructed to maintain central fixation while covertly attending to the scene

on the left or right (nine blocks each). The participants made a manmade/natural judgment for the attended scene.

fMRI Acquisition

All imaging data were acquired using a 3-T Siemens (Erlangen, Germany) Skyra MRI scanner with a 16-channel head coil. Functional images were obtained with a T2*-weighted EPI sequence: repetition time = 1500 msec, echo time = 28 msec, matrix = 64, field of view = 192 mm, flip angle = 64°, thickness = 4 mm (3 × 3 × 4 mm voxels). Twenty-seven oblique axial slices aligned to the AC–PC line were collected in interleaved order. The encoding runs contained 278 volumes each, and the localizer runs contained 364 volumes each. To align scans in all cases, coplanar FLASH and high-resolution MPAGE T1-weighted anatomical images were collected.

fMRI Analysis

The first four volumes of each functional run were discarded for T1 equilibration. Functional data were preprocessed and analyzed using FSL (www.fmrib.ox.ac.uk/fsl), including correction for head motion and slice-acquisition time, spatial smoothing (5-mm FWHM Gaussian kernel), and high-pass temporal filtering (120-sec period). Preprocessed data were aligned to the anatomical images and the standard MNI152 brain and interpolated to 2-mm isotropic voxels.

With the exception of the trial-by-trial analysis below, statistical analyses were performed using a general linear model (GLM) in FEAT. For every run, BOLD activity was modeled with a delta function at stimulus onset convolved with a double-gamma hemodynamic response function. Separate regressors were specified for each of the three jittered events per condition (SR, SN, and DN). The third event was further subdivided into whether the novel scene to be probed in the memory test appeared on the left or right side. Analyses of overall repetition attenuation collapsed over left and right third events, but later, trial-by-trial analyses examined repetition attenuation in regions contralateral to the repeated scene.

Regressors-of-no-interest were specified for trials with inverted targets and for motion parameters. For each convolved regressor, temporal derivatives were also modeled. This resulted in 32 regressors (event number in subscript): SR₁, SR₂, SR_{3_left}, SR_{3_right}, SN₁, SN₂, SN_{3_left}, SN_{3_right}, DN₁, DN₂, DN_{3_left}, DN_{3_right}, and targets (all ×2 for temporal derivatives) as well as six motion directions. Parameter estimates were normalized to percent signal change by scaling with the amplitude of the predicted effect, dividing by the run mean, and multiplying by 100 (mumford.fmripower.org/perchange_guide.pdf).

The trial-by-trial subsequent memory analysis was performed by *z* scoring the preprocessed data and extracting the BOLD signal three volumes (4.5 sec) after event onset. A trial-specific activity difference was then calculated for each condition by subtracting the activity in the first event from the third event. This estimate was then *z* scored within

ROI (left vs. right) and separated according to whether it was taken from the ROI contralateral to the repeated scene or the novel scene. Overall activity was higher on the third event than that on the first event because the former contained two scenes and the latter contained one scene. However, we interpreted the third-minus-first-event difference as a relative measure of repetition attenuation for the repeated scene on the third event. At the extreme, a completely attenuated response for the repeated scene would lead to zero difference, as the response for both first and third events would be dominated by activity for the one novel scene. Thus, the smaller the difference, the greater attenuation on the third event. We then related this activity difference to the binary subsequent memory outcome (hit = 1, miss = 0) for the novel scene on that trial using logistic regression. The reliability of resulting beta values was tested at the group level for each condition. We hypothesized that the average beta would be negative, with a smaller activity difference (i.e., more repetition attenuation) associated with better subsequent memory. One participant was excluded from this analysis as he or she had no misses in one condition.

The localizer runs were analyzed with a GLM like above. Separate regressors were specified for face and scene blocks (category localizer) and right and left blocks (peripheral localizer). An ROI was defined in each hemisphere from voxels showing both greater activity for scenes versus faces and for contralateral versus ipsilateral locations (both $ps < .05$, cluster corrected).

Experiment 2

The goal of Experiment 2 was to replicate the findings of Experiment 1 while more cleanly isolating the cortical processing of old and new items. The repeated and novel stimuli on the third event of SR trials were now drawn from face and scene categories, respectively (Figure 2), which are selectively processed by distinct areas of ventral temporal cortex. The design was otherwise identical to Experiment 1, except that we eliminated the DN condition to increase statistical power for the primary SR condition and its tightest control, the SN condition. Moreover, eye tracking was not used because all stimuli were centered at fixation.

Participants

Thirty-two adults (17 women, mean age = 21.3 years) participated in the second fMRI experiment. All participants had normal or corrected-to-normal visual acuity, received monetary compensation, and provided informed consent to a protocol approved by the Princeton University Institutional Review Board.

