Self-perspective in episodic memory after parietal damage and in healthy ageing

Highlights:

- Damage to right parietal cortex leads to a specific deficit in episodic memory
- This deficit is in recognition of the perspective from which a memory was encoded
- MVPA in neuroimaging shows parietal involvement in recalling from own perspective
- Supramarginal and angular gyri regions crucial for these aspects of episodic memory

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Self-perspective in episodic memory after parietal damage and in healthy ageing

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Abstract

Although there is strong support from functional imaging studies for lateral parietal lobe involvement in episodic memory, patients with damage to these regions do not appear to suffer from severe deficits in this cognitive domain. As such there has been no definitive explanation of this area's precise involvement. Here, we hypothesised that parietal regions play a crucial role in episodic memory - specifically in recollecting details from an egocentric perspective. In order to test this hypothesis systematically, we designed a novel experimental task utilising a head-mounted camera to record images from the participant's perspective, enabling us to evaluate the integrity of memory from the individual's own point of view. In the first study we examined patients with parietal damage and in a second study, using fMRI, we examined young and older healthy participants. Right-hemisphere patients with parietal damage were able to recall information accurately when recollecting what items had been present and where these items had been. However, patients were significantly impaired when attempting to judge from which perspective they had viewed the scenes. Critically, the patient group showed no evidence of impairment on standard tests of episodic and working memory. Examination of healthy participants in the second study utilised multi-voxel pattern analysis on neural activity during the recognition phase of a similar task. This revealed sensitivity to be highest around the angular gyrus of the lateral parietal cortex for our critical comparison - that is, when viewing stimuli that were the same as their egocentric view during encoding versus the identical scene but presented from an alternative angle. Our results provide important evidence that parietal cortex is directly involved in egocentric spatial perspective aspects of episodic memory and demonstrate for the first time a specific deficit in episodic memory in patients with right parietal damage.

Key words: Episodic memory; parietal cortex, neuropsychology, ageing

1. Introduction

Patients with damage confined to lateral parietal cortex are not thought to suffer from episodic memory problems. Right hemisphere lesions affecting this region often result in the striking attentional deficits that form the core symptoms of spatial neglect (e.g., Mort *et al.*, 2003; Corbetta and Shulman, 2011), with left hemisphere damage leading to other deficits including those considered part of Gerstmann's syndrome or aphasias (e.g., Fridriksson *et al.*, 2010; Rusconi *et al.*, 2010). There has been a surge of interest in the apparent contradiction between activity consistently seen in lateral parietal cortex during functional neuroimaging studies of episodic memory (Cabeza *et al.*, 2008; Schoo *et al.*, 2011 and see Rugg & King, 2017; Sestieri et al , 2017 for recent reviews) and the assumption, followed by accruing evidence, of preserved episodic recall skills in patients with damage to this region (Ally *et al.*, 2008; Simons *et al.*, 2008). This contrasts with the clear relationship between neural activity in medial temporal regions elicited during episodic recall and the debilitating long-term memory loss associated with damage to those regions (Scoville and Milner, 1957; Wagner *et al.*, 1998; Squire *et al.*, 2004; Rugg and Vilberg, 2013).

Despite the fact that lateral parietal cortex lesions do not reduce recall accuracy in standard episodic memory tasks, careful investigation by a number of groups has delineated subtle impairments. For example, even with preserved overall recall accuracy, patients with bilateral parietal lesions show an atypical relationship between self-rated confidence in their performance and their actual performance. In some paradigms they rate themselves less confident than controls despite accurate performance, whereas in other paradigms they rate themselves as confident despite failures to recognise previously presented items (e.g., Berryhill *et al.*, 2009; Olson and Berryhill, 2009; Simons *et al.*, 2010; Hower *et al.*,

2014). Perhaps relating to this altered confidence, patients make fewer false alarms than healthy controls and are less susceptible to falsely recalling semantically related lures (Drowos *et al.*, 2010). In autobiographical tasks where patients are asked to freely recall an event from their own life, patients with parietal damage can recall personal memories but description of these events is independently rated as vague and imprecise, suggestive of impairments in vividly recalling the event (Berryhill *et al.*, 2007; Davidson *et al.*, 2008; Berryhill, 2012). Consistent with this suggestion is evidence that individuals with parietal damage are less likely to rate the responses given in a recall task as explicit 'Remember' versus the implicit 'Know' (e.g., Drowos *et al.*, 2010), as are reports from patients that even when accurately recalling an autobiographical event they do not have the subjective feeling of having experienced the memory themselves (see Davidson *et al.*, 2008).

Complementary to this neuropsychological work a number of groups have examined disruption to relevant parts of posterior parietal cortex in healthy participants, focusing on the left angular gyrus. Repetitive TMS (Sestieri et al, 2013) and continuous theta burst stimulation (Yazar et al 2014) has suggested that disrupting this region affects the subjective experience of remembering without loss of overall accuracy of recall. Further, using functional imaging Bonnici et al (2016) demonstrated that classification accuracy in multi-voxel pattern analysis increased within angular gyrus as participants reported greater vividness of recall.

The nature of these neuropsychological impairments and the results of experimental disruption make it pertinent to consider well-documented functions of parietal cortex. Computational and neuroimaging evidence suggests a key role for parietal cortex in

egocentric spatial representation of visual input (see Burgess *et al.*, 2001; Burgess, 2008; Lambrey *et al.*, 2012). In order to create an accurate image of the world around us- from our own first-person perspective - we rely on parietal cortex. Evidence of impaired route learning when only egocentric (as opposed to allocentric) cues are available in parietal patients further supports this (Weniger *et al.*, 2009). As does evidence that deficits in visuo-spatial awareness commonly seen after right hemisphere parietal damage predominately affect egocentric rather than allocentric space (Rorden et al., 2012). Consideration of the features of episodic memory highlights the potentially critical role for egocentric spatial recall in this function. If we are asked to remember the event of having dinner last night, we would not feel that we were accurately recalling our memory if we did not construct a visuospatial mental image of the scene as we perceived it at the time. Accurate recall of egocentric perspective appears critical to episodic recall. Several studies have shown that as memory declines in ageing there is increased recall from a third person 'observer' perspective and that this is associated with a lack of vivid recalling of autobiographical events (Piolino *et al.*, 2006; Piolino *et al.*, 2009). Ciaramelli and colleagues directly examined topographical memory for route planning tasks in parietal patients and their data revealed more severe impairments on the tasks loading on egocentric representations as compared to allocentric representations (Ciaramelli *et al.*, 2010). In a recent study Ciaramelli and colleagues (2017) in an assessment on patients with parietal damage, confirmed that although memory for word stimuli were accurately recalled, patients (compared to healthy controls) were less likely to select 'Remember' as opposed to 'Know', suggestive of a changed subjective experience of the recalled memory after this damage.

Related to this, St Jacques and colleagues have examined, in healthy individuals shifting the perspective from which they encoded an event at retrieval (St Jacques et al, 2018; St Jacques, Szpunar & Schacter, 2017; Marcotti & St Jacques, 2018). These studies have revealed that posterior parietal cortex appears intrinsically involved in this shift and that the requirement to shift visual perspective at recall reduces the overall accuracy of the memory and – crucially- this effect leads to a reduction in reported subjective vividness of the memory.

