

Neural correlates of contextual cueing are modulated by explicit learning

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ABSTRACT

Contextual cueing refers to the facilitated ability to locate a particular visual element in a scene due to prior exposure to the same scene. This facilitation is thought to reflect implicit learning, as it typically occurs without the observer's knowledge that scenes repeat. Unlike most other implicit learning effects, contextual cueing can be impaired following damage to the medial temporal lobe. Here we investigated neural correlates of contextual cueing and explicit scene memory in two participant groups. Only one group was explicitly instructed about scene repetition. Participants viewed a sequence of complex scenes that depicted a landscape with five abstract geometric objects. Superimposed on each object was a letter T or L rotated left or right by 90°. Participants responded according to the target letter (T) orientation. Responses were highly accurate for all scenes. Response speeds were faster for repeated versus novel scenes. The magnitude of this contextual cueing did not differ between the two groups. Also, in both groups repeated scenes yielded reduced hemodynamic activation compared with novel scenes in several regions involved in visual perception and attention, and reductions in some of these areas were correlated with response-time facilitation. In the group given instructions about scene repetition, recognition memory for scenes was superior and was accompanied by medial temporal and more anterior activation. Thus, strategic factors can promote explicit memorization of visual scene information, which appears to engage additional neural processing beyond what is required for implicit learning of object configurations and target locations in a scene.

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1. Introduction

As we gaze at the world, the visual system extracts information to generate an internal representation of scene after scene. The redundant co-occurrence of objects and events can serve as a basis for these representations, and over time, repeating stimulus patterns can be used to predict the location of task-relevant items (Chun & Jiang, 1998; Chun & Nakayama, 2000). Invariant contextual information can thus be thought of as enabling an “accumulation of knowledge” as the visual system fine-tunes representations to reflect these constancies (Dienes & Altmann, 1997).

To investigate ways in which such knowledge influences performance, Chun and Jiang (1998) devised a paradigm in which participants scanned displays for a rotated “T” amongst rotated “L” distracters. In this paradigm, searches were speeded for displays that were repeated several times throughout the experiment compared with novel scenes that appeared only once. The authors dubbed this phenomenon *contextual cueing* and suggested that

invariant contexts facilitate the shifting of attention to corresponding locations, streamlining search. Subsequent findings indicated that the global, unchanging configuration of stimuli, rather than specific perceptual details, were responsible for this effect. For example, contextual cueing was not attenuated when the identity of distracter items was changed but their configuration was preserved (Chun & Jiang, 1998).

Implicit memory refers to a collection of phenomena in which facilitated stimulus processing occurs in the absence of awareness of memory retrieval. These behavioral adaptations typically depend on plasticity in brain areas such as the basal ganglia, cerebellum, and neocortex (Squire, 2004). In contrast, for the awareness of memory retrieval that characterizes explicit memory, a contribution from the medial temporal lobe (MTL), which includes the hippocampus and adjacent cortex (entorhinal, perirhinal, and parahippocampal cortices), appears to be essential. The MTL is thought to operate in conjunction with other cortical regions to bind together the constituent elements of a scene or event into a relational representation that makes subsequent explicit retrieval possible (Eichenbaum & Cohen, 2001).

Contextual cueing is considered to be a type of implicit memory because it commonly occurs in the absence of conscious awareness of retrieval of the repeating context. As evidence of the independence of contextual cueing from explicit memory, participants who

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had learned to locate targets in repeated displays more quickly were still unable to discriminate repeated from new displays (Chun & Jiang, 1998). The few participants who claimed to notice that displays repeated still performed at chance levels when trying to recognize repeated displays and also showed search benefits with repeated displays that were equivalent to those in other participants. Chance recognition was also observed in another inquiry with more sensitive explicit memory measures (Chun & Jiang, 2003). Furthermore, individuals given foreknowledge about the repetition performed similarly to naive individuals and had equally poor explicit memory for displays.

Recent evidence suggests that contextual cueing may be an atypical form of implicit memory, as MTL damage has been shown to disrupt contextual cueing. In an initial study, patients with damage to the hippocampus and surrounding cortical regions did not show contextual cueing (Chun & Phelps, 1999). Given that many forms of implicit memory are intact after MTL damage (Squire, 2004), this work received considerable attention. Yet, it is not the only instance of impaired implicit memory following MTL damage. Impairments have been observed in priming for new verbal associations (e.g., Paller & Mayes, 1994; Shimamura & Squire, 1989; Verfaellie, Martin, Page, Parks, & Keane, 2006) and in an implicit measure of relational memory for scenes derived from eye movements in patients with hippocampal amnesia (Ryan, Althoff, Whitlow, & Cohen, 2000). However, complicating matters, a subsequent contextual-cueing study showed that patients with damage to the hippocampus but not surrounding cortical regions of the MTL exhibited near-normal contextual cueing (Manns & Squire, 2001). These studies sparked considerable debate about the neural basis of memory underlying contextual cueing.

In the current study, neuroimaging data were collected to identify brain activity involved in contextual cueing. Previous neuroimaging studies have sought to clarify the role of the MTL in contextual cueing, though it remains unclear whether the hippocampus, the surrounding MTL cortex, or both, contribute to contextual cueing. In one study with functional magnetic resonance imaging (fMRI), the hippocampus was implicated in contextual cueing, as differential hippocampal activity for repeat versus novel displays correlated with the reaction-time facilitation for repeated displays (Greene, Gross, Elsinger, & Rao, 2007). These results are consistent with fMRI studies implicating the hippocampus in other forms of complex implicit learning (Greene, Gross, Elsinger, & Rao, 2006; Harrison, Duggins, & Friston, 2006). Potential relationships between contextual cueing and neighboring MTL cortical regions were not assessed. In another study, contextual cueing was linked with MTL cortical regions but not the hippocampus, as activity in perirhinal and entorhinal cortex, but not in the hippocampus, predicted the magnitude of contextual cueing (Preston & Gabrieli, 2008).

One difficulty in drawing a strong conclusion from previous reports is that MTL regions are very small and can suffer from alignment and co-registration inaccuracies in typical fMRI analyses (Stark & Okado, 2003; Yassa & Stark, 2009). Such inaccuracies could be responsible for these mixed findings across studies. To minimize this problem, here we used a region-of-interest analysis guided by anatomical landmarks to examine MTL activity. In this way, our study may help to discern how different regions within the MTL contribute to contextual cueing.

