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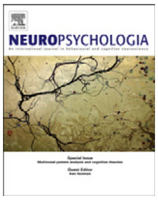

Use of explicit memory cues following parietal lobe lesions

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ABSTRACT

The putative role of the lateral parietal lobe in episodic memory has recently become a topic of considerable debate, owing primarily to its consistent activation for studied materials during functional magnetic resonance imaging studies of recognition. Here we examined the performance of patients with parietal lobe lesions using an explicit memory cueing task in which probabilistic cues (“Likely Old” or “Likely New”; 75% validity) preceded the majority of verbal recognition memory probes. Without cues, patients and control participants did not differ in accuracy. However, group differences emerged during the “Likely New” cue condition with controls responding more accurately than parietal patients when these cues were valid (preceding new materials) and trending towards less accuracy when these cues were invalid (preceding old materials). Both effects suggest insufficient integration of external cues into memory judgments on the part of the parietal patients whose cued performance largely resembled performance in the complete absence of cues. Comparison of the parietal patients to a patient group with frontal lobe lesions suggested the pattern was specific to parietal and adjacent area lesions. Overall, the data indicate that parietal lobe patients fail to appropriately incorporate external cues of novelty into recognition attributions. This finding supports a role for the lateral parietal lobe in the adaptive biasing of memory judgments through the integration of external cues and internal memory evidence. We outline the importance of such adaptive biasing through consideration of basic signal detection predictions regarding maximum possible accuracy with and without informative environmental cues.

1. Introduction

The wide range of topics covered in this Special Issue illustrates how Andrew Mayes has been a formative influence across the field of memory research. One of the areas that he has helped to develop most recently relates to the role of the parietal lobe in human memory. Soon after a symposium at the annual meeting of the Memory Disorders Research Society highlighted an intriguing discrepancy between neuroimaging and neuropsychological findings concerning the parietal lobe contribution to memory, Andrew rapidly organized a Special Section of *Neuropsychologia* on the subject (Simons & Mayes, 2008). Containing papers from many of the leading researchers in the area, the Special Section helped to lay the foundations for what has become a major focus in the field.

The reason that this topic has generated such interest is that traditionally, the parietal lobes have not been considered relevant for human memory: patients with parietal lesions often have difficulty with visuospatial attention or visually-guided action (Corbetta & Shulman, 2002; Milner & Goodale, 2008), but do not exhibit severe or even mild amnesia. However, neuroimaging methods like fMRI have revealed consistent involvement of parietal regions in healthy volunteers during performance of memory tasks (Wagner, Shannon, Kahn, & Buckner, 2005). This raises the possibility that subtle memory deficits may be present in parietal patients that are missed by standard neuropsychological testing batteries but may nonetheless impact on the patients' functioning. Consistent with this notion, patients themselves sometimes report that although they can recall previous events, their memories can lack vividness and detail.

In the last few years, a number of groups have investigated empirically whether circumscribed lesions to the parietal lobe areas identified by neuroimaging studies do actually cause a measurable impairment on tests of human memory. For example, Simons et al. (2008) reported results from two fMRI experiments in which parietal lobe activity was observed in healthy volunteers during source memory tasks that involved recollecting the context in which stimuli were previously encountered. Patients with unilateral parietal lobe lesions that overlapped closely with the

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regions activated in the healthy volunteers were then administered the same source memory tasks, exhibiting unimpaired performance (Simons et al., 2008). Similarly intact performance following unilateral parietal lesions has been reported on a number of recognition memory tasks that require participants to distinguish previously encountered "old" items from non-presented "new" items (Davidson et al., 2008; Haramati, Soroker, Dudai, & Levy, 2008). Preserved item recognition and source recollection has also been demonstrated in patients with bilateral parietal lesions, although these patients appear to exhibit reduced trial-by-trial subjective confidence in their accurate recollection (item recognition confidence was unimpaired) (Simons, Peers, Mazuz, Berryhill, & Olson, 2010). This finding might explain observations that parietal lesions are associated with reduced subjective "remember" responses on the remember/know task (Davidson et al., 2008) and diminished vividness and detail in spontaneous autobiographical narratives (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007). Evidence has also been reported that parietal lesions may be associated with diminished parietal electrophysiological activity but enhanced activity over frontal electrodes relative to controls, perhaps indicating the recruitment of frontally mediated compensatory mechanisms to support accurate memory performance (Ally, Simons, McKeever, Peers, & Budson, 2008).

Among the theories proposed to account for the neuroimaging and neuropsychological results is the *attention to memory* model which, drawing on theories of frontoparietal networks that support attention (Corbetta & Shulman, 2002), posits that the parietal lobe may support the attentional control of memory (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). According to the model, dorsal parietal regions support top-down attentional processes guided by episodic retrieval goals, whereas ventral parts of the parietal lobe subserve bottom-up attentional processes captured by retrieval output. Thus, the preserved source recollection observed following parietal lobe lesions might be attributable to intact orienting of attention towards the context details required by the task, whereas the reduced "remember" responses and diminished autobiographical detail reported might be due to impaired spontaneous capture of bottom-up attention by salient features of mnemonic representations (Cabeza et al., 2008).

The attention to memory model is supported by much neuroimaging and neuropsychological evidence, but a number of its predictions have been questioned. For example, Hutchinson, Uncapher, and Wagner (2009) highlighted that whereas recent meta-analyses have linked bottom-up attention primarily with the right temporoparietal junction (Corbetta, Patel, & Shulman, 2008), activity relating to memory retrieval is typically observed in more posterior regions in the left lateral parietal lobe (Hutchinson et al., 2009; Vilberg & Rugg, 2008). In addition, the model's suggestion that differences in "remember" response rates and autobiographical recall might be due to reduced attentional capture by behaviorally-relevant mnemonic information was tested by administering to bilateral parietal lesion patients a source memory task that included a manipulation of the behavioral relevance of the mnemonic information required for success (Simons et al., 2010). Even though this experiment included the two patients who exhibited reduced detail in their autobiographical narratives in Berryhill et al. (2007) study, the behavioral relevance manipulation did not disproportionately impair the ability of the patients to recollection source information.

Another patient study did find evidence consistent with predictions of the attention to memory model. Ciaramelli, Grady, Levine, Ween, and Moscovitch (2010) had participants study word-pairs (e.g., BUN–DEER, HOME–LIME) and then undergo a cued old-new recognition memory task in which they were presented with a studied or non-studied cue (e.g., BUN) or a baseline cue (e.g., @@@) that might predict whether a subsequent target word (e.g., DEER) was likely to be old or not. Top-down attention to memory was considered to be engaged when the cue was a studied word that might elicit attentional orienting towards the expected target. On occasions, an old target (e.g., DEER) was preceded by a studied cue that did not predict it (e.g., HOME). Such invalid cueing was considered to engage bottom-up attention to memory. Supporting the predictions of the model, recognition accuracy of patients with dorsal parietal lesions was found not to benefit from the provision of memory cues, and patients with ventral parietal lesions were reported to be slower to respond to invalidly cued targets (Ciaramelli et al., 2010).