In the studies presented here we aim to further probe the functions of parietal cortex – in particular the angular gyrus and nearby regions –in relation to recalling novel scenes from a self – *egocentric*- perspective. Within our design we are able to directly compare memory for egocentric perspective with memory for allocentric spatial relationships. This allows us to examine differences in recall between these conditions in patients with damage to these parietal regions and, in a second study, in older versus younger participants. Our intention to additionally examine the effect of ageing on memory for egocentric perspective was motivated by the seeming harmony between descriptions of memory change in parietal patients with those in the ageing literature – albeit more dramatic in the patient groups. For example, in older people episodic recall is also frequently reported as lacking detail and specificity (e.g, Levine et al, 2002; Addis et al, 2011; Schacter et al, 2013). Further, the evidence for an increase in memories reported from an 'observer's viewpoint rather than 'field' perspective harmonises with the processes we are directly probing with our paradigm (see, Piolino et al, 2006; 2009). Additionally, the second study was a direct attempt to address the apparent contradiction of parietal involvement in episodic memory in functional neuroimaging despite there being only subtle changes to these processes in patients with

damage here. Using fMRI based multi-voxel pattern analysis (MVPA) we will decode which areas of parietal cortex differentiate between self-perspective of a previously presented scene compared to the same scene from another perspective. This analysis enables us to examine whether specific patterns of activity can predict whether the participant is currently viewing their own view of the scene or an alternative perspective. Note that this analysis differs from univariate analysis in which we might predict parietal activity during recollection of a scene but without this activity necessarily discriminating whether they are viewing their own view or that of another. Using MVPA analysis with healthy participants we aim to confirm that parietal cortex is involved in the aspects of episodic memory that we hypothesise to be affected by acquired damage to these regions.

In summary, in our first study we were interested in two things. First, whether right hemisphere damage to parietal cortex can result in deficits in episodic memory. Second, whether these deficits are specifically related to memory for egocentric self-perspective. In Experiment 2 we adapt our neuropsychological paradigm to examine changes in this aspect of episodic memory with age and to directly examine whether areas of interest within parietal cortex are involved in differentiating our own self-perspective of an episodic memory.

2. Experiment 1

2. 1 Materials and Methods

2.1.1 Participants

Six patients (3 females) with chronic lesions affecting parietal cortex were recruited. All had been patients on the stroke unit at Imperial College Healthcare NHS Trust. All previously suffered from spatial neglect, which had recovered at the time of testing – confirmed at the start of the session with the Behavioural Inattention Test Star Cancellation task (Wilson *et al.*, 1987). They were aged 66 to 79 (mean = 71.2 years) and had a right hemisphere stroke more than 6 months previously. They were compared to a group of eight healthy age-matched participants (6 females), aged 64 to 83 (mean = 71.6 years). Inclusion criteria for patients were: a lesion affecting right parietal cortex; no current visuo-spatial neglect or extinction; no reports of memory problems; no other neurological impairment; no diagnosis of psychiatric impairment. Individuals were excluded if these criteria were not fulfilled. Healthy participants confirmed they had no current diagnosis of neurological or psychiatric illness and no memory problems. All participants also completed the mini-mental state exam (MMSE), no individual scored below 27/30 (patient group mean = 29.4; healthy group mean = 29.9), anyone scoring below 27 was excluded. All participants gave written consent according to the Declaration of Helsinki, with the study having been approved by the local research ethics committee (Figure 1).

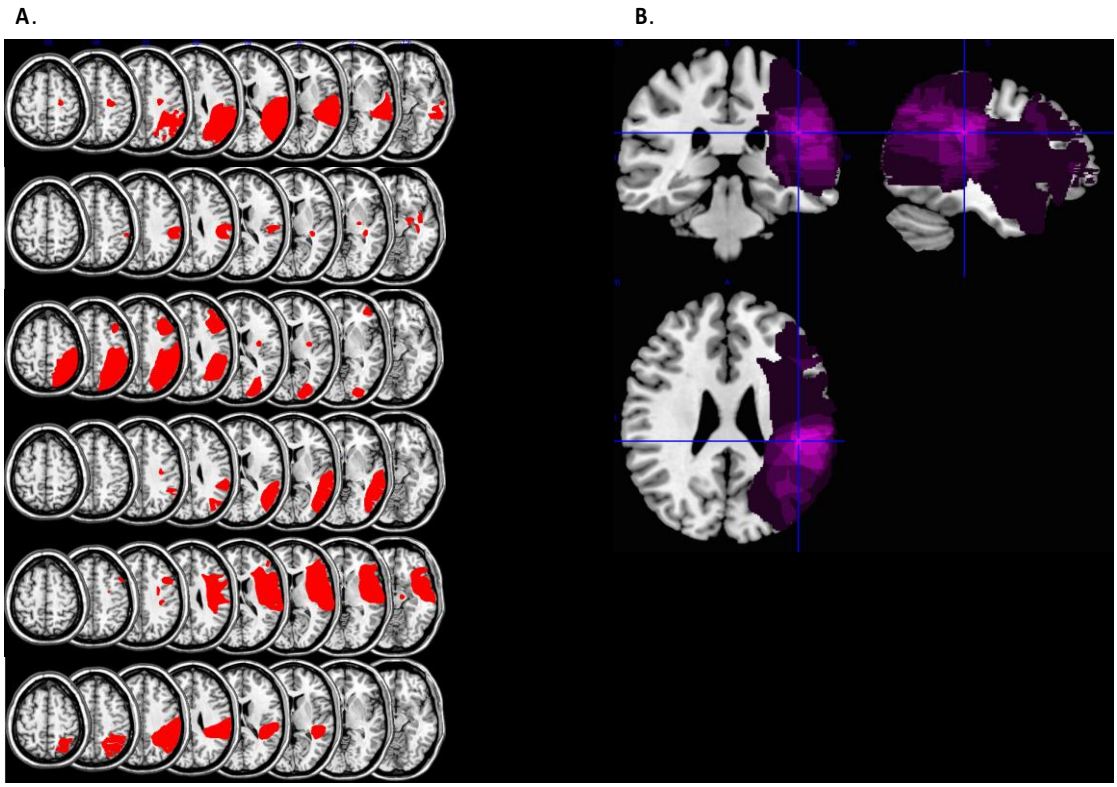


Figure 1

Individual Lesions and Lesion Overlap

Four of the six patients' lesions were mapped directly onto patients' native MRI scans using MRIcron software (www.mccauslandcenter.sc.edu/mricro/mricron). The anatomical scan and lesions were subsequently mapped onto stereotaxic space using Clinical Toolbox (www.mccauslandcenter.sc.edu/CRNL/clinical-toolbox) for spatial normalisation, implemented via SPM8 software (www.fil.ion.ucl.ac.uk/spm/software/spm8). The remaining two lesions were plotted using onto a T1 weighted template in MRIcron software (www.mccauslandcenter.sc.edu/crnl/mricron/) by direct comparison with the native scan. All scans were mapped by trained neurologists (KL and PM).

A. Lesions mapped for each of 6 patients individually

B. Lesion overlap. Lesions are represented in purple, with regions damaged in increasing numbers of patients shown in brighter shades. All patients had strokes affecting the middle cerebral artery territory, with varying degrees of frontal and temporal involvement. The

single region of maximal overlap (all 6 patients affected) was in the right supramarginal gyrus, centred around MNI coordinates (46, -33, 26) extending laterally to (59, -29, 26) and superiorly to (46,-33,27).

2.1.2 Standardised Memory tasks

These tasks were used to assess episodic and spatial working memory:

Rivermead Behavioural Memory Test – Line drawing delayed recognition (RBMT-3). Line drawings of common objects were shown for three seconds each. A delayed recognition task followed after 30 minutes*; Corsi Block Tapping Task*. Participants observed a sequence of taps and then repeated this in the identical ('Forward span') or reverse order ('Backward span'). The task starts with a short sequence increasing in length to a maximum of nine or until the participant is incorrect in both trials of a particular length.

2.1.3 Experimental task

Participants were presented with 14 novel 3D scenes to remember. Each scene consisted of two items positioned in separate squares of a 2 x 2 grid pattern, placed on the table in front of the participant (see Figure 2). For half of the scenes participants sat to the left of the grid, for the other half to the right, seating position was randomly allocated across the trials with an equal distribution of both angles – the order in which left and right were used was counterbalanced across participants. Participants were asked to move seats for this manipulation. If they were in a wheelchair, their wheelchair was moved for them. Viewing position, items used and the order of presentation were counterbalanced across participants. Pilot testing with a similar group of patients had confirmed suitability of this number of scenes.