A few studies have investigated the contributions of brain regions outside of the MTL to contextual cueing. In a study of event-related potentials (ERPs) recorded from intracranial locations, late-onset potentials in early visual areas were identified during contextual cueing, suggesting that context may modulate visual activity via an attentionally guided top-down mechanism (Olson, Chun, & Allison, 2001). Neuroimaging studies have revealed several regions exhibiting attenuated neural activity for repeated

versus novel displays that could be involved in top-down modulation, including visual areas as well as frontal, temporal, and parietal areas (Greene et al., 2007; Preston & Gabrieli, 2008). Suppressed activity for repeated stimuli has been linked with behavior for other types of implicit memory, including perceptual priming (Buckner et al., 1998; Henson, Shallice, & Dolan, 2000; Maccotta & Buckner, 2004). Although systematic relationships have been observed between contextual cueing and brain activity in the MTL, as described above, it is unknown whether such relationships hold for other brain regions that may be instrumental for implicit learning. Based on the extant findings, we expected contextual cueing to correlate with repeat-novel differences in early visual cortex, perhaps in conjunction with modulations of attentional network components such as the anterior cingulate, posterior parietal cortex, and frontal eye fields (Mesulam, 2000; Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006).

Another problem with previous contextual cueing studies is that participants could potentially acquire and retrieve explicit memories during the procedure, thus contaminating neural measures attributed to contextual cueing. Here, the role of explicit memory during contextual cueing was manipulated by directing half of the participants to memorize specific object configurations and corresponding target locations (*explicit group*). Other participants were treated in a typical fashion such that they were not informed that scenes repeated (*implicit group*). Accordingly, neuroimaging data were examined to compare brain activity as a function of the involvement of explicit memory. We hypothesized that brain activity would be modulated by the degree to which scene repetition engendered the acquisition and retrieval of explicit memories. We predicted that an explicit-learning strategy, whereby people robustly recognize repeated scenes, would engage MTL regions to a greater extent than typical procedures whereby manifestations of contextual cueing are attributed to implicit learning.

To our knowledge, instructions encouraging explicit learning have been used in only one contextual-cueing study, but participants were largely unsuccessful in forming durable explicit memories, and associated neural activity was not examined (Chun & Jiang, 2003). Whereas most previous studies employed configurations of colored letters on a monochromatic gray background, here we used intricate and memorable scenes resembling snapshots of a surrealistic landscape. Contextual cueing has been observed with complex scenes (Kunar, Flusberg, Horowitz, & Wolfe, 2007; Kunar, Flusberg, & Wolfe, 2008), but brain activity was not measured in these studies. In our paradigm, each scene contained five complex geometric objects superimposed on a colorful computer-generated landscape (Fig. 1a). These scenes arguably provide a good simulation of search facilitation outside the laboratory and are more amenable to explicit memorization than displays typically used to study contextual cueing.

2. Methods

2.1. Participants

Twenty-four right-handed, native English-speaking individuals (20–30 years old; mean age = 24.9 years) were recruited from the Northwestern University community. All participants gave informed consent prior to the experiment and received monetary compensation. Participants were randomly assigned to either the implicit group ($n = 12$) or the explicit group ($n = 12$). Data were excluded from analyses due to excessive error rates during the visual search task (greater than 2.5 *SD* above the group average) in two participants, due to poor signal quality of the fMRI data (signal-to-noise ratio greater than 2.5 *SD* below the group average) in one participant, and due to inadequate scan coverage of the MTL in one participant. The final sample included 10 participants per group.

2.2. Stimuli

Stimuli consisted of 60 scenes, each containing 5 unique, abstract objects that were created by combining geometric shapes and altering their colors and textures