Stimuli

Face stimuli consisted of colorful photographs of male and female faces subtending $\sim 3^\circ \times 3^\circ$, and scene stimuli

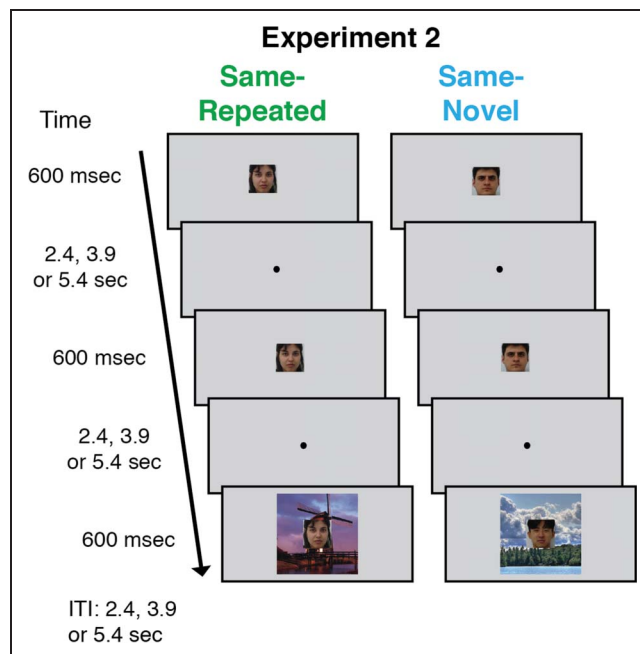


Figure 2. Trial structure of Experiment 2. Participants viewed a series of images while performing a cover task of detecting inverted images. A single face was presented at fixation for the first two events, and the third event contained either a repeated face (SR) or a novel face (SN) surrounded by a novel scene. Afterward, participants were given a surprise memory test for the novel scenes from the third event.

consisted of colorful photographs of indoor and outdoor places subtending $\sim 16^\circ \times 16^\circ$. Photographs were projected on a screen behind the scanner bore.

Procedure

The encoding phase was very similar to Experiment 1, with a couple of changes noted here. For all trials in the encoding phase, the first two events contained the same, trial-unique face at fixation. The third event contained either the same face (SR condition) or a new face (SN condition) presented centrally, surrounded by a novel scene. There were fewer trials overall (120 trials across four scanning runs), but because there was no DN condition, the number of trials per condition was higher (48, after excluding 12 inverted targets per condition). The test phase was nearly identical to Experiment 1, except that there were 96 old items and 48 lures (144 trials in total).

The face/scene localizer was adapted from Experiment 1. It contained six blocks each of novel face and scene stimuli for a total of 12 blocks and lasted 6 min 6 sec. The stimuli were presented at the same size as in the encoding phase ($3^\circ \times 3^\circ$ and $16^\circ \times 16^\circ$ for faces and scenes, respectively). To equate overall visual stimulation, however, face stimuli were presented in the middle of a $16^\circ \times 16^\circ$ checkerboard pattern. Scene stimuli contained a $3^\circ \times 3^\circ$ checkerboard square in the central location where the faces appeared in the encoding phase. The localizer was completed between the encoding and test phases.

fMRI Acquisition

Data were acquired in an identical manner to Experiment 1, except that there were fewer volumes in the face/scene localizer (244).

fMRI Analysis

Preprocessing and analysis steps were very similar to Experiment 1. There were fewer regressors in the GLM analysis (20 in total) because the DN condition was eliminated, with regressors for each of the three events per condition (SR₁, SR₂, SR₃, SN₁, SN₂, SN₃) and trials with inverted targets (all ×2 for temporal derivatives) as well as for the six motion directions. The trial-by-trial subsequent memory analysis was performed similar to before, but with the third-minus-first-activity differences obtained from both face- and scene-selective ROIs. The beta value for each participant relating the face-selective activity difference to subsequent memory for the scene was obtained from a multiple logistic regression with the scene-selective activity difference included as an additional predictor. This model isolated the unique variance within each ROI that related to subsequent scene memory. A second logistic regression analysis assessed how the interaction between ROIs related to memory, using the *z* score of activity in scene-selective voxels minus the *z* score of activity in face-selective voxels to predict subsequent memory for the scene. The reliability of the beta values was tested at the group level for each condition. One participant was excluded as an outlier (beta > 3 SDs away from mean).

The localizer run was analyzed with a GLM as described in Experiment 1. ROIs were defined for voxels showing greater activity for faces versus scenes and vice versa ($p < .05$, cluster corrected). We were only able to identify a face-selective ROI in the right hemisphere (consistent with Peelen & Downing, 2005; Kanwisher, McDermott, & Chun, 1997) and so also restricted the scene-selective ROI to the right hemisphere to avoid hemispheric differences.

RESULTS

Experiment 1

Cover Task

To ensure that encoding was incidental, participants were not told in advance about the memory test and were given a cover task of detecting occasional scenes that were inverted. Accuracy was excellent on this cover task (behavioral pilot: mean $d' = 3.48$, $SEM = 0.09$, vs. chance: $t(35) = 38.83$, $p < .001$; Experiment 1: mean $d' = 3.22$, $SEM = 0.13$, $t(28) = 24.85$, $p < .001$).

