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Subjective recollection independent from multifeatural context retrieval following damage to the posterior parietal cortex

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ABSTRACT

This study investigated whether damage to the posterior parietal cortex (PPC) impairs the capacity to retrieve multiple aspects of the encoding context in which items were studied, or whether it impairs the subjective awareness of recollection. Patients with lesions to the PPC (PPC patients) and healthy controls memorized words along with the position in which the words were presented on the screen and the ink color in which they were printed. We studied PPC patients' recognition and source memory performance, as well as subjective recollection as indexed by Remember/Know judgments. PPC patients had preserved recognition memory, and gave a similar number of R responses as did controls. Moreover, PPC patients' source memory performance, including memory for multiple contextual features, was similar to the controls'. However, whereas healthy controls were more likely to select R responses with correct multifeatural source judgments compared to K responses, PPC patients were not. These findings indicate that the PPC plays a role in the subjective experience and metamnemonic evaluation of memory contents.

1. Introduction

Episodic memory is the ability to recollect specific past experiences. One prominent – if not defining – property of episodic memory retrieval is the reinstatement of multiple contextual features characterizing the original event. It is this aspect of episodic memory retrieval that makes it "mental time travel" (Tulving, 1985): re-living a past event with a level of vividness and an experiential richness comparable to that of direct (perceptual) experience. In the laboratory, episodic memory

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retrieval typically is assessed by investigating individuals' ability to retrieve contextual aspects of the learning episode, such as the original position or color of an item at study (in source memory tasks), or by examining individuals' ability to judge whether memory retrieval is accompanied by a feeling of re-accessing the learning context as opposed to merely having a sense of familiarity (in the Remember (R)/Know (K) paradigm).

Functional neuroimaging (fMRI) and neuropsychological studies of brain-damaged patients converge in showing that the medial temporal lobes (MTLs) and prefrontal cortex are crucial for episodic memory retrieval, orchestrating search, reinstatement and monitoring of past experiences (Cabeza & St. Jacques, 2007; Dobbins, Foley, Schacter, & Wagner, 2002; Gilboa et al., 2005; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Ranganath, Johnson, & D'Esposito, 2003; Rugg, Fletcher, Chua, & Dolan, 1999; Simons & Spiers, 2003). More recent research has called attention to the posterior parietal cortex (PPC) as an additional neural correlate of episodic memory retrieval. There is, indeed, fMRI evidence of a "retrieval success effect" in PPC, characterized by greater activity for recognition hits compared to correct rejections (for reviews, see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Gilmore, Nelson, & McDermott, 2015; Vilberg & Rugg, 2008; Spaniol et al., 2009; Wagner, Shannon, Kahn, & Buckner, 2005). Successful autobiographical memory retrieval is also associated with activity in PPC (Cabeza & St. Jacques, 2007; Philippi, Tranel, Duff, & Rudrauf, 2015; Svoboda, McKinnon, & Levine, 2006). The ventral PPC is particularly active during retrieval of memories rich in contextual details (Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins et al., 2002; Kahn, Davachi, & Wagner, 2004) and memories vividly recollected rather than simply familiar (Duarte, Henson, & Graham, 2008; Eldridge, Engel, Zeineh, Bookheimer, & Knowlton, 2005; Wheeler & Buckner, 2004; Yonelinas, Otten, Shaw, & Rugg, 2005).

Drawing brain-behavior inferences in cognitive neuroscience requires converging methods. Lesion studies, in particular, have the potential to relate brain activity causally with behavior, and constrain the interpretation of the function of target brain regions in a way that is not possible with neuroimaging data alone (Rosenbaum, Gilboa, & Moscovitch, 2014). Despite the fMRI evidence for a role of PPC during episodic memory retrieval, there have been few studies of memory in patients with damage to PPC. In general, such patients show subtle memory deficits, certainly not as severe as those observed in patients with lesions to the MTLs or prefrontal cortex. Nonetheless, the neuropsychological findings align with fMRI evidence implicating PPC in episodic recollection. PPC patients, indeed, do not generally have a recognition memory impairment (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; Ciaramelli, Rosenbaum, Solcz, Levine, & Moscovitch, 2010; Haramati, Soroker, Dudai, & Levy, 2008; Simons, Peers, Mazuz, Berryhill, & Olson, 2010), but may show a lower frequency of subjective states of remembering (i.e., R responses; Ciaramelli, Rosenbaum, et al., 2010; Davidson et al., 2008; Drowos, Berryhill, Andre, & Olson, 2010), and reduced confidence in memory (Hower, Wixted, Berryhill, & Olson, 2014; Simons et al., 2010). Surprisingly, PPC patients have preserved source memory (Davidson et al., 2008; Simons et al., 2008, 2010). Together, these findings have suggested that PPC may be more concerned with the *subjective* experience of one's recollections, rather than the *objective* ability to recollect contextual details of past experiences (Simons et al., 2010). Alternatively, PPC may mediate the automatic capture of attention by vivid memory contents (supposedly associated with remembering states), which remain accessible voluntarily during source memory tasks (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Ciaramelli et al., 2008; see also Berryhill, 2012, and Cabeza et al., 2008, for reviews of competing accounts of the role of PPC in memory retrieval).

