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# Mental *Space* Travel: Damage to Posterior Parietal Cortex Prevents Egocentric Navigation and Reexperiencing of Remote Spatial Memories

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The ability to navigate in a familiar environment depends on both an intact mental representation of allocentric spatial information and the integrity of systems supporting complementary egocentric representations. Although the hippocampus has been implicated in learning new allocentric spatial information, converging evidence suggests that the posterior parietal cortex (PPC) might support egocentric representations. To date, however, few studies have examined long-standing egocentric representations of environments learned long ago. Here we tested 7 patients with focal lesions in PPC and 12 normal controls in remote spatial memory tasks, including 2 tasks reportedly reliant on allocentric representations (distance and proximity judgments) and 2 tasks reportedly reliant on egocentric representations (landmark sequencing and route navigation; see Rosenbaum, Ziegler, Winocur, Grady, & Moscovitch, 2004). Patients were unimpaired in distance and proximity judgments. In contrast, they all failed in route navigation, and left-lesioned patients also showed marginally impaired performance in landmark sequencing. Patients' subjective experience associated with navigation was impoverished and disembodied compared with that of the controls. These results suggest that PPC is crucial for accessing remote spatial memories within an egocentric reference frame that enables both navigation and reexperiencing. Additionally, PPC was found to be necessary to implement specific aspects of allocentric navigation with high demands on spontaneous retrieval.

*Keywords:* posterior parietal cortex, remote spatial memory, memory retrieval, spatial reference frames

The rich and varied spatial environments in which humans often navigate are processed within multiple, complementary frames of reference to achieve efficient navigation to unseen goal locations. Aguirre and D'Esposito (1999) developed a taxonomy, grounded in developmental and environmental cognitive theory, to characterize the collaborative effort of varied, segregated neural processes that support the many ways in which mental navigation and landmark identity may be represented. Though largely guided by anecdotal observation of relatively small patient samples, and published at a time when neuroimaging studies on memory for large-scale space were just beginning to emerge, this framework has proved effective in predicting focal deficits in diverse cases with restricted and larger lesions to neocortex (e.g., Ciaramelli, 2008; Rosenbaum, Gao, Richards, Black, & Moscovitch, 2005; Rosenbaum et al., 2000; Takahashi & Kawamura, 2002; Weniger & Irle, 2008; Wilson et al., 2005). There are four major components to this network: (a) egocentric processing of locations in the posterior parietal cortex (PPC; Levine, Warach, & Farah, 1985; Stark, Coslett, & Saffran, 1996), (b) allocentric heading direction in the retrosplenial–posterior cingulate cortex (Cammalleri et al., 1996; Maguire, 2001; Takahashi, Kawamura, Shiota, Kasahata, & Hirayama, 1997), (c) coding new spatial locations and forming allocentric spatial configurations ("cognitive maps") based on those locations in the medial temporal lobe (including parahippocampal cortex and hippocampus; Bohbot et al., 1998; Habib & Sirigu, 1987; O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978), and (d) perceptual identification of landmarks in a posterior parahippocampal-lingual region of inferior temporal cortex (Incisa della Rocchetta, Cipolotti, & Warrington, 1996; Whiteley & Warrington, 1978).

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## The PPC and Egocentric Coding of Space

As part of the dorsal visual stream, the PPC is needed to represent positions in terms of body-centered coordinates that allow for accurate reaching toward objects and movement with respect to landmarks in the environment (Milner & Goodale, 1995). Neurons coding spatial position relative to body parts have been found in the monkey's PPC and in connected regions in prefrontal cortex (e.g., Colby & Goldberg, 1999). Functional neuroimaging research in humans has confirmed that egocentric coding of space recruits a frontoparietal network along the dorsal stream (Committeri et al., 2004; Galati et al., 2000; Vallar et al., 1999).

Egocentric coding of space needs continuous updating as one moves about the environment and is necessary for the online organization of movements in space. Indeed, patients with lesions to PPC may show inaccurate visuomotor coordination (i.e., optic ataxia; Perenin & Vighetto, 1988) and fail to explore the contralesional side of external space (i.e., hemispatial neglect) or internal representations derived from memory (i.e., representational neglect; Vallar, 1998). Damage to PPC can disrupt new spatial learning and cause disorientation in familiar environments, possibly because the individual has lost the ability to represent the location of objects (and landmarks) with respect to the self, though the landmarks themselves may be recognizable (De Renzi, 1982; Guariglia, Piccardi, Iaria, Nico, & Pizzamiglio, 2005; Levine et al., 1985; Stark et al., 1996).

## The PPC and Egocentric Processing of Remote Spatial Memory

The neuroimaging literature on normative way finding in real-world and virtual-reality environments and the neuropsychological literature on topographical disorientation in patients with PPC lesions have largely focused on novel or recently encountered environments. One important question for theories of remote spatial memory is whether navigation in very familiar environments is equally reliant on PPC function and vulnerable to its disruption.

Early theories of mental mapping of large-scale environments emphasized that spatial representations advance in stages from the simple encoding of landmarks in relation to the organism (i.e., undifferentiated egocentric) to a more complex mental representation of the spatial relationships among landmarks (i.e., differentiated allocentric and abstractly coordinated). These stages are believed to apply to an adult's acquisition of the spatial structure of a new environment as much as to a child's acquisition of spatial competence (e.g., Hart & Moore, 1973; Piaget & Inhelder, 1967). If it is the case that long-standing representations of familiar environments can be represented in allocentric terms without the need for egocentric processing, then remote spatial memory should not require the support of the PPC.