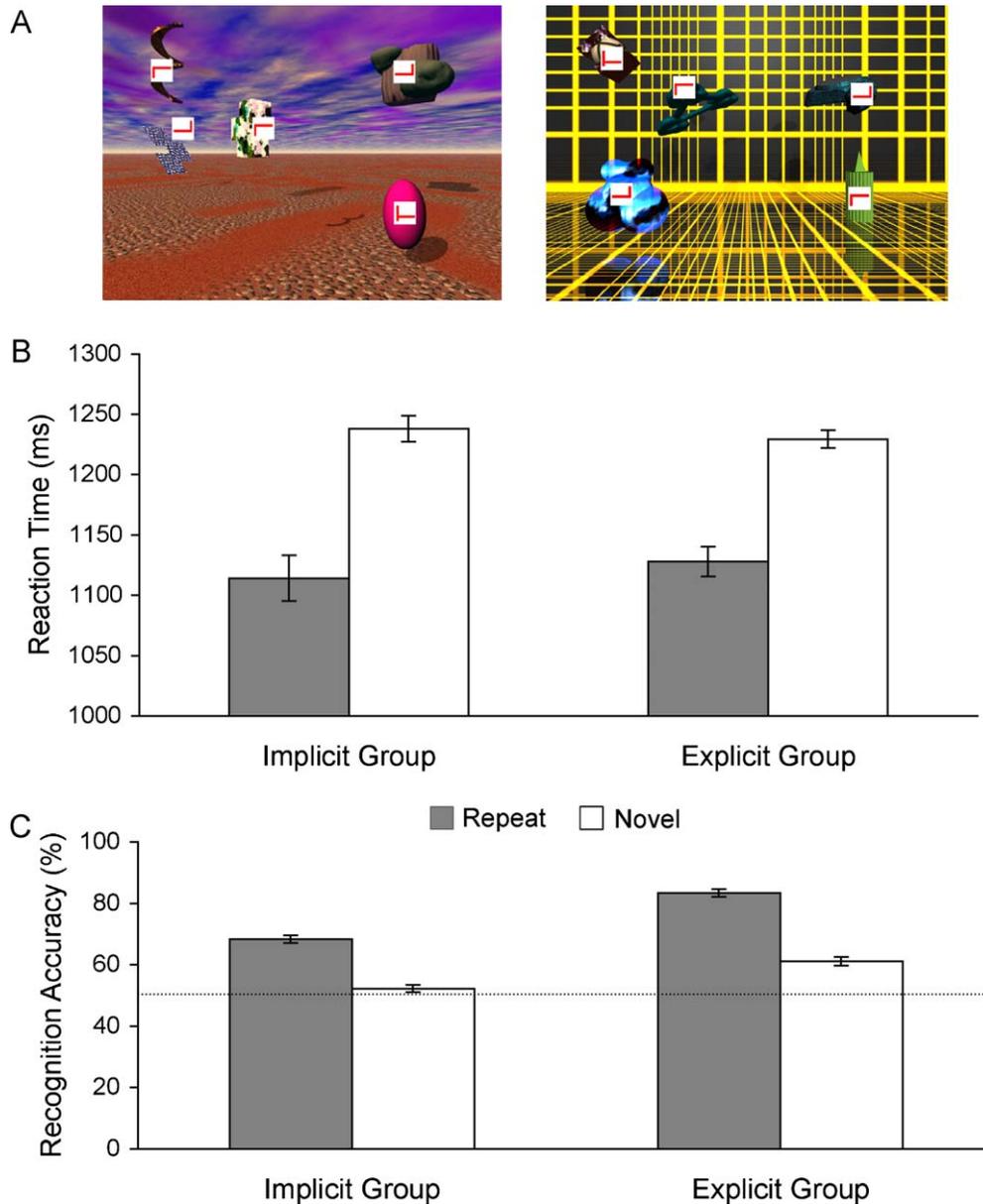


Fig. 1. (A) Two examples of scenes used in this experiment. Participants located the target (“T”) amongst the distracters (“L’s”) and then indicated its orientation (rotated left or rotated right). (B) Reaction time data plotted as a function of participant group (explicit or implicit) and scene type (novel or repeated). Bars represent standard errors of the mean. (C) Forced-choice recognition accuracy plotted as a function of scene type (repeat or novel) and participant group (implicit or explicit). Dashed line represents chance level. Bars represent standard errors of the mean.

(Fig. 1a). Each scene was divided into five areas (the four quadrants and an area surrounding the center), and one object was placed within each area. The target letter, a “T” rotated right or left by 90°, was superimposed on one randomly selected object. A distracter, an “L” rotated right or left by 90°, was superimposed on each of the remaining four objects. The base of each target T was slightly offset to increase the difficulty of target-distracter discrimination. Across all scenes, targets appeared in each area an equal number of times. Two sets of 60 scenes were created, one with the target T rotated right and the other with it rotated left.

Scenes were arranged into 9 blocks, each containing 6 novel scenes (never viewed before), and 6 repeat scenes (scenes that were presented in every block). For repeat scenes, the orientation of the target differed across blocks such that the context was predictive of the target location but not the motor response. Target orientation was equated across novel and repeat scenes for each block.

2.3. Procedure

Prior to entering the scanner, participants viewed a page containing the 6 repeat scenes to familiarize themselves with the stimuli and to practice discriminating targets from distracters. For participants in the explicit group, the experimenter also explained that this subset of scenes would repeat multiple times throughout

the study, that all aspects of these scenes except for target orientation would remain invariant, and that they should memorize stimulus features in these scenes such that search could be facilitated because they would know where to find the target whenever they recognized a repeat scene.

Once inside the scanner, participants completed a practice block to acquaint them with completing the search task in the scanner. None of the practice stimuli appeared in the actual experiment.

The task was comprised of two 6.75-min runs, termed *epoch1* and *epoch2* each containing 9 blocks of 12 visual search trials randomly intermixed with 6 odd-even judgment trials (with the constraint that the same repeat scene could not be presented on the last trial of one block and the first trial of the next block). On odd-even trials, a single digit appeared on the screen for 2000ms followed by a fixation cross for 500ms and participants indicated whether it was odd or even by pressing one of two buttons. These trials were used to estimate baseline activity levels, based on previous evidence that MTL activity during such trials is lower and less variable than during fixation viewing (Stark & Squire, 2001). On visual search trials, a scene appeared for 2000ms, followed by a fixation cross for 500ms. Participants pressed one of two buttons to indicate the orientation of the target T. Participants were instructed to respond as quickly and as accurately as possible and were discouraged from guessing.

After exiting the scanner, participants were queried about their knowledge of the experiment. This debriefing provided evidence concerning participants' awareness of the repeated scene manipulation, and about whether they used this knowledge to facilitate visual search. In particular, participants were asked to report what strategies they used to complete the task and if they were aware that scenes repeated throughout the task. If repetition was reported, they were further asked at what point in the experiment the repetition was noticed, and if the target was always in the same location in the repeated scenes.

Finally, recognition for novel and repeat scenes presented during the visual search task was tested using forced-choice procedures. For repeat scenes, participants viewed two side-by-side pages containing the 6 repeat scenes and 6 foil scenes in random order. None of the foil scenes had appeared earlier in the experiment. Participants were given 2 min to select the 6 displays that were seen previously. Next, recognition for novel scenes was tested. Participants viewed three side-by-side pages containing 9 novel scenes and 9 foil scenes in random order. The novel scenes were randomly selected from the set of 54 novel scenes used in the experiment. Participants were given 3 min to select the 9 displays that were seen previously. Recognition accuracy was measured as the percentage of scenes correctly identified as having been seen previously, yielding for each participant a percent-correct score for repeat scenes and a percent-correct score for novel scenes.

2.4. Neuroimaging

Event-related fMRI data were collected on a Siemens TRIO 3T scanner. Whole-brain gradient-recalled echo-planar images (35 axial 3.0-mm slices, 0-mm gap) were collected using the following parameters: TR = 2500 ms; echo time = 20 ms; flip angle = 80°; field of view = 22 cm; voxel size = 3.44 mm × 3.44 mm × 3 mm; for a total of 174 volumes in each functional run. The initial 6 volumes in a run occurred prior to stimulus presentation and were used for T1 stabilization. After the second functional run, 3D MP-RAGE T1-weighted scans (voxel size = .859 mm × .859 mm × 1 mm; 160 axial slices) were collected for anatomical localization.

