Published in final edited form as:

Psychophysiology. 2018 October ; 55(10): e13197. doi:10.1111/psyp.13197.

Neural activation and memory for natural scenes: Explicit and spontaneous retrieval

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Abstract

Stimulus repetition elicits either enhancement or suppression in neural activity, and a recent fMRI meta-analysis of repetition effects for visual stimuli (Kim, 2017) reported cross-stimulus repetition enhancement in medial and lateral parietal cortex, as well as regions of prefrontal, temporal, and posterior cingulate cortex. Repetition enhancement was assessed here for repeated and novel scenes presented in the context of either an explicit episodic recognition task or an implicit judgement task, in order to study the role of spontaneous retrieval of episodic memories. Regardless of whether episodic memory was explicitly probed or not, repetition enhancement was found in medial posterior parietal (precuneus/cuneus), lateral parietal cortex (angular gyrus) as well as in medial prefrontal cortex (frontopolar) which did not differ by task. Enhancement effects in the posterior cingulate cortex were significantly larger during explicit, compared to implicit, task, primarily due to a lack of functional activity for new scenes. Taken together, the data are consistent with an interpretation that medial and (ventral) lateral parietal cortex are associated with spontaneous episodic retrieval, whereas posterior cingulate cortical regions may reflect task or decision processes.

Keywords

repetition; retrieval; spontaneous memory; posterior parietal; fMRI

1 Introduction

Stimulus repetition can elicit either enhancement or suppression in neural activity (Grill-Spector et al. 2006; Segaert et al. 2013) and a recent fMRI meta-analysis of repetition effects for visual stimuli (e.g., words, faces, scenes; Kim, 2017) reported cross-stimulus repetition enhancement in the precuneus, posterior cingulate cortex, inferior parietal cortex, dorsolateral prefrontal cortex, and superior temporal cortex. Because of the overlap in regions showing repetition enhancement with those typically showing enhanced functional activity during episodic recognition (e.g., see reviews by Rugg and Vilberg, 2013; Gilmore

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et al. 2015; Sestieri et al., 2017; Rugg & King, 2017), these regions have been associated with processes involved in episodic memory retrieval, with the functional role of specific regions based on the pattern of enhancement effects. For example, because regions of the lateral parietal cortex (angular gyrus) show enhanced activation for both hits and false alarms, Wheeler & Buckner (2004) suggested this region is associated with perceived, rather than actual “oldness”.

In addition to explicit retrieval, in which episodic memory is deliberately probed for prior occurrence, episodic representations can also be spontaneously activated when current cues (either external or internal) contact memory in a bottom up fashion, a process called “reminding” (Hintzman, 2010, 2011), “involuntary explicit remembering” (Hall et al., 2014), involuntary autobiographical memory (Berntsen, 2010), or simply “spontaneous retrieval” (e.g., McDaniel & Einstein, 2007; Bradley et al., 2015). Spontaneous episodic retrieval is typically studied in the context of a task that does not require an explicit memory decision but rather a non-memory related judgment or categorization decision (“implicit”) which nonetheless shows facilitatory effects of repetition on performance. For words, however, prior exposure can also prompt priming effects, in which repetition facilitates performance, but which is typically accompanied by neural repetition suppression, rather than enhancement (see Gotts, Chow & Martin, 2012, for an overview). Schott and colleagues (2005) attempted to separate priming and spontaneous retrieval processes using implicit word stem completion: word stems completed with a previously studied word that were not recognized as on the study list were considered to be relatively pure instances of “primed” items, as episodic memory was not evident. The data indicated that, whereas primed words showed repetition suppression in a number of regions (see also Kim, 2017; Grill-Spector et al. 2006; Segaert et al. 2013), items that were both primed and recognized showed enhancement effects in bilateral parietal cortex, temporal cortex, and left frontal cortex.

Whereas some recently presented word stimuli can not be recognized on an immediate test, recognition performance for pictures is almost perfect (Ferrari et al., 2013; Weymar et al., 2013; “picture superiority effect”, Shepard, 1967) which suggests that neural enhancement for pictures on an implicit task will reflect spontaneous retrieval, rather than priming. Consistent with this, when pictures are simply repeated across a free viewing phase (an “implicit” task), Bradley et al. (2015) reported significant repetition enhancement effects for natural scenes in bilateral posterior parietal cortex including regions of the precuneus and cuneus, as well as lateral parietal cortex (in the region of the angular gyrus), concluding that these regions may specifically be implicated in spontaneous retrieval, as no other decision or motor response was required. In the current study, we assessed functional activity in repetition enhancement regions in a task context in which both a decision and a response was required to each picture, varying whether episodic memory retrieval was explicit (yes/no recognition test) or implicit (a person judgment task).