Data on patients with representational neglect due to PPC damage suggest this is not the case. When required to describe a familiar route, patients with representational neglect tend to omit turns on the left-hand side and typically describe long detours with mostly right instead of left turns (Bisiach, Brouchon, Poncet, & Rusconi, 1993). In the now classic study by Bisiach and Luzzatti (1978), two patients with representational neglect were asked to describe Piazza del Duomo in Milan (with which they were very familiar) when facing the Duomo or facing away from it. Patients omitted the buildings to the left of the given point of view (facing the Duomo), yet described those same buildings when given the opposite point of view (facing away from the Duomo). Patients' lack of awareness for the (egocentrically defined) left side of Piazza del Duomo, in the face of retained knowledge of all the features of the familiar square, suggests that the PPC is necessary to process remote spatial information in an egocentric, rather than allocentric, reference frame (Aguirre & D'Esposito, 1999; Levine et al., 1985; Milner & Goodale, 1995). The egocentric remote spatial memory deficit in patients with representational neglect likely results from a failure to attend to the contralesional side of internal representations. It is unclear, however, whether PPC patients without neglect, who can activate a complete representation of the environment, would also show impaired egocentric processing of remote spatial memory.

Additional evidence in support of a role of the PPC in egocentric components of remote spatial memory comes from the case study of patient M.U., an individual with bilateral PPC damage (Wilson et al., 2005). Testing on a comprehensive battery of spatial memory tasks involving places that he had experienced since before his neural insult revealed that M.U. was able to recognize famous and local landmarks, and to judge the proximity of locations in relation to one another, suggesting intact allocentric remote spatial memory representations. M.U., however, could not orient himself to different locations from a given landmark that he imagined facing, and could not describe routes between landmarks, suggesting a deficit in processing remote spatial memory in an egocentric reference frame (Wilson et al., 2005). M.U.'s pattern of preserved and impaired performance, however, was in the context of impaired episodic memory, spatial imagery, visually guided pointing and reaching to objects, picture scanning and matching, and visuospatial short-term memory (some of which are features of Balint's syndrome), making it difficult to delineate the basis of his performance on the topographical measures. These variables may further interact with side of lesion. The majority of cases of egocentric disorientation reported in the literature have bilateral or mostly right-sided PPC damage, with a few studies further specifying that the lesioned area is within superior parts of PPC. M.U., however, was reported to have greater left than right PPC damage, and a recent large-group patient study of new spatial learning reported no difference between left- and right-lesioned patients in learning to navigate a virtual maze based on egocentric memory (Weniger & Irle, 2008).

In summary, previous research is in line with the hypothesis that PPC might mediate egocentric components of remote spatial memory. However, the PPC is implicated in a host of cognitive processes, including attentional capture and control (Corbetta & Shulman, 2002), working memory (WM; Berryhill & Olson, 2008), and episodic memory retrieval (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Olson & Berryhill, 2009; Vilberg & Rugg, 2008), which may impinge on navigational ability. Greater coordination across functional domains and methodologies, with attention paid to laterality and localization of functions within PPC, is needed to gain a more complete understanding of whether, and through which mechanisms, PPC crucially and selectively supports egocentric components of remote spatial memory.

## The Present Study

The present study examines performance of patients with focal left or right lesions to PPC who had extensive premorbid experience navigating in downtown Toronto to determine whether this region makes a necessary and selective contribution to egocentric components of remote spatial memory. The patients did not have obvious signs of neglect and did not all have deficits in WM or executive function, though there was a trend toward episodic memory impairment. Patients underwent a set of experimental tasks designed to simulate relatively higher demands on allocentric versus egocentric components of remote spatial memory posed by environmental circumstances in places that had been navigated frequently over a long period (Experiment 1), as well as a test of recognition of environmental landmarks (Experiment 2).

### Selecting Allocentric and Egocentric Remote Spatial Memory Tasks

Table 1 provides a list of the remote spatial memory tasks used in the present study, together with the assumed predominant frame of reference (allocentric vs. egocentric), and the extant evidence that enabled us to select the allocentric versus egocentric reference frame as the predominant one for each of the tasks.