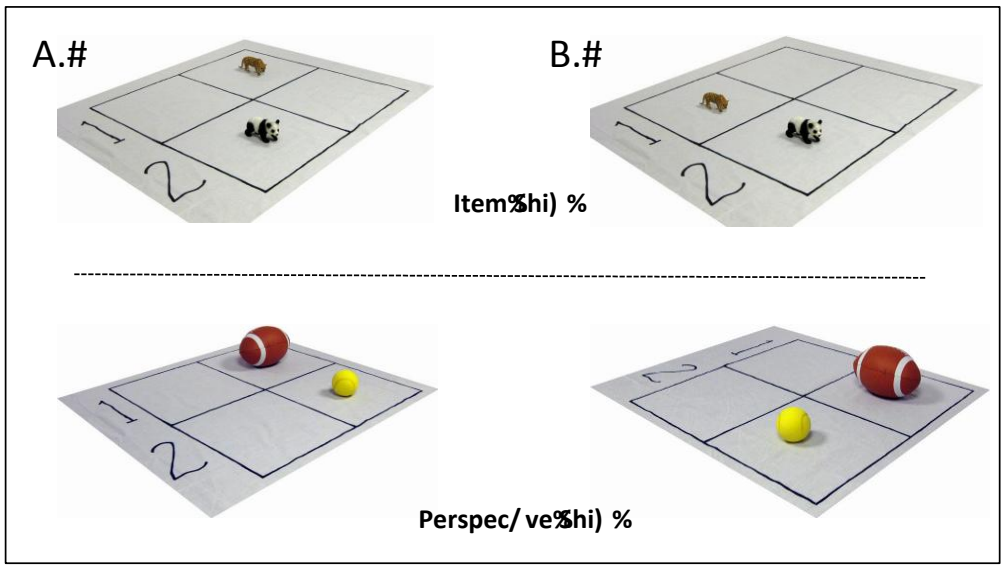


Figure 2

Experimental task stimuli and conditions

Pictures shown in column A are indicative of the original scenes shown to participants. Each scene consisted of two items taken from a total of 14 individual categories. Examples of possible categories included kitchen items, toy vehicles, models of musical instruments, and fruit. There were 8 potential exemplars from each category. No category was used more than once. In each encoding trial, two items from separate categories were placed on the grid in front of participants. Note that during encoding photographs were not used but the actual 3-D image, test images were purported to be from the head camera participants wore during encoding. Seen in this figure are examples from the animal and sports equipment categories. In the recognition task, items such as those shown in column B were used alongside the veridical images of what they had seen as shown in column A. During the 'Item shift' condition shown in the top panel of Figure 2, the lure image was taken from the same perspective but one of the items had moved by one square. In the critical 'Perspective Shift' condition in the lure image, the items occupied the same squares as in original image but the photograph was taken from the opposite angle.

During encoding, the two items for each scene were placed onto the grid by the experimenter and left for 1 minute. Participants were told that their memory for the scenes and what they looked like to them would be probed later. Each scene was explicitly given a category name, e.g., 'Stationery'. Scenes were presented in two blocks of seven. After each block, participants were cued with the category name of each scene and then asked to recall the items, their positions, and the viewing perspective they experienced that scene from. For example, they could be asked, 'when we showed you the stationery scene can you tell us what items we showed to you, where they were on the grid and where you viewed this scene from?'

All participants were wearing a head camera during encoding. They were shown this camera and it was explained that a still would be taken from each scene, which they would need to identify in the memory test. In reality we pre-prepared stills of each scene – facilitating the later memory test and making the images as clear as possible on the screen. In our pilot studies the head camera images were too unclear to faithfully represent the scene as shown, e.g., similar items like a leopard and tiger were frequently confused. Importantly, no participant in either group questioned that the images were taken from their head camera or mentioned being suspicious during debrief when we explained what had been done. The head camera was used to emphasise that it was how the scenes appeared to the participants that was crucial and not – for example – what objects were in the scene.

Recognition tests took place approximately 2 hours after encoding. Two images were presented on the screen simultaneously. Participants were required to select the image taken from their head camera and that therefore represented the scene that they had seen,

as they remembered it. One of the images was identical to a pseudo-image from the participants' head camera while viewing one of the scenes, i.e., the same scene (same objects in same grid squares) taken from the same viewing angle as presented to that particular participant. The identity of the other simultaneously presented scenes were split into two experimental categories. Half were 'Item Shift' lures; that is, the same exemplars from the category were used with the same viewing angle but one item had moved squares within the grid. This condition was designed to assess the maintenance of allocentric spatial information from the scenes as one object had changed in its spatial relationship to the other object within the grid. Alternatively, the lure could be a 'Perspective Shift'; that is, the same category exemplars were presented on the same grid squares but the picture was taken from the opposite viewing angle. Note that inherent in this design is that the perceptual demands are similar for the two conditions ('Perspective shift' and 'Item shift') and that simultaneous presentation of the previously seen image and the 'lure' scenes minimised any requirement for mental rotation.

Participants verbally selected which image they believed they had seen (the correct image was randomly presented on the left or right side of the screen). There were 14 trials, one for each unique scene. Participants were given as long as they needed and the images remained on the screen while they decided. They were then asked how confident they were of their decision, rating their confidence on a scale of 1-4 (4 being most confident).

2.2 Results and Discussion

Analysis was carried out using non-parametric statistics as Shapiro-Wilk tests revealed that some data were not normally distributed (see Table 1 and Figure 3).

2.2.1 Standard Memory Tasks

Patients and controls were statistically equivalent ($U = 30$, $p = .49$) in the line-drawing delayed recognition test. Spatial working memory performance (Corsi Block task) was also equivalent across the groups both for the 'Forward' ($U = 21$, $p = .76$) and the 'Backward span' conditions ($U = 36$, $p = .14$).

	Patients	Healthy Controls
Line drawing – memory task (proportion)	.97 (.03)	.99 (.02)
Corsi blocks forward span	6.83 (1.72)	6.50 (1.51)
Corsi blocks backwards span	6.17 (1.94)	7.88 (1.64)
Experimental Task		
Item Shift		
Accuracy (proportion)	.83 (.17)	.97 (.07)
Confidence (/4)	3.60 (.27)	3.73 (.46)
Perspective Shift		
Accuracy (proportion)	.53 (.20)	.86 (.15)
Confidence(/4)	3.39 (.50)	3.46 (.61)
Recap Condition in encoding session (proportion)		
Item identity	.89 (.08)	
Item position	.88 (.14)	N/A
Viewing angle	.87 (.10)	

Table 1:

Data from all tasks in Experiment 1, standard deviations in brackets.

Additional information on percentage correct recall in the recap questions asked during the encoding session:

'Item Identity' indicates responses to the question: 'Which items did you see in the (e.g.) Sports equipment trial?'

For 'Item position' the question was: 'Where were the items shown in (e.g.) sports equipment trial?

For the 'Viewing Angle' question they were asked: "Where were you sitting when you saw the (e.g.) sports equipment trial?'

2.2.2 Experimental Task

First, patients' performance in the encoding session was assessed. Analysis was carried out on their performance against ceiling (i.e., examining whether scores were significantly different from 100%, see Table 1) as, although the control group answered the same questions at the same time and experienced the encoding sessions in exactly the same way, data were not systematically collected. Patients scored significantly lower than ceiling when recalling the actual items ($U = 44$, $p = .01$) and repeating positions on the grid ($U = 40$, $p = .04$). Given the failure of data collection from the older group, this is a conservative estimation of patient performance. It is important to note that any mistakes were corrected in this part of the encoding session. For the element of greatest interest (perspective from which they viewed the scene) their scores did not significantly differ from 100% ($U = 30$, $p = .07$).