Previous neuroimaging studies comparing effects of repetition in explicit and implicit memory tasks have suggested that similar patterns of activation may be found, at least in some regions. Thus, Donaldson, Petersen & Buckner (2001) presented repeated and new words in either an explicit recognition task or semantic judgment task, reporting enhanced activity in regions including posterior parietal (lateral and medial) and prefrontal cortex as a

function of “retrieval success” in recognition (i.e., correct old vs new decision in the recognition task). On the other hand, these regions were also activated during the semantic task, leading them to conclude that retrieval success regions are activated even though “... subjects need not be required to actively seek to retrieve episodic information in the pursuit of current task demands” (pg. 1052). Because the task manipulation was within subject, however, prior experience making episodic memory decisions may have persisted when making semantic judgments. In the current study, the task manipulation was conducted between subjects in order to re-assess repetition enhancement in explicit recognition or judgment tasks, with those making non-episodic judgments never exposed to the explicit recognition task.

Bradley et al. (2015) found that the hedonic content of natural scenes had little effect on repetition enhancement when pictures were simply repeated in a free viewing context. On the other hand, previous data suggest that emotional (unpleasant), compared to neutral, scene recognition is associated with greater activation in inferior frontal gyrus, amygdala and precuneus during an explicit memory task (old/new contrast: Keightley et al., 2011; “remember” old/miss contrast: e.g., Dolcos et al., 2005; remember/know contrast: e.g., Sterpenich et al., 2009). Therefore, we included both emotionally evocative and neutral scenes in the current study to assess effects of both repetition and task.

Thus, for all participants, emotional and neutral scenes were initially presented (6 s) in a free viewing context without any information regarding a subsequent task. Repeated (“old”) and new scenes were then presented in the context of either an explicit recognition task or a judgment task. In the recognition task, the participant decided whether each scene had been presented during the viewing phase or not, and pressed a button (yes/no) following picture offset; in the judgment task, the participant decided whether each scene depicted one person or more than one person, and pressed a button (one/more) following stimulus offset. Although enhancement effects were expected in the precuneus and lateral parietal cortex regardless of whether retrieval was explicit or spontaneous (based on effects of mere scene repetition on functional activity, Bradley et al., 2015), it is possible that explicit retrieval prompts larger differences. Moreover, evidence of old-new differences in additional regions associated with episodic memory retrieval would suggest effects of decision-making or other task requirements. Of secondary interest were differences in repetition suppression effects and effects of hedonic content.

2 Method

2.1 Participants

Participants were 24 healthy students (9 male, 15 female; mean age: 19.1 years; two left-handed) from a General Psychology course at the University of Florida who participated for course credit or financial compensation with normal or corrected-to normal vision. All participants reported no previous experience of claustrophobia during a phone interview. The study was approved by the UF Institutional Review Board and informed consent was obtained prior to the experiment.

2.2 Materials and Procedure

Overall, 72 photographs¹ depicting people were selected from the International Affective Picture System (IAPS; Lang et al. 2008) consisting of 48 emotional pictures that included 24 unpleasant (violence), 24 pleasant (erotica), and 24 neutral (everyday contexts) pictures. Based on the IAPS ratings, picture categories differed in both rated pleasure ($F(2, 46) = 288.13, p < .0001$) and arousal ($F(2, 46) = 130.17, p < .0001$). Pleasure ratings were lower for unpleasant (mean pleasure = 2.2) compared to neutral (mean pleasure = 4.9), $t(23) = 15.34, p < .0001$ or pleasant pictures (mean pleasure = 6.3), $t(23) = 30.00, p < .0001$, and pleasure ratings were higher for pleasant than neutral pictures ($t(23) = 7.06, p < .0001$). Rated arousal was higher for unpleasant (mean arousal = 6.1) and pleasant pictures (mean arousal = 5.9) compared to neutral scenes (mean arousal = 3.5) ($t(23) = 15.05, p < .0001$ and $t(23) = 14.97, p < .0001$, respectively), and pleasant and unpleasant scenes did not differ in arousal ($t(23) = 1.16, p = .26$).

Two sets of 36 pictures were matched based on pleasure and arousal ratings as well as semantic content and the number of people portrayed in the picture (one or more). Mean ratings from the IAPS did not differ statistically between sets in terms of either pleasure ratings (unpleasant pictures: 2.1, 2.2; neutral pictures: 5.1, 4.7; pleasant pictures: 6.2, 6.4) or arousal ratings (unpleasant pictures: 6.1, 6.1; neutral pictures: 3.5, 4.5; pleasant pictures: 5.9, 5.9). All pictures were presented in grayscale and sets were matched for brightness, contrast, spatial frequency and complexity using Adobe Photoshop 7 and subjective ratings.