First of all, we focused on the standard definitions and geometrical properties of allocentric and egocentric reference frames. In an allocentric reference frame, the location of an object is computed with respect to environmental landmarks, whereas in an egocentric reference frame, the location of an object is computed with reference to the body (Aguirre & D'Esposito, 1999). It is commonly assumed, therefore, that tasks emphasizing the spatial relations between objects within the environment (e.g., probing a maplike representation of space), such as drawing a map, localizing landmarks on a map, judging the distance between landmarks, judging the proximity of landmarks, and estimating the angular distance between landmarks (i.e., Tasks 1–5 in Table 1), activate preferentially an allocentric reference frame (Aguirre & D'Esposito, 1999). All these tasks, indeed, require retrieving the allocentric position of relevant streets and landmarks on an internal map of the environment and, in case, computing the linear or angular distance between pairs of landmarks. An allocentric coordinate system appears as the most suited for these tasks, because Euclidean relations between places in the environment are preserved within this system, and therefore angle and distance relations are readily available. In contrast, egocentric representations become increasingly daunting as distances and numbers of locations increase, because a simple movement requires updating of the locations of every object in the environment (see Burgess, 2006, for a discussion). On the other hand, tasks probing a route-based representation of space, such as sequencing landmarks along a route or describing a route between landmarks (i.e., Tasks 6 and 7 in Table 1), are assumed to activate preferentially an egocentric reference frame. These tasks, indeed, emphasize the relations between the egocentric position and the environment. For example, landmark sequencing involves judging the order of relevant landmarks with respect to one's own walking direction. As well, describing a route through a well-known environment typically involves engaging in an imaginary walk along the route (Farrell, 1996). An egocentric coordinate system appears as the most suited for these tasks. Within this system, spatial knowledge is the linear representation of a sequential record of steps leading from a starting point, through landmarks, and finally to a destination. Each landmark is coupled with a given instruction (e.g., go right at the church) that leads to another landmark and another instruction until the goal destination is reached (Aguirre & D'Esposito, 1999).

Although the standard definitions of allocentric and egocentric reference frames support the view that the selected tasks differed in their relative demands on allocentric and egocentric processing, the tasks were likely not process pure, but relied on the interplay between allocentric and egocentric representations (Burgess, 2006). Individuals may rely on a variety of navigational strategies to solve way-finding problems. For example, distance judgments and proximity judgments, which are arguably solved within an allocentric reference frame (i.e., recalling an internal cognitive map and accessing the two locations and their locations within it), could also, in principle, be solved within an egocentric reference frame (i.e., imagining moving between the landmarks and estimating the path length). The fact that most remote spatial memory tasks are, to some extent, amenable to different strategies, which are determined by a host of interacting factors (reviewed in Aguirre & D'Esposito, 1999; see also Ward, Newcombe, & Overton, 1986), may complicate the interpretation of performance in these tasks.

To gain inferential power upon the cognitive mechanisms mediating different spatial memory tasks, we adopted the following strategies. First, we coupled behavioral and functional magnetic resonance imaging (fMRI) evidence from a previous study (Rosenbaum, Ziegler, Winocur, Grady, & Moscovitch, 2004) to determine the preferential use of allocentric versus egocentric reference frames during relevant mental navigation tasks. In that study, subjects were scanned while performing remote spatial memory tasks (i.e., Tasks 3, 4, 6, and 7 in Table 1) and, in postscan interviews, reported whether they had accomplished the tasks by adopting an allocentric strategy (i.e., recalling a maplike representation of Toronto and the position of relevant landmarks within it) or an egocentric strategy (i.e., imagining their own body position with respect to the relevant landmarks). Proximity judgments and distance judgments (i.e., Tasks 3 and 4) were reportedly accomplished by adopting an allocentric strategy, whereas landmark sequencing and route navigation (i.e., Tasks 6 and 7) were reportedly accomplished by adopting an egocentric strategy. Subjective reports were mirrored in dissociable neural activation patterns that have been associated previously with different types of representations: The PPC, commonly associated with egocentric processing, was activated more strongly during tasks classified as egocentric (i.e., Tasks 6 and 7) than during tasks classified as allocentric (i.e., Tasks 3 and 4), whereas the retrosplenial cortex, commonly associated with allocentric processing, showed the reverse pattern (Rosenbaum et al., 2004; see Table 1).

As further evidence in support of the preferential use of allocentric versus egocentric reference frames during navigation tasks, we asked participants to qualify their mental navigation experience, as suggested by Aguirre and D'Esposito (1999). The fact that participants consistently reported having accomplished route navigation (i.e., Task 7 in Table 1) adopting a first-person (as opposed to third-person) perspective constitutes additional evidence for the egocentric nature of the task.

Table 1

*Experimental Remote Spatial Memory Tasks and Prominent Reference Frames*

| Task | Description | Prominent reference frame | Support for the task's A versus E nature | Implicated process according to Aguirre and D'Esposito (1999) | Performance in PPC patients |
|---|---|---|---|---|---|
| Experiment 1 | | | | | |
| Map drawing | Drawing a map of the streets and landmarks of Toronto | A | Emphasis on the relations between objects within the environment | Coding (and retrieval) of A spatial configurations | Impaired |
| Landmark localization | Indicating the location of landmarks on a map of Toronto | A | Emphasis on the relations between objects within the environment | Coding (and retrieval) of A spatial configurations | Unimpaired |
| Proximity judgments | Indicating which of two Toronto landmarks is closer in distance to a reference landmark. | A | (a) Emphasis on the relations between objects within the environment; (b) subjective reports of using an A strategy; (c) RC activity > PPC activity | Coding (and retrieval) of A spatial configurations | Unimpaired |
| Distance judgments | Indicating whether the distance between pairs of Toronto landmarks is greater or less than 2.5 km. | A | (a) Emphasis on the relations between objects within the environment; (b) subjective reports of using an A strategy; (c) RC activity > PPC activity | Coding (and retrieval) of A spatial configurations | Unimpaired |
| Vector mapping | Indicating the angular distance between two Toronto landmarks. | A | Emphasis on the relations between objects within the environment | Coding (and retrieval) of A spatial configurations | Impaired (impairment is secondary to that in map drawing) |
| Landmark sequencing | Indicating whether pairs of Toronto landmarks are in the correct order that would be passed if walking in a given direction. | E | (a) Emphasis on the relations between the E position and the environment; (b) subjective reports of using an E strategy; (c) PPC activity > RC activity | Representation of the location of objects with respect to the self | Unimpaired in right-PPC patients; marginally impaired in left-PPC patients |
| Route navigation | Describing the most efficient route from one specified Toronto landmark to another. | E | (a) Emphasis on the relations between the E position and the environment; (b) subjective reports of using an E strategy; (c) subjective reports of adopting a first-person perspective; (d) PPC activity > RC activity | Representation of the location of objects with respect to the self | Impaired (impairment is accompanied by reduced subjective experience and adoption of first-person perspective, and independent from that in map drawing) |
| Experiment 2 | | | | | |
| Landmark recognition | Recognizing Toronto landmarks from distractor landmarks from other cities | | | Perceptual identification of landmarks | Unimpaired |