The results reported by Ciaramelli et al. (2010) are very interesting and the task used is ingenious. However, there are a number of issues worth considering. First, the task relies on successful associative retrieval in order to cue later item recognition expectations. That is, participants must recover the second word of a paired associate pair (cued by the first word of the pair) to form an expectation about the upcoming recognition target. This is quite an indirect way of assessing top-down influences on memory, because retrieved memories would not normally be characterized as top-down attentional cues. In fact, one memory triggering retrieval of another memory would often be thought of as bottom-up cuing. In addition, it may be that participants are not using the recovered associates as cues to facilitate their recognition of the subsequent target, but instead are simply matching with respect to the lexical item recovered during the preceding paired associate retrieval phase. In other words, if BUN triggers cued recall of DEER and the subsequent recognition target is DEER, there is no need to actually assess DEER for its memory content when a participant could more easily just decide whether the target item DEER lexically matches the previously recalled associate DEER. Consistent with this alternative interpretation, Ciaramelli et al. report that invalid associative cues facilitate correct rejections compared to uncued recognition trials. This implies that participants are making their recognition decision to new items on the basis of lexical mismatch with the recovered associate, and are thus able to reject new items more easily than when uncued.

To address some of these issues, the present study takes a different approach, using a close memory analogue of the Posner visual cueing task to identify whether patients with parietal lobe lesions are intact in their ability to utilize explicit memory cues. In previous work using fMRI, O'Connor, Han, and Dobbins (2010) demonstrated a dissociation between parietal lobe activity associated with episodic retrieval and expectancy violation induced by the cueing procedure. Briefly, the explicit memory cueing task involves studying lists of words followed by a memory test that includes the explicit presentation of valid or invalid anticipatory memory cues ("Likely Old" or "Likely New") before each recognition memory probe. O'Connor et al. found that healthy volunteers show declining recognition accuracy for invalidly versus validly cued trials, which was associated with prominent differential activity in inferior parietal regions in particular. Because cue validity modulated activation even for new materials in this region, it was concluded that the contribution of the region to recognition was linked with memory expectations or their violation and not with successful retrieval of episodic content per se (O'Connor et al., 2010). The present study involves administering a version of this task to patients with parietal lobe lesions with the prediction that lesions that overlap with the areas of activity identified in healthy volunteers will be associated with atypical and perhaps inefficient cue use in patients. The task was also administered to patients with frontal lobe lesions to explore the degree to which an ability to make use of external memory cues might depend on frontoparietal networks (Corbetta & Shulman, 2002), rather than having a specific locus in lateral parietal regions.

2. Methods

2.1. Participants

2.1.1. Lesion patients

Twenty-one patients with stable, non-traumatic parietal or frontal lobe brain lesions were included. Eleven patients aged 45 to 78 years (6 female, mean age 61.6 years, SD 10.1 years) with parietal lobe lesions, and 10 patients aged 46 to 79 years (7 female, mean age 61.8 years, SD 12.4 years) with frontal lobe lesions, were recruited from the Cambridge Cognitive Neuroscience Research Panel. Each was paid UK£7.50 per hour for their participation and informed consent was obtained in a manner approved by the UK National Research Ethics Service. Patients were recruited without regard for behavioral profile, on the basis of their neuroradiological assessment indicating stable, non-traumatic brain injury principally affecting either the lateral parietal or frontal lobe. Lesion overlap diagrams for the patients with parietal and frontal lobe lesions are displayed in Fig. 1. Lesions in seven of the parietal patients appeared confined to the left hemisphere, with some bilateral involvement in the other four. In the frontal patients, three had predominantly unilateral left hemisphere lesions, five primarily right, and in two the lesions were spread across both hemispheres. The groups did not differ in overall lesion volume (mean volume 36,551 mm^3 for the parietal patients and 39,140 mm^3 for the frontal patients), t (19)=0.19, p=0.85. See Supplementary information for information about individual patient lesions, aetiology, and performance on background neuropsychological tests.

All patients and controls were administered the North American or UK versions of the National Adult Reading Test (Uttl, 2002).

2.1.2. Controls

Thirty-three healthy control participants were included. Fifteen individuals aged 43 to 77 years (9 female, mean age 61.4 years, SD 8.4 years) were recruited from the Washington University older adults volunteer pool. Each was paid U$10 per hour for their participation and informed consent was obtained in accordance with the institutional review board of the university. Eighteen individuals aged 41 to 71 years (9 female, mean age 59.2 years, SD 8.4 years) were recruited from the healthy volunteer panel at the MRC Cognition and Brain Sciences Unit, Cambridge. Each was paid UK£7.50 per hour for their participation and informed consent was obtained in a manner approved by the UK National Research Ethics Service. The patient and control groups were closely matched on age (parietal 61.64 (10.12), frontal 61.09 (12.02), control 60.21 (8.34); $F<1$) and IQ estimated via NAART (parietal 115.18 (9.61), frontal 119.10 (4.51), control 115.24 (7.35); F(2, 51)=1.10, p=.341). The parietal and control groups comprised 45% and 48% males, respectively, (p=.863). The frontal patient group was 27% male, but this proportion did not significantly differ from the parietal group (p=.379) or the control group (p=.215).

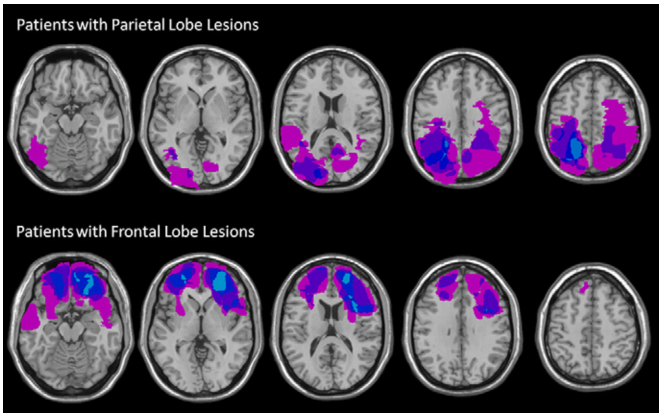

Fig. 1. Diagrams displaying areas of lesion overlap of the patients with parietal and frontal lobe lesions, manually traced on a structural MRI scan of their brain, normalized to MNI space, and displayed on axial slices of a canonical structural image.

2.2. Materials

A total of 150 words were randomly drawn for each subject from a pool of 1216 words. From this sample, 100 items were studied (50 deeply and 50 shallowly encoded) and 50 items reserved for new items during the subsequent recognition test. The items in the pool had on average 7.09 letters, 2.34 syllables, and a Kucera–Francis corpus frequency of 8.85.

2.3. Procedures

During the study phase, two incidental encoding tasks were administered. For half the items participants performed an “Alphabetical order?” shallow encoding task in which they indicated whether the first and last letters of each word were in alphabetical order. For the other half of the items they semantically rated the words using a “Concrete or Abstract?” deep encoding task. This levels of processing manipulation was randomly intermixed during the study phase, and the task to be performed on each trial was indicated via a prompt appearing 500 ms prior to the word onset positioned on the top of the screen (“Alphabetical order?” versus “Concrete or Abstract?”). Responses were self-paced and a blank screen was displayed for 500 ms between study trials.