Analysis was then carried out on scores in the two conditions of the main task. Between-subjects analysis compared the two groups' scores in the Item Shift condition to those obtained in the Perspective Shift condition. These data revealed that patients and controls were equivalently accurate in the Item Shift condition ($U = 37$, $p = .11$). However, in the

condition assessing memory for personal perspective (Perspective Shift) the patient group performance was significantly worse than the healthy controls (U = 43.5, p = .01).

Data were then compared within-subject group. Whereas the control group were equivalently accurate in the Item Shift and Perspective Shift conditions (W = 10, p = .06), the Patient group were significantly more accurate in the Item Shift condition (W = 15, p = .04).

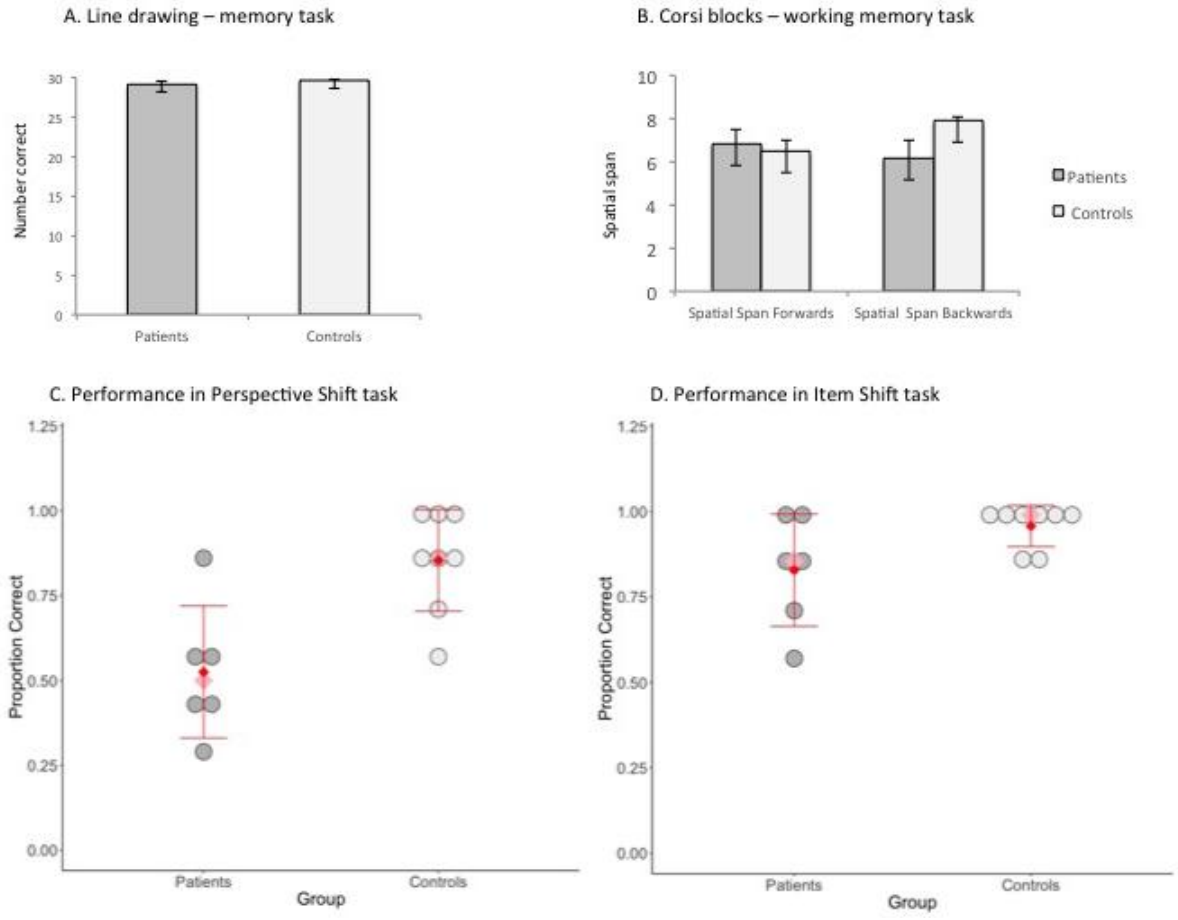


Figure 3

A. Overall number correct for each group in the line drawing recognition task (standard error mean bars)

B. Spatial span in Corsi blocks task. Both the forwards and backwards conditions are shown for each group (standard error mean bars).

C. Performance in the Perspective Shift task. Dots plot scores of individual participants. Red diamond indicates mean. Red lines are standard error bars and the pink diamond indicates median.

D. Performance in the Item Shift task. Red diamond indicates mean. Red lines are standard error bars and the pink diamond indicates median.

Five out of the six patients demonstrated the expected deficit –performing more accurately in the Item Shift task compared to the Perspective shift task. When subtracting the patients' scores in Perspective Shift from those achieved in Item Shift the decrement in performance from the Item Shift to the Perspective Shift task was sizable, ranging from 14% to 57% (M = 36.80; median = 29). The only patient who did not show this effect was accurate on only 57% of trials for both tasks - their performance can be seen as the lowest dot on the Item Shift task for this group in this condition. This abnormally weak performance in Item Shift might indicate a wider memory problem or reflect occipital damage, which was not present in the other patients.

Finally, we assessed whether the patients' confidence in their responses differed from that of controls. Self-rated scores of confidence were equivalent across groups for both the Perspective Shift and Item Shift conditions (U = 29, p = .57; U = 33.5, p = .23 respectively). The patient group's confidence in their performance also did not differ for the two experimental conditions (W = 10, p = .50). However, the control group were significantly more confident in their answers to the Item Shift condition compared to the Perspective Shift condition (W = 20, p = .05).

Experiment 1 reveals impairments in self-perspective aspects of episodic memory in patients with damage to right parietal cortex. These individuals were not impaired on a

standard episodic memory task, were at ceiling in a task assessing encoding of scenes, were unimpaired in spatial working memory tasks and – crucially - were not impaired in an experimental memory condition in which allocentric spatial relationships were manipulated (i.e. Item Shift trials). However, they were impaired when compared to neurologically healthy volunteers when judging which image - purporting to be from the head camera they wore during encoding- was the one they had experienced *only* when they were required to differentiate their own versus another image of the same scene taken from another angle. This is important, as the use of these egocentric visuo-spatial mechanisms in episodic memory has not been previously studied in research interrogating the role of these regions in long-term memory. Here we directly assessed this aspect of episodic memory and demonstrate that it is impaired following parietal damage. These novel findings are potentially important for these patients. This group has been previously overlooked in analysis of episodic memory impairments, and delineating long-lasting cognitive deficits after right hemisphere stroke is important as evidence suggests that these have been underestimated (Bonato, 2012).

The two conditions within the novel paradigm directly compare the ability to select a participant's own scene in the presence of a lure that varies in either perspective information (Perspective Shift) or in allocentric spatial information (Item Shift). It was in the Perspective Shift condition *only* that the patient group revealed a deficit. This suggests that parietal damage does not result in an overall impairment in episodic memory or indeed visuo-spatial aspects of episodic memory *per se* (as tested by Item Shifts), which harmonises with previous research. In addition, these patients performed the standard test of spatial working memory – the Corsi block task- at a level not significantly different to controls. As a

result, the data cannot be explained by impairments in spatial working memory (Malhotra *et al.*, 2005). Further, overall task difficulty is unlikely to explain the results as the Corsi block task is challenging, particularly the backwards condition, and here patients' performance was statistically equivalent to healthy control participants.