Eye Tracking

Gaze position was monitored to ensure that there were no differences in eye movements between conditions.

Of primary interest was the proportion of samples where fixation fell on the peripheral stimuli in the third event of encoding trials. There was no main effect of Condition on peripheral fixations ($F(2, 50) = 0.10$, $p = .91$). Moreover, for the SR condition, peripheral fixations did not differ between repeated and novel scenes ($t(25) = 0.87$, $p = .39$).

Subsequent Memory

During the recognition memory test, participants performed above chance in detecting old versus new items (behavioral pilot: mean $d' = .32$, $SEM = 0.04$, $t(35) = 8.54$, $p < .001$; Experiment 1: mean $d' = .27$, $SEM = 0.04$, $t(29) = 6.11$, $p < .001$). Consistent with the idea that old items facilitate encoding of concurrent new items, the behavioral pilot revealed better memory for novel scenes in SR (mean $d' = .39$, $SEM = 0.04$) versus SN trials (mean $d' = .29$, $SEM = 0.04$; $t(35) = 2.23$, $p = .02$, one-tailed). Critically, these conditions differed only in the presence of a repeated scene in the third event. Memory was also better for the SR versus DN conditions (mean $d' = .26$, $SEM = 0.06$, $t(23) = 2.28$, $p = .01$, one-tailed), although these conditions differed in both the second and third events. We did not have any predictions about the SN versus DN conditions, and indeed, they did not differ ($t(23) = 1.03$, $p = .31$, two-tailed). The independent sample of participants in Experiment 1 displayed a similar pattern of results, but the hypothesized effects were less reliable: SR (mean $d' = .32$, $SEM = 0.06$) versus SN conditions (mean $d' = .24$, $SEM = 0.05$, $t(29) = 1.43$, $p = .08$, one-tailed) and SR versus DN conditions (mean $d' = .25$, $SEM = 0.05$, $t(29) = 1.44$, $p = .08$, one-tailed); SN and DN conditions again did not differ ($t(29) = 0.08$, $p = .94$, two-tailed).

Despite being weaker, the behavioral effects in Experiment 1 were not statistically smaller than those in the pilot study (Sample [pilot, Experiment 1] × Condition [SR, SN] interaction: $F(1, 64) = 0.08$, $p = .77$). Indeed, pooling the SR-minus-SN difference in memory across samples preserved the effect ($F(1, 64) = 6.47$, $p = .01$). More importantly, the critical test of our hypothesis is that stronger repetition attenuation for a particular repeated scene on an SR trial will produce better later memory for the novel scene initially encountered on that trial. In other words, there should be a trial-by-trial relationship between the amount of repetition attenuation for the repeated stimuli and subsequent memory for the novel stimuli, with lower activity for the former predicting better memory for the latter.

Repetition Attenuation

To estimate repetition attenuation, we localized bilateral ROIs that responded selectively to scene stimuli presented in the periphery and examined evoked activity during the encoding phase (Figure 3). In a repeated-measures ANOVA with Event (first, second, third) and Condition