As we noted earlier, episodic memory serves retrieval of complex, multi-featural experiences. Source memory tasks, therefore, may be underpowered to detect subtle source memory deficits. This is all the more relevant when focusing on the role of PPC in source memory. The ventral PPC is thought to mediate the integration of perceptual information for attention and action, both within and between sensory modalities. For example, the PPC has been associated with color–form binding in conjunction visual search tasks (i.e., visual search for a target defined by a conjunction of features; Ashbridge, Walsh, & Cowey, 1997; Donner et al., 2002), and patients with bilateral PPC lesions have difficulty in conjoining shape and color (Freidman-Hill, Robertson, & Treisman, 1995). Suppression of PPC excitability with transcranial magnetic stimulation (TMS) decreases individuals' sensitivity in conjunction (but not single feature) visual search tasks (Ashbridge et al., 1997; Muggleton, Cowey, & Walsh, 2008), and impairs the integration of audio-visual (Bertini, Leo, Avenanti, & Làdavas, 2010) and audio-tactile information (Serino, Canzoneri, & Avenanti, 2011). TMS over the PPC also attenuates the unusual induction of color from graphemes characteristic of some forms of synesthesia (Esterman, Verstynen, Ivry, & Robertson, 2006), further confirming the role of PPC in perceptual feature binding (Robertson, 2003; Seghier, 2013). Shimamura (2011) has recently proposed that the ventral PPC may play a similar integratory role in memory as it does in perception, helping bind and retrieve multiple episodic features, processed in different cortical regions. One prediction of this hypothesis is that the involvement of PPC in source memory (and source memory deficits following PPC damage) should be magnified when the task requires retrieval of ensembles of episodic features as opposed to isolated features, especially if the features rely on processing in disparate brain regions. A recent fMRI study tested this prediction empirically. Bonnici and colleagues investigated brain activity while participants recalled memories for items viewed on a computer screen, heard through headphones, or presented concurrently both auditorily and visually (Bonnici, Richter, Yazar, & Simons, 2016). They showed that the angular gyrus was more engaged during retrieval of audio-visual episodic memories than during retrieval of unimodal auditory or visual memories, supporting the view that ventral PPC may support retrieval of rich, multifeatured episodic memories (Bonnici et al., 2016; Shimamura, 2011).

The fact that PPC may support the integration of multiple features of episodic memories is relevant for interpreting the pattern of results including impaired subjective recollection with preserved source memory observed in PPC patients. This

dissociation may relate to the fact that subjective memory judgments reflect a global assessment of recollection which is likely informed by multiple memory features (Parks, 2007; Yonelinas & Jacoby, 1996). In contrast, source memory studies typically assess retrieval of individual contextual features (e.g., color, position, presentation modality). A problem with feature integration during memory retrieval in PPC patients, therefore, could result in reduced remembering states with preserved source memory judgments for the individual features of an experience. To test this hypothesis, we had PPC patients and healthy controls memorize words as well as the color in which they were presented (red vs. green) and their position on the screen (top vs. bottom). We studied PPC patients' recognition performance, subjective experience of retrieval, and source memory for color and position information. If PPC patients have a problem at retrieving multifeatural context (Bonnici et al., 2016; Shimamura, 2011), they should be able to identify single contextual features (color *or* position), but be less likely to recollect items in their "multifeatural" context than controls, specifying both their color *and* position at study. In contrast, if PPC patients' main problem concerns the subjective experience of recollection, they should show preserved (multifeatural) context retrieval, and yet reduced subjective recollection experience resulting from an inability to translate the reinstatement of multiple contextual features into the typical subjective experience.

2. Methods

2.1. Participants

Seven individuals with damage to the PPC and 38 age-matched healthy individuals participated in the study. Patients were recruited at Baycrest Hospital, Toronto, Canada (3 cases), at the Centre for Studies and Research in Cognitive Neuroscience, Cesena, Italy (2 cases), and at the Spedali Riuniti, Brescia, Italy (2 cases; see Table 1 for demographic and clinical data). Patients were selected on the basis of the location of their lesion evident on magnetic resonance imaging (MRI) or computed tomography (CT) scans. Included patients had a lesion in PPC, in no case invading the medial/limbic region, and no other diagnosis likely to affect cognition or interfere with the participation in the study (e.g., psychiatric or cerebrovascular disease, alcohol abuse). All patients were in the stable phase of recovery (at least 12 months post-morbid).

The boundary of the lesion was manually delineated on each MRI/CT scan using the software MRIcro (Rorden & Brett, 2000). Fig. 1 shows the extent of damage for each patient. Two patients had right-hemisphere lesions, and five patients had left-hemisphere lesions. In general, the lesion encompassed both ventral parietal cortex (BA 39, BA 40; mean lesion volume in BA 39 = 31.49 cc, mean lesion volume in BA 40 = 11.28 cc) and dorsal parietal cortex (BA 7; mean lesion volume = 24.74 cc; see Fig. 1), and in four cases it involved the angular gyrus (BA 39). In three patients, the lesion extended to the occipital lobe (BA 19; mean lesion volume = 30.85 cc, corresponding to 14% of total lesion volume). In one patient, the lesion also involved the ventrolateral prefrontal cortex (BA 44, BA 45). Considering that the size of this patient's parietal lesion was almost double that of his frontal lesion, we decided to include him in the patient sample. Excluding this patient from the analyses did not alter the pattern of results.

PPC patients' general cognitive functioning was preserved (see Table 1), as indicated by the scores they obtained in the Mini Mental State Examination and in verbal fluency (for normative data, Spinnler & Tognoni, 1987; Spreen & Strauss, 1998), which was normal in all cases. Immediate and delayed long-term memory were assessed with the Hopkins Verbal Learning Test – Revised in Canadian patients (Benedict, Schretlen, Groninger, & Brandt, 1998), and with the Rey Auditory Verbal Learning Test (Spinnler & Tognoni, 1987) or the Buschke–Fuld test (Buschke & Fuld, 1974) in Italian patients. Only one patient had impaired long term memory recall (and our results do not change if we exclude this patient from the analyses). In addition, there were no documented cases of aphasia among the patients with damage in left PPC, and no documented cases of hemispatial neglect among those with damage in right PPC.