*Note.* A = allocentric; E = egocentric; PPC = posterior parietal cortex; RC = retrosplenial cortex.

## Predictions

We expected PPC patients to have particular difficulty on tests with predominantly egocentric components, whereas tests of landmark recognition and those with predominantly allocentric components were expected to be unimpaired. As Table 1 shows, our results were, for the most part, consistent with predictions. Compared with the controls, all patients showed impaired performance in route navigation, and left-damaged patients also showed weak performance in landmark sequencing. In contrast, all patients performed normally on landmark recognition, as well as most allocentric tasks (e.g., distance judgments and proximity judgments).

## Experiment 1: Remote Memory for Landmark Location and Mental Navigation

In the first experiment, participants underwent a series of mental navigation tasks that require spatial judgments based on the knowledge of an extensively experienced environment (i.e., downtown Toronto). The tasks were designed to probe allocentric and egocentric representations to a different degree. If PPC is crucially and selectively implicated in egocentric navigation, then patients with lesions to PPC should fail on tasks that probe egocentric components of remote spatial memory but perform normally on tasks that probe allocentric components of remote spatial memory.

## Method

**Participants.** Seven individuals with damage to PPC and 12 age-matched healthy controls participated in the study. Patients were recruited from Baycrest Hospital, Toronto, Canada. Patients were selected on the basis of the location of their lesion evident on CT or MRI scans. Included patients had lesions in PPC, had no other diagnosis likely to affect cognition or interfere with participation in the study (e.g., psychiatric disease, alcohol abuse, head injury), and were in the stable phase of recovery (at least 12 months postmorbid; see Table 2 for demographic information).

The area of damage was determined by visual inspection on axial view by a radiologist. For a lesion to be traced, it had to appear in more than one slice, with a diameter of at least 3 mm on one of the slices. The boundary of the lesion was traced from MRI or CT images on a standardized brain with the software MRIcro (Rorden & Brett, 2000). Figure 1 shows the extent of damage for each patient. Brain lesions varied in terms of their precise location within lateral parietal cortex. Three patients had lesions in the left PPC: Patient 1050 and patient A.S. had superior parietal damage, and patient 1022 had damage in the temporoparietal junction (TPJ), including the angular gyrus. The other four patients had lesions in the right PPC: Patient S.S. had superior parietal damage; patient 1047 had damage centered on the TPJ, including the angular gyrus. This patient also had minimal damage in right orbitofrontal cortex, accounting for about 5% of total lesion size; patient P.K. had TPJ damage; patient F.F.C. had damage in the inferior parietal lobe, extending into the temporo-occipital junction. In no case did patients' lesions invade the medial–limbic region. Patients had a mean age of 67.5 years (range: 48–88) and a mean education of 13.2 years (range: 8–17). Their "experience with downtown Toronto," defined as the number of years they had lived, or worked daily, in downtown Toronto, was of 38.8 years (range: 5–88).

Patients did not report problems navigating in real life. For example, with the exception of F.F.C., all patients arrived at Baycrest Hospital for the experimental sessions on their own, either by driving (five cases of six) or by bus (patient A.S.). More generally, patients assured us that they were able to go about their daily activities independently and never got lost or confused while driving. They admitted, however, that their life was rather repetitive since the brain accident and that, as a consequence, their trips revolved around a few, overlearned routes. F.F.C. preferred not to drive and to be accompanied always by her daughter. She attributed this choice exclusively to her old age and health problems, not to problems in way finding.

The control group comprised 12 individuals matched to the patients on mean age ($M = 70.1$ years; range: 43–83), education ($M = 14.5$ years; range: 12–18), and experience with downtown Toronto ($M = 38.7$ years; range: 5–83). Thus, the participant groups were equated with respect to mean age, education, and experience with downtown Toronto ($p > .30$ in all cases). Partic-

Table 2
*Patients' Demographic and Lesion Data*

| Patient | Gender | Age (years) | Education (years) | Experience with downtown Toronto (years) | Etiology | Lesion location |
|---|---|---|---|---|---|---|
| 1050 | Male | 48 | 12 | 30 | Meningioma | Left superior parietal lobe |
| A.S. | Male | 62 | 17 | 51 | Intracerebral hemorrhage | Left superior parietal lobe |
| 1022 | Male | 74 | 12 | 25 | Stroke | Left inferior parietal lobe, including TPJ and angular gyrus |
| S.S. | Male | 75 | 17 | 40 | Intracerebral hemorrhage | Right superior parietal lobe |
| 1047 | Female | 67 | 13 | 33 | Stroke | Right inferior parietal lobe, including TPJ and angular gyrus |
| P.K. | Female | 59 | 14 | 5 | Stroke | Right TPJ |
| F.F.C. | Female | 88 | 8 | 88 | Stroke | Right inferior parietal lobe and TOJ |
| Normal controls (*M*) | | | | | | |
| Experiment 1 | 7 female | 70.17 | 14.58 | 38.75 | | |
| Experiment 2 | 4 female | 67.50 | 13.58 | 40.25 | | |

*Note.* TPJ = temporoparietal junction; TOJ = temporo-occipital junction.