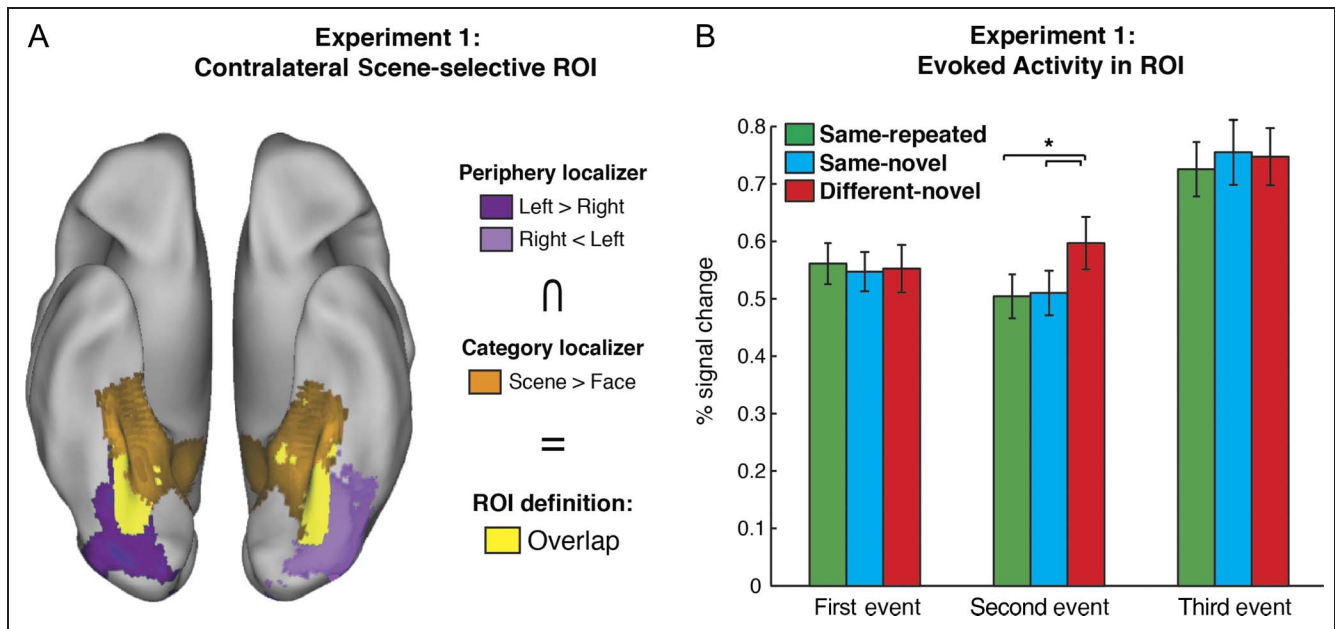


Figure 3. ROI selection and evoked activity for Experiment 1. (A) Ventral surface of right and left hemispheres, respectively. ROIs (yellow) were defined in each hemisphere with functional localizer tasks by identifying voxels with greater activity for scene versus face blocks ($p < .05$; orange) and greater activity for contralateral versus ipsilateral blocks ($p < .05$; dark purple: left > right, light purple: right > left). (B) Evoked activity in the encoding phase of Experiment 1 for the first, second, and third events of each trial and in the SR, SN, and DN conditions. Error bars reflect ± 1 SEM. $*p < .05$.

(SR, SN, DN) as within-subject factors, there was a main effect of Event ($F(2, 116) = 68.22, p < .001$), a main effect of Condition ($F(2, 116) = 4.74, p = .01$), and an interaction ($F(4, 116) = 6.09, p < .001$). Planned comparisons focused on the second event, which provided a pure measure of repetition attenuation because a single novel (DN) or repeated (SR, SN) scene was presented. As expected, there was less activity for SR versus DN conditions ($t(29) = -4.72, p < .001$) and SN versus DN conditions ($t(29) = -4.85, p < .001$).

We also tested for repetition attenuation in the third event by comparing SR with SN and DN conditions. Although numerically in the right direction, with lower activity for SR, these comparisons did not reach significance: SR versus SN conditions ($t(29) = -1.52, p = .07$, one-tailed) and SR versus DN conditions ($t(29) = -1.15, p = .13$, one-tailed). The third event in the SR condition contained a novel scene in addition to the repeated scene, which may have masked the attenuated response for the repeated scene (which had been observed in the second event). Regardless, our hypothesis concerned how variance in repetition attenuation on the third event related to memory.

Relating Repetition Attenuation to Subsequent Memory

Repetition attenuation was measured for each trial as the difference in activity between the third and first events in the ROI contralateral to the repeated scene. This measure was then related to memory outcome with logistic regression (Figure 4A). Consistent with our hypothesis,

the mean beta for the SR condition was negative (vs. 0: $t(28) = -4.26, p < .001$; Figure 4B)—that is, lower activity on the third event (greater attenuation) was related to better memory outcome for the novel scene.

Importantly, this relationship required a repeated scene: When the same analysis was performed in the SN and DN conditions by predicting memory for one of the novel scenes on the third event from the activity for the other novel (rather than repeated) scene in that event, the mean betas were unreliable (SN: $t(28) = -0.37, p = .71$; DN: $t(28) = 0.66, p = .52$). Moreover, the mean SR beta was significantly lower than both the mean SN and mean DN betas ($ps < .04$). Taken together, these results suggest that the degree of neural activation to a repeated stimulus, but not a novel stimulus, has a trial-by-trial relationship to the encoding and hence subsequent memory of a competing novel stimulus.

Furthermore, the relationship for SR trials was specific to our measure of repetition attenuation: When memory for the novel scene was predicted from the activity for the repeated scene on the third event alone—that is, without accounting for stimulus-specific attenuation from the first event—the beta became unreliable (mean = $-0.15, SEM = 0.09, t(28) = -1.70, p = .10$). Indeed, the repetition attenuation needed to occur during the competitive third event to be influential: Attenuation for the repeated scene during the second event (second-minus-first-activity difference) was not predictive of memory for the novel scene on the third event (mean = $-0.12, SEM = 0.12, t(28) = -1.00, p = .32$).

Surprisingly, the relationship for SR was not specific to the contralateral ROI: The mean beta was also reliably negative in the ROI ipsilateral to the repeated scene ($t(28) = -3.88, p < .001$; SN and DN mean betas were still unreliable, $ps > .42$). By defining ROIs that responded more strongly to contralateral versus ipsilateral scenes, we had hoped to isolate processing of the repeated and novel stimuli on SR trials. However, the similar pattern of results suggests that these ROIs were not purely responsive to contralateral stimuli. Thus, the purpose of Experiment 2 was to better disentangle processing of the repeated and novel stimuli using visual categories represented in distinct areas of ventral temporal cortex.

Experiment 2

Cover Task

Participants were highly accurate in detecting the infrequent inverted targets during the encoding phase (mean $d' = 4.25, SEM = 0.13$, vs. chance: $t(31) = 31.87, p < .001$).