The four Italian patients (2 males; mean age = 58 years; mean education = 11 years) were matched to a group of 24 healthy Italian individuals (11 males; mean age = 52 years; mean education = 12 years) on the basis of gender balance, age, and education. The three Canadian patients (3 males; mean age = 61 years; mean education = 17 years) were matched to a group of 14 healthy Canadian individuals (11 males; mean age = 63 years; mean education = 14 years) on the basis of gender balance and age. In the Canadian sample, education was slightly higher in patients than in controls. Participants were screened for clinically significant depression, alcohol and drug abuse, epilepsy, and any other known neurological conditions. The ratio of patients to healthy controls was similar for the Italian and Canadian sample, $\chi 2$ (1) = .09, p = .76. For analysis purposes, we collapsed Italian and Canadian participants into one group of seven PPC patients (5 males), with a mean age of 59 years (range 47–76) and a mean education of 13 years (range 5–17), and one group of 38 healthy controls (22 males), with a mean age of 56 years (range 34–75) and a mean education of 13 years (range 5–17). PPC patients did not differ in age, $t(43) = .78$, $p = .43$, $\eta_p^2 < .01$, education, $t(43) = .31$, $p = .75$, $\eta_p^2 < .01$, or gender balance, $\chi 2$ (1) = .45, p = .50. All participants gave informed consent, and the study procedures were approved by the ethics committees of the University of Bologna, Baycrest Hospital, and Ryerson University, and in line with the Declaration of Helsinki (International Committee of Medical Journal Editors, 1991).

2.2. Materials

Ninety medium frequency words, between 4 and 8 letters long, were selected from the Kucera and Francis (1967) pool (for the Canadian task; mean frequency per million = 39.35; mean concreteness = 6.05) or the Barca, Burani, and Arduino (2001) pool (for the Italian task; mean frequency = 55.3 per million; mean concreteness = 6.13). The frequency of Italian words was slightly higher than that for English words, but we think this does not constitute a problem since an equal ratio of

Table 1 – Patients' demographic and clinical data.

PPC patients' initials	Sex	Age (years)	Education (years)	Etiology	Lesion side	MMSE	Verbal (phonemic) fluency	LTM retrieval	LTM retention
AC (C)	M	47	16	Stroke	L	29	17 (44.7 ± 11.2)	19* (28.8 ± 3.8)	8 (10.3 ± 1.7)
DZ (I)	F	57	13	Tumor	L	28	42 (30.7 ± 11.3)	106 (85.1 ± 50.8)	8 (8.6 ± 1.7)
AE (I)	F	49	13	Stroke	L	27	53 (33.9 ± 9.1)	53 (44.4 ± 8.8)	12 (9.8 ± 2.6)
AF (I)	M	76	5	TBI	L	26	20 (25.9 ± 9.2)	36 (34.3 ± 6.7)	6 (6.6 ± 2.2)
AS (C)	M	62	17	Stroke	L	28	22 (42.0 ± 12.1)	19 (27.5 ± 4.3)	8 (9.8 ± 1.8)
SS (C)	M	75	17	Stroke	R	30	55 (42.0 ± 12.1)	24 (25.2 ± 5.5)	5 (8.7 ± 2.8)
DB (I)	M	51	8	Stroke	R	25	–	36 (41.8 ± 8.4)	11 (8.8 ± 2.5)

Note: PPC = posterior parietal cortex; M = male, F = female, C = Canadian, I = Italian, L = left, R = right, MMSE = Mini Mental State Examination, LTM = long term memory. Note that immediate and delayed LTM were assessed with the Hopkins Verbal Learning Test – Revised in Canadian patients (Benedict et al., 1998), and with the Rey Auditory Verbal Learning Test (Spinnler & Tognoni, 1987) or the Buschke–Fuld test (Buschke & Fuld, 1974) in Italian patients. We report the patients' uncorrected scores, and, in parentheses, the mean and standard deviation of the normative sample. The asterisk signals a score deviating from the mean more than 2.5 standard deviations, and the dash indicates missing data.

patients/controls received the Italian and English version of the task. Sixty words were studied and the other 30 words were not studied but served as distractors during the recognition phase. The assignment of words to target or distractor status was counterbalanced across participants.

2.3. *Procedure*

At study, 60 words were presented visually at a rate of one word every 3 sec, with an inter-stimulus-interval of 1 sec. Words appeared either in the upper or in the lower half of the screen, and were printed either in a green or in a red ink. Moreover, to investigate laterality effects on memory performance, half of the items appeared on the left side of the screen, and the other half appeared on the right. Participants were told to do their best to memorize each word, whether it appeared on the top or the bottom of the screen (regardless of the side), and whether it was presented in a green vs. red ink. The assignment of words to the left vs. right side of the screen, to the top vs. bottom position, and to the green vs. red ink color, was randomized for each participant.

The recognition test, which immediately followed the study session, comprised the 60 studied words and 30 new items. All words were presented in the center of the screen, and in black ink. Participants were requested to indicate, for each word, whether they had seen it at study, by pressing one of two buttons, and to indicate the confidence associated with their decision on a scale from 1 (low confidence) to 7 (high confidence). For each word they judged "old", they were additionally asked to indicate whether they remembered or knew the word (Tulving, 1985). Participants were instructed to give a "Remember" (R) response if they could mentally travel back to the moment of seeing the word and remember something about that encounter. In contrast, participants were instructed to give a "Know" (K) response if they believed that the word was presented earlier, but they could not recollect anything specific about the moment of its occurrence (Yonelinas, 2002). To ensure that participants understood the distinction between R and K responses, they were asked to explain the R/K distinction to the experimenter, using their own words. Finally, for each recognized item, participants were asked to indicate whether at study it had been presented on the top or the bottom of the screen (i.e., position identification task), and whether it was printed in a red or a green ink (color identification task).

3. Results

One PPC patient gave no K responses, and one control participant gave no R responses. Moreover, confidence data were lost for one healthy participant due to a technical problem. Therefore, the analyses of recognition and source memory associated with R and K responses were conducted on 6 patients and 37 controls, and the analyses of confidence for R and K responses were conducted on 6 patients and 36 controls. PPC patients and controls were still matched in age, $t(40) = .36$, $p = .72$, $\eta_p^2 < .01$, education, $t(40) = -.76$, $p = .94$, $\eta_p^2 < .01$, and gender balance, $\chi^2\ (1) = .15$, $p = .70$. The results obtained for items presented on the left and on the right side of the screen were not statistically different, for both PPC patients and controls ($p > .11$ in all cases). For clarity, we present the results collapsed across items presented on the left and right side of the screen.