We were concerned with delineating whether patients with right-hemisphere damage might suffer from specific and subtle episodic deficits rather than outlining precise lesion sites; however it is interesting to examine the lesion anatomy. The region of damage overlapping in all patients centres on the right supramarginal gyrus (Brodmann's area 40). This is relevant as evidence suggests these ventral parietal regions are involved in explicit 'Remember' as opposed to more implicit 'Know' responses in standard episodic tasks (e.g., Wheeler and Buckner, 2004). There is a large body of evidence implicating ventral lateral parietal cortex in episodic retrieval - specifically with the *quality* of the memory, as involvement of these regions enables retrieval of richer more vivid information (see Vilberg & Rugg, 2008 and Rugg & King, 2017). Although this relationship is often shown in the left hemisphere, frequently the episodic tasks used to investigate neural response use word stimuli as the to-be-remembered items (e.g., Wheeler and Buckner, 2004; Gonzalez *et al.*, 2015) which might be one factor leading to greater recruitment of left-hemisphere regions. The data here suggest that it is likely that the act of explicitly visually recalling an event (leading to accurate 'Remember' responses) relies in part on the ventral parietal region damaged in our patients. Here, we suggest that in right hemisphere the 'Remember' act involves accurate recall of visuospatial relations from an egocentric viewpoint.

Data examining the self-rated confidence of our participants complements findings suggesting that accurate insight of episodic recall accuracy is altered after parietal damage (e.g., Berryhill *et al.*, 2009; Simons *et al.*, 2010). Patients were equivalently confident in their responses to both perspective and item shift conditions despite their poor performance in the first condition.

The task developed in Experiment 1 reveals a specific deficit in right hemisphere stroke patients in episodic recall from self-perspective. The area of maximal overlap is consistent with evidence for the lateral posterior parietal cortex and vividness of episodic recall. An interesting avenue to develop this paradigm is with healthily ageing adults. Older adults' episodic recall is frequently reported as lacking specificity and detail, as has been reported in parietal patients (e.g., see Levine et al 2002; Addis et al, 2011; Schacter et al, 2013). There is also an increase in memories being recalled from an 'observer' rather than 'field' perspective (Piolino et al 2006; 2009), which correlates with reports of a weaker subjective feeling of experiencing the memory and a lack of rich detail (e.g., Piolino et al, 2006). The task used here is suited to probing which areas of parietal cortex are involved in discriminating between one's own versus another perspective in episodic memory. By introducing a critical design adaptation (simply showing only one image to the participants at a time in the recognition task) with MVPA we can use it to decode parts of the parietal cortex that are involved in this discrimination.

3. Experiment 2

3. 1 Materials and Methods

3. 1. 1 Participants

Twenty-eight individuals took part: 16 healthy younger participants (11 females) between the age of 19 and 24 years (*M* = 20.87, *SD* = 1.73) and 12 healthy older participants (8 females) aged from 62 to 81 years (*M* = 69.25, *SD* = 6.18). Younger participants were recruited from the local student population and older participants were recruited from an over 50s exercise class and from the local University of the Third Age (U3A). Data are presented for 23 of these individuals. Two people opted out of going in the MRI scanner on day 2, a further two experienced technical problems on the second day and one person's performance was below chance in all memory tests and conditions. The remaining 25 were 13 younger participants (19-24 year olds, *M* = 21) and 10 older adults (62-81 year olds, *M* = 69.30). Each participant was reimbursed £15 in total for their attendance costs. All participants were asked to confirm that they had no current diagnosis of neurological or psychiatric illness. They all gave written consent according to the Declaration of Helsinki, with the study having been approved by the local research ethics committee.

3.1.2 Standardised Memory tasks

As in the previous study, the following tasks were used to assess episodic and spatial working memory: *Rivermead Behavioural Memory Test – Line drawing delayed recognition* (RBMT-3); *Corsi Block Tapping Task – forwards and backwards*. This experiment ran over two days, permitting further examination. Extra assessments were, *Buschke's Selective Reminding Test* (Buschke, 1973) and the *Rey-Osterrieth Complex Figure (ROCF) test*. The Buschke task consisted of a series of 12 unrelated words presented over 12 trials, or until the subject was able to recall the entire list on three consecutive trials. A delayed recall test was given without warning 30 minutes after completion. In the *ROCF* participants were asked to copy a complex visuo-spatial design as accurately as possible. Once complete, the

design was removed and participants were asked to immediately draw it again from memory. After 20-30 minutes they had a delayed-recall task for the figure.

3.1.2 Experimental Task

The task was modified in several ways. First, in order to make the memory test more challenging for healthy participants, double the number of scenes were shown at encoding. The same 14 categories were used with the same 8 exemplars but two different scenes from each category were presented (both contained different exemplars). For example, in the stationery category one scene might contain a stapler and a highlighter pen and the other a roll of tape and a ruler. Scenes from the same category were not presented in the same encoding block. Encoding was split into 4 blocks of 7 scenes. As before, at the end of each block participants were cued with the category name and then asked to recall the items, their positions, and the viewing angle they experienced that scene from. To increase the difficulty further the recognition test in the scanner for the novel scenes took place the day after encoding, rather than on the same day.

Again all participants wore a head camera during encoding. They were shown this camera and it was explained to them that a still would be taken of each scene to be used in a memory test in the scanner on the following day. As in Experiment 1, we had pre-prepared stills of each scene. On the first day, encoding was followed by administration of standardised tests. At the end of the session participants were presented again with the to-be-encoded scenes, but for only 15 seconds. This was added, as piloting revealed this facilitated maintenance of the scenes for the next day in the older group.

In the recognition test in the scanner on day 2 the task was adapted to enable us to interrogate the imaging data. We sought to decode neural activity in response to images from within specific conditions and it was therefore necessary to have only one visible at a time. Participants saw 28 individual scenes, two times during the scanning session. Ten of these scenes were identical to the ones shown in the lab the day before (i.e., the scene that they saw from the angle in which they had viewed it, *identical* condition), 10 were of the same scene but taken from the opposite viewing perspective (*perspective shift* condition), 4 were taken from the same viewing angle with the same items but they were placed in different position (*item shift* condition), and 4 were from the same viewing angle, the same category and same squares used but contained different exemplars (*object change* condition).

Images were displayed for five seconds. After the stimulus disappeared a question was presented on screen: “Did you see this scene in the lab yesterday?” It was emphasised that the viewing angle of these images was not relevant for the first question. They were required to respond whether those items in those grid positions were seen during encoding. If participants responded ‘yes’ then they were asked: “Was the scene taken from your viewpoint (i.e. it is the image from your head-camera)?” The task took approximately eight minutes, after which an anatomical scan of the participants’ brain was taken for 4 and half minutes. The participant then repeated the recall experiment in order to increase discrimination power.

3.1.3 Imaging & data analysis

Data were acquired at the Combined Universities Brain Imaging Centre (CUBIC) with a 3T MRI scanner (Magnetom Trio, Siemens, Erlangen, Germany) using a standard Siemens eight-channel array headcoil. Functional images were acquired with a gradient-echo, echoplanar (EPI) sequence (TR 3000 ms, TE 31 ms, voxel size 3 x 3 x 3 mm) comprising 41 axial slices (64 x 64 matrix) covering the entire brain, and acquired continuously during each experimental run (231 timepoints). A high-resolution (1 x 1 x 1 mm) anatomical scan of the whole brain was also acquired.

All data were pre-processed using SPM8 (www.fil.ion.ucl.ac.uk/spm/) and included slice-time correction, motion correction, and spatial smoothing using a Gaussian kernel with FWHM of 6mm. A general linear model approach was used to model each individual correct trial as a separate regressor, and convolved with the canonical hemodynamic response function. Modelled trials represented the 5s presentation of the visual scene plus the time leading to their response. The 'object change' and item shift' trials were also included as regressors of no interest, as were the realignment parameters as calculated during motion correction. Participant-specific parameter estimates were calculated for each regressor and transformed into t-values resulting in a series of t-maps representing trial-specific activation for use in the subsequent MVPA analysis.