AFNI software (Cox, 1996) was used to co-register the functional images in time and space, remove voxels that exhibited low or erratic signal, spatially smooth the images with a 7.5-mm FWHM gaussian kernel, and concatenate data from the two functional runs. For the whole-brain analysis, data were transformed into standard stereotaxic space, and deconvolution of the hemodynamic signal was achieved with a general linear model identifying four trial types – repeat-epoch1, repeat-epoch2, novel-epoch1, and novel-epoch2 – where *epoch1* refers to the first functional run and *epoch2* to the second functional run (blocks 1–9 and 10–18, respectively, following the analysis procedures used by Chun & Jiang, 1998). Eight nuisance variables were also included (6 for motion, 2 for drift). Signal was averaged from 5 to 12.5 s after stimulus onset to account for hemodynamic lag. Brain regions exhibiting consistent changes in activity were assessed across participants in a standard second-pass random-effects analysis (*t*-test). As a correction for multiple comparisons, a Monte Carlo simulation was performed in which matched noise data were subject to the same analysis path as the real data. Contiguous regions in which each voxel was found to be activated at $t > 3.5$ were found to be reliable at $p < .01$.

Region-of-interest (ROI) analyses were performed to provide sensitive tests for MTL regions that may not overlap adequately in standard group analyses. Using the high-resolution T1 scan for each participant, identifiable landmarks described by Insausti and colleagues (1998) and Reber, Wong, & Buxton (2002) guided the drawing of five MTL regions bilaterally: anterior hippocampus, posterior hippocampus, parahippocampal cortex, perirhinal cortex, and entorhinal cortex (Fig. 2a). Next, signal values from non-normalized functional data were averaged across all voxels in each ROI, yielding a single time series for the region. This technique was applied to every region in each participant, followed by deconvolution as described above.

3. Results

3.1. Behavior

In the visual search task, contextual cueing was observed in both groups as a reaction-time facilitation for repeat scenes compared to novel scenes. The accuracy of these responses to targets exceeded 94% for all trial types (Table 1). Accuracy data were subjected to a repeated-measures analysis of variance (ANOVA) with within-subjects factors of epoch (1 or 2) and condition (repeat or novel) and a between-subjects factor of group (explicit or implicit). Main effects indicated that target detection was more accurate in epoch2 than in epoch1 [$F(1,18) = 8.4, p < .01$], and more accurate for repeat than for novel scenes [$F(1,18) = 8.2, p < .05$]. However, the condition × group interaction [$F(1,18) = 4.6, p < .05$] indicated that target detection was more accurate for repeat than for novel scenes in the explicit group [$t(9) = 3.3, p < .01$] but not in the implicit group

[$t(9) = 0.6, p > .5$]. Accuracy was also high in the baseline odd-even task (96%).

Reaction time (RT) data are depicted in Fig. 1b. Formal analyses revealed reliable contextual cueing effects in both groups, as RTs to discriminate target orientation were faster for repeat scenes compared with novel scenes, with the same magnitude of contextual cueing in the two groups (implicit = 116 ms, explicit = 102 ms). RT data from correct trials were submitted to an ANOVA with within-subjects factors of epoch (1 or 2) and condition (repeat or novel) and a between-subjects factor of group (implicit or explicit). Main effects of epoch [$F(1,18) = 90.1, p < .0001$] and condition [$F(1,18) = 23.3, p < .0001$] were significant, as participants responded more quickly in epoch2 (1120 ms) than in epoch1 (1231 ms), and faster to repeat scenes (1121 ms) than to novel scenes (1230 ms). A significant epoch × condition interaction was also found [$F(1,18) = 17.3, p < .001$], as the magnitude of contextual cueing was greater in epoch2 (137 ms) than in epoch1 (80 ms). The main effect of group was not significant (p value $> .9$). Likewise, the group × condition interaction was not significant (p value $> .3$) and the group × epoch × condition interaction was not significant (p value $> .08$).

Recognition accuracy was superior in the explicit group compared to the implicit group, as expected (Fig. 1c). Percent correct scores were submitted to an ANOVA with factors of condition (repeat or novel) and group (implicit or explicit). A significant main effect of group [$F(1,18) = 11.9, p < .005$] confirmed that the explicit group had superior recognition compared with the implicit group (73% versus 60% correct, respectively). A main effect of condition [$F(1,18) = 21.9, p < .0001$] indicated that memory accuracy was higher for repeat scenes (77%) than for novel scenes (57%). The group × condition interaction was not significant ($p > .3$). Paired *t*-tests confirmed that the explicit group showed above-chance recognition (50%) for both repeat and novel scenes [$t(9) = 9.0, p < .001$, and $t(9) = 2.5, p < .05$, respectively]. The implicit group performed above chance for repeat scenes [$t(9) = 4.7, p < .01$] but not for novel scenes [$t(9) = 0.6, p > .5$].

Verbal reports during debriefing provided compelling evidence that participants in the implicit group were largely unaware of scene repetition whereas participants in the explicit group used a recollection-based strategy to complete the task. In the implicit group, five of ten individuals reported that they noticed some repetition, but they provided scarce details (e.g., “Something repeated, but I’m not sure what it was” or, “I think I saw the same object a few times”), and they all incorrectly reported that the location of the target in repeated scenes varied across trials. Furthermore, none of these five participants reported using explicit search strategies. In contrast, most participants in the explicit group offered highly detailed descriptions of specific repeated scenes and intricate search strategies for recognized scenes (e.g., “When I saw the background with green clouds, I knew to look on the pink egg in the lower left corner”). In describing their search strategies, eight of ten participants in the explicit group concluded that foreknowledge of the repetition manipulation allowed for more efficient search.

3.2. Whole-brain analyses

To reveal brain areas active during the visual search task, activity during all visual search trials (collapsed across group, condition, and epoch) was contrasted with activity during baseline trials. Bilateral engagement of large portions of the ventral and dorsal visual pathways was observed, including the fusiform gyrus, inferior temporal lobe, parahippocampal gyrus, and posterior parietal cortex (Fig. 3a).