3.1. *Recognition accuracy*

Table 2 shows mean hit rates, false-alarm rates, memory accuracy (hit rates minus false-alarm rates), as well as confidence levels associated with hits for both R and K responses in PPC patients and healthy controls. An analysis of variance (ANOVA) on recognition accuracy with Group (PPC patients,

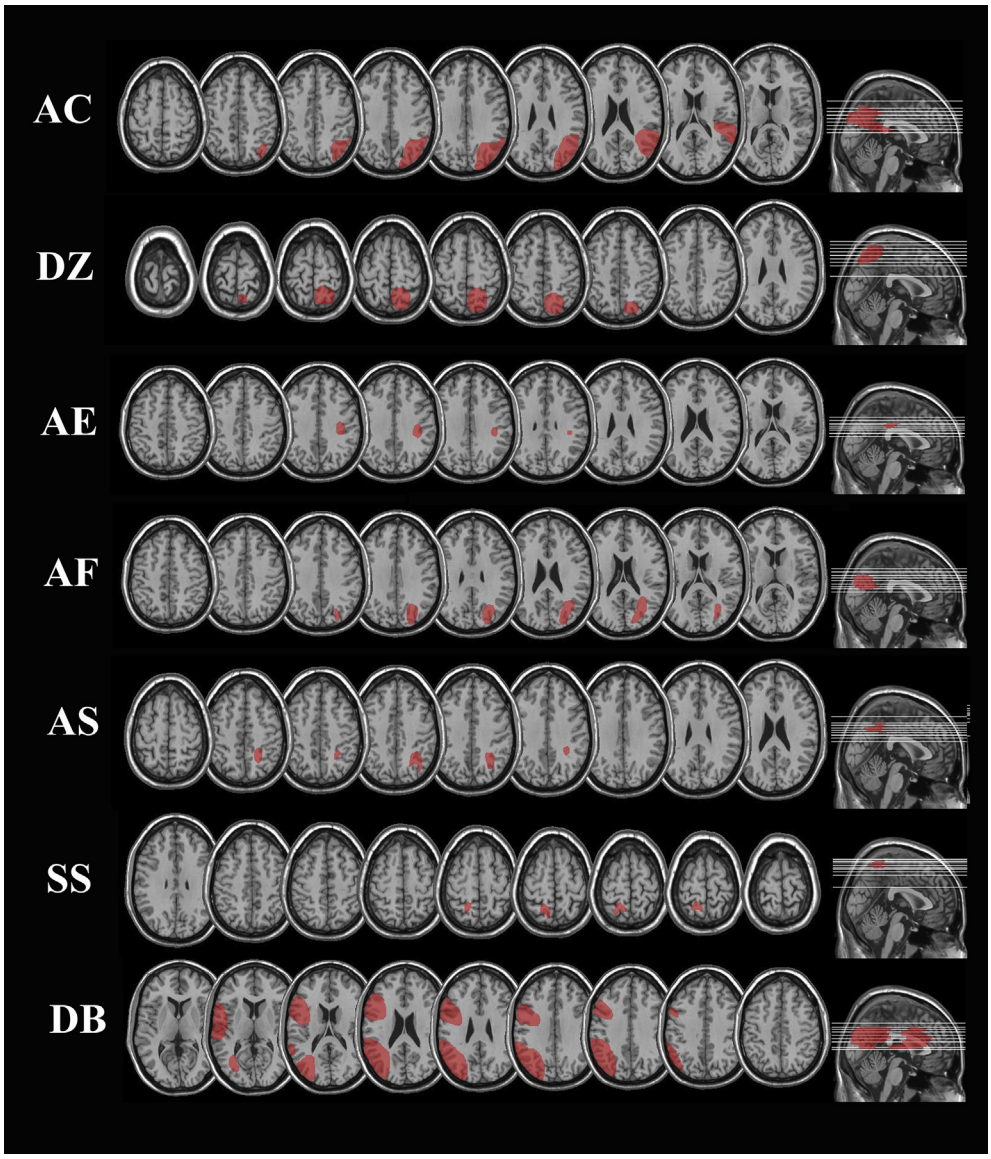

Fig. 1 – Individual PPC patients' lesions. In each slice, the left hemisphere is on the right side.

healthy controls) as the between-subjects factor and Response (R vs. K) as the within-subject factor yielded a marginal effect of Response, $F(1, 41) = 3.75$, $p = .06$, $\eta_p^2 = .08$, indicating a trend toward higher accuracy in association with R ($M = .26$) compared to K responses ($M = .15$), in both PPC patients and controls. The effects of Group and the Group × Response interaction were not significant ($p > .38$, $\eta_p^2 < .02$ in both cases).

3.2. *Sensitivity and response bias*

Table 2 also reports signal-detection indexes of sensitivity and response bias associated with R and K responses. Given the relatively small number of subjects in the study, we used signal-detection measures that do not assume that the signal and noise distributions are normally distributed (as in the case of d', see MacMillan & Creelman, 1991). Specifically, we

Table 2 – Recognition accuracy, sensitivity, bias, and confidence data.