During encoding, one of the two picture sets was shown to approximately half of the participants in each experimental group (recognition vs. judgment). Each picture was presented for 3000 ms and followed by an intertrial interval (ITI) of 15 s or 18 s. A fixation cross was present in all picture trials and ITIs to ensure that participants fixated the center of the screen. Half of the pictures were cued by a colored screen (9 s) that signaled the upcoming content of the picture (unpleasant, neutral, or pleasant) in order to assess brain activity during anticipation (see Sege, Bradley, Weymar, & Lang, 2017). Cueing, however, did not affect later task performance (cueing: $F(1, 22) = .05, p = .83$; cueing $\times$ task: $F(1, 22) = .20, p = .67$; cueing $\times$ hedonic valence $\times$ task: $F(2, 44) = .43, p = .64$).

After encoding, participants were engaged in a brief distractor task in which textual descriptions of different events (e.g., “I receive the registered letter confirming the news that I’ve won ten million dollars”) were first read and then the participant imagined themselves as an active participant in the described event; this task lasted about 10 minutes.

Following the retention interval, 36 old pictures from initial encoding and 36 new pictures were presented. Each picture was presented for 3000 ms and followed by an intertrial interval (ITI) of 9 s or 12 s. Participants in the explicit recognition group, ($n = 12$; 6 female) were instructed to decide if each picture has been viewed earlier in the study, and, at picture

¹Scenes selected from the IAPS include: Set 1: unpleasant: 3120, 3001, 3016, 3059, 3069, 3190, 6571, 6313, 6315, 9433, 6838, 2799; neutral: 2210, 2215, 2101, 2441, 9210, 2026, 2396, 2890, 2359, 2590, 2308, 2393; pleasant 4520, 4525, 4559, 4180, 4220, 2300, 4697, 4659, 4669, 4687, 4693, 4666; Set 2: unpleasant: 3010, 3068, 3017, 3051, 3225, 3191, 3530, 6350, 6561, 9420, 6520, 9900; neutral: 2220, 2190, 2102, 2305, 2104, 2038, 2579, 2397, 2312, 2595, 2222, 2850; pleasant: 4505, 4530, 4470, 4085, 4003, 4008, 4695, 4658, 4668, 4660, 4647, 4698

offset, to press a button marked “old” or “new”. In the judgment group, participants ($n = 12$; 9 female) were instructed to decide if the picture portrayed one person or more than one person, and, at picture offset, to press a button marked “one” or “more”. Responses were made using the pointer and ring finger of the dominant hand and hand of response (e.g., old/new; one/many) was counterbalanced across participants.

After entering the scanner, each participant was instructed to view each picture while it was displayed on the monitor. No mention of a later test was made (incidental encoding).

Following a 10-minute distractor task, old and new pictures were presented in the context of either a judgment task or explicit recognition, depending upon group assignment.

2.3 Data Acquisition and Analysis

A T1-weighted anatomical volume was acquired using a Phillips 3T MR scanner. Functional volumes were 53 coronal slices (3 mm thick, 0.5 mm gap) acquired using a T2*-weighted echo planar imaging sequence with a 3000 ms TR, 30 ms TE, 72×68 acquisition matrix, and 180 mm FOV (2.5×2.5 inplane voxel resolution) resulting in a total of 335 functional volumes. Data were processed offline using the Analysis of Functional Neuroimages software (AFNI; Cox, 1996) in which structural images were aligned to functional images, and the functional data were then slice-time adjusted, motion corrected, spatially smoothed (5 mm FWHM Gaussian kernel), and expressed as percent blood oxygen level-dependent (BOLD) signal relative to the mean BOLD activity across the entire timeseries for each voxel. These data were deconvolved using a general linear regression model that estimated the amplitude of the hemodynamic response for old and new scenes and included regressors of non-interest that modeled motion residuals and baseline drift. The resulting beta values for old and new scenes for each participant were spatially normalized and resampled to a 2.5 mm isotropic voxel size.

To identify regions that showed repetition enhancement or suppression, the functional data were assessed in a repeated measures ANOVA (whole brain analysis) across participants that tested the mean beta change at peak activation ($TR = 3 + 4$) using repetition (old, new) as a repeated measure. Each volume was thresholded at $F(1, 24) = 9.34$ (uncorrected $p < .01^2$) with a cluster size criterion of 55 voxels. To avoid inflation of type II error when findings are restricted to large clusters based on statistical criteria, the cluster threshold was selected based on cluster sizes reported in previous memory retrieval studies (e.g., Hall et al., 2014). Voxels were then neuroanatomically labeled using macrolabels derived from the MNI-single subject template brain (Eickhoff et al. 2005) and transformed into Talairach space (Brett et al. 2001).