To isolate brain regions involved in contextual cueing, activity for novel trials was subtracted from activity for repeat trials (henceforth referred to as the *contextual cueing contrast*). This

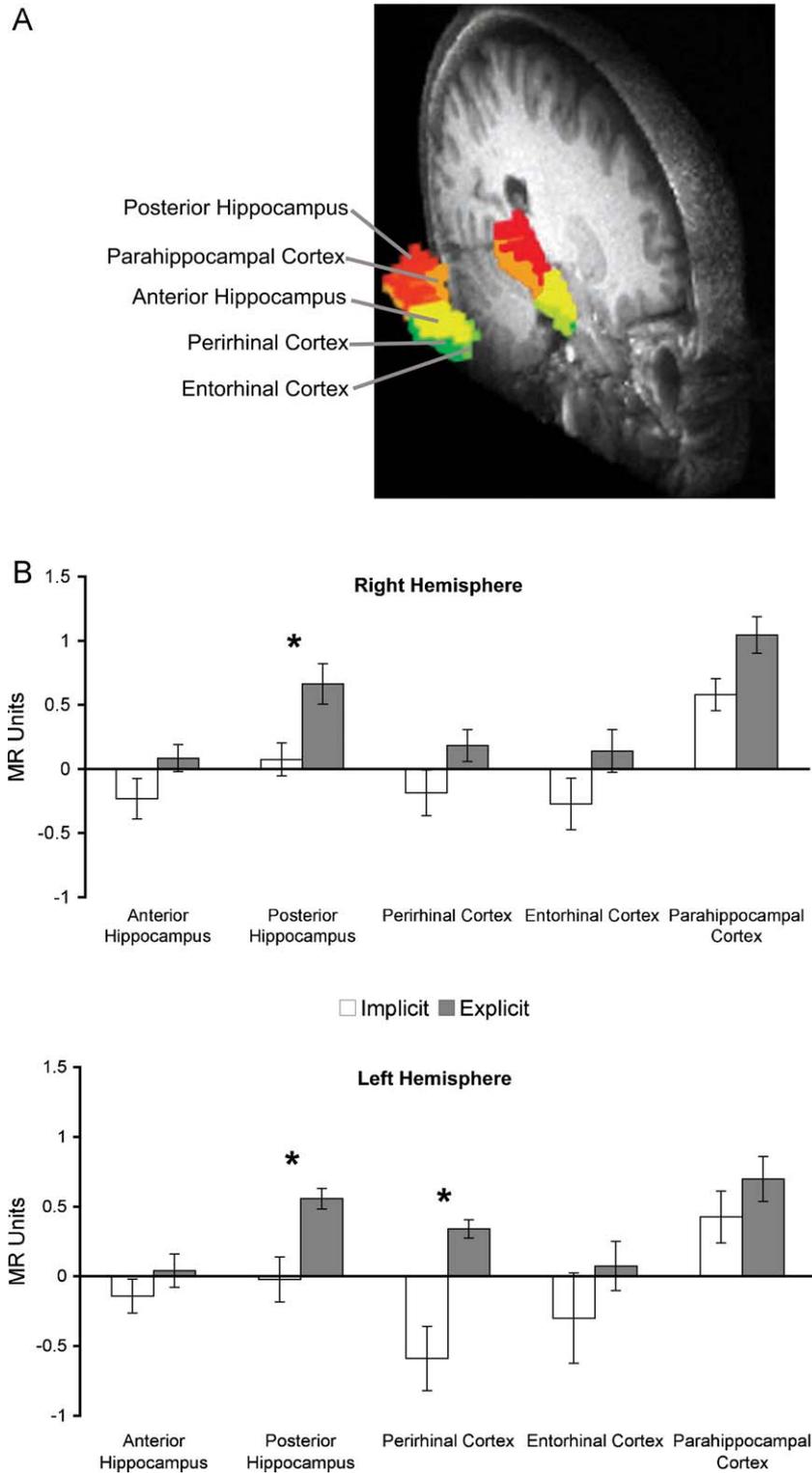


Fig. 2. (A) Anatomically defined medial temporal regions of interest superimposed on a high-resolution structural scan. The anterior hippocampus, posterior hippocampus, entorhinal cortex, perirhinal cortex, and parahippocampal cortex were defined bilaterally for each participant. (B) Neural activity during the visual search task was greater in the explicit group than the implicit group in the left and right posterior hippocampus and the left perirhinal cortex. Bars represent standard errors of the mean.

Table 1
Accuracy of responses to targets, with standard error of the mean in parentheses.

	Epoch 1		Epoch 2	
	Repeat	Novel	Repeat	Novel
Explicit group	97.0% (1.1)	94.3% (1.5)	98.3% (.64)	97.2% (.63)
Implicit group	97.2% (1.0)	97.2% (0.6)	98.7% (.56)	98.1% (.92)