Subsequent Memory

During the recognition memory test, participants performed above chance in detecting old versus new items (mean $d' = .44, SEM = 0.08, t(31) = 5.58, p < .001$). The pattern of results

across conditions was qualitatively similar to the behavioral pilot study and to Experiment 1, but the overall difference between SR (mean $d' = .46, SEM = 0.08$) and SN (mean $d' = .40, SEM = 0.08$) conditions did not reach significance ($t(31) = 1.28, p = .11$, one-tailed). As in Experiment 1, the effect was not reliably weaker in Experiment 2 than in the behavioral pilot study (Sample [pilot, Experiment 2] \times Condition [SR, SN] interaction: $F(1, 56) = 0.31, p = .58$). Regardless of these overall effects, the key question was again whether trial-wise variance in subsequent memory for the novel scene on SR trials was predicted by repetition attenuation for the repeated face presented concurrently.

Repetition Attenuation

The only stimuli that were repeated in this experiment were faces, and so, we measured repetition attenuation in a face-selective ROI (Figure 5). A repeated-measures ANOVA with Event (first, second, third) and Condition (SR, SN) as within-subject factors revealed a main effect of Event ($F(2, 62) = 12.88, p < .001$) and a main effect of Condition ($F(1, 62) = 5.03, p = .03$) but no interaction ($F(2, 62) = 1.05, p = .36$). Repetition attenuation was manifested in two ways in this experiment. First, collapsing over condition, there was less activity in the second event with a repeated face than in the first event with a

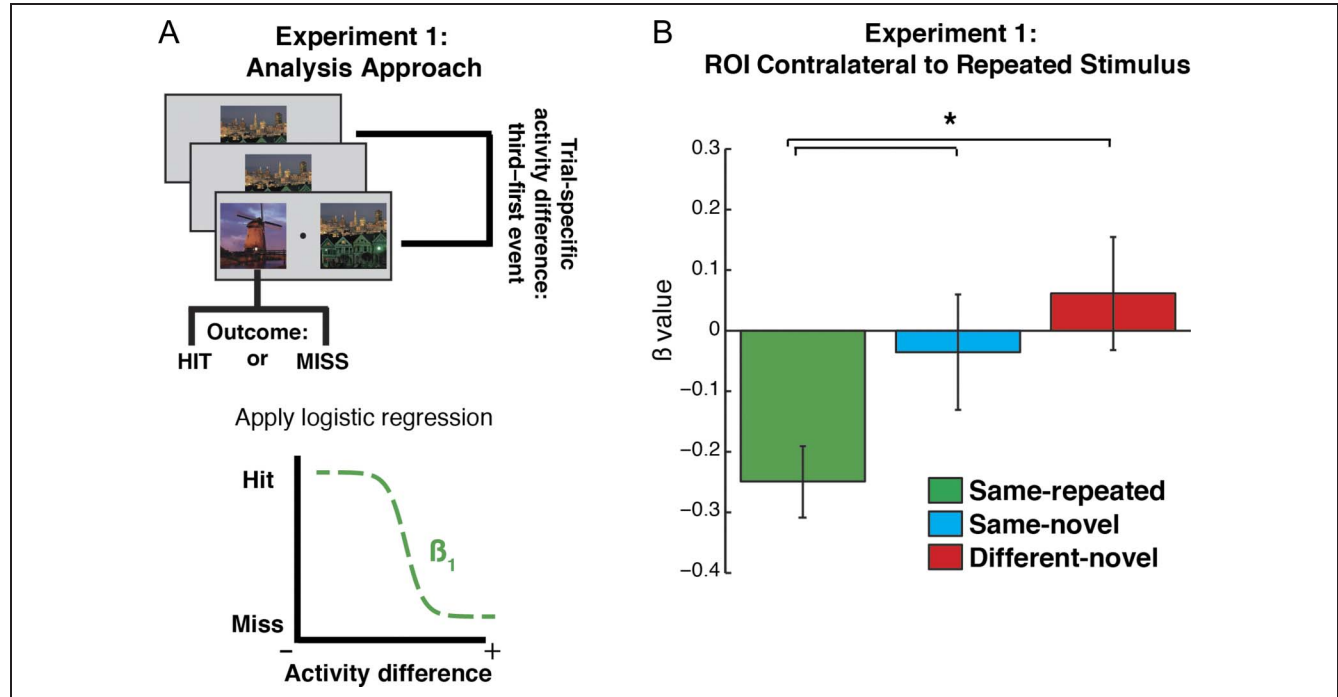


Figure 4. Relationship between BOLD activity and behavior for Experiment 1. (A) For SR trials, the difference in evoked activity between the third and first events in ventral temporal cortex contralateral to the repeated scene was extracted as a measure of repetition attenuation. This difference was then used to predict with logistic regression whether the novel scene in the third event would be remembered (hit) or forgotten (miss) in the recognition memory test. For SN and DN trials (not shown), the difference was calculated contralateral to one of the novel scenes, providing a baseline of what happens without attenuation (because there was no repeated scene). The regression was used to predict memory for the other novel scene, which was not used to calculate the difference. (B) For SR trials, lower relative activity for the third event versus the first event (more repetition attenuation) was related to better memory. For SN and DN trials, when the competing scene was novel rather than repeated, the relationship was eliminated. Error bars reflect $\pm 1 SEM$. $*p < .05$.