The whole-brain voxel approach identified regions reliably showing repetition enhancement, in which significant differences in which signal change were greater for old, compared to new, scenes, and included precuneus, posterior cingulate cortex, angular gyrus, and

²The regions showing effects of repetition replicate those reported in many previous studies involving repetition and/or episodic retrieval, which suggests that, based on existing data, functional activity in these regions could be assessed, even in the absence of an overall old/new effect. Nonetheless, we opted to first confirm that significant old/new effects were found before exploring differences in regions as a function of task. Because replication, rather than statistical significance, is the more convincing finding in psychological studies, utilizing the stated significance level is appropriate.

prefrontal cortex (Kim, 2013, 2017). Differences in repetition enhancement in these regions of interest were tested in a mixed ANOVA that included task (recognition, judgment) as a between-subject factor and repetition (old, new) and hedonic content (pleasant, neutral, unpleasant) as repeated measures. In the recognition task, trials with incorrect behavioral responses (false alarms/misses) were not used in analysis of the fMRI data. Relatedly, regions showing repetition suppression were identified as significant differences in which signal change was reduced for repeated, compared to new, scenes, and similarly tested in a mixed ANOVA that included task (recognition, judgment) as a between-subject factor and repetition (old, new) and hedonic content (pleasant, neutral, unpleasant) as repeated measures.

Accuracy of task performance (hits, recognition; % correct, judgments) was analyzed in a 2 (task) $\times$ 3 (hedonic content) mixed ANOVA. Because the button response was delayed until picture offset (to reduce motor related activity/artifact), reaction time is not informative and was not analyzed.

3 Results

3.1 Performance

Accuracy was high on both tasks (88 %, recognition; 98 %, judgment), but significantly better on the judgment, compared to the recognition, task ($F(1, 22) = 31.65, p < .0001$). Hedonic content of the scenes did not influence performance on either task.

3.2 Repetition Enhancement

Repetition enhancement, in which functional activity was enhanced when processing repeated, compared to new, scenes was obtained in all of the key regions listed in a recent meta-analysis (Kim, 2017) except for superior temporal cortex. Figure 1 illustrates BOLD changes when viewing old and new scenes in repetition enhancement regions overall, as well as functional activation when either explicit recognition or a judgment task was required (see also Table 1).

Heightened BOLD activity was observed bilaterally in regions of the posterior parietal cortex involving the precuneus and cuneus (BA 7/31; repetition: $F(1, 22) = 17.37, p < .0001$; Figure 1A) which did not vary as a function of task (task: $F(1, 22) < 1, p = .45$; repetition $\times$ task: $F(1, 22) = 1.95, p = .18$). Thus, in this medial parietal region, viewing old scenes was associated with greater signal change, compared to when viewing new scenes, regardless of whether the task explicitly probed episodic memory, $F(1, 11) = 10.80, p = .007$ or did not, $F(1, 11) = 6.78, p = .02$. An interaction between valence, repetition and task just reached significance ($F(2, 44) = 3.63, p = .04$) indicating that the old/new difference for unpleasant and neutral scenes was (slightly) enhanced during explicit recognition, relative to judgement task ($F(1, 22) = 5.28, p = .03$; $F(1, 22) = 3.31, p = .08$). No scene content differences were observed between unpleasant and neutral old/new effects ($F(1, 22) = 2.38, p = .14$) indicating no difference between neutral and emotionally unpleasant contents in this region. On the other hand, the old/new effect for pleasant scenes was not significant ($F(1, 22) < 1, p = .46$) for either task ($F(1, 22) = 1.38, p = .25$).

Repetition enhancement was also found for left prefrontal cortex, comprising the middle and superior frontal gyrus (BA 10; repetition: $F(1, 22) = 22.27, p < .0001$; Figure 1D), which again did not differ by task (task: $F(1, 22) < 1, p = .69$; repetition $\times$ task: $F(1, 22) = 1.53, p = .23$). Thus, activation in this prefrontal region was enhanced for repeated, compared to new, scenes both when explicit memory was explicitly probed, $F(1, 11) = 12.95, p = .004$, and when it was not, $F(1, 11) = 11.58, p = .006$. However, hedonic content did not influence activation in this region (Repetition ($F(2, 44) = 1.13, p = .32$; task ($F(2, 44) = 2.76, p = .09$; hedonic content $\times$ repetition $\times$ task, $F(2, 44) < 1, p = .69$).

A main effect of repetition, as well as an interaction of repetition and task were found in middle (BA 23) and posterior cingulate cortex (BA 29, repetition: $F(1, 22) = 19.30, p < .0001$; repetition $\times$ task: $F(1, 22) = 6.19, p < .05$; Figure 1B). Although both recognition and judgment tasks prompted significant repetition enhancement (recognition: $F(1, 11) = 13.76, p < .001$; judgment: $F(1, 11) = 6.50, p < .05$), the difference was significantly larger when episodic memory was explicitly probed, compared to when it was not (one-way ANOVA on old/new difference; $F(1, 23) = 6.19, p < .05$). Hedonic content did not interact with repetition ($F(2, 44) = 3.03, p = .07$) and task ($F(2, 44) < 1, p = .45$) (hedonic content $\times$ repetition $\times$ task: ($F(2, 44) < 1, p = .63$).