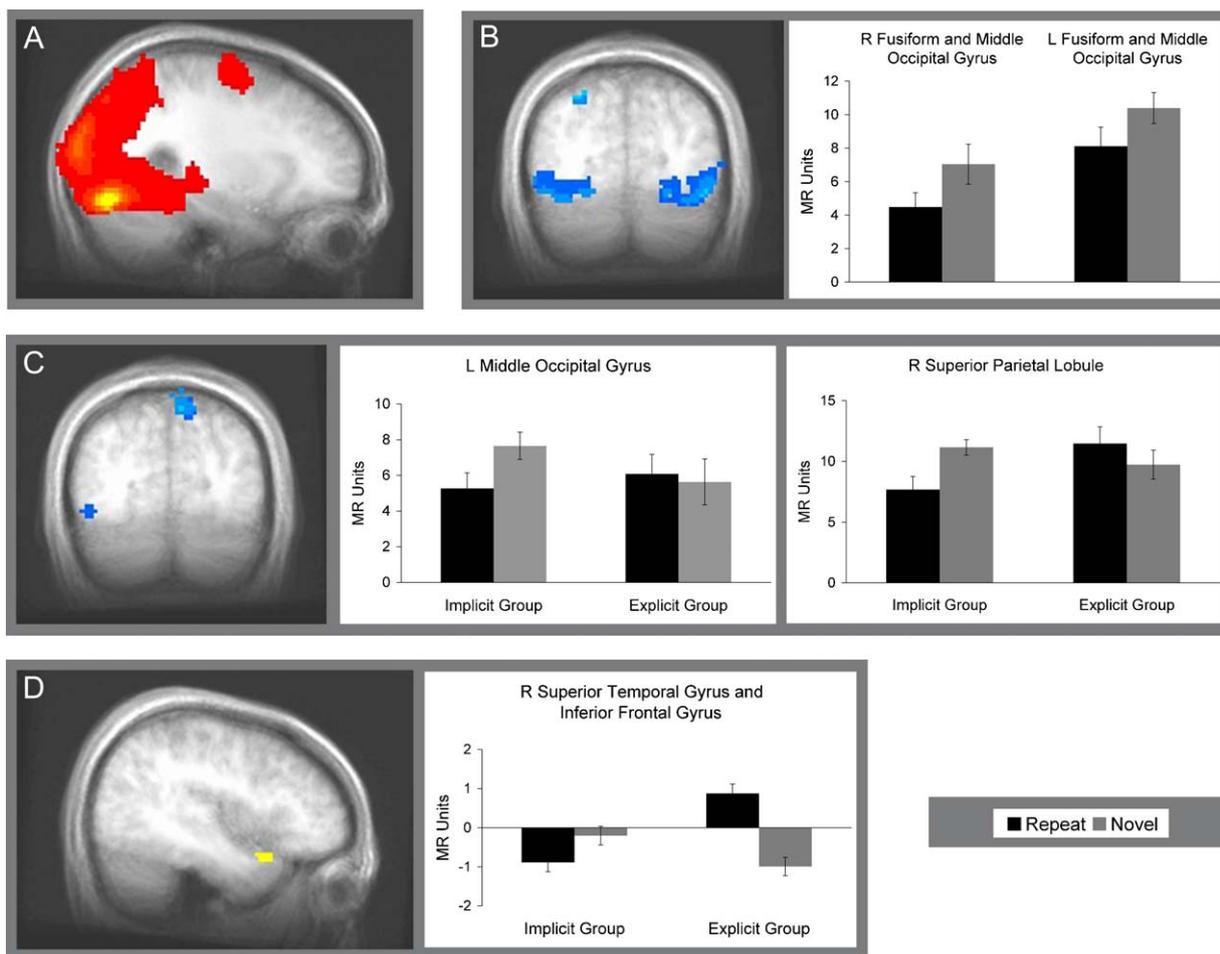


Fig. 3. Sagittal view of neural activity present when (A) all search trials were contrasted with baseline trials for all participants, and (B) repeat trials were contrasted with novel trials for all participants. (C) The contextual cueing contrast showed a larger deactivation of the right superior parietal lobule and the left middle occipital gyrus for the implicit group than the explicit group. (D) The contextual cueing contrast was larger in the right superior temporal gyrus for the explicit group in epoch 2.

contrast was associated with widespread, bilateral deactivations within the ventral visual stream (Fig. 3b), with the largest clusters of activity occurring in the right fusiform gyrus and the left middle occipital gyrus (see Table 2 for location, size, and mean activation level of all regions). Paired *t*-tests were performed to determine if the magnitude of contextual cueing effects differed across epoch within each of these regions of interest. In the left inferior parietal lobule, cueing effects were larger during epoch1 than during epoch 2 [$t(18) = 2.7, p < .05$], whereas cueing effects were larger during epoch2 than during epoch1 in the left inferior frontal gyrus [$t(18) = 4.2, p < .001$]. Epoch-dependent differences were not observed in any other region.

To determine whether the magnitude of the contextual cueing contrast was associated with memory performance, average neural activation values within each ROI identified in the contextual cueing contrast were correlated with contextual cueing

scores (computed as novel RT minus repeat RT). For this analysis, only RT and fMRI data from epoch2 were considered, as contextual cueing behavior was not robust in each participant in epoch1. A significant negative correlation was observed in both the right fusiform gyrus ($r = -.57, p = .009$) and the left middle occipital gyrus ($r = -.60, p = .006$). That is, larger deactivations of these regions were associated with larger contextual cueing scores. No significant correlations were observed between contextual cueing scores and average neural activation values in other regions of interest identified in Table 2. Furthermore, neural activation values for regions that did show correlations with contextual cueing scores did not show correlations with recognition memory for repeat or novel scenes (p values $> .3$).

Follow-up analyses examined these correlations in each group separately. Correlations between epoch2 contextual cueing and activation in the right fusiform gyrus approached significance in

Table 2
Deactivations for the contextual cueing contrast (repeat scenes versus novel scenes, both groups together).

Brain region	BA	Talairach coordinates (x,y,z)	Cluster size (ml ³)	Mean intensity
R fusiform gyrus	37	37, -65, -8	6031	3.14
L middle occipital gyrus	19	-37, -71, -4	5797	2.28
R lingual gyrus	17	26, -88, 2.4	2875	2.68
L postcentral gyrus/inferior parietal lobule	1, 40	-45, -30, 55	2078	2.83
R inferior frontal gyrus	9, 6	47, 0, 35	1750	1.64
L inferior frontal gyrus	6	-41, 2, 33	797	1.75

Note. BA = Brodmann's area, L = left, R = right.

the implicit group ($r = -.63, p = .05$) but did not reach significance in the explicit group ($r = -.48, p < .17$). Correlations between epoch2 contextual cueing and activation in the left middle occipital gyrus was significant in the explicit group ($r = -.84, p < .005$) but not in the implicit group ($r = -.47, p < .18$). Given the magnitude of these r values, the relatively small sample size when each group is considered separately ($n = 10$), and the comparable magnitude of contextual cueing in the two groups, a reasonable inference is that the significant correlations observed when both groups were considered together were not strongly driven by relationships present in only one group.

Further analyses were conducted to determine whether repeat-novel activity differences identified through the contextual cueing contrast were influenced by explicit/implicit search strategy. For these analyses, across-group t -tests were performed on the repeat-novel activity difference for each epoch. Monte Carlo simulations revealed a minimum cluster size of 200 mm^3 , where each voxel exhibited $t(18) > 3.5, p < .005$, was sufficient to achieve significance at the $p < .05$ level. In epoch1, voxel clusters in the right superior parietal lobule (516 mm^3) and left middle occipital gyrus (266 mm^3) showed significantly larger deactivations in the implicit group compared with the explicit group (Fig. 3c). In epoch2, a cluster of voxels (203 mm^3) showed greater repeat-novel activation in the right superior temporal gyrus (partially overlapping with the right inferior frontal gyrus) in the explicit group compared with the implicit group (Fig. 3d).