Immediately after the study phase, the 100 old items were randomly intermixed with 50 new items and presented serially for a recognition judgment using a six-point confidence rating scale (very confident old, somewhat confident old, guessing old, guessing new, somewhat confident new, and very confident new). Participants used the “1” to “6” keys on the computer keyboard to rate their confidence. The key assignment was counterbalanced between subjects (i.e., for about half of the participants the “1” key stood for very confident old and the 6 to very confident new, whereas for the other half the opposite key assignment was used). Responses were self-paced. For some trials, the test probe was preceded by a cue that probabilistically forecast the memory status of the upcoming probe (“Likely Old” or “Likely New”). Each cue appeared one second before its associated test probe. Seventy five percent of the cues were valid, while 25% were invalid. Thus, a total of 120 items were cued (40 deep, 40 shallow, 40 new) with the remaining items uncued. Thus for each item type (deep, shallow, new), 30 items were validly cued, 10 invalidly cued, and 10 were not cued. In order to emphasize perceived cue utility, participants were told that 80% of the cues were valid. The order of the items and cueing type was random.

3. Results

Because our main focus was examining the effect of parietal lobe lesions on the use of explicit memory cues, we concentrate primarily on comparisons between the parietal patients and controls. Following this, the lesion specificity of any observed dissociations is tested by comparing the performance of parietal patients directly to that of patients suffering from frontal lobe lesions. Before analyzing the data, it is important to discuss the specific pattern of performance that is expected if subjects optimally use external cues under the theory of signal detection, since this helps motivate the ANCOVA regression analyses used below. Under signal detection theory, observers respond to external recommendations by shifting a decision criterion along an internal evidence dimension comprised of normally distributed evidence values for studied and new materials (Fig. 2). Thus, a subject given a “Likely Old” cue will shift the criterion markedly to the left (from the neutral point midway between the distributions) as he or she accommodates the expectation that the upcoming item is likely to be old. Fig. 2 illustrates the statistically ideal locations for these shifted decision criteria for an observer whose accuracy, d', is 1.0. Focusing on the “Likely Old” cue condition it is clear that when this cue is valid then items from the old distribution will be endorsed very accurately. In fact, 95% of these items will fall to the right of the criterion leading to a correct response. In the case of old items occurring during the “Likely New” cue, an invalidly cued trial, a considerably smaller proportion, only 27% will fall to the right of the shifted criterion because the expectation has been violated. However, invalid trials are the minority because the cues are 75% valid across the entire test, thus the effective hit rate of the observer under the two cues is not the simply average of .95 and .27, but instead the weighted average, $.75\times.95+25\times.27$, or 78%. This is 9% higher than the maximum possible without environmental cues and the same effects occur for correct rejections. Thus observers are expected to shift their criterion given generally valid cueing because it noticeably increases their total accuracy of judgment across a wide range of baseline skills and external cue validities (see Selmeczy and Dobbins (in press) for further detail).

Fig. 3 shows the expected relationships between baseline and cued performance across a group of observers with different discrimination indices (d') if they are using an external cue that is 75% valid, and if they are capable of placing the criterion in the statistically ideal location during the three cue conditions (baseline (no cue), "Likely Old", and "Likely New"). The plot relates baseline performance (percentage of correct responses) in the absence of cues to performance in the presence of valid cues (circles) and invalid cues (squares). The predictions are equivalent for hits and correct rejections because the assumed evidence distributions are symmetric. In the case of valid cues performance falls well above the main diagonal simply indicating that validly cued correct percentages are more accurate than without cues. Additionally, the rates are extremely high, near ceiling and so the relationship between validly cued and baseline performance is fairly flat. In the case of invalid cues performance falls below the main diagonal indicating that cued performance is lower than uncued performance reflecting the misleading nature of the cues. However, performance is not at floor during cueing and instead there is a clear positive relationship between baseline and performance during invalid cueing.

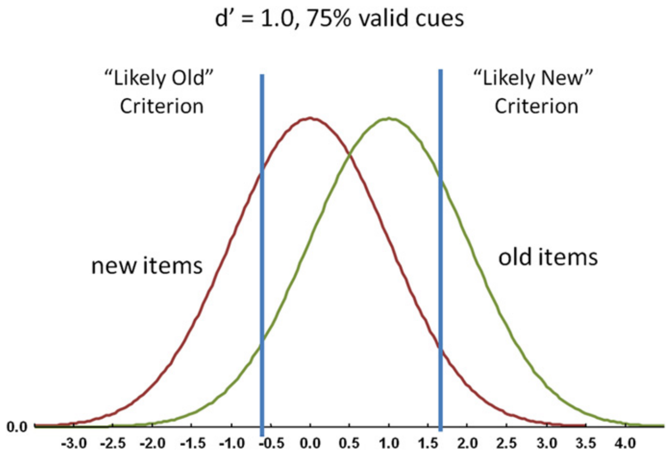

Fig. 2. Signal detection model of optimal criterion placement during explicit memory cueing task. The figure demonstrates the optimal criterion placement for an observer with a d' of 1 under the current cueing manipulation. In the absence of cues the criterion should be placed at the intersection of the distributions. In contrast, the two criteria show the ideal placement under "Likely Old" and "Likely New" cues.

Real observers however demonstrate considerable noise in their criterion placement and so panel (b) illustrates the predictions for observers with moderately noisy criterion placement. The basic patterns remain. Finally, panel (c) shows the expected performance for observers who are unable or unwilling to use the cues to improve performance. During both valid and invalidly cued trials performance falls along the main diagonal. This reflects the fact that baseline and cued performance should closely track one another if the cues are not being integrated into recognition decisions.

In summary, the signal detection model predicts that observers who cannot incorporate cues will fall largely along the main diagonal when one compares their baseline to their cued performance, reflecting the fact that their recognition judgments are insensitive to the external cues. In other words, the best predictor of cued performance in an individual who is insensitive to

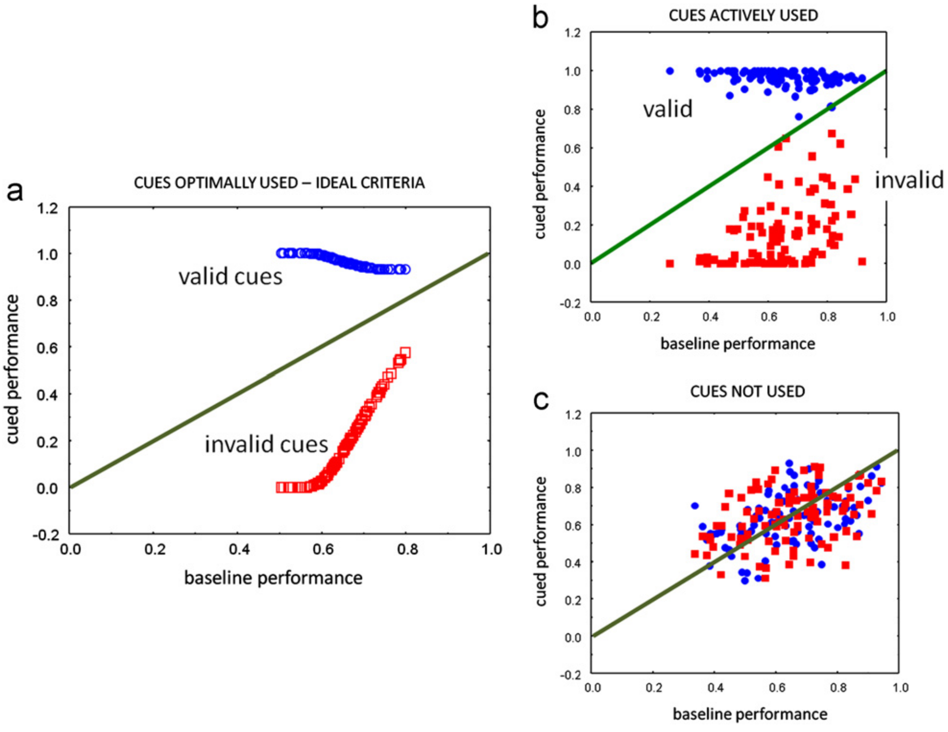

Fig. 3. Accuracy predictions under the signal detection model of adaptive criterion shifts in response to external cues with a 75% validity. Panel (a) shows the accuracy relationships between cued and baseline performance across observes with a range of d' values, assuming observers place all criteria ideally. Circles illustrate performance under valid cues (both hits and correct rejections) whereas squares illustrate performance under invalid cues (both hits and correct rejections). Panel (b) demonstrates the model's predictions if observers have moderate noise in their criterion placement across the three cueing conditions (baseline, valid, and invalid). Panel (c) illustrates the predictions for observers who are insensitive to the external cues. Here performance during valid and invalid cueing is similar to baseline, demonstrating insensitivity to the external cues.