A repetition “enhancement” difference was also found in lateral parietal cortex (angular gyrus; Figure 1C), $F(1, 22) = 31.92, p < .0001$, which did not differ by task (task: $F(1, 22) < 1, p = .84$; repetition $\times$ task: $F(1, 22) = 2.74, p = .11$). This difference, however, was primarily due to a significant decrease in BOLD activity for new, compared to old, items, rather than due to enhanced BOLD activity when viewing repeated scenes. Thus, for new scenes, BOLD change indicated a significant decrease from zero, $t(23) = -5.27, p < .0001$, that was significant both during the explicit task, $t(11) = -4.55, p = .0008$, and the implicit task, $t(11) = -2.97, p = .01$, whereas BOLD changes when viewing repeated scenes did not differ from zero in either group. Hedonic content did not impact repetition ($F(2, 44) = 2.45, p = .10$) and task ($F(2, 44) = 1.70, p = .20$) (hedonic content $\times$ repetition $\times$ task: ($F(2, 44) = 1.83, p = .18$) in this analysis.

3.3 Repetition Suppression

Regions in which BOLD activity was reduced for old, compared to new, scenes, is listed in Table 1. Consistent with Kim (2017) and Bradley et al. (2015), suppression effects for these visual stimuli were found in a broad network including bilateral fusiform gyrus ($F(1, 22) = 15.55, p < .001$), inferior and middle occipital gyrus ($F(1, 22) = 14.00, p < .001$), as well as in the hippocampus ($F(1, 22) = 34.35, p < .0001$). There were no effects involving task in any of these regions (repetition $\times$ task: $F(1, 22) = 1.52, p = .23$ for fusiform gyrus; $F(1, 22) < 1, p = .41$ for occipital gyrus; $F(1, 22) = 2.90, p = .10$ for hippocampus).

Replicating previous studies (e.g., Sabatinelli et al. 2011; Bradley et al. 2015), emotional pictures, whether old or new, prompted heightened BOLD activity, compared to neutral scenes, in regions showing repetition suppression effects, including fusiform cortex, $F(2, 44) = 13.38, p < .0001$ (emotion $M = .63/1.01$, neutral $M = .51/.84$ for recognition and judgment, respectively), and inferior/middle occipital gyrus, $F(2, 44) = 29.85, p < .0001$ (emotion M

= .56/.78, neutral $M = .35/.59$ for recognition and judgment, respectively). Task and repetition did not affect emotional and neutral differences in these regions ($F < 1$).

4 Discussion

Whether repeated and novel scenes were presented in a task that explicitly probed episodic memory, or in an implicit task that required a judgment regarding the number of people in the scene, enhanced functional activity was found for old, compared to new, scenes in medial parietal cortex, including the precuneus/cuneus, and in ventral lateral parietal cortex in the region of the angular gyrus, as found during mere scene repetition (Bradley et al., 2015). Repetition enhancement effects were also apparent in posterior cingulate cortex and in anterior prefrontal cortex, regions previously showing enhanced activity when correctly recognizing old, compared to new, items on episodic memory tests (e.g., Spaniol et al., 2009; Kim, 2013). Similarities and differences in the pattern and amplitude of repetition enhancement as a function of whether episodic retrieval was explicit or spontaneous across regions sheds additional light on potential underlying mechanisms.

4.1 Medial parietal cortex

Medial posterior parietal activation, in the region of the precuneus and cuneus, was enhanced for repeated, compared to novel, items, regardless of whether episodic memory was explicitly probed or not. The location and amplitude of the enhancement effect is practically identical to the activation of medial parietal cortex found when pictures were merely repeated in the absence of a task, consistent with a hypothesis that activation in this region reflects, in part, spontaneous episodic retrieval (Bradley et al., 2015). Spontaneous or involuntary retrieval has been proposed as a common and fundamental memory process, in which cues automatically access memory representations in a bottom-up fashion. Such “reminding” (Hintzman, 2011) is ubiquitous in daily life, and is a fundamental cognitive process mediating retrospective, as well as prospective, memory (McDaniel & Einstein, 2007; Beck, Ruge, Walser, & Goschke, 2014).

Cabeza et al. (2008) postulate that a dorsal parietal region including the precuneus is specifically engaged in top-down directed retrieval, which does not contradict our findings. Despite repetition enhancement in a task that does not explicitly require episodic memory retrieval, as in the person judgment task studied here, or as found previously for mere scene repetition (Bradley et al., 2015) we also found stronger repetition enhancement for unpleasant and neutral scenes during explicit recognition. Gilmore and colleagues (2015), on the other hand, include the medial posterior parietal region in a general “parietal memory network” that operates on the basis of a bottom-up match between a retrieval cue and a memory representation. The similar pattern of medial posterior parietal enhancement found for repeated items in both the explicit and implicit tasks in the current study (and during free viewing) is consistent with a process in which cues spontaneously retrieve episodic representations in the absence of an explicit search.