3.3. Medial temporal lobe

To determine MTL involvement in memory processing and modulation by learning strategy, we submitted data from each MTL region to an ANOVA with factors condition (repeat or novel), epoch (1 or 2), and group (implicit or explicit). A main effect of group was observed in the posterior hippocampus bilaterally [right, $F(1,18) = 5.06, p < .05$; left, $F(1,18) = 5.36, p < .05$] and in left perirhinal cortex [$F(1,18) = 7.34, p < .05$]. In these regions, greater activity was observed in the explicit group compared to the implicit group (Fig. 2b). Additionally, a main effect of epoch was present in left entorhinal cortex [$F(1,18) = 6.08, p < .05$], such that activations were greater in epoch1 compared with epoch2. No other main effects or interactions reached significance.

Given previous reports of contextual cueing effects in the MTL (Greene et al., 2007; Preston & Gabrieli, 2008), planned paired t -tests were performed for each MTL region comparing activity for repeat trials versus novel trials. Two significant effects were found in the explicit group. In right parahippocampal cortex, activity was greater for novel trials than for repeat trials in epoch2 [$t(9) = -2.27, p < .05$], revealing contextual cueing effects of the sort found in previous studies using implicit learning instructions. In epoch1, the explicit group showed the reverse effect in right perirhinal cortex, in that activity for repeat trials was significantly greater than for novel trials [$t(9) = -2.73, p < .05$]. No significant effects were present in the implicit group.

To determine if the magnitude of the contextual cueing effect differed across MTL regions, an ANOVA was conducted with factors region (ten MTL ROIs), epoch (1 or 2), and group (implicit or explicit). No main effects or interactions approached significance [all p values $> .1$].

The extent to which MTL activity predicted recognition memory was also examined. In the explicit group, recognition memory for repeat scenes was positively correlated with epoch2 neural activity in the right perirhinal cortex ($r = .77, p < .05$), and to a marginal degree in the left perirhinal cortex ($r = .62, p < .06$) and in the left anterior hippocampus ($r = .63, p < .06$). Furthermore, repeat scene recognition was negatively correlated with epoch2 neural activity in the left entorhinal cortex ($r = -.73, p < .05$) in the explicit group.

Novel scene recognition was not correlated with activity in any MTL region in the explicit group. In the implicit group, recognition for novel scenes was negatively correlated with epoch2 neural activity in the right perirhinal cortex ($r = -.64, p < .05$). Recognition for repeat scenes did not correlate with activity in any MTL region in the implicit group.

4. Discussion

Target detection in the visual search task was systematically speeded for repeated scenes. As in prior contextual cueing experiments, participants in the implicit group completed the task largely on the basis of implicit learning, in that they claimed to have minimal or no explicit knowledge about what repeated while performing the search task. Yet, approximately the same magnitude of contextual cueing was exhibited in both groups. That is, the response facilitation was not greater for participants who relied more strongly on explicit learning during the visual search task and who were thus able to provide precise descriptions of the repeated scenes and of their strategies for remembering those scenes. Furthermore, neuroimaging findings supported the notion that in both groups the same basic learning mechanisms were responsible for the response facilitation for repeated scenes. Regions of the ventral visual processing stream were deactivated in the contextual cueing contrast, and these deactivations were correlated with the magnitude of the advantage for repeat versus novel scenes. Whereas conscious memory retrieval was most prevalent during visual search in the explicit group, in both groups responses for repeated scenes were evidently speeded due to neural processing that is typically attributed to non-conscious memory retrieval.

Despite these similarities between the two groups, a greater reliance on explicit learning was shown to modulate neural activity during the visual search task. Participants encouraged to use an explicit learning strategy, when compared with participants in the implicit group during epoch2, showed a greater difference in activation for repeat compared with novel scenes in a region that spanned the right superior temporal gyrus and the inferior frontal gyrus. Furthermore, only the explicit group showed greater activation for repeat compared with novel scenes in the perirhinal cortex during epoch1, confirming our hypothesis that this strategy entails the recruitment of brain areas typically responsible for explicit memory. Superior scene recognition and greater MTL activity during the visual search task in the explicit compared to the implicit group corroborate this conclusion.

Contextual cueing is typically reported to occur in the absence of recognition that some displays repeated (e.g., Chun & Jiang, 1998, 2003; Greene et al., 2007; Manns & Squire, 2001; but see Preston & Gabrieli, 2008). In the current study, scene recognition at the conclusion of the experiment was above chance in the implicit group for repeated scenes, though their accuracy did not reach the level of that in the explicit group, and they did not recognize novel scenes above chance levels. The ability to recognize scenes was probably superior for our participants compared to participants in prior contextual cueing paradigms because of the vastly different types of scenes used; here the scenes included complex multicolored visual objects and exotic backgrounds, whereas most prior studies used colored letters against a monochromatic background, producing relatively uninteresting and undifferentiated scenes (e.g., Chun & Jiang, 1998). Furthermore, given that implicit memory may help guide successful forced-choice recognition judgments in some circumstances (Voss & Paller, 2009), such mechanisms may have contributed to recognition of the complex scenes used here. According to debriefing results, participants in the implicit group did not rely on explicit memory retrieval during visual search, and in general, a participant's successful memory

retrieval during forced-choice recognition testing does not imply that explicit retrieval was used during visual search.

Implicit and explicit groups were considered together to identify brain regions involved in contextual cueing. This analysis revealed deactivations in areas typically involved in visual processing and spatial attention, and similar areas have been implicated in previous studies of contextual cueing (e.g., Greene et al., 2007; Olson et al., 2001; Preston & Gabrieli, 2008). These results are consistent with two possible explanations for contextual cueing in our study. One explanation is that it reflects implicit learning regardless of the degree to which individuals additionally engage in explicit learning. The other explanation is that the brain mechanisms of implicit learning are always operative, but the behavioral improvement for repeated scenes is driven by different mechanisms depending on the extent to which explicit learning is engaged. Yet, the correlations between behavior and deactivations, particularly in right fusiform gyrus and left middle occipital gyrus, suggest that brain areas typically involved in implicit learning contributed to the behavioral improvement for repeated scenes in both groups.