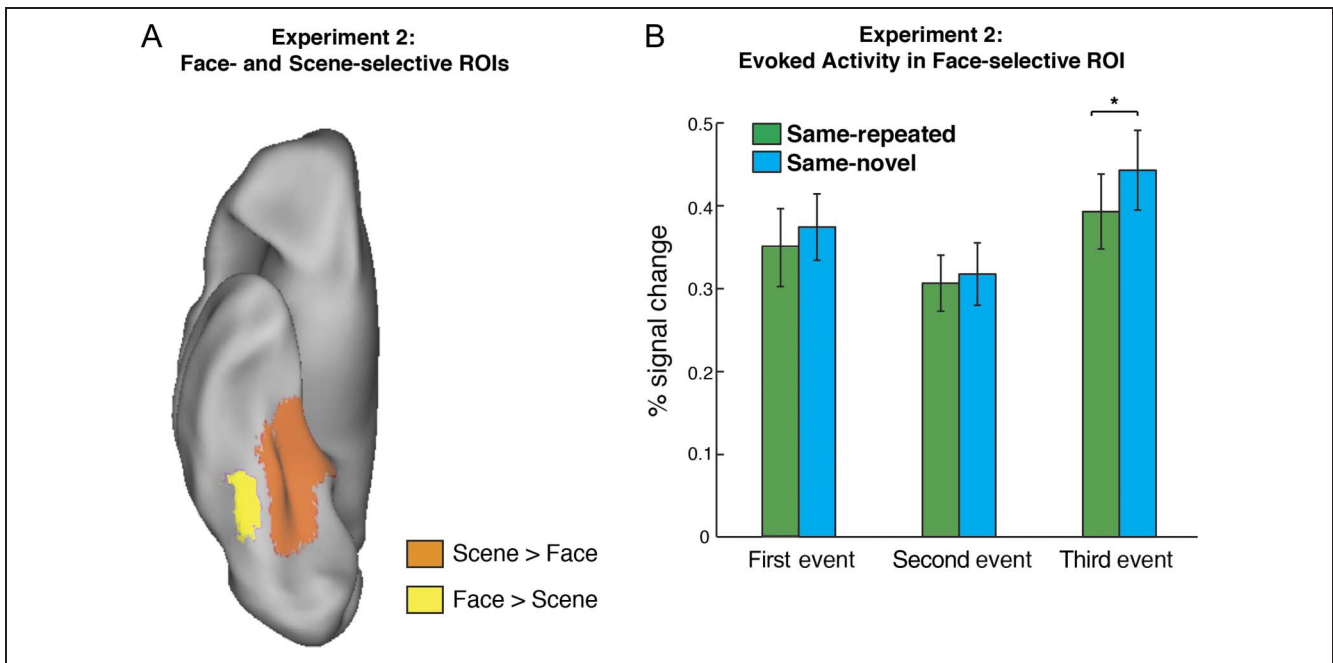


Figure 5. ROI selection and activity for Experiment 2. (A) Ventral surface of right hemisphere. Using an independent localizer, ROIs were defined as voxels with greater activity for face versus scene blocks ($p < .05$; yellow) and scene versus face blocks ($p < .05$; orange). (B) Evoked activity within the face-selective ROI in the encoding phase for the first, second, and third events of each trial in the SR and SN conditions. Error bars reflect ± 1 SEM. * $p < .05$.

novel face ($F(1, 31) = 8.53, p = .007$). Second, within the third event, there was less activity for the SR condition with a repeated face than the SN condition with a novel face ($t(31) = -2.46, p = .01$, one-tailed).

Relating Repetition Attenuation to Subsequent Memory

Repetition attenuation was measured for each trial as the difference in activity between the third and first events in

the face-selective ROI, and this measure was then related to memory outcome for the scene with logistic regression. Because our face-selective ROI can show a weak response to scenes (Weiner & Grill-Spector, 2010), we also calculated the third-minus-first-event activity difference from a scene-selective ROI as a control and entered it into the same regression model to partial out variance related to scene processing. Consistent with our hypothesis, the mean beta for the SR condition in the face-selective ROI