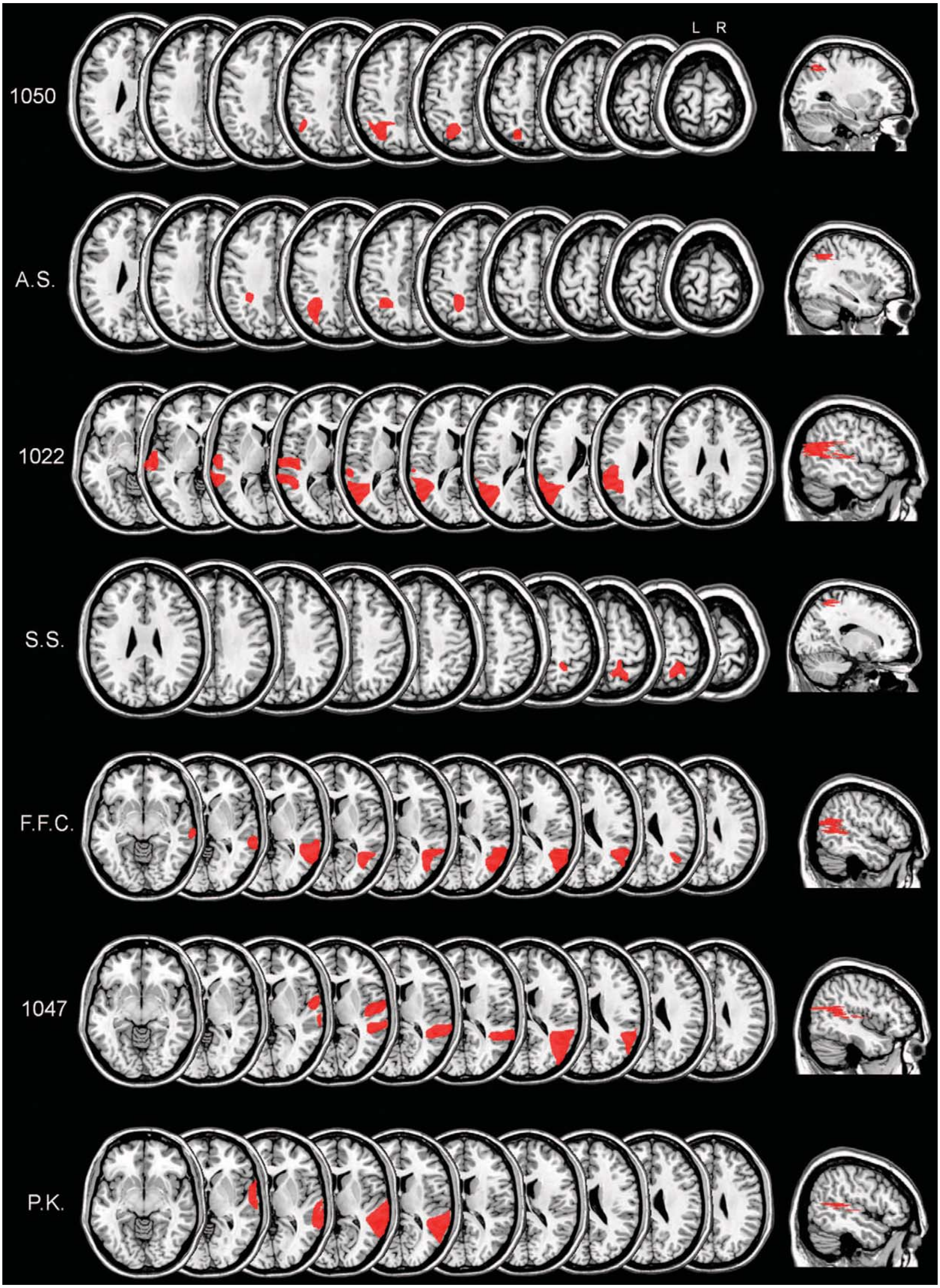

*Figure 1.* Location of brain damage in patients.

ipants were screened for clinically significant depression, alcohol and drug abuse, epilepsy, and any other known neurological conditions. All participants gave informed consent, and all study procedures were approved by the ethics committees of Baycrest Hospital and York University.