A searchlight approach was adopted to identify those regions of the brain sensitive to differences between ‘identical’ and ‘perspective shift’ scenes. MVPA was performed with custom written Matlab scripts utilizing a linear support vector machine (LIBSVM; www.csie.ntu.edu.tw/~cjlin/libsvm/). A spherical ROI (radius = 3 voxels) was defined that moved sequentially through every voxel in the functional volume space providing 123 t-

values from each ROI for classification purposes. Thus the feature matrix for pattern classification comprised 40x123 elements (20 exemplars of the 'identical' response and 20 exemplars of the 'perspective shift' response [from 2 recording sessions], 123 voxels ROI), with each feature normalised to unit length. The information content of each searchlight ROI was assessed using a k-fold cross validation approach (k=5). Partitioning of the feature matrix into training and test sets was balanced such that there were always two examples of each condition from both sessions. Classifier accuracy was calculated by averaging over the 5 folds. In order to generalise the results and assess overall classification performance, the final three-dimensional maps of decoder accuracies for each participant were normalised to MNI space and smoothed with a 6mm Gaussian filter.

Group analysis, testing whether decoding performance was above chance between subjects, was conducted using a voxelwise non-parametric permutation test (FSL Randomise; Winkler et al, 2014) and corrected for multiple comparisons using threshold-free cluster enhancement. In order to investigate the functional role of the parietal lobe as well as the lesioned areas as identified in Experiment 1, we restricted this group analysis to two regions of interest: The lesion region as determined from the patient study (Figure 1), and a broader bi-lateral parietal lobe ROI defined using WFU Pickatlas (Ver. 3.0.4; Maldjian et al, 2003).

3. 2 Results

3.2.1 Standardised Tests (Table 2)

Rivermead Behavioural Memory Test:

Recognition by older participants did not significantly differ from younger participants after a 30-minute delay, $U = 49$, $z = -1.29$, $p = .31$.

Corsi Block Tests:

Scores on the forward tapping task did not significantly differ between younger and older participants, $t(21) = -1.34$, $p = .19$. This was also true in the backwards condition, $t(21) = -.97$, $p = .34$.

Bushcke Selective Reminding Task:

Younger participants were able to recall significantly more words after a 30-minute delay than the older participants, $U = 23$, $z = -2.80$, $p = .01$.

Rey Complex Figure:

Figures were scored according to the Boston Qualitative Scoring System (Stern et al, 1994). There were no significant differences between the groups $t(17) = -.20$, $p = .84$.

	Older Group	Younger Group
Line drawing – memory task (proportion)	.96 (.56)	.99 (.39)
Corsi blocks forward span	6.20 (1.32)	6.92 (1.26)
Corsi blocks backwards span	5.80 (1.55)	6.31 (.95)
Bushcke Selective Reminding Task (30 min delay - /12)	9.3 (2.98)	11.69 (.48)
Rey-Osterrith Complex Figure Task (delayed retention %tile)	47.25 (15.63)	48.91 (18.82)
Experimental Task		
Question 1	d' 2.96 (.80)	d' 3.86 (.43)
'Did you see this scene in the lab yesterday?'	Hit rate .94 (.06)	Hit rate .97 (.02)
	False alarm .16 (.16)	False alarm .04 (.06)
Question 2		
'Is this the image from your own view (your head camera)?'	d' 1.10 (.94)	d' 2.51 (.94)
	Hit rate .71 (.15)	Hit rate .90 (.08)
	False alarm .34 (.17)	False alarm .17 (.13)

Table 2

Data from behavioural measures in Experiment 2 (standard deviations in brackets).

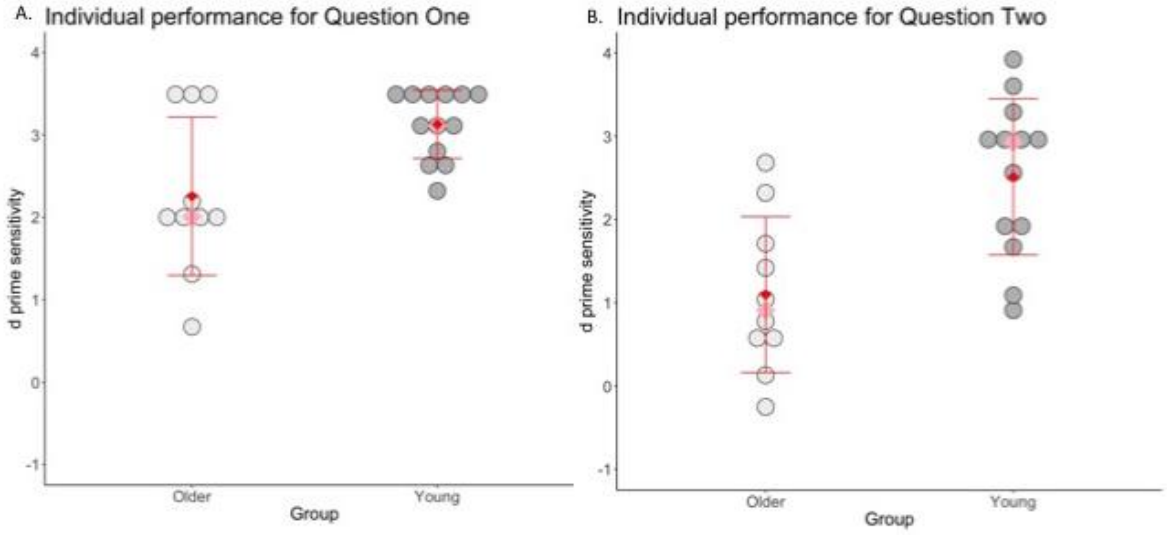


Figure 4

Dots plot scores of individual participants: Red diamonds indicate mean; red lines are standard error bars; pink diamonds indicate median.

3.2.2 Experimental task

First, responses to Question 1 ('Did you see this scene yesterday?') were analysed. There were 4 conditions (Identical; Perspective shift; Object Change; Item shift). The correct answer to this question for Identical and Perspective shift should be 'yes' and 'no' for the other two conditions. The paradigm lends itself well to analysis with a sensitivity measure such as d'prime. Questions such as 'Is this the image from your head camera?', are potentially affected by response bias – somebody might be more prone to respond 'yes' and achieve a similar percentage correct to another participant who is more selective. Therefore, we analysed target sensitivity (d') according to signal detection theory, taking account of proportion for hit rates and false alarms in each question (Table 2). For question 1 'Did you see this scene in the lab yesterday?' saying 'yes' to the 'Identical' and 'Perspective-Shift' trials was correct –the hit rate - whereas saying 'yes' to object change

and item shift constituted false alarms. Independent samples t-test on this sensitivity analysis revealed the older group to be significantly worse than that younger group ($t(21) = -3.50$, $p = .002$).

Responses to the second question (Is this the image from your head camera?) were then analysed. As participants were only asked this question if they answered that they had seen the scene yesterday, data here were analysed only for the relevant conditions –'Identical' and 'Perspective shift' stimuli. Here responding 'yes' to 'Identical' trials constituted the hit rate whereas responding 'yes' to 'Perspective shift' trials was considered a false alarm. Here, the older group were again significantly worse than the younger group $t(21) = -3.59$, $p = .002$). Although the older participants were not significantly worse than the younger group in the Rivermead recognition task, Rey Complex Figure task and the forwards and backwards Corsi blocks, they were less sensitive than the younger group to the correct answers for both questions in our experimental paradigm. They also recalled significantly fewer words in the Bushcke task than younger participants.