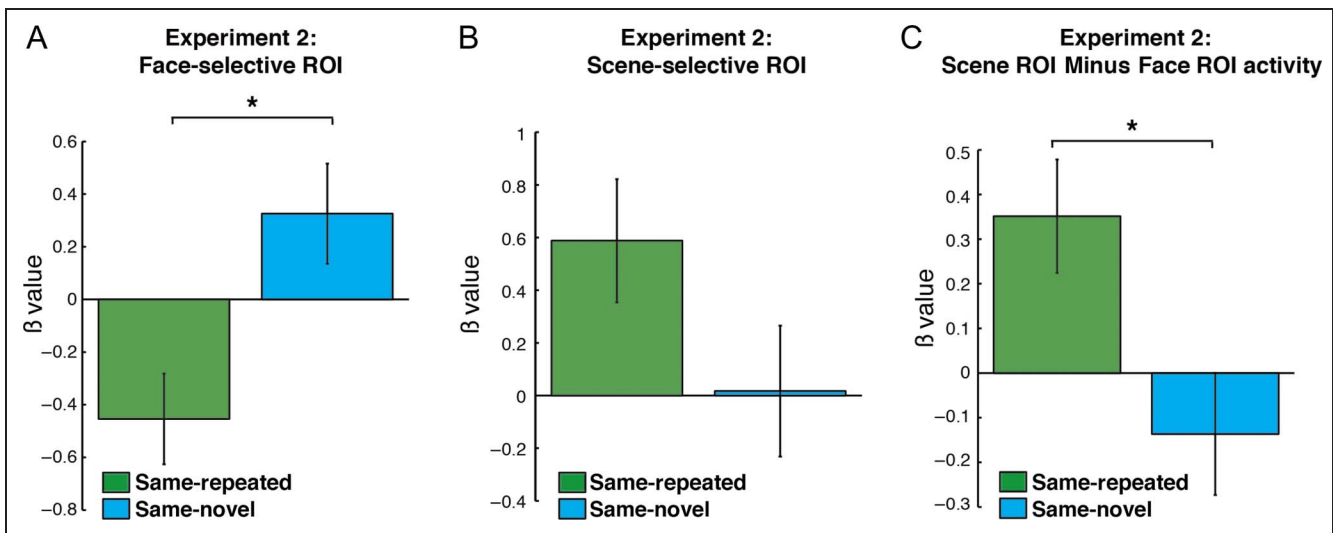


Figure 6. Relationship between BOLD activity and behavior for Experiment 2. (A) Lower face-related activity was associated with better scene memory in the SR but not SN conditions. (B) Greater scene-related activity was associated with better scene memory in the SR but not SN conditions. (C) The difference in raw activity between regions coding for the novel scene and repeated face was associated with the likelihood of encoding the novel scene in the SR but not SN conditions. Error bars reflect ± 1 SEM. * $p < .05$.

was negative (vs. 0: $t(30) = -2.63, p = .01$)—that is, lower face-related activity (greater attenuation) was related to better memory for the scene (Figure 6A). Importantly, this negative relationship required a repeated face on the third event, as the mean beta for the SN condition was numerically positive ($t(30) = 1.71, p = .10$) and significantly different from the mean SR beta ($t(30) = 3.17, p = .003$). Moreover, the relationship for SR was specific to our measure of repetition attenuation (third-minus-first-event activity), as memory could not be predicted from activity on the third event alone (mean beta = $-0.22, SEM = 0.24, t(30) = -0.88, p = .39$), nor from attenuation during the second event (mean = $-0.14, SEM = 0.15, t(30) = -0.94, p = .35$).

By better isolating processing of the repeated and novel stimuli in this experiment, we were able to conduct two further analyses. First, whereas lower face-related activity was beneficial for scene memory, studies of subsequent memory (e.g., Turk-Browne et al., 2006; Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998) suggest that greater scene-related activity during encoding of scenes should be beneficial for memory. Indeed, the mean beta from the multiple logistic regression above for the SR condition in the scene-selective ROI (controlling for face-related processing) was positive (vs. 0: $t(30) = 2.52, p = .02$; Figure 6B). There was no relationship for the SN condition ($t(30) = 0.07, p = .95$), and the two conditions differed marginally ($t(30) = 1.78, p = .09$).

Second, this regression model identified unique variance in the face- and scene-selective ROIs (because they were entered as simultaneous regressors), but biased competition theory suggests that their activity might be yoked—that is, lower face activity because of repetition attenuation might result in higher scene activity. If so, a greater difference in the raw activity of scene- and face-selective ROIs should be associated with a greater bias toward processing and encoding the scene. Indeed, this difference positively predicted memory outcome in the SR condition ($t(30) = 2.76, p = .01$; Figure 6C). There was no such relationship when both were novel in the SN condition ($t(30) = -1.00, p = .33$), and the difference between conditions was reliable ($t(30) = 2.73, p = .01$).

DISCUSSION

Our findings provide insight into how prior experience influences memory encoding. We found that memory is enhanced for new items presented with old items that elicit repetition attenuation in ventral temporal cortex. This extends the biased competition framework—wherein sensory representations compete for processing and conscious awareness (Desimone, 1996; Desimone & Duncan, 1995)—to the domain of long-term episodic memory. Specifically, during the third event of SR trials, the relatively weaker (i.e., attenuated) response for a repeated scene (Experiment 1) or face (Experiment 2) bi-

ased processing toward a novel scene presented at the same time and enhanced its episodic encoding.