external cues, is their baseline recognition performance. This should occur regardless of whether one examines validly or invalidly cued trials because in neither case do the participants incorporate the cues into their judgments. Observers who optimally use the cues will instead show two effects. Their validly cued response rates will be above the main diagonal and the relationship between baseline and cued performance will be fairly flat because of near ceiling performance during validly cued trials. In contrast, their invalidly cued performance will fall below the main diagonal, but will not be at floor. Instead there should be a positive relationship between baseline and invalidly cued performance. Thus when comparing a group expected to not use the cues, with one expected to use them optimally, the statistical model should ideally jointly asses a) whether there is an overall difference in the level of cued performance across the groups (a main effect of group when predicting cued performance) and (b) whether or not the groups have fundamentally different slopes relating baseline to cued performance which could potentially occur when comparing valid cueing performance across the groups. These tests are possible using ANCOVA regression models that can jointly test both of these effects.

3.1. Accuracy

Descriptive statistics for accuracy, confidence and reaction time are listed in Table 1. Because accuracy for deeply processed materials was uniformly high (limiting the utility of external cues), we analyzed only the hit rates for shallowly encoded items and the correct rejections rates. Beginning with validly cued hits (“Likely Old” cue), Fig. 4 suggests similar performance for parietal patients and controls (circles Fig. 4). This was confirmed with an ANCOVA model that predicted validly cued hits using variables of baseline hit rates (baseline), group (parietal patients[1] versus controls[0]), and the interaction of baseline and group (Table 2). The latter variable tests whether the relationship between baseline and cued performance reliably differs across the parietal

Table 1
Descriptive statistics for patients and controls.

		Accuracy		Confidence		Reaction time	
		Control	Parietal	Control	Parietal	Control	Parietal
Hits	Baseline	0.42(0.24)	0.50(0.26)	2.13(0.56)	2.33(0.54)	3.88(1.64)	4.10(1.46)
	LO-cue	0.60(0.24)	0.67(0.22)	2.04(0.43)	2.22(0.50)	4.19(1.87)	4.27(1.38)
	LN-cue	0.27(0.22)	0.43(0.33)	2.14(0.70)	2.28(0.60)	4.09(2.07)	4.61(2.10)
CR	baseline	0.84(0.19)	0.78(0.28)	2.33(0.65)	2.53(0.34)	3.33(1.43)	4.10(2.31)
	LO-cue	0.65(0.28)	0.63(0.28)	2.15(0.70)	2.03(0.66)	4.00(1.78)	5.50(2.18)
	LN-cue	0.94(0.07)	0.78(0.31)	2.40(0.51)	2.33(0.42)	3.11(1.08)	4.50(1.62)

Note: Means with standard deviations in parentheses.

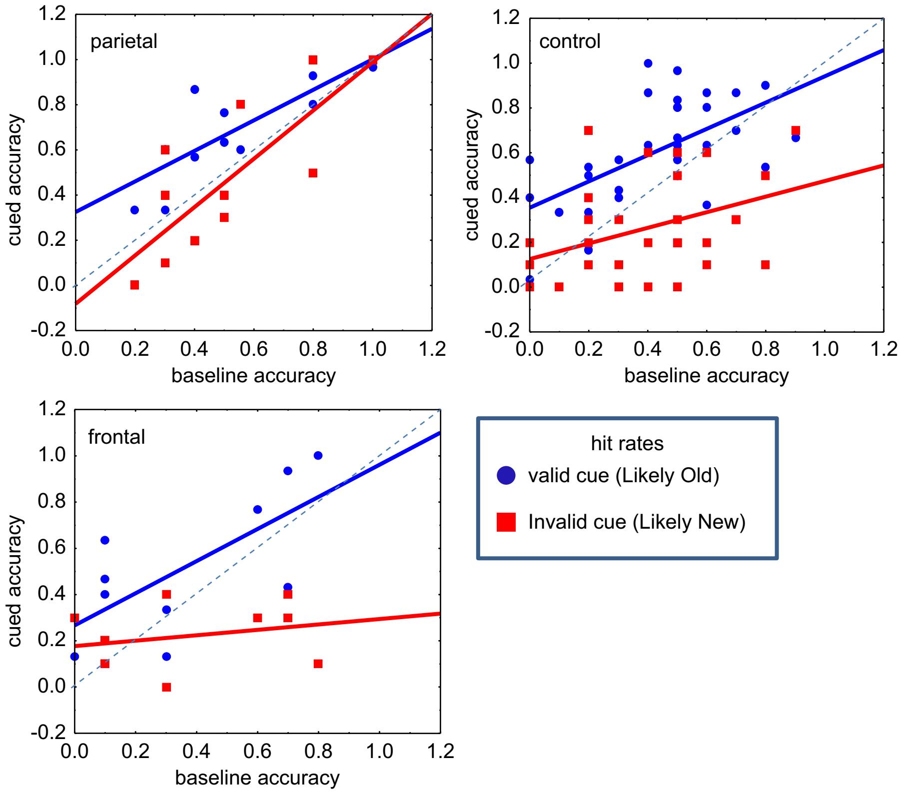

Fig. 4. Empirical data linking baseline and cued performance for parietal patients, control participants, and frontal lobe patients during correct detection of old materials-hits. For these materials, “Likely Old” cues are valid whereas “Likely New” cues are invalid. Dotted lines indicate anticipated relation between cued and baseline performance if individuals are insensitive to cues. Solid blue lines demonstrate relationship between baseline and validly cued performance. Solid red lines demonstrate relationship between baseline and invalidly cued performance.

Table 2
Full ANCOVA model, parietal patients vs. controls.