	Hit rates		False alarm rates		Recognition accuracy		Sensitivity (A′)		Bias (B″)		Confidence (hits)	
	R	K	R	K	R	K	R	K	R	K	R	K
PPC patients	.36 (.09)	.30 (.07)	.07 (.03)	.18 (.05)	.29 (.07)	.12 (.07)	.77 (.04)	.61 (.08)	.57 (.14)	.36 (.10)	5.30 (.78)	4.38 (.54)
Controls	.29 (.03)	.29 (.02)	.05 (.01)	.18 (.03)	.24 (.02)	.17 (.03)	.78 (.01)	.69 (.02)	.73 (.05)	.50 (.06)	6.10 (.14)	5.01 (.21)

Note: PPC = posterior parietal cortex; R = Remember, K = Know. Values in parentheses are standard errors of the mean.

computed A′ and B″, which provide estimates of sensitivity and response bias analogous to d′ and β (see also Schacter, Verfaellie, Anes, & Racine, 1998b). Values of A′ can vary between 0 and 1, with .5 indicating chance performance and higher values indicating greater sensitivity. Values of the bias measure, B″, can vary between −1, indicating extremely liberal responding, and 1, indicating extremely conservative responding. When hit rates < false-alarm rates, modified formulas by Aaronson and Watts (1987) were used. An ANOVA on A′ values with Group and Response as factors showed a significant effect of Response, $F(1, 41) = 11.19$, $p = .001$, $\eta_p^2 = .21$, such that R responses ($M = .78$) were associated with higher levels of sensitivity than K responses ($M = .68$), in both PPC patients and controls. The effect of Group and the Group × Response interaction were not significant ($p > .27$, $\eta_p^2 < .03$ in both cases). The same ANOVA on B″ values showed a significant effect of Response, $F(1, 41) = 5.67$, $p = .02$, $\eta_p^2 = .12$, indicating a more liberal response bias in association with R responses ($M = .71$) compared to K responses ($M = .48$), in both PPC patients and controls. The effect of Group and the Group × Response interaction were not significant ($p > .20$, $\eta_p^2 < .04$ in both cases).

3.3. Confidence

The ANOVA on confidence ratings for hits with Group and Response as factors yielded a significant effect of Response, $F(1,40) = 8.79$, $p = .01$, $\eta_p^2 = .18$, indicating that, in both groups, R responses ($M = 5.70$) were associated with higher memory confidence than K responses ($M = 4.70$). There was a marginal effect of Group, $F(1,40) = 3.63$, $p = .06$, $\eta_p^2 = .08$, such that PPC patients were less confident about their memory contents ($M = 4.84$) than healthy individuals ($M = 5.56$). The Group × Response interaction was not significant ($p = .79$, $\eta_p^2 = .002$) (see Table 2).

This first set of analyses shows that PPC patients have preserved recognition memory, though they show a tendency to be less confident about their memory than healthy controls. The fact that PPC patients showed the same pattern of recognition accuracy, confidence, sensitivity and response bias across R and K responses as did controls indicates that their labeling of memory products as R or K was not erratic, but demonstrably tied to other (objective and subjective) measures of memory.

3.4. Source memory

Fig. 2 shows the frequency of correct position identifications for R responses (i.e., number of correct position identifications for targets receiving a R response divided by the number of R responses to targets) and K responses (i.e., number of correct position identifications for targets receiving a K response divided by the number of K responses to targets) and the frequency of correct color identifications for R responses and K responses, calculated analogously. Note that the count of correct position/color identifications comprises both cases in which participants identified correctly only the probed feature (e.g., position) and cases in which they identified both the probed feature and the other (position and color), which is the habitual way of reporting source memory data. Fig. 3 focuses on the frequency with which participants correctly identified both the color and the position of recognized items.

We first investigated whether PPC patients were generally impaired at recollecting source information about color and position. An ANOVA on the frequency of correct source identifications with Group, Response, and Source (location, color) as factors yielded no significant effects or interactions ($p > .10$, $\eta_p^2 < .06$ in all cases), indicating, in line with previous literature (Davidson et al., 2008; Simons et al., 2008; 2010), that PPC patients, compared to controls, are not significantly impaired at retrieving some aspects of the encoding context, in this case the original position ($p = .26$) or color ($p = .92$) of studied items (see Fig. 2). We obtained similar results when we repeated the ANOVA without the factor Response. No

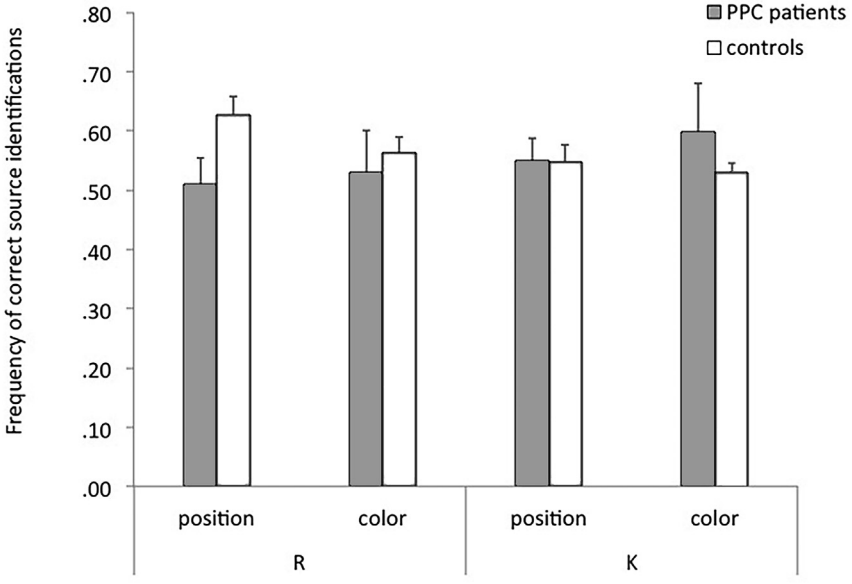

Fig. 2 – Frequency of correct source identifications for R and K responses in PPC patients and controls as a function of type of contextual feature. Standard errors of the mean are shown in the error bars.