Repetition attenuation may reflect facilitated processing of the repeated stimulus, such that more attentional resources were available for processing the novel stimulus. Such resources may be allocated in a competitive manner because of an object-based capacity limit or because of a central processing bottleneck (Chun, Golomb, & Turk-Browne, 2011). Alternatively, such resource sharing need not be related to selective attention per se and could instead reflect constraints on cognitive control or working memory processes that support memory encoding (Blumenfeld & Ranganath, 2007; Craik et al., 1996).

The current findings expand on prior work in two additional ways. First, previous studies have examined the relationship between repetition attenuation for one item and subsequent memory for that same item (Xue et al., 2011; Turk-Browne et al., 2006; Wagner, Maril, & Schacter, 2000). Our study suggests that attenuation for an item has broader consequences, including influencing how other items are encoded. Second, most previous studies of subsequent memory have found that greater activity in perceptual regions during encoding increases the likelihood of later retrieval (for reviews, see Kim, 2011; Paller & Wagner, 2002). Here, we show that this is not a universal principle, with greater activity at encoding in these same regions being detrimental if it reflects processing of competing items.

There are potential interpretations of the current results that do not rely on competitive processing per se. For example, the presence of an old item alongside a new item in the critical SR condition might enhance encoding of the new item, insofar as the old item serves as contextual “scaffolding” for the formation of new associative memories (e.g., Poppenk & Norman, 2012). Although consistent with the observed behavioral results, the neuroimaging results from the second experiment—in which the difference in activity for the new and old items predicted memory for the new item—suggest that competition played some role. The presence of an associative benefit could be tested in future work by comparing encoding of a new item in the context of an old item (as in our SR condition) against encoding of a new item presented alone (without competition). This would establish whether old items serve only to mitigate competition or can in fact enhance memory above baseline.

Another consideration is that the novelty of recently encoded items has been shown to influence mnemonic processing of the current item (e.g., Duncan, Sadanand, & Davachi, 2012). For example, when viewing an object that is similar to a previously encoded object, it is easier to detect that it differs from the original when the preceding (unrelated) item was new versus old. This suggests that novelty primes pattern separation—that is, the formation of new memory traces—even for related inputs. On the surface, this might predict enhanced

encoding of new items presented in the context of other new items, seemingly contrary to the present results—better memory for new items presented concurrently with old items. However, the effect of novelty on pattern separation has only ever been tested for sequential presentations, and whether it occurs for simultaneous items is unknown. Perhaps, the closest proxy to prior work comes from the first experiment, in which the two new items on the third event of SN and DN trials were preceded on the second event by old and new items, respectively. However, we did not observe a difference between these two conditions. Future work could better examine the influence of mnemonic states on competitive encoding by presenting an unrelated old or new item immediately preceding events containing both old and new items.

There are also potential interpretations of our results that maintain the emphasis on competitive processing but where repetition attenuation does not play a primary role. For example, novel stimuli can capture attention in the context of repeated stimuli (e.g., Downing, 2000; Johnston, Hawley, Plewe, Elliott, & DeWitt, 1990), which is consistent with our interpretation insofar as the capture reflects an automatic, stimulus-driven shift of attention caused by an attenuation-related imbalance in activity for the repeated and novel stimuli. However, an alternative possibility is that the repeated stimulus is recognized as old and attention is shifted in a volitional, goal-directed manner to the novel stimulus. Accordingly, the reduced activity for the repeated stimulus is a consequence of the withdrawal of attentional resources toward the novel stimulus. Although both of these accounts fall within the purview of the biased competition model (Desimone & Duncan, 1995), an important difference is whether repetition attenuation is the bias signal that redirects attention or whether the bias signal emanates from elsewhere (e.g., control areas in frontoparietal cortex).

Our results suggest that both accounts might apply. Consistent with the notion that attention was shifted to the novel scene, in Experiment 2, the difference in activity between regions coding for the scene and face positively predicted subsequent scene memory. That is, a strong shift of attention to the novel scene would both enhance encoding of the scene and result in greater relative activity for the scene than the face. However, other results are consistent with the notion that repetition attenuation played a central role. In Experiment 2, there was a negative relationship between face-related activity and subsequent scene memory when controlling for scene-related activity, suggesting that the predictive power of reduced activity for the repeated stimulus was not solely a consequence of processing the novel stimulus. Moreover, in both experiments, the activity difference between the third and first events for the repeated stimulus—a measure of stimulus-specific attenuation—and not the activity on the third event alone predicted memory for the novel stimulus. Collectively, these findings suggest that both attention may have been shifted

to the novel stimulus and that repetition attenuation was involved.

In summary, our findings suggest that past experience facilitates the formation of new memories and that repetition attenuation may be an underlying mechanism. Given that attenuation is only one of many signatures of memory for old information, a fruitful direction for future research will be to relate other signatures such as behavioral priming (Schacter, Dobbins, & Schnyer, 2004; Henson, 2003), eye movements (Hannula & Ranganath, 2009), and neural pattern similarity (Xue et al., 2010) to the encoding of new information.

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