	Cue Cond.	IV	**B**	**SE of B**	***t*(40)**	***p*-level**
Hit rates						
Valid	Likely Old	**Baseline**	**0.586**	**0.137**	**4.272**	**0.000**
		Group	−0.025	0.143	−0.174	0.863
		$b \times g$	0.099	0.266	0.372	0.712
Invalid	Likely New	**Baseline**	**0.349**	**0.151**	**2.303**	**0.027**
		Group	−0.220	0.157	−1.400	0.169
		$\boldsymbol{b \times g}$	**0.697**	**0.293**	**2.375**	**0.022**
			B	**SE of B**	***t*(40)**	**p-level**
Correct rejection rates						
Invalid	Likely Old	**Baseline**	**0.885**	**0.218**	**4.055**	**0.000**
		Group	0.202	0.283	0.713	0.480
		$b \times g$	−0.225	0.337	−0.668	0.508
Valid	Likely New	Baseline	0.120	0.085	1.406	0.168
		Group	**−0.831**	**0.111**	**−7.500**	**0.000**
		$\boldsymbol{b \times g}$	**0.862**	**0.132**	**6.545**	**0.000**

Note: Significant predictors are in bold. Baseline = uncued performance, group = parietal (1) or control (0), $b \times g$ = interaction of group and baseline performance when predicting cued performance.

patients and controls. Consistent with the plots, there was a significant relationship between baseline and cued performance, however cued accuracy did not differ across groups, nor did the relationship between baseline and cued performance differ across groups. This overall pattern suggests that the groups are using the cues similarly, although clearly not optimally given that the rates were not near ceiling (c.f. Fig. 3b). Nonetheless, both groups benefited from the cues because the performance during cued trials was higher than that during baseline for each (Parietal: $t(10)=3.18$, $p=.003$; Control: $t(32)=4.81$, $p<.001$). These results are the first piece of evidence that "Likely Old" cues similarly influenced performance of the two groups. When valid, these cues similarly benefited the performance of the two groups.

For invalidly cued hit rates ("Likely New" cue), Fig. 4 instead suggests potential differences across parietal and control participants (squares). Patient performance falls primarily along the main diagonal suggesting that they are responding no differently when invalidly cued versus when uncued. In contrast the performance of control participants appears to be reduced under the invalid cues because the slope of the relationship between uncued and cued performance is fairly shallow and below that of the main diagonal. Consistent with this the full ANCOVA model demonstrated a group × baseline interaction demonstrating that the slope relating baseline and invalidly cued performance was significantly more positive in the patients than controls (Table 2). These findings coupled with Fig. 4 support the conclusion that the patients were unaffected by invalid "Likely New" cues whereas control group performance was somewhat worse. This was further confirmed with separate *t*-tests contrasting baseline and invalidly cued performance, which demonstrated no reduction for parietal patients ($t(10)=1.23$, $p=.245$) but a sizeable effect for controls ($t(32)=3.29$, $p=.002$). These results suggest that only control subjects were adversely affected by the "Likely New" cue when it preceded old materials. It is important to note that the above findings anticipate that group differences should not be present for the "Likely Old" cue, but should be present for the "Likely New" cue when next considering response rates to new materials below. This is because subjects cannot categorically choose, as a function of material type (old or new), when to rely upon external cues. Because the control group is clearly influenced by the "Likely New" cue when responding to old materials (a cost) then they should also be heavily influenced by the same cues when they precede new materials (a benefit). In contrast, because the parietal group demonstrates no discernible response to the "Likely New" cue when it precedes old materials then it is expected that this same lack of influence will be evidenced when one considers their performance to the "Likely New" cue when it precedes new materials. As we show below, these expectations were confirmed and converge in demonstrating that the parietal patients do not appropriately integrate the "Likely New" cues into their memory judgments.

For invalidly cued correct rejections ("Likely Old" cues) Fig. 5 (squares) does not suggest strong differences across parietal patients and controls. Both groups evidence a similar slope relating baseline and cued performance and the cases fall marginally below the main diagonal for the parietal patients and clearly so for the controls. This was confirmed via regression which did not demonstrate a group difference or an interaction between group and baseline predictors (Table 2). Post hoc *t*-tests confirmed that both parietal patients and controls were significantly worse during invalid "Likely Old" cues versus baseline (parietal: $t(10)=2.28$, $p=.046$; $t(32)=4.69$, $p<.001$).

Finally, for validly cued correct rejections ("Likely New" cues) Fig. 5 (circles) suggests a prominent dissociation across the groups. The performance of parietal patients appears unaffected by the cues, falling along the main diagonal relating baseline to cued performance. This matches the pattern observed when these patients encountered "Likely New" cues preceding old materials (Fig. 4) demonstrated above. In contrast, the control participants appear to perform near ceiling suggesting optimal or near optimal cue use. The regression model confirmed these impressions, yielding a significant group effect demonstrating significantly worse cued performance for the patients, and more importantly a significant group by baseline interaction, demonstrating a significantly tighter coupling between baseline and cued performance for the patients. Post hoc t-tests confirmed that patient performance was similar during baseline and cued trials ($t<1$) whereas it was significantly improved during cued versus baseline trials for control participants ($t(32)=3.25$, $p=.003$).

Overall, the accuracy data demonstrate that parietal patients and controls differed considerably in their use of the external cues, but only during the "Likely New" cue condition. During this condition, the performance of controls was largely in line with the predictions of the signal detection model with performance being nearly at ceiling during trials in which these cues were valid, and being hampered but not at floor when these cues were invalid. In

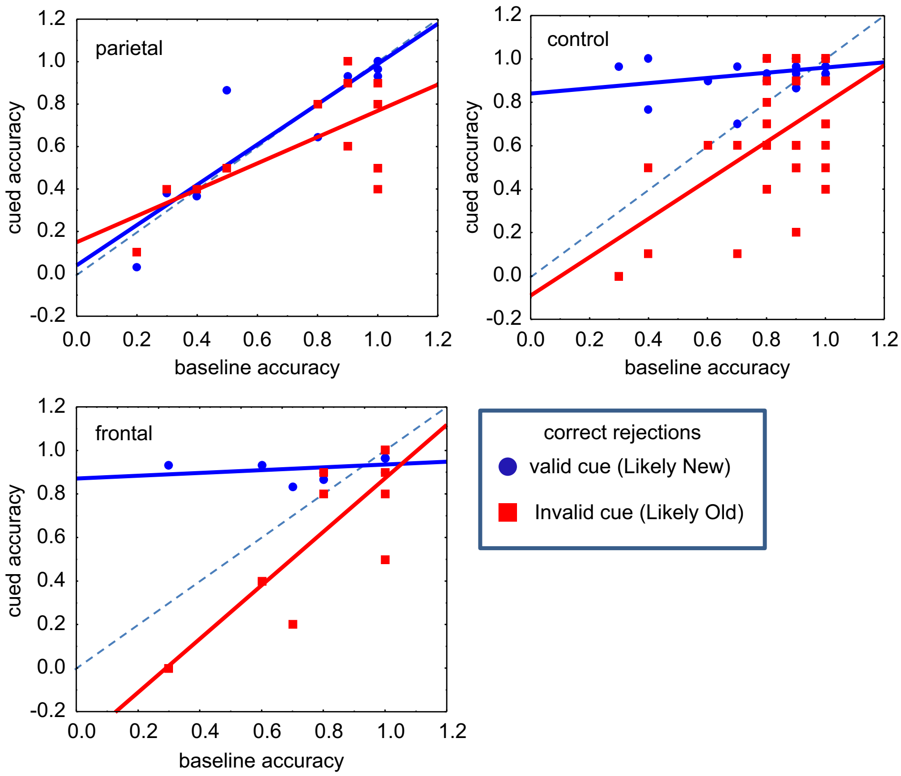

Fig. 5. Empirical data linking baseline and cued performance for parietal patients, control participants, and frontal lobe patients during correct rejection of new materials. For these materials, "Likely Old" cues are invalid whereas "Likely New" cues are valid. Dotted lines indicate anticipated relation between cued and baseline performance if individuals are insensitive to cues. Solid blue lines demonstrate relationship between baseline and validly cued performance. Solid red lines demonstrate relationship between baseline and invalidly cued performance.

contrast, the performance of parietal patients closely approximated baseline performance in both instances, demonstrating that they were incapable of incorporating these cues or unwilling to do so. In the case of the "Likely Old" cue condition there were no notable differences between the groups, however, neither group appears to have used the cues as optimally as possible. Although, the results suggest a clear group dissociation in the use of the "Likely New" cues the differences were more statistically robust when these cues were valid ("Likely New" preceding new materials) than when invalid ("Likely New" preceding old materials). This likely reflects the fact that the invalid condition is necessarily based on much smaller trial counts than the valid condition given that the external cues were 75% accurate. Thus the estimates of each subject during invalidly cued trials are expected to be noisier than the estimates obtained during validly cued trials. Nonetheless, it is important to note that these findings provide convergent evidence that the parietal patients and control subjects process the external cues differently, with only the latter integrating them in a manner expected based on an optimal decision model.