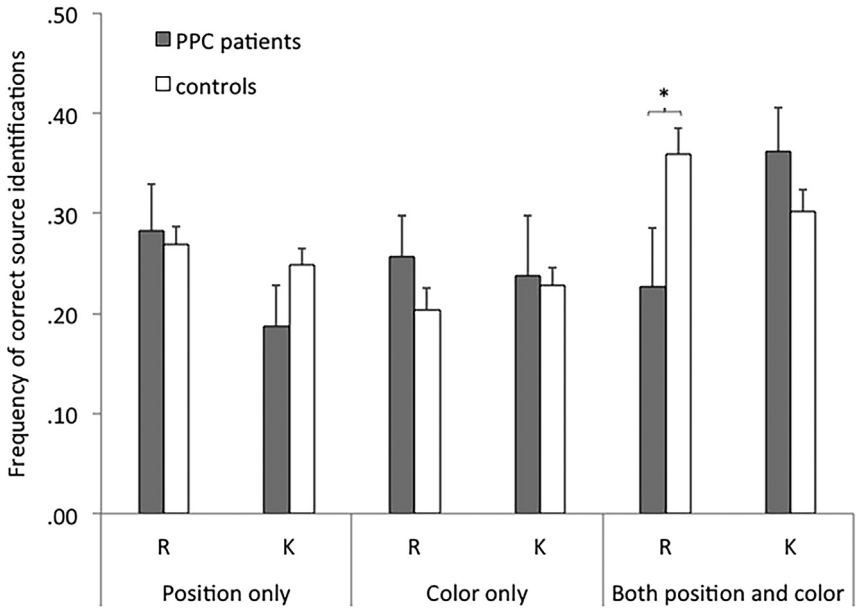

Fig. 3 – Frequency of correct identifications of position only, color only, and both color and position for R and K responses in PPC patients and controls. Standard errors of the mean are shown in the error bars.

significant effect of Group, Source, or Group × Source interaction emerged ($p > .11$, $\eta_p^2 < .05$ in all cases), confirming no significant difference in the frequency with which PPC patients and controls correctly identified the original position ($p = .19$) or color ($p = .35$) of recognized items.

We then investigated PPC patients' ability to retrieve multiple aspects of the encoding context of studied items. We looked separately at the frequency of correct source identifications of both the position and the color of recognized items, as opposed to position only or color only. An ANOVA on the frequency of correct source identifications with Group, Response, and Source (position only, color only, both color and position) as factors yielded a significant effect of Source, $F(2,82) = 3.39$, $p = .038$, $\eta_p^2 = .08$, which was qualified by a significant Group X Response × Source interaction, $F(2,82) = 3.59$, $p = .032$, $\eta_p^2 = .08$. Post hoc Fisher comparisons revealed that in PPC patients R responses were associated with a lower frequency of correct identifications of both position and color for recognized items compared to controls ($p < .005$), whereas the frequency of such "multifeatural" source identifications for K responses was not significantly different between groups ($p = .09$), and numerically higher in patients than in controls. In four of the six PPC patients, the frequency of correct multifeatural source identifications for R responses was at least one standard deviation below the controls' mean. Three of these patients had lesions in the angular gyrus. We examined the relation between extent of lesion in the angular gyrus and multifeatural context retrieval directly in Section 3.6. PPC patients and controls did not differ statistically in the frequency with which they retrieved single contextual features, for both R responses ($p > .13$ in both cases) and K responses ($p > .08$ in both cases). In healthy controls, the frequency of correct multifeatural source identifications was higher for R than K responses, though this difference just failed to reach conventional levels of statistical significance ($p = .05$). A trend in the reverse direction (i.e., with, notably, more frequent correct multifeatural source identifications for K than R responses; see Fig. 3) was present in PPC patients ($p = .06$), suggesting these patients, unlike controls, did not use the successful retrieval of multifeatural context to select R responses, failing to demonstrate the same link between (multifeatural) source memory and subjective remembering observed in healthy controls.

It is important to note that among remembered items healthy controls were more likely to identify both the color and position than position only ($p < .003$) or color only ($p < .00002$). This finding likely depends on participants being explicitly required to memorize the word along with its color and position. Therefore, encoding efforts were directed at forming memories integrating items with multiple (as opposed to single) contextual features. This finding also suggests that PPC patients' difficulties at retrieving multifeatural context in association with R responses were not due to specific costs associated with retrieval of multiple contextual features vs. single contextual features. No other effects in the ANOVA were significant ($p > .20$, $\eta_p^2 < .04$ in all cases). Specifically, there was no significant effect of Group, nor a significant Group × Source interaction ($p > .49$ in both cases), confirming that PPC patients were not generally impaired at retrieving source information.

This second set of results indicates that although the frequency of correct source identifications was not significantly different between PPC patients and controls, the retrieval of (bound) contextual features is not as tied to subjective remembering states in patients as it is in the controls. In this respect, we note that R responses in controls were associated with above-chance identification of position ($t = 4.45$, $p < .0001$; Fig. 2), color ($t = 2.31$, $p < .05$; Fig. 2), or both contextual features ($t = 4.29$, $p < .0001$; Fig. 3), whereas this was not the case in PPC patients (position: $t = .17$, $p = .43$; color:

$t = .27$; $p = .39$; both color and position: $t = .39$, $p = .35$). The fact that PPC patients claimed recollection as frequently as the controls, therefore, further suggests that remembering states were not triggered by accurate retrieval of contextual features. The results on multifeatural source identification are the most relevant here, because it was joint retrieval of position and color (and not single source retrieval) that differentiated R vs. K responses in healthy controls. Paradoxically, PPC patients showed above-chance levels of multifeatural source retrieval for K responses ($t = 2.56$, $p < .05$), confirming a misalignment of objective and subjective recollection following PPC damage.