Indeed, brain–behavior relationships like those found in right fusiform and left middle occipital regions have not been previously reported in contextual cueing paradigms. Deactivations in fMRI signal during memory paradigms are typically thought to reflect more fluent processing of repeated stimuli, a phenomenon referred to as repetition suppression (Henson & Rugg, 2003; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005). In the contextual cueing paradigm, deactivations in visual areas likely reflect more fluent processing of repeated visual scenes, which facilitates detection of a target within this context. This idea fits with findings from other types of implicit memory. In perceptual priming, the magnitude of priming effects is systematically related to the degree of activity reductions in visual cortex and perirhinal cortex observed for primed stimuli (Maccotta & Buckner, 2004; Voss, Hauner, & Paller, 2009), and in perceptual skill learning, the degree of skill acquisition is related to activity reductions in occipital and fusiform areas (Poldrack, Desmond, Glover, & Gabrieli, 1998; Schiltz et al., 1999; Schiltz, Bodart, Michel, & Crommelinck, 2001). These deactivations are also consistent with theories of cortical tuning, whereby changes associated with learning occur in the same cortical areas involved in the initial processing of information (Cohen, 1984; Cohen & Eichenbaum, 1993).

In addition to visual areas, deactivations were also observed in the inferior parietal lobule and inferior frontal cortex. These regions have been identified as components of an attentional network involved in perceptually guided spatial orienting, such that processing in these regions is thought to promote more efficient visual guidance of spatial attention (Mesulam, 2000; Summerfield et al., 2006). In the contextual cueing paradigm, reduced activity in these regions may reflect the guidance of attention to facilitate search through the programming and execution of learned eye movement patterns in response to repeated scenes.

To determine if an explicit search strategy modulates neural activity in the contextual cueing paradigm, neural activity patterns associated with contextual cueing were directly contrasted between the two groups. During epoch1, the implicit group showed larger repeat-novel deactivations in the left middle occipital gyrus and the right superior parietal lobule than the explicit group. As described above, deactivations in occipital and parietal areas likely reflect the operation of implicit memory mechanisms. Deactivations in the middle occipital gyrus may reflect more fluent processing of the repeated scenes, whereas deactivations in the superior parietal lobule may facilitate target detection within a scene through the deployment of spatial attention (Kastner & Ungerleider, 2000). The superior parietal lobule has been specifically implicated in shifts of attention between spatially distinct objects (Yantis et al., 2002) and therefore this region could facilitate

search for the target object within a scene. Smaller epoch1 deactivations in these regions in the explicit group than in the implicit group may reflect initial competition for processing resources between explicit and implicit memory mechanisms that was resolved later in learning (epoch2). Supporting this conjecture, behavioral cueing effects were numerically larger in the implicit compared with the explicit group during epoch1 (93 ms and 66 ms, respectively), whereas behavioral cueing effects were nearly identical in the two groups during epoch2 (138 ms and 137 ms).

During epoch2, the explicit group showed greater repeat-novel activity in a region spanning across the right superior temporal gyrus and the right inferior frontal gyrus compared with the implicit group. Greater activity in this region in the explicit group could reflect cognitive control mechanisms involved in accessing representations of visual scenes stored in long-term memory. Consistent with this suggestion, increased activity in right inferior frontal regions concomitant with increased fusiform activity has been shown during the processing of visual scenes (Kirchhoff, Wagner, Maril, & Stern, 2000), and this region has been hypothesized to mediate access to and evaluation of visuospatial stimuli (Wagner, 2002). Such circuits may become involved only when an explicit, elaborative strategy is used to process repeated stimuli. Collectively, results from brain regions showing different patterns of activity across explicit and implicit participant groups suggest that there is a greater involvement of explicit memory in contextual cueing when participants are encouraged to use their knowledge of scene repetition.

Results from the MTL ROI analysis also revealed that explicit learning modulates neural activity in this paradigm. Contextual cueing deactivations were observed in the parahippocampal cortex in the explicit but not in the implicit group, indicating that the MTL is involved in cueing when an explicit learning strategy is used. Furthermore, explicit learning of both novel and repeated scenes was associated with greater activity in the posterior hippocampus and perirhinal cortex compared with implicit learning, and neural activity during epoch 2 in the entorhinal and perirhinal cortex was related to subsequent recognition of repeated scenes with explicit learning. In contrast, recognition of novel scenes was associated with neural activity in the perirhinal cortex in the implicit group, indicating a differential involvement of MTL regions based on learning strategy.

Regarding the current debate over how different MTL regions may be involved in contextual cueing, our results are consistent with previous studies that suggest that MTL cortical regions contribute (Manns & Squire, 2001; Preston & Gabrieli, 2008), as the parahippocampal cortex showed a significant contextual cueing deactivation. Yet, cross-region comparisons failed to yield significant differences, likely due to low statistical power. Thus, future research is necessary to disentangle the relative contributions of different MTL regions to contextual cueing.

The present juxtaposition of neural activity related to varying degrees of implicit and explicit learning during repeated visual search mirrors similar observations with several other types of memory. For example, neural dissociations and possible competition between implicit versus explicit learning strategies have been observed in studies of perceptual-motor skills (Willingham, Salidis, & Gabrieli, 2002), category learning (Nomura et al., 2007; Reber, Gitelman, Parrish, & Mesulam, 2003), probabilistic classification (Poldrack et al., 2001), and habit learning (Foerde, Knowlton, & Poldrack, 2006). Multiple learning strategies are engaged in many learning situations in the laboratory, and probably also in everyday circumstances.

Collectively, the current results suggest that efficient search within repeating complex scenes can result from implicit-learning mechanisms that are evidenced by brain deactivations of a broad band of regions involved in visual perception and spatial attention.

Performing this task with a search strategy that emphasizes explicit memory for repeated scenes engages additional brain regions, including portions of the MTL, even though the neural signals of the implicit-learning mechanism remain operative. The emphasis on explicit learning makes possible the added benefit of episodic awareness of when a scene occurs repeatedly, along with facilitated recognition of those scenes when explicit memory is tested.

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