3.2. *Examining lesion specificity*

Although parietal lobe patients were the main focus of the manuscript, the paradigm was also administered to patients suffering frontal lobe lesions, providing a critical test of the specificity of the observed dissociation. We examined the lesion specificity of "Likely New" cue processing dissociation by contrasting the performance of parietal lobe and frontal lobe patients during valid and invalid "Likely New" trials to verify whether the pattern seen when contrasting the parietal patients to controls replicated when comparing the parietal patients to frontal patients. For invalid "Likely New" cues (Fig. 4) the regression suggested a trend towards higher parietal patient performance during invalid cueing, and replicating the finding with controls, there was a significantly steeper slope relating baseline to cued performance in the parietal patients (viz., a group by baseline interaction) (Table 3). Thus as with the controls, the frontal lobe patients were more adversely affected by the invalid "Likely New" cues than the parietal patients because the slope relating their baseline and cued performance was depressed compared to the parietal patients. Turning to valid "Likely New" trials (Fig. 5 circles) the parietal patients were significantly less accurate than the frontal lobe patients as a group, and there was a group by baseline interaction demonstrating a significantly shallower slope relating baseline and cued performance for the frontal lobe patents who where performing near ceiling when cued (Table 3).

The two key findings observed when contrasting parietal patients to controls replicated when they were compared to a frontal lesion group. In the case of invalid "Likely New" cues to old materials, the frontal lobe patients demonstrated a significantly shallower slope relating baseline and cued performance compared to the parietal patients, a pattern suggesting a more deleterious effect of the invalid cues in the former. In the case of valid "Likely New" cues, there were both group differences and differences in the interaction of group and baseline measures when predicting validly cued correct rejection rates. The frontal lobe patients had reliably higher cued performance and this benefit flattened the relationship between baseline and cued performance yielding the significant interaction Table 4.

3.3. *Interim summary of results*

Overall, the accuracy data demonstrate a dissociation of parietal patients from controls and frontal lobe patients in the processing of "Likely New" cues. This dissociation is modest when

Table 3
Full ANCOVA model, parietal vs. frontal patients.

	Cue Cond.	IV	B	SE of B	*t*(17)	p-level
Hit rates						
	Likely Old	**Baseline**	**0.695**	**0.207**	**3.362**	**0.004**
		Group	0.064	0.161	0.396	0.697
		b × *g*	−0.010	0.310	−0.032	0.975
	Likely New	Baseline	0.117	0.198	0.592	0.562
		Group	−0.272	0.154	−1.771	0.094
		b* × *g	**0.929**	**0.296**	**3.136**	**0.006**
Correct rejection rates						
			B	**SE of B**	***t*(17)**	**p-level**
	Likely Old	**Baseline**	**1.230**	**0.306**	**4.018**	**0.001**
		Group	0.470	0.328	1.433	0.170
		b × *g*	−0.570	0.390	−1.462	0.162
	Likely New	Baseline	0.065	0.159	0.407	0.689
		Group	**−0.862**	**0.170**	**−5.069**	**0.000**
		b* × *g	**0.917**	**0.202**	**4.540**	**0.000**

Note: Significant predictors are in bold. Baseline = uncued performance, group = parietal (1) or control (0), $b \times g$ = interaction of group and baseline performance when predicting cued performance.

Table 4
Full ANCOVA model, parietal patients vs. Control—stringent lesion criterion.

	Cue Cond.	IV	B	SE of B	*t*(37)	p-level
Hit rates						
	Likely Old	**Baseline**	**0.586**	**0.142**	**4.129**	**0.000**
		Group	−0.049	0.169	−0.292	0.772
		b × *g*	0.151	0.342	0.442	0.661
	Likely New	**Baseline**	**0.349**	**0.155**	**2.243**	**0.031**
		Group	−0.163	0.186	−0.879	0.385
		b × *g*	0.625	0.374	1.671	0.103
Correct rejection rates						
			B	**SE of B**	***t*(37)**	**p-level**
	Likely Old	**Baseline**	**0.885**	**0.216**	**4.093**	**0.000**
		Group	0.348	0.358	0.972	0.338
		b × *g*	−0.386	0.423	−0.913	0.367
	Likely New	Baseline	0.120	0.080	1.506	0.140
		Group	**−0.605**	**0.132**	**−4.580**	**0.000**
		b* × *g	**0.617**	**0.156**	**3.960**	**0.000**

Note: Significant predictors are in bold. Baseline = uncued performance, group = parietal (1) or control (0), $b \times g$ = interaction of group and baseline performance when predicting cued performance.

these cues are invalid and is characterized by a tendency for the slope relating baseline and cued performance to be shallower in controls and frontal lobe patients compared to parietal lobe patients. Thus control subjects and frontal patients mildly suffer when "Likely New" cues are invalid, demonstrating that they are influenced by the external recommendations. In contrast, because the slope is near unity for the parietal patients, this finding indicates that they are insensitive to the invalid "Likely New" cues. The more robust dissociation occurs for the valid "Likely New" cue condition. Here the parietal patients differed from the controls and frontal lobe patients in terms of overall cued performance (significantly worse) and the slope relating baseline and cued performance (significantly steeper). The latter effect occurred because the controls and frontal lobe patients were performing near ceiling when validly cued whereas the parietal lobe patients had a slope near unity, again suggesting they were insensitive to the external cues and were performing largely as they would have if the cues were absent.

One concern that potentially arises when considering small patient groups is the potential for one or two behavioral outliers in the patient group to drive the statistical conclusions. However, that concern is not warranted for the parietal patients examined here for two reasons. First, the range of baseline, uncued performance during both hits (Fig. 4) and correct rejections (Fig. 5) is quite similar for the parietal patients and controls as reflected by a similar distribution across the *x*-axes for both groups. Thus, in the absence of external cues, it is clear the groups have similar recognition accuracy. Second, the dissociation in response to cueing occurs because the performance of the control subjects, not the parietal patients, is altered in response to the cues. Thus control performance departs markedly from baseline when the "Likely New" cue is valid and departs moderately from baseline when the same cue is invalid. In contrast, patient performance is remarkably consistent across cued and uncued conditions for both hits and correct rejections. Indeed, for the patients, the correlation between uncued and cued performance is .81 for hits and .89 for correct rejections. This high degree of consistency highlights the reliability of their responses across the uncued and "Likely New" cued conditions and contrasts with the control participants who demonstrated lower correlations between baseline and cued performance for hits ($r=38$; group difference $p=.075$) and correct rejections ($r=33$; group difference $p=.010$) which should necessarily occur if control participants are influenced by the external cues. Thus overall, it is clear that the results are not driven by extreme scores in response to cueing on the part of the parietal patients and that these patients demonstrate remarkable consistency in their responding, supporting the reliability of the conclusions that can be drawn.