3.2.3 Imaging Data

MVPA searchlight analysis was carried out to identify areas of the brain sensitive to changes in viewing angle (i.e. brain areas whose responses differ such that they differentiate between identical and perspective shift scenes). We restricted the group level analysis to two ROIs: the lesion region and bilateral parietal lobes. The statistical maps derived from this group analysis of both the young and old individual classifier accuracy maps (testing for classifier accuracy > 50% and thresholded at $p<0.05$, FWE corrected for multiple comparisons) are shown in Figure 5.

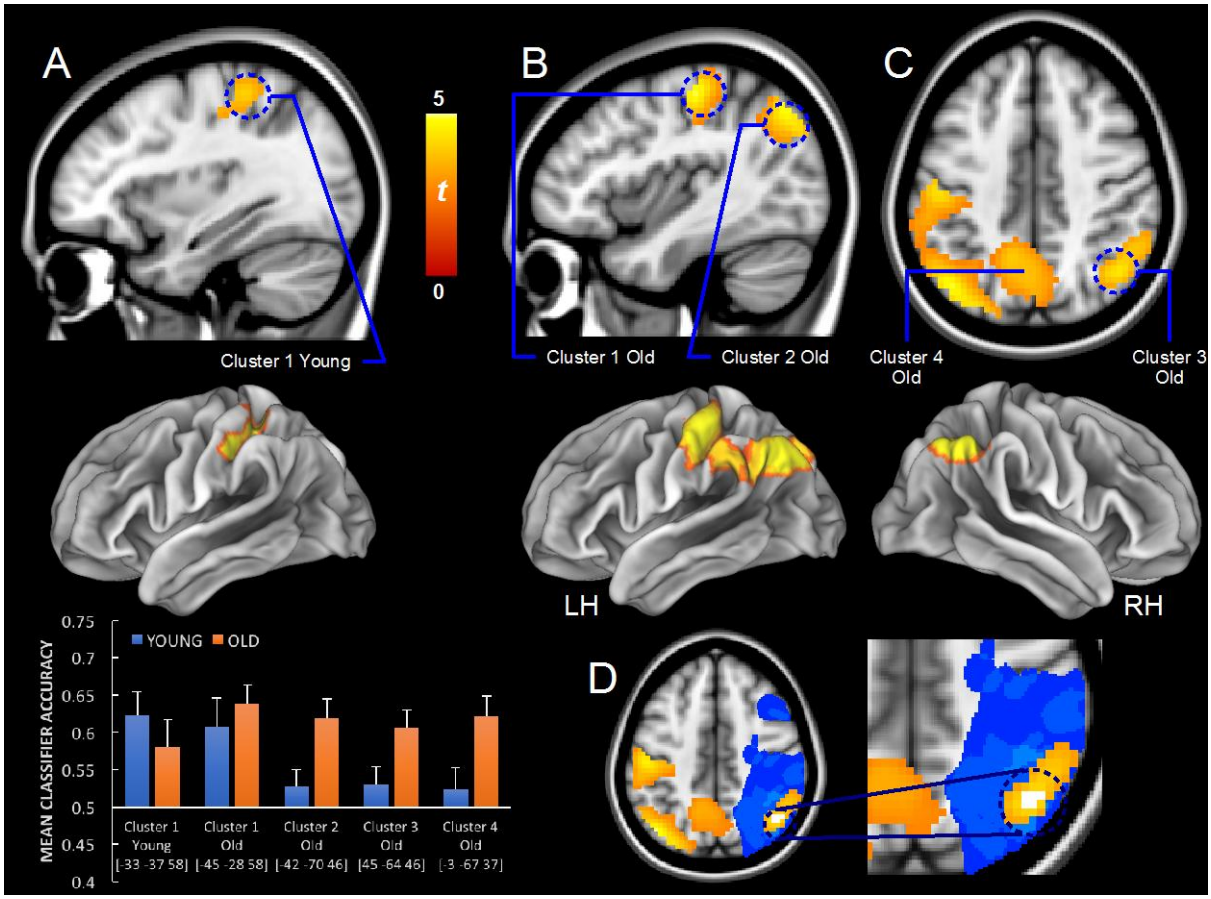


Figure 5

Group classifier maps indicating areas of significant decoder performance in differentiating the neural response associated with correctly identified identical/perspective-shift scenes (classifier accuracy > 50%; threshold p<0.05, FWE corrected for multiple comparisons). These are all superimposed on a template brain in the MNI coordinate space. Blue circles highlight statistically significant cluster peaks. (A) Young group; (B) & (C) Older group; (D) Blue overlay represents the lesion map ROI, orange/yellow overlay represents the group classifier map established in the older group parietal ROI (as shown in B & C), white overlay represents the group classifier map from the lesion ROI in the older group.

Independent t-tests comparing each cluster across groups revealed that there were no significant differences between old and young for the left hemisphere circled cluster in 5A (Cluster 1 Young; t(21) = -.88, p = .39) and the left hemisphere circled anterior cluster in 5B (Cluster 1 Old; t(21) = .62, p = .55). Whereas the classifier accuracy in the other three areas of significance in the old group

significantly differed between the two groups: posterior circled region in 5B (Cluster 2; t(21) = -2.70, p = .01); circled region in 5C (Cluster 3; t(21) = -2.24, p = .04); and the precuneus region (Cluster 4; t(21) = 2.37, p = .03).

See Supplementary methods for whole brain analysis.

The analysis within the larger bilateral parietal ROI reveals a number of distinct clusters in both groups. In the young participants, 'Cluster 1 Young' emerges with a peak within the inferior parietal lobe of the left hemisphere (Fig 5A, mean classifier accuracy at statistical peak 66%; *t*=3.98; MNI -33, -37, 58). The older group in contrast shows much larger networks of the parietal region sensitive to differences between identical and perspective shift scenes. In the left hemisphere, two lateral parietal clusters can be seen (Fig 5B) - one more anterior, close to the postcentral gyrus ('Cluster 1 Old',accuracy 61%; *t*=4.89; MNI -45, -28, 58) and corresponding to that observed in the younger group; the second in the inferior parietal lobe and encompassing the angular gyrus ('Cluster 2 Old', accuracy 53%; *t*=4.86; MNI -42, -70, 46). A similar cluster to this is observed in the right hemisphere again in the region of inferior parietal and angular gyrus (Fig 5C, 'Cluster 3 Old', accuracy 55%; *t*=4.47; MNI 45, -64, 46). Finally, a midline cluster spanning both hemispheres is observed in the region of the precuneus (Fig 5C 'Cluster 4 Old', accuracy 53%; *t*=4.18; MNI -3, -67, 37).

When the group analysis is restricted to the ROI defined by the lesion map, a smaller cluster centred around the same right hemisphere angular gyrus region as identified above is evident in the older group. This is shown in Fig 5D as the small white cluster overlayed on the parietal lobe map as described above as well as the lesion ROI (shown in blue). Unsurprisingly, no clusters were observed in the younger group within this ROI.

Results revealed by MVPA show that specific patterns of activity in areas of parietal cortex were indicative of whether participants were viewing either a scene they encoded the previous day *from the view in which it was experienced* or the same scene from a *different perspective*. This reinforces the proposal, supported by the results of Experiment 1, that the role for parietal cortex within episodic memory is directly related to recalling from one's own eyes –egocentric – encoding perspective. In the young group it would appear that left parietal cortex is vital– for example the area of supramarginal gyrus indicted in our classification analysis - whereas in the older group we revealed evidence of a wider network, which encompasses the angular gyrus in both hemispheres. The involvement of angular gyri in our task harmonises with evidence from previous neuropsychological, neural disruption and functional imaging studies that these regions are involved with the subjective experience of recalling an episodic memory (eg.,Davidson et al 2008; Sestieri et al, 2013; Marcotti and St Jacques, 2018). We suggest that recall of our memory from an egocentric perspective – as we experienced it at the time – is crucial to this sense of subjective experience.