3.5. *R responses in PPC patients and controls*

The previous analyses show that the propensity to give R responses was not reduced in PPC patients compared to controls, though these patients, unlike controls, did not provide R responses in association with successful multifeatural context retrieval. One may then ask what information drives R responses in PPC patients. To begin to tackle this question, we conducted non-parametric correlations between recognition sensitivity (A′) associated with R and K responses, and the frequency of correct multifeatural source identifications and confidence for R and K responses. In healthy controls, recollection sensitivity correlated significantly with multifeatural source retrieval for R responses, $r_{Spearman} = .40$, $p = .01$, not with confidence in R responses, $r_{Spearman} = .18$, $p = .29$. In PPC patients, on the other hand, recollection sensitivity correlated most strongly with confidence for R responses, $r_{Spearman} = .83$, $p = .04$, and less so with multifeatural source retrieval for R responses, $r_{Spearman} = .37$, $p = .47$. A′ for K responses was not related to multifeatural source retrieval or confidence in either group ($r_{Spearman} < .31$, $r > .06$ in all cases). Thus, whereas in healthy controls accurate remembering states were associated with the retrieval of multifeatural context of study items, in PPC patients they were mainly associated with recognition confidence.

3.6. *Source memory and PPC*

Because patients' lesions were, in some cases, not limited to the PPC, we performed additional analyses to confirm that our main findings were attributable to parietal (as opposed to occipital) damage. We computed non-parametric correlations between lesion volume in PPC (collapsing across BA 39, BA 40, BA 7) and in the occipital cortex (collapsing across BA 17, BA 18, BA 19) and three measures of interest: the frequency of correct multifeatural source identifications for R responses, the general capacity to retrieve multifeatural context (collapsing across R and K responses), and recognition confidence (collapsing across R and K responses). We also looked at lesion volume in BA 39 separately, as recent research has pointed to the angular gyrus specifically as a crucial structure for multifeatural context retrieval (Bonnici et al., 2016). We found that the frequency of correct multifeatural source identifications associated with R responses correlated with lesion volume in PPC, $r_{Spearman} = -.78$, $p = .04$ (but not specifically in BA 39, $r_{Spearman} = -.48$, $p = .27$), and not with lesion volume in the occipital cortex, $r_{Spearman} = -.39$, $p = .38$. On the other hand, recognition confidence correlated with lesion volume in the occipital cortex, $r_{Spearman} = -.79$, $p = .03$, but not with lesion volume in PPC, $r_{Spearman} = -.36$, $p = .42$ (or in BA 39 specifically, $r_{Spearman} = -.63$, $p = .12$). Interestingly, the general capacity to retrieve multifeatural context correlated with lesion volume in BA 39, $r_{Spearman} = -.81$, $p = .02$, though not with total lesion volume in PPC, $r_{Spearman} = -.67$, $p = .09$, or in the occipital cortex, $r_{Spearman} = -.63$, $p = .12$. We elaborate more on this pattern of results in the Discussion.

4. Discussion

The present study investigated accuracy and subjective experience of recognition and source memory judgments in PPC patients and healthy controls. The question motivating this research was whether PPC damage impairs the retrieval of multifeatural episodes (Shimamura, 2011), or whether it impairs the subjective awareness of retrieval, in line with a role of PPC in metamemory (Hower et al., 2014; Simons et al., 2010). To address this question, we studied PPC patients' recognition and source memory accuracy, including multifeatural source memory, as well as subjective recollection as indexed by Remember/Know judgments.

Consistent with previous studies (Ciaramelli, Grady, et al., 2010; Ciaramelli, Rosenbaum, et al., 2010; Haramati et al., 2008; Simons et al., 2010), we found that PPC patients have preserved recognition memory. We note that PPC patients in the present study attained normal recognition accuracy in association with both R and K responses, whereas previous studies had detected a reduction of remembering states following PPC damage (Ciaramelli, Rosenbaum, et al., 2010; Davidson et al., 2008; Drowos et al., 2010). There were two important differences between the paradigm we used and previous ones: first, we used intentional as opposed to incidental encoding; second, we explicitly instructed participants to encode the item along with its color and position. Intentional encoding of compounds of item and contextual features likely maximized recollection across groups. PPC patients may have benefited particularly from this encoding procedure, being presumably less likely than controls to use strategies to encode source information spontaneously when performing incidental tasks. PPC patients' subjective experience of retrieval was not completely unaffected, however, as they showed lower recognition confidence compared to the controls. Differences in memory confidence between PPC patients and controls were only marginally significant, likely due to the small sample size, but in line with anecdotal evidence (Davidson et al., 2008, Study 2) and experimental findings (Ally, Simons, McKeever, Peers, & Budson, 2008; Hower et al., 2014; Simons et al., 2010) of reduced memory confidence following PPC damage. Turning to objective recollection, PPC patients' ability to identify information about the color *or* the position of the recognized items did not differ significantly from controls'. This evidence is again in line with previous reports of preserved source memory in PPC patients using similar experimental paradigms (Davidson et al., 2008; Simons et al., 2008, 2010).

A closer inspection of the data, however, revealed significant differences between PPC patients and controls. Healthy controls typically retrieved both the position and the color of recognized items receiving an R response. It was multifeatural

context retrieval, and not retrieval of position or color information in isolation, that distinguished R from K responses in healthy individuals. This finding is consistent with participants' subjective experience of re-living the learning episode during remembering states (see Ciaramelli & Ghetti, 2007; Dudukovic & Knowlton, 2006; but also Hicks, Marsh, & Ritschel, 2002). Indeed, retrieving not just one but multiple features of an episode is the hallmark feature of recollection as conceptualized in dual-process theories of episodic memory (e.g., Tulving, 1985; Yonelinas, 2002). The frequency of multifeatural source retrieval for R responses was significantly lower in PPC patients than in controls, suggesting that PPC damage reduced the frequency with which multifeatural memories translated into the typical subjective experience of recollection. In contrast, the frequency of multifeatural source retrieval associated with subjective familiarity was not significantly different between PPC patients and controls, and, if anything, it was slightly inflated in PPC patients, who showed paradoxically more frequent multifeatural source retrieval in association with K than with R responses, failing to demonstrate the same link between multifeatural source retrieval and subjective remembering observed in healthy controls.