3.4. Reaction time

Reaction times were quite variable. In an initial analysis we contrasted parietal patients and controls across the six conditions examined above, namely baseline trials (hits and correct rejections) and "Likely Old" and "Likely New" cued trials for hits and correct rejections. The parietal patients were significantly slower during validly and invalidly cued correct rejections ($t(41)=3.22$, $p=.003$; $t(40)=2.25$, $p=.030$) (Table 1). Since this might reflect merely a general slowing on the part of the patients we attempted to replicate these differences with baseline performance statistically controlled via ANCOVA. The group difference during invalid cueing did not survive the ANCOVA, however, that during valid cueing did. Thus the patients appear slower than what would be predicted given their baseline reaction time during the presentation of valid "Likely New" cues. This was also the condition producing the most robust accuracy differences across the groups.

3.5. Confidence

The confidence data were quite variable and direct comparison of confidence for the cued and baseline conditions across the parietal and control groups did not yield any significant differences.

3.6. Lesion location and cue influence

Recent consideration of parietal activations during fMRI studies of recognition have typically distinguished between dorsal responses in the supramarginal gyrus/intra-parietal sulcus and a more ventral activation sometimes observed in the angular gyrus. The latter is often assumed to reflect processes critically linked with contextual recollection during recognition judgments (perhaps the bottom-up capturing of attention by retrieved information) whereas the former has been linked to familiarity monitoring or the top-down guiding of attention by retrieval goals (e.g., Cabeza et al., 2008). However, there is currently little support for such dorsal/ventral functional dissociations in the patient memory literature (although see Ciaramelli et al., 2010). Because of the small size of the present parietal group, a voxel-based lesion symptom mapping analysis (Bates, Wilson, & Saygin, 2003) to investigate possible dorsal/ventral distinctions is obviously impossible. However, based on visual inspection of lesion extent (see Supplementary Fig.), we divided the cohort into mainly dorsal ($n=4$) and mainly ventral ($n=7$) subgroups. Exploratory t-tests conducted on all of the response categories in Table 1 failed to suggest any differences in accuracy, confidence, and reaction time. Indeed there was only one comparison that fell below a p value of .31 which was the comparison of confidence for invalidly cued new materials ($t(9)=2.06$, $p=.07$) with the dorsal subgroup showing numerically lower confidence ($M=1.56$) than the ventral subgroup ($M=2.30$). However, given the exploratory nature, large number of comparisons, and small sample sizes, this trending difference may only reflect sampling variability.

4. Discussion

As outlined in the introduction there are essentially two broad hypotheses about the role of the parietal lobe in memory retrieval, which can be segregated into models suggesting either a primary or secondary contribution to retrieval performance. In terms of a putative primary contribution, Berryhill and colleagues have documented impairments in the level of detail in the retrieval of remote autobiographical content in two parietal lesion patients (Berryhill et al., 2007). However, a growing body of research suggests minimal if any impairment in basic recognition or source memory abilities (Ally et al., 2008; Davidson et al., 2008; Haramati et al., 2008; Simons et al., 2008, 2010) and the current report joins this cohort. There was very little to distinguish the current parietal lobe patients and controls on item recognition performance when cues were not available in the environment. The groups demonstrated similar accuracy (all p's > 31), confidence (all p's > 32) and reaction times (all p's > 20) in the baseline condition during correct responses to deeply encoded targets, shallowly encoded targets, and new materials. Thus there is nothing in the baseline, uncued performance of the parietal patients to suggest a recognition memory impairment for rejection of new materials or detection of deeply or shallowly encoded targets.

Instead, group differences were observed when a valid external memory cue was presented that should have biased attributions towards judgments of stimulus novelty ("Likely New" cues). Parietal patients were less accurate and markedly slower compared to controls when these cues were available and valid. Additionally, they were less adversely affected by these same cues on the small proportion of trials in which they were invalid (shallow old materials); an outcome that would also occur if they were less vigorously incorporating these cues into their recognition attributions.

These findings are most broadly compatible with a secondary role for the parietal lobe during memory attribution and in particular with accounts suggesting the region supports attention (Cabeza et al., 2008), integration (Binder, Desai, Graves, & Conant, 2009; Shimamura, 2011) or decision biasing (O'Connor et al., 2010) processes during recognition attribution. As outlined in the introduction, the attention to memory framework holds that dorsal and ventral parietal regions support top-down and bottom up attentional functions, respectively. The current data would have to be interpreted within the dorsal mechanism for two reasons. First, because the ventral region is assumed to enable the attentional capture of recollective content, the model presumably predicts clear recognition memory impairments with ventral lesion whereas as noted above, there is no evidence for a recognition impairment in the current parietal cohort. Second, the lesion analysis suggests that the maximal overlap among the parietal patients is in the left superior parietal lobule, extending laterally into supramarginal gyrus. Although caution is warranted given the large and variable lesion extents, these areas correspond to those representing the dorsal function in the attention to memory framework. However, it is not clear that the top down component within that model naturally predicts the current effects. The top down role for the dorsal parietal lobe is characterized as crucial for sustained effortful episodic memory search operations, hence its prominent activation during low confidence judgments (Cabeza et al., 2008). However, the "Likely New" cueing condition used in the current report poorly fits this characterization because it should not induce sustained effortful memory searches, since for the majority of trials it correctly predicts novel materials. Instead, detection theoretic accounts suggest that in this situation, participants should shift the decision criterion such that new items will more easily characterized as such reflecting a search for, or expectation of experienced novelty. The signal detection approach also corresponds to the Bayesian solution to this paradigm when assuming normal evidence distributions along a single dimension. Importantly, this decision biasing model does not assume that the region instantiates or potentiates only the search for episodic content, but instead assumes the region biases judgments either towards or against judgments of familiarity depending upon external environmental cues. Thus the region is assumed to influence the decision process for both old and new materials and materials consistent with the cued expectations are predicted more likely to be endorsed than in the uncued case. These predictions arise not only in single process or unidimensional decision models of recognition but also under dual process models of recognition that assume that familiarity based judgments operate in accordance with basic detection theory principles (Yonelinas, 1994). Indeed, Jaeger, Cox and Dobbins (2012) successfully simulated the pattern of confidence and accuracy that arises under the explicit memory cueing procedure using a dual process decision model. Under the model, the cues are assumed to only influence the familiarity judgment process through the placement of the familiarity decision criterion. In contrast, when an old item evokes contextual recollection, the model assumes that the environmental cues are ignored. Using this framework, the current data would reflect a failure on the part of the parietal patients to appropriately shift their familiarity decision criterion in response to the "Likely New" cue, leading to the strong correspondence between their cued and uncued performance. The lack of any discernible difference in the baseline recognition performance of the controls and parietal patients is also consistent with this decision model since environmental cues are absent.

Thus unlike the current version of the attention to memory hypothesis, a decision biasing framework emphasizing the integration of external cues and internal evidence is capable of predicting divergence between patients and controls under conditions in which cues correctly instill an expectation of upcoming novelty, even though this is precisely the kind of situation in which sustained and effortful memory search will usually be unnecessary and inappropriate.