4.2 Posterior cingulate cortex

Repetition enhancement effects were also significant in a region of medial posterior cortex that extended into posterior cingulate cortex, in which old, compared to new, scenes prompted greater BOLD activity, regardless of whether retrieval was explicit or not. Repetition enhancement in this region was significantly larger during explicit recognition, however, compared to the person judgment task, and this difference was primarily due to the lack of functional activity specifically for novel items during explicit recognition. Although BOLD deactivation for novel items is a major mechanism in Gilmore et al.'s (2015) parietal memory account, the region of the posterior cingulate included in that episodic network is slightly more anterior (middle cingulate cortex) than what was found here. Moreover, the level of functional activity for novel items during the explicit recognition test never fell below baseline in this region, and the novel items in the person judgment task did not show the same lack of activation, which are not completely consistent patterns of functional activation in the two tasks.

Like the precuneus, the posterior cingulate cortex is often considered part of the default mode network that is sometimes associated with internally directed cognition (Buckner et al., 2008). Based on the lack of activation specifically for new items during episodic recognition in the current study, one possibility is that activity in this region indexes an internal cognitive process that “accumulates” evidence for task decisions (e.g., Sestieri et al., 2014). If so, the data provide support for speculations that episodic decisions for new items can be made on the basis of lack of evidence of prior occurrence. Thus, whereas decisions regarding prior occurrence, as well as person judgments for repeated or novel scenes require accumulation of evidence, decisions regarding whether new items were presented previously in the experiment can be made on the basis of the lack of episodic evidence. On the other hand, this pattern of findings could simply reflect sampling error in the relatively small between-subject study reported here, and should be replicated before drawing strong conclusions. Regardless of the mechanism, posterior cingulate activity is consistently related to a network supporting episodic retrieval, and was found here during both explicit and implicit memory tasks.

4.3 Lateral parietal cortex

A role for the lateral parietal cortex in episodic retrieval has been widely acknowledged, with a distinction often made between a dorsal region, including the interparietal sulcus, and a more ventral region that includes the angular gyrus, with a variety of different region-specific processes proposed (e.g., Cabeza, Ciaramelli, & Moscovitch, 2012; Hutchinson, Uncapher & Wagner, 2009; Kuhl & Chun, 2014; Olson & Berryhill, 2009; Rugg & King, 2017; Sestieri, Shulman & Corbetta, 2017; Vilburg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). In the current study, repetition enhancement effects were confined to ventral lateral parietal cortex, including the angular gyrus, and were similar regardless of whether retrieval was explicit or spontaneous, which may be also in line with Cabeza and colleagues (2008) linking this region to bottom-up processing. As noted by Bradley et al. (2015), however, the “enhancement” difference in this region of lateral parietal cortex is primarily due to a significant decrease in BOLD activity when viewing new, compared to

old, scenes, in which functional activity in the angular gyrus region for repeated scenes often does not increase above baseline.

In fact, the majority of fMRI studies providing signal change data in the region of the angular gyrus for old, compared to new, items similarly show functional activity that generally decreases below baseline, with a smaller decrease found for old, compared to new, items, prompting a significant “enhancement” effect (e.g. Figure 3, Criss, Wheeler, & McClelland, 2013; Figure 2, Rugg & King, 2017; Figure 5, Wheeler & Buckner, 2004; Figure 4b, Sestieri et al., 2014; Figure 2, Schott et al., 2005; Figure 2, Hutchinson et al., 2009; Figure 2, Gilmore et al., 2015). As noted previously, greater deactivation (compared to baseline) for novel items is a key feature in Gilmore et al.’s (2015) parietal memory network and is purported to index stimulus novelty (within experiment). This provides a mechanism for ‘negative subsequent memory effects’ (Gilmore et al., 2015), in which items showing more deactivation in angular gyrus during encoding prompt better subsequent memory, presumably due to increased attention and more elaborative encoding for novel items.

Whereas Gilmore et al. (2015) suggest that all regions in the parietal memory network exhibit this “encoding/retrieval flip” activation pattern, significant deactivation for novel scenes was only apparent in the current study, and in many other studies, in the region of the angular gyrus. Functional activity in the other regions in Gilmore’s parietal memory network (i.e., medial parietal cortex, posterior cingulate cortex) showed less evidence of significant deactivation for novel items. Regardless of the specific mechanism, studies using multivoxel pattern classification to characterize neural networks underlying episodic retrieval consistently include the angular gyrus as key region (Kuhl & Chun 2014; Rissmann et al., 2016), which shows similar effects of repetition on both explicit and implicit episodic tasks, as well as when scenes are repeated during free viewing (Bradley et al., 2015).