Poor subjective experience of multifeatural context retrieval in PPC patients is unlikely to be attributed to task difficulty, because identifying both the position and the color of studied items was not more difficult than identifying one of these features only. Multifeatural source retrieval was in fact more frequent than single feature retrieval in healthy controls, a pattern that may be explained by retrieval of bound episodes. We note that previous studies have shown differences between R vs. K responses in the level accuracy of retrieval of single contextual features (e.g., Ciaramelli & Ghetti, 2007; Dudukovic & Knowlton, 2006; Perfect, Mayes, Downes, & Van Eijk, 1996); this difference was not found in the present study. As we noted earlier, our task encouraged memorizing ensembles of contextual features, not single ones, and therefore at test multifeatural, but not single, source retrieval proved a diagnostic indicator of recollection. As well, our results are unlikely to be due to poor comprehension, on the PPC patients' part, of the R/K distinction. Patients were able to repeat the difference between R and K responses back to the experimenter, and correctly linked this difference to context, consistent with their preserved cognitive functioning. Moreover, the fact that patients, as well as controls, showed the expected differences in accuracy, confidence, and signal-detection indexes associated with R and K responses suggests that R and K judgments were not given erratically, but demonstrably related to other measures of memory. Specifically, although R responses in PPC patients were not tied to multifeatural context retrieval, they were strongly related to memory confidence, a more holistic indicator of memory quality. Thus, we cannot exclude a misunderstanding of the R/K distinction on the PPC patients' part based on these data, but a deficit in appreciating/using the contextual features of their memories seems a more reasonable interpretation.

Although accruing evidence points towards a causal role for the PPC in recollection, its mechanistic role is not yet clear (for reviews of different accounts, see Berryhill, 2012; Cabeza, Ciaramelli, & Moscovitch, 2012; Rugg & Vilberg, 2013). Our results are most obviously consistent with the hypothesis that PPC is implicated in the subjective experience of contextual recollection (Hower et al., 2014; Moscovitch et al., 2016; Simons et al., 2010; Yazar, Bergstrom, & Simons, 2014). As anticipated, this hypothesis stems from the observation that PPC patients show reduced subjective confidence along with preserved objective recollection of contextual details (Davidson et al., 2008; Hower et al., 2014; Simons et al., 2010), as if they failed to appreciate subjectively the qualitative features of their memory products. Our data are consistent with this hypothesis, showing a misalignment of objective and subjective recollection following PPC damage. In the present study, PPC patients gave R responses as frequently as controls. However, they were at chance in retrieving the color and/or the position of items associated with R responses, while being paradoxically above chance in retrieving those associated with K responses. Thus, on the one hand, PPC patients can claim remembering states in the absence of memory for context; on the other, when PPC patients' memories are demonstrably rich in (multifeatural) context, patients do not seem to experience recollection, but instead they experience (atypically) a sense of familiarity.

Exploratory correlation analyses showed that lesion volume in PPC was significantly and negatively related to the frequency of multifeatural source retrieval associated to R responses, and not to the ability to retrieve multifeatural context in general, which supports the hypothesis that PPC mediates the subjective appreciation of memory contents rather than their objective retrieval. It is important to note, however, that a different pattern of correlations emerges if we focus on lesion volume in BA 39 specifically: this lesion volume was related to the objective capability to retrieve multifeatural context, not the propensity to select R responses upon successful multifeatural retrieval. It is known that functional divisions exist within PPC (e.g., Nelson et al., 2010), and it is possible that PPC subregions differ with respect to their specific contribution to the objective retrieval and subjective apprehension of memory contents. The present results point to a prominent role of PPC in the subjective experience of (multifeatural) memory contents. Future studies on patients with lesions focused to the angular gyrus, however, may be able to reveal remembering states more strongly tied to objective recollection measures. As well, it will be important to confirm whether our findings hold even in multimodal (as opposed to multifeatural unimodal) source memory tasks, which should be even more sensitive to processing in the angular gyrus (Bonnici et al., 2016; Shimamura, 2011).

This experiment was not designed to test alternative accounts of the role of PPC in memory, and therefore cannot favor one theory over the other. We did not have enough patients to compare the effect of lesion to the ventral vs. dorsal PPC, and therefore we could not test the merit of the Attention to Memory hypothesis, which proposes different mnemonic roles for the two regions (Cabeza et al., 2012, 2008; Ciaramelli et al., 2008). We note, however, that these results are also consistent with the Attention to Memory model, according to which PPC patients have detailed memories that fail to capture attention bottom-up. Moreover, attention is crucial for feature binding in perception (Robertson, 2003). Patients with unilateral neglect, who have problems attending to the

contralesional side of space, fail to detect targets on the neglected side based on the conjunction of two features (e.g., colour and shape), but not single features (color or shape alone) (Eglin, Robertson, & Knight, 1989; Estermann, McGlinchey-Berroth, & Milberg, 2000). This may relate to PPC being more crucial for the subjective experience of multiple rather than single contextual features. This observation also fits with the mnemonic buffer hypothesis (Rugg & Vilberg, 2013; Vilberg & Rugg, 2008), according to which PPC is necessary to hold and manipulate multiple episodic details.

We conclude by noting an important limitation of the study, the lack of a control group of brain-damaged individuals. We have shown that our main findings relate to lesion volume in PPC, and not in the occipital lobe, providing some evidence of regional specificity. Future studies that include a control group, and a larger group of PPC patients, will help specify the mnemonic role of PPC's subregions. For the time being, we show that objective memory performance – including multifeatural source memory – is not significantly different in PPC patients compared to healthy controls. Yet, there was a significant group difference in the link between multifeatural context retrieval and subjective recollection, as predicted by the subjective memory hypothesis.

Conflict of interest statement

The authors declare no conflict of interest.

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