**Neuropsychological assessment.** Patients underwent a standardized neuropsychological examination, including measures of general cognitive functioning (Mini-Mental State Examination), neglect (bell cancellation test, Gauthier, Dehaut, & Joanette, 1989; clock drawing task, Van der Horst, 1934), vocabulary (Shipley, 1946), executive function (Wisconsin Card Sorting Test, Stuss et al., 2000; Trail Making Test, Spreen & Strauss, 1998; and verbal fluency, Spreen & Strauss, 1998), and verbal learning and memory (Hopkins Verbal Learning Test–Revised; Benedict, Schretlen, Groninger, & Brandt, 1998). WM was assessed with a self-ordered pointing task (see Davidson et al., 2008; Petrides & Milner, 1982), which consisted of a booklet containing sheets with arrangements of pictures of items (objects, people, and animals). The position of items on each sheet varied, and subjects were asked to touch all the items in the set, a different one on each sheet. Set size increased as the task progressed (i.e., 6, 8, 10, or 12 items per sheet). We computed the total number of errors (e.g., selecting an item more than once).

Table 3 reports the patients' results. For each measure, we show each patient's raw score, with those beyond the normal range for their age-appropriate control groups ($z < -1.96$) in bold. Overall, patients were within the normal range on general cognitive functioning and vocabulary. Patients did not show symptoms of neglect, as assessed by the bell cancellation test or the clock drawing task. Two patients (A.S., 1022) were impaired on the executive measures: They both showed increased response times on Part B of the Trail Making Test compared with healthy controls; patient 1022 exhibited additional impairment on the Wisconsin Card Sorting Test. On the verbal memory tasks, patients' scores were within the normal range but with a trend toward impairment. WM was generally within the normal range, except for patient 1022.

**Materials and procedure.** All remote spatial memory tasks included as stimuli either single or pairs of names of well-known landmarks located in downtown Toronto and required participants to make a variety of spatial judgments. Before testing, participants were reminded of the streets bordering the area of downtown Toronto relevant to the study. The tasks were presented in a fixed order. We now describe each task in more detail. We placed in parentheses, next to the task, the prominent framework that was presumed to be used (see also Table 1).

**Map drawing (allocentric).** Participants were requested to reproduce the configuration of streets and landmarks of downtown Toronto on an outline map containing only the streets bordering downtown Toronto. As measures of map accuracy, we report the number of streets and the number of landmarks participants reported in the correct location on the map.

**Landmark localization (allocentric).** Participants were presented with a map containing only the main streets of downtown Toronto and were asked to draw a dot on the map representing the location of each of 11 specified landmarks. Deviation of each landmark from its true location (in kilometers) was measured.

**Proximity judgments (allocentric).** Participants indicated which of two landmarks was closer in distance (i.e., shorter linear distance) to a reference landmark (specified for each trial). The actual distance among the 12 sets of landmarks varied from trial to trial. For half the trials, the difference in distance between the reference and the choice landmarks was less than 1 km (difficult trials). For the other half, the difference in distance between the reference and the choice landmarks was more than 1 km (easy trials). Difficult and easy trials were intermixed randomly. Percent correct was calculated.

**Distance judgments (allocentric).** Participants judged whether the distance (i.e., shortest linear distance) between each of

Table 3
*Patients' Results in the Standardized Neuropsychological Tests*

| Test | 1050 | A.S. | 1022 | S.S. | 1047 | P.K. | F.F.C. |
|---|---|---|---|---|---|---|---|
| MMSE | 29 | 28 | — | 30 | 29 | 26 | 28 |
| Shipley vocabulary | 29 | 34 | **27** | 35 | 32 | 32.7 | 29 |
| Bell cancellation test (number of bells left/right) | 17/17 | 15/15 | 15/16 | 18/17 | 15/16 | 18/17 | 15/15 |
| Clock drawing task | 3 | 3 | — | 3 | 3 | 3 | 3 |
| WCST | | | | | | | |
| Number of categories | 7 | 6 | 3 | 6 | 5 | 6 | 6 |
| PPC | 18 | 7 | **43** | 11 | 40 | 22 | 10 |
| PPR | 3 | 7 | 16 | 7 | 11 | 17 | 10 |
| Verbal fluency | 38 | 22 | 31 | 55 | 42 | 30 | 30 |
| Trail Making Test | | | | | | | |
| Part A | 26 | 50 | **66** | 61 | **51** | 52 | 52 |
| Part B | 80 | **170** | **408** | 81 | 73 | 149 | 112 |
| HVLT-R | | | | | | | |
| Recall | 24 | 19 | 19 | 24 | 25 | 21 | 22 |
| Retention | 10 | 8 | 7 | 5 | 8 | 9 | 4 |
| Recognition | 11 | 11 | 10 | 8 | 12 | 10 | 10 |
| WM (number of errors) | 12 | 7 | **35** | 4 | 12 | 19 | — |

*Note.* Values in bold are two standard deviations below average. Dashes indicate patient not tested. MMSE = Mini-Mental State Examination; WCST = Wisconsin Card Sorting Test; PPC = perseverations of previous criterion; PPR = perseverations of previous response; HVLT-R = Hopkins Verbal Learning Test–Revised; WM = working memory.

14 pairs of landmarks was greater or less than 2.5 km. The actual distance among the 14 pairs of landmarks varied from trial to trial. For half the trials, the distance between landmarks was between 1.5 and 3.5 km (difficult trials). For the other half, the distance between landmarks was less than 1.5 km, or more than 3.5 km (easy trials). Difficult and easy trials were intermixed randomly. Percent correct was calculated.