4.4 Prefrontal cortex

Activation of multiple regions in lateral prefrontal cortex, often divided into a ventral (vlPFC) and dorsal (dlPFC) region, is commonly reported in studies of episodic memory (e.g., Blumenfeld & Ranganath, 2007), and Kim’s (2013) meta-analysis lists five separate regions of “dorsolateral” prefrontal cortex that prompt reliable enhancement effects across studies. The coordinates listed for largest dorsolateral cluster reported there, however, are very similar to the left prefrontal region showing enhancement in the current study, but is somewhat more ventral and medial, located in or near what is more often called frontopolar, rostral prefrontal cortex, or anterior frontal cortex, in the region of BA10 (rather than BA 9). Repetition enhancement in this region did not differ as a function of whether episodic memory was explicitly probed or not, but was not significantly activated when repeated scenes were simply presented for free viewing (Bradley et al., 2015).

Using faces, Ranganath, Johnson, & D’Esposito (2003) reported activation in the same left anterior region of prefrontal cortex when participants explicitly made recognition decisions on either immediate or delayed tests, but not during initial encoding, suggesting a task context might be critical for activating this region. In their “gateway” theory of the rostral prefrontal cortex (BA 10), Burgess, Gilbert & Dumontheil (2007) suggest that a medial region taps stimulus-oriented processing, defined by tasks or activities that require stimulus-

based decisions, whereas a more lateral region is associated with stimulus-independent processing in mind-wandering and other tasks that do not direct attention to external stimulation. Both the recognition and person judgment tasks in the current study clearly required processing external stimuli, and activated this medial prefrontal regions, which was not found when repeated scenes were simply repeated without a task during free viewing (Bradley et al., 2015), which might suggest a role for task-oriented stimulus processing in this medial prefrontal region.

4.5 Repetition Suppression

Repetition suppression effects, in which enhanced BOLD activation was found for novel, compared to repeated, scenes were found in fusiform and occipital cortex replicating many previous neuroimaging studies (e.g., Bradley et al. 2015; Schacter and Buckner, 1998; Donaldson et al. 2001; Jessen, Manka, Scheef, Schild, & Heun, 2002). Heightened activation in the anterior hippocampal region, irrespective of task, was also found for new, compared to old, scenes, which has also previously been obtained when processing novel stimuli (e.g., Bradley et al., 2015; Kim, 2013; Tulving et al. 1996; Nyberg, 2005; Jessen et al. 2002; Rugg et al. 2012).

Based on the similarity in the regions showing repetition suppression effects and those showing subsequent memory effects (Kim, 2011), Kim (2017) suggests that repetition suppression may reflect reduced elaborative encoding. That is, although regions that show better later memory performance (“subsequent memory”) are similar to those showing repetition suppression effects, it is enhanced activity in these regions that is associated with improved memory, whereas decreased functional activity (which occurs during repetition suppression) is associated with poorer later performance (“negative subsequent memory”). For scenes, Bradley et al. (2015) found repetition suppression effects only in regions that also showed enhanced BOLD activity (from baseline) during novel picture encoding, consistent with the interpretation that repetition suppression is linked to less elaborative encoding.

4.6 Hedonic scene content

Valence differences in repetition enhancement were only observed in the precuneus/cuneus region, which showed no old/new effect for pleasant contents. This lack of repetition enhancement is consistent with activation differences reported between pleasant and unpleasant contents during recognition in frontal, mesiotemporal and parietal regions (Keightley et al., 2011). Moreover, because pleasant scenes depicted erotica, feature similarity among old and new exemplars may have contributed to this null effect (Versace, Bradley & Lang, 2010). Retrieval activation was not different between unpleasant and neutral scenes, on the other hand, suggesting the difference was not mediated by emotional arousal. In each of the other repetition enhancement and suppression regions, effects of hedonic content were not significant, which is largely in line with Bradley et al. (2015) when emotional and neutral scenes are simply repeated across a free viewing phase. It is also in line with other studies, using the same short-term delays, in which neither recognition performance nor old/new recognition ERP amplitude differed as a function of hedonic scene content (e.g., Ferrari et al. 2013; Ferrari, Codispoti & Bradley, 2017; Weymar et al. 2013).

Rather, effects of emotional scene content on recognition memory performance have been reported when recognition tests are delayed (up to a year), and picture memory is no longer on the ceiling (e.g., Dolcos, LaBar & Cabeza, 2005; Weymar, Löw, Melzig, & Hamm, 2009; Weymar, Löw, & Hamm, 2011). On the other hand, some studies have reported enhanced recognition memory and neural activation for unpleasant contents (scenes and faces) on an immediate recognition test (e.g. Keightley et al., 2011) which, of course, could be related to differences in experimental features, such as stimulus set composition and task (picture ratings during encoding).