Regarding the results from the younger group there is a question regarding why classification accuracy in decoding differences between the key conditions did not activate the larger network of areas identified in the older group. First, we draw attention to functional imaging studies of memory with standard univariate analysis comparing young and older groups. There are many examples of greater neural recruitment in older adults, potentially as compensation for less efficiency (e.g., Angel et al, 2014, Stern et al, 2012; Zarahn et al, 2007). Morcom & Friston (2012), used an analysis similar to that adopted here,

to decode neural activity patterns associated with successful recall in younger and older adults. Their analysis revealed wider involvement of bilateral networks in the older as compared to the younger group. In contrast, Wang et al (2016), using MVPA, revealed no differences between young and old adults but this was in the context of no group differences in the behavioural assessment of memory – in contrast to our study. We would suggest that a key reason for our results is that the young group found the task rather easy as, in order to achieve reasonable accuracy in the older group across a complicated set of stimuli and a long time gap, there were only 28 scenes and these scenes were shown twice. It is possible that the younger group did not need to use the same strategy as the older group – a strategy that is key to our design i.e. recreating a mental image of the scene when encoded. A hint of this is that at debrief some younger participants reported recalling which chair they sat in for the different scenes as a mnemonic - older participants never reported this strategy. We believe that in follow-up work, if this strategy is counteracted and the task more challenging for younger participants, they would show the same regions are being used for this task.

4. General Discussion

In the two studies presented here we have introduced a novel paradigm that demonstrates a key role for ventral parietal regions in egocentric perspective information within episodic memory. This is important as accurately recalling experienced events from one's own perspective is linked with increased accuracy and stronger sense of subjective experience (e.g., Marcotti and St Jacques, 2018). Our data support research implying a role for vividness of recall in activation of ventral regions of parietal cortex, and suggest, an alternative or additional account to those currently posited-that these regions are involved in multimodal

representations and processing of context per se in episodic memory (e.g., Bonnici et al 2016 and Ramanan, Piquet & Irish, 2017). It appears likely from this evidence (where modality was the same across conditions) that the visual-spatial representation from one's own encoding view is perhaps a critical context processed by these areas of parietal cortex.

In Experiment 1, our paradigm revealed a deficit in egocentric visuospatial memory in patients with right parietal damage. This is the first demonstration of a specific episodic memory deficit in this patient group using a new task. The next step is to carry out a larger study clarifying whether this deficit in accurate recall from an egocentric perspective might explain previous findings in patients with parietal damage who lacked vivid detail in recalling and had a reduced feeling of recalling a personally experienced event when remembering (e.g., Drowos et al, 2010). The results described here help to explain the role of parietal cortex in episodic memory and suggest that patients with parietal damage may have long-lasting deficits in this domain. Another important avenue for further exploration, would involve assessment of patients with damage to analogous left-hemisphere regions. This would be valuable as evidence suggests that the right hemisphere may be specialised for egocentric processing (e.g. Iachini, Ruggiero, Conson & Trojano, 2009).

It is difficult to draw strong conclusions about the relative roles of the left and right hemispheres from the existing literature concerning episodic memory following parietal damage. Some studies have only tested very small groups of patients with bilateral damage (n=2: e.g., Berryhill et al, 2009; 2007; Drowos et al, 2010; Hower et al, 2014). Or their critical impairment has only been found in a bilateral group and not in either group of unilateral patients (e.g., Simons et al, 2010). Davidson et al (2008) assessed a group of four left

hemisphere patients and one right hemisphere patient, precluding separate analysis of the two groups. Recently Ciaramelli et al (2017) tested six patients in their main analysis from an original group of five with left and two with right hemisphere damage but did not state which hemisphere was damaged in the patient who did not complete the study and analysis was not separated according to lesion side. To our knowledge only one study has separately analysed patients with left (n = 3) versus right (n = 4) parietal damage (Ciaramelli et al, 2010), revealing those with left hemisphere damage to be more impaired on two topographical tasks loading on egocentric as opposed to allocentric memory. However, pertinent to our current paradigm, there were similar impairments in both groups when patients were directly asked if they recalled their route from a first ('field') or third ('observer') person perspective (only two left hemisphere patients and two right hemisphere patients used a first person perspective) and both groups were abnormal when asked if they 're-experienced' the route during recall. Only one individual reported 're-experiencing' the memory and they had left hemisphere damage. This was a small group but it is relevant that no right hemisphere patient reported re-experiencing the memory. Right hemisphere regions might be particularly important for re-experiencing an event, for which it is crucial to reconstruct the visual spatial image of the event as we experienced it, from our own eyes' perspective.

Our study is an important development as, to our knowledge, this is the largest patient study examining episodic memory in patients with parietal damage in which they are matched for lesion hemisphere. Given the disparity in stroke outcome after left versus right hemisphere damage in attention as demonstrated by the far greater number of patients with spatial neglect after right hemisphere damage (e.g., Stone et al, 1993), it is important

to analyse patients with damage to each hemisphere separately. Further, evidence suggests that any spatial neglect after left hemisphere stroke impairs allocentric spatial processing more than egocentric (see Kleinman et al, 2007).

In the second experiment healthy older participants were impaired in judging whether a presented scene was from the same perspective they viewed it from - in contrast to performance in most other tests of episodic and working memory. Functional imaging using MVPA in older participants during our task revealed that ventral parietal regions, including angular gyrus, were sensitive to differences between stimuli from a self or other perspective. In the older group, ROI analysis of bilateral parietal cortex revealed the angular gyrus to be involved in correctly discriminating whether a scene at retrieval was the same as one's own perspective. Therefore, both left and right hemisphere are involved in making the judgment critical to our task. Regions around the angular gyri bilaterally were significantly accurate in distinguishing between self versus another's visual perspective in previously encoded scenes. It is clear that the left hemisphere is critically involved in episodic memory and the previous focus on this area is not simply a result of the nature of the stimuli or language requirements in the task – in our task verbal encoding of the scenes would be very unlikely to encapsulate the visuo-spatial differences between one's own versus another's angle of view. This raises the question of why were patients had an intact left hemisphere impaired in our task? Taken together, our results might suggest that although the left hemisphere is important, the right hemisphere regions are necessary to reliably make the judgement required here. As discussed above, examination of neuropsychological evidence for the role of the different hemispheres of parietal cortex in episodic memory is not fully informative at present. Though we would draw attention to evidence from other studies

that these regions in the right hemisphere might be concerned with recalling personally experienced episodic information regarding the self both visuo-spatially (e.g. St Jacques et al, 2016) and auditorily (e.g., Levine et al 2004). This is consistent with the separate analysis of right and left hemisphere patients in Ciaramelli et al (2010) – that is, the right hemisphere patients did not 're-experience' the memory and were poor with first-person recall. As well as examining left-hemisphere patients, study of the connectivity between these regions in a task similar to ours might enable further clarification. Bellana et al (2016) carried out analysis of bilateral angular gyrus connectivity with the default mode network (DMN). They found that left and right angular gyri were strongly connected to this DMN at retrieval, with right angular gyrus being more strongly connected to medial temporal lobe (MTL) regions and the left angular gyrus with other units of the DMN. This provides converging evidence that the hemispheres have differing roles during episodic recall.

In conclusion, our studies reveal egocentric episodic deficits in patients with right parietal damage and delineate the role for ventral lateral parietal regions in egocentric representation in a functional imaging studying using classification analysis. The results presented here provide important evidence that parietal cortex activity is directly associated with egocentric spatial perspective aspects of episodic memory and demonstrate for the first time a specific deficit in this cognitive process in patients with right hemisphere parietal damage.

5. Acknowledgements

We thank all our participants for their incredibly valuable help. This work was supported by a grant from the Bial Foundation, Portugal (155/10) and the National Institute for Health Research (NIHR) Imperial Biomedical Research Centre.

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