**Vector mapping (allocentric).** Participants were asked to draw arrows indicating the correct direction from a reference landmark specified by a mark to an unmarked location on 10 maps that included only the northern- and southernmost borders of downtown Toronto. Deviation of estimates from actual directions (in degrees) was measured.

**Landmark sequencing (egocentric).** Participants determined whether each of 10 pairs of landmarks was in the correct order that would be passed if walking in a given direction (e.g., west to east). Percent correct was calculated.

**Route navigation (egocentric).** In each of 11 trials, participants described the most efficient route from one specified landmark to another given that the street vital to taking the most direct route was inaccessible.[1] Percent correct was calculated. Trials in which participants arrived at their destination but gave an impoverished description of the route (e.g., not remembering the name of the street they were taking) were given 0.5 points.[2] At the end of the task, participants were additionally asked whether they felt they were experiencing the simulated navigation episodes from a first-person perspective (i.e., as being actually involved in the episode; e.g., driving or walking on the streets) or from a third-person perspective (i.e., as being an observer of the episode, or adopting a survey perspective) (first- vs. third-person report). In addition, participants were asked to report whether their experience of the simulated navigation episodes had been vivid, rich in perceptual and emotional details, as if they were truly driving or walking through downtown Toronto (reexperiencing report).

**Statistical analyses.** For each task, the variables of interest were entered as dependent measures in a between-subjects analysis of variance (ANOVA) with Group (patients vs. controls) as a factor. To control for the effect of age, education, and experience with downtown Toronto, we entered these variables as covariates in the analysis of covariance (ANCOVA). In addition to the ANCOVA analysis, we performed individual modified *t* tests based on Crawford and Garthwaite's (2002) method for comparing single cases with small control samples to analyze the behavior of individual subjects. When appropriate, the performance of relevant subgroups of patients was compared by means of nonparametric statistics.

## Results

Table 4 shows patients' performance and that of the controls on all mental navigation tasks.

**Map drawing (allocentric).** The ANCOVA on the number of streets correctly reported in the map revealed a significant effect of Group, $F(1, 14) = 4.82$, $p < .05$, $\eta^2 = .25$: Patients correctly reported significantly fewer streets on a map of downtown Toronto than controls. A significant effect of Group also emerged when the ANCOVA was run on the number of landmarks reported on the map, $F(1, 13) = 14.26$, $p < .005$, $\eta^2 = .46$, such that patients drew significantly fewer landmarks than controls. No significant effect of age, education, or experience with Toronto emerged either on the number of streets ($p > .53$ in all cases) or on the number of landmarks drawn on the maps ($p > .10$ in all cases).

**Landmark localization (allocentric).** The ANCOVA on mean deviation (in kilometers) of landmarks from their true location revealed no significant effect of Group, $F(1, 14) = 0.03$, $p = .86$, $\eta^2 = .001$. Age, education, and experience with Toronto had no significant effect on performance ($p > .23$ in all cases).

**Proximity judgments (allocentric).** The ANCOVA on percent correct (collapsed across easy and difficult trials) revealed no significant effect of Group, $F(1, 14) = 0.36$, $p = .55$, $\eta^2 = .01$. There was, however, a significant effect of education ($\beta = .72$, $p < .01$), indicating better performance in more compared with less educated individuals, and a marginal effect of age ($\beta = .50$, $p = .08$), suggesting better performance in older compared with younger individuals. No effect of Group emerged even when the ANCOVA took into account easy trials, $F(1, 14) = 0.74$, $p = .40$, $\eta^2 = .04$, and difficult trials separately, $F(1, 14) = 0.002$, $p = .96$, $\eta^2 = .0001$. None of the covariates had a significant impact on performance on easy trials ($p > .23$ in all cases). As for difficult trials, education had an effect on performance, although only marginal ($p = .06$), whereas age and experience with Toronto did not ($p > .22$ in both cases).

**Distance judgments (allocentric).** The ANCOVA on percent correct (collapsed across difficult and easy trials) revealed no significant effect of Group, $F(1, 14) = 0.08$, $p = .77$, $\eta^2 = .004$, and no significant effect of any of the covariates ($p > .25$ in all cases). The same results were observed when the ANCOVA was run on easy trials $F(1, 14) = 0.11$, $p = .77$, $\eta^2 = .007$, and difficult trials, $F(1, 14) = 0.13$, $p = .71$, $\eta^2 = .008$, separately. For both types of trial, the effect of the covariates was not significant (for easy trials, $p > .12$; for difficult trials, $p > .25$).

**Vector mapping (allocentric).** The ANCOVA on mean deviation of estimates (in degrees) from actual directions revealed a significant effect of Group, $F(1, 14) = 0.67$, $p < .05$, $\eta^2 = .19$, such that patients were less accurate than controls at specifying the direction from an imaginary landmark to another on an unmarked map. There was also a significant effect of education ($\beta = -.70$, $p < .01$), indicating better performance in more compared with less educated individuals.