Replicating many previous studies (e.g., Bradley et al., 2015; Lang et al. 1998; Phan et al. 2004; Sabatinelli et al. 2011), enhanced BOLD activity was found when viewing emotionally arousing, compared to neutral, scenes, regardless of repetition, in occipital cortex (inferior and middle) and fusiform cortex, which was found whether viewing repeated or new scenes. Interestingly, heightened functional activity for emotional, compared to neutral, scenes is only found in regions involved in novel picture processing (Bradley et al., 2015) and which also show suppression effects as a function of repetition, consistent with a hypothesis that these effects are linked to enhanced encoding, presumably reflecting the “natural selective attention” in which motivationally relevant cues reflexively direct attention and elaborative processing (Bradley et al., 1992; Bradley, 2009; Lang & Bradley, 2010).

4.7 Summary

Regardless of whether a task explicitly probed episodic memory for natural scenes or did not, equivalent repetition enhancement effects were found in medial (precuneus/cuneus) and lateral (angular gyrus) parietal cortex that are similar to the functional differences found when repetitions are simply encountered in the context of free viewing, (Bradley et al. 2015), consistent with the hypothesis that these regions may be involved in spontaneous episodic retrieval. On the other hand, variations in the effects in posterior cingulate cortex (and medial anterior prefrontal cortex) suggest these regions may index other aspects of the task context, rather than, or perhaps, in addition to, episodic retrieval. Taken together, however, the neural regions activated in the context of an explicit and implicit episodic task for natural scenes are broadly similar to those found for repeated visual stimuli of many types (Kim, 2017), and, because scenes are well-recognized on immediate tests, provides a method for studying spontaneous retrieval which minimizes the contribution of priming.

Acknowledgments

This research was supported in part by NIMH grants MH094386 & MH098078 to Peter J. Lang and by grants from the German Research Society (Deutsche Forschungsgemeinschaft, DFG) to Mathias Weymar (WE 4801/1-1 & WE 4801/3-1).

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Figure 1.

Left panel: Waveforms illustrate the change in BOLD activity when viewing old (black) and new (gray) scenes in regions showing repetition enhancement (Old > New) in the precuneus/cuneus region (A; coordinates L: $-6 -70 25$, R: $13 -68 25$), posterior cingulate cortex (B; $0 -42 27$), angular gyrus (C; coordinates L $-35 -56 36$; R $44 -52 28$) and left prefrontal cortex (D; L $-31 52 16$). Middle panel: Significant enhancement differences (red) are overlaid on the anatomical image averaged across participants. Right panel: The mean

BOLD change for old and new items in each region is plotted separately for participants in the explicit recognition or person judgment task.

Table 1

Brain regions showing repetition enhancement and suppression effects, in which BOLD activity was greater when viewing new, compared to repeated, items, during either an explicit recognition or judgment task.

Anatomical Region	Recognition				Judgment			
	LPI coord ^a	Voxel count	Old	New	Repetition $F(1, 11) =$	Old	New	Repetition $F(1, 11) =$
<i>Enhancement Effect (Old > New)</i>								
Precuneus/Cuneus	L/R -6 13	25 25	.26 (.05)	.11 (.05)	10.80; $p = .01$	.18 (.05)	.10 (.05)	6.80; $p = .03$
Middle + Posterior Cingulate	M 0	27	.19 (.04)	-.00 (.03)	13.76; $p = .00$	.13 (.03)	.08 (.03)	6.50; $p = .03$
Prefrontal Cortex	L -31	16	.13 (.05)	-.06 (.06)	11.58; $p = .01$	.06 (.07)	-.06 (.06)	12.95; $p = .00$
Angular gyrus ^b	L/R -35 44	36 28	.04 (.05)	-.14 (.03)	16.19; $p = .00$	-.02 (.04)	-.11 (.04)	22.67; $p = .00$
<i>Suppression Effect (Old < New)</i>								
Fusiform gyrus	L/R -31 27	-17 -15	.57 (.08)	.62 (.09)	4.65; $p = .05$	.91 (.11)	0.99 (.11)	11.08; $p = .01$
Inf + Middle Occipital	L/R -39 45	-70 -63	.47 (.05)	.52 (.06)	4.11; $p = .07$	.68 (.09)	.76 (.09)	10.74; $p = .01$
Hippocampus ^c	L/R -17 19	-11 -14	-.00 (.04)	.05 (.04)	7.94; $p = .02$	.03 (.04)	.12 (.05)	31.42; $p = .00$

^aCoordinates for x, y, z are in MNI space; L: left; R: right; M= medial.

^bAlthough BOLD changes were significantly different for old and new scenes, the difference was due to a reliable decrease in BOLD for new scenes, rather than BOLD enhancement for old scenes.

^cMain part of cluster that also included voxels within parahippocampal gyrus, lentiform nucleus and amygdala