A recent fMRI report by O'Connor et al. (2010) linked activation in the supramarginal gyrus/inferior parietal lobule region to decision biases in participants by demonstrating that parietal activation during recognition was strongly contingent upon the violation of cued expectations, and that in the absence of external cues, parietal lobe activation covaried with individual differences in observer decision criteria. Both effects led to the conclusion that activation in the parietal lobe during recognition was a reflection of the violation of observer expectations, occurring for subjectively unexpected recognition judgments. However, the most natural prediction arising from that study was that behavioral deficits accompanying parietal lobe damage would be most noticeable under invalidly cued trials because these were the circumstances under which activation was greatest for both new and old materials when correctly judged as such. That is, parietal lobe activation was greatest when expectations were violated, regardless of whether those incorrectly cued expectations were of upcoming novelty or familiarity. Consistent with other frameworks investigating cognitive control (Braver, Paxton, Locke, & Barch, 2009), these responses were hypothesized to putatively reflect a form of reactive control, in which mnemonic evidence was used to overcome inappropriate a priori expectations. The current data instead suggest a more prominent role in the implementation of proactive or anticipatory biases during memory attribution because the clearest group differences arose during validly cued performance. Bringing the attention to memory and detection theoretic models together, the current findings argue for a role of the parietal lobe in the implementation of anticipatory decision or attribution biases in which observers integrate external cues and internal evidence, using the external information to bias judgments by dynamically adjusting the mapping between memory evidence and overt judgments. As illustrated in the rationale preceding the results section, the adaptive value of such biases is that they serve to increase one's overall accuracy above what would be possible from relying solely upon internal evidence.

Although the data indicate a dissociation across the parietal patients and controls in terms of adaptive decision biases, this dissociation was selective to the "Likely New" cue condition. We can only speculate as to why this effect did not generalize to the "Likely Old" condition, but it seems likely that this was a result of the fact that old materials outnumbered new materials two to one in the design and relatedly because of the presence of deeply encoded materials intermixed with the shallowly encoded materials during testing. Both factors may have led participants to feel that old materials were being easily and/or adequately detected and hence they may have focused their efforts on trying to improve the detection of the subjectively rarer new materials via use of the external cues. Because neither controls nor parietal patients incorporated the "Likely Old" cues particularly strongly, subsequent work will be required that tests the utility of these cues, perhaps by contrasting conditions in which old materials are rare, versus conditions in which they are predominant. Regardless, the current findings suggest a clear inability to adaptively use "Likely New" cues on the part of the parietal patients.

Accruing evidence from non-human primate research supports the linkage of parietal cortex to top down attentional modulation of perceptual representations during stimulus judgment. For example, when competing stimuli are simultaneously present in the environment, early sensory regions for the trial relevant stimulus type demonstrate greater activity than the trial irrelevant type and this differential biasing has been hypothesized to rely upon parietal cortex (Kastner & Ungerleider, 2001). Additionally, neurons in the lateral intraparietal region of monkeys are sensitive to both prior probabilities and animal analogues of confidence reports (Hanks, Mazurek, Kiani, Hopp, & Shadlen, 2011; Kiani & Shadlen, 2009), two characteristics that would be essential for implementing adaptive decision biases based on external contingencies. Recent fMRI support for a key role of the parietal lobe in the top down biasing of human attention has also been garnered by directly comparing cued recall and perceptual search tasks (Sestieri, Shulman, & Corbetta, 2010). Given this convergence, casting the role of the parietal lobe during episodic recognition in terms of biasing processes seems well justified, and perhaps more importantly, helps explain why parietal patients are not characteristically associated with prominent memory deficits. Because typical experimental memory tasks are designed to avoid the potential for participants to use external cues to bias judgments, a decision biasing model of the parietal lobe naturally anticipates that standard memory assessments should appear largely normal in this population. It is only under conditions in which judgments should be situationally biased that this model anticipates deficits.

Although the current data, in light of previous findings, suggest a secondary or indirect role for the parietal lobe during memory attribution, it is important to emphasize that this role is likely extremely important for accurate performance outside the laboratory. Because signal detection accuracy parameters are designed to remain constant under static shifts of criterion (i.e., shifts that persist throughout a given test), this often leads researchers to mistakenly believe that criterion shifts largely represent nuisance variables. This is a misconception because while useful, the signal detection accuracy estimate d' generally obscures the fact that criterion positioning can have large consequences on the cumulative success rate of the observer across trials, if the observer is able to advantageously place the criterion on each trial. For example, imagine two observers whose d' accuracy values are 1.5 and 2.0 when measured in isolation. If the criterion of the former remains fixed and neutral across stimulus encounters, then her maximum success rate is 77% under the standard signal detection model. However, now consider if she traveled with the observer whose d' was 2.0, and if she shifted her internal decision criterion based on the reports of the highly accurate companion from encounter to encounter. Under this scenario her maximum success rate elevates to 87%. Of course, the ability to use such a strategy depends upon establishing the long term reliability of the source of the cues. In the current study this information is explicitly given to the participants, in the anecdote discussed above it would presumably result from either extensive trial and error, or observational learning about the companion's superior memory skills. In either case the key point is the same; adaptive biasing of decision criteria enables observers to use external sources of information to maximize correct responding.

Although a decision biasing interpretation of parietal lobe activation during recognition fits fairly well with the prior literature, it is worth considering how well some of the previous parietal lesion memory findings fit within this conceptualization. For example, Simons et al. (2010) observed unimpaired item recognition and source memory accuracy in groups of parietal patients, but reliably reduced patient confidence in their source attributions. The patients' confidence in their item recognition judgments was comparable to controls, consistent with the recognition confidence findings of the present experiment. Because the experiments reported by Simons et al. involved relatively deep encoding tasks and did not use external cueing at retrieval, the correspondence of the two findings is difficult to judge. The other relevant previous patient study is that by Ciaramelli et al. (2010), who found that patients with parietal lesions did not benefit from the availability of memory cues, and were slower in responding to invalidly cued targets. Although these results appears on the surface to be consistent with some of the present findings, there are important differences between the paradigms. As discussed in the introduction, it is arguable whether the memory cues in Ciaramelli et al.'s task correspond to the external explicit cues provided in the present paradigm. Given this, future work comparing indirect and explicit cueing procedures both during item and source memory for parietal patients is likely to be informative.

In conclusion, the current study suggests that the parietal lobe plays an important role in the ability to dynamically bias recognition judgments based on external explicit memory cues. Using a recently developed explicit memory cueing paradigm (O'Connor et al., 2010), the data demonstrated that parietal patients were less accurate than both healthy and lesion controls when responding to new materials that followed a valid, predictive memory cue. The failure to capitalize on such cues reflects a considerable judgment deficit, albeit one that would tend not to be captured on typical memory tasks. However, outside the laboratory, optimal memory functioning ideally requires that one situationally bias judgments because the recognition status of stimuli is often heavily anticipated by the contexts in which they are encountered. One important contextual cue is the recommendation of others, at least in social species such as ours. An individual who can use external cues such as these can in principle elevate his or her own memory performance considerably by judiciously biasing reports towards those of conspecifics when internal memory evidence is lacking. In order to do so however, one must be able to dynamically revalue or remap the internal memory evidence scale onto overt decisions and the lateral parietal lobe may be critical in this integrative ability.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2012.07.037.

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