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[1] It should be noted that this specific version of the task, requiring to overcome a blocked street, was originally intended (Rosenbaum et al., 2000) as a test to assess internal cognitive maps based on Tolman (1948). In two studies (Rosenbaum et al., 2007, 2004), however, we have found that participants reported an egocentric, route-based strategy to solving the test (see introduction). That is, the blocked street was not viewed by participants as an obstacle, who easily described a route that moved around that street by means of the next arterial street parallel or perpendicular to it. This likely depends on the very regular and predictable (gridlike) layout of Toronto that makes navigation relatively simple and mostly based on major, well-practiced streets that can be used somewhat interchangeably to get to a destination. London's irregular, unpredictable structure may tap allocentric representations more heavily. Indeed, patients with medial temporal lobe lesions can navigate in Toronto (Rosenbaum et al., 2000) but may fail in London (Maguire et al., 2006).

[2] Comparable results were obtained when such responses were considered completely correct, and given 1 point.

Table 4
*Patients' Results in the Experimental Tasks*

| | | | | | | | | Normal controls | |
|---|---|---|---|---|---|---|---|---|---|
| Task | 1050 | A.S. | 1022 | S.S. | 1047 | P.K. | F.F.C. | *M* | *SD* |
| Experiment 1 | | | | | | | | | |
| Map drawing | | | | | | | | | |
| Number of streets | 11 | 14 | **6** | **8** | **8** | 12 | **8** | $12.50^{a}$ | 2.32 |
| Number of landmarks | 2 | 4 | 2 | 3 | 2 | 3 | 2 | $8.37^{a}$ | 4.65 |
| Landmark localization (mean deviation, in kilometers) | 0.49 | 0.23 | 0.37 | 0.34 | 0.23 | **0.86** | 0.43 | 0.42 | 0.13 |
| Proximity judgments (proportion correct) | **.33** | .83 | .58 | .83 | .75 | .67 | .83 | .80 | .12 |
| Distance judgments (proportion correct) | .86 | .93 | .78 | .86 | .86 | .71 | .71 | .83 | .08 |
| Vector mapping (mean deviation, in degrees) | **34** | 7 | **32** | 15 | **36** | 22 | **27** | $14.28^{a}$ | 4.82 |
| Landmark sequencing (proportion correct) | .90 | **.70** | **.70** | 1.00 | **.50** | 1.00 | .90 | .89 | .09 |
| Route navigation | | | | | | | | | |
| Proportion correct | **.55** | **.50** | **.25** | .77 | **.30** | **.55** | .73 | $.79^{a}$ | .09 |
| First person | Yes | Yes | No | No | No | Yes | Yes | $\text{Yes}^{a,b}$ | |
| Reexperiencing | No | Yes | No | No | No | No | No | $\text{Yes}^{a,c}$ | |
| Experiment 2 | | | | | | | | | |
| Landmark recognition | | | | | | | | | |
| Accuracy | **.25** | .75 | — | .50 | .65 | .55 | .55 | .60 | .13 |
| Familiarity | 5.11 | 6.22 | — | 5.69 | 5.29 | 4.85 | **1.68** | 4.73 | 1.47 |
| Reexperiencing | 1.00 | .89 | — | .77 | .57 | .46 | .21 | .57 | .21 |

*Note.* Landmark recognition accuracy was computed as hit rates to Toronto landmarks minus false-alarm rates to distractor landmarks from other North American cities. Values in bold are significantly lower to the controls' data, based on Crawford and Garthwaite (2002). Dashes indicate patient not tested.
[a] Significant difference between patients and controls ($p < .05$). [b] All 11 normal controls. [c] Nine subjects.

Individual *t* tests revealed that four of the seven patients were impaired in this task compared with the controls (patients 1050, 1047, 1022, F.F.C.). In particular, only one of the three patients with superior parietal lesions was impaired, whereas three of the four patients with inferior parietal lesions were. We therefore tested the possibility that the site of lesion had an impact on vector mapping performance. The scores obtained by patients with superior versus inferior parietal lobe lesions were not significantly different ($p = .28$). However, because demographic variables were found to have a significant impact on vector mapping performance in the ANCOVA, patients with superior and inferior parietal lesions were also compared with two subgroups of normal controls ($N = 5$), closely matched with patient groups for age, education, and experience with Toronto. A significant difference in performance emerged between patients with inferior parietal lesions ($M = 29.03$) and their controls ($M = 16.42$, Mann–Whitney $U = 0$, $p < .05$) but not between patients with superior parietal lesions ($M = 18.77$) and their controls ($M = 12$, $p = .45$). Thus, patients with inferior parietal lesions appeared more susceptible to deficits in vector mapping than patients with superior parietal lobe lesions.

Vector mapping is a complex task that requires recalling and holding in mind sufficient information about a relevant map for a time sufficient to estimate accurate vectors between two locations on the map. It is possible, therefore, that patients' deficit in vector mapping was related to their problems at recalling a detailed map of downtown Toronto (see performance on map drawing) to draw vectors with respect to it. To investigate this hypothesis, we reran the ANCOVA including the number of streets and landmarks recalled during map drawing as two additional regressors. The effect of Group on vector mapping was no longer significant, $F(1, 14) = 0.18$, $p = .67$, $\eta^2 = .004$. In contrast, the number of streets reported on the map ($\beta = -.43$, $p < .05$) and, marginally, the number of landmarks reported on the map ($\beta = -.38$, $p = .055$) had an impact on performance. Together, these results support the hypothesis that lower vector mapping accuracy in PPC patients may be secondary to a deficit recalling a detailed spatial map upon which to operate.

Finally, although our patients did not suffer from neglect, we investigated whether the side of space vectors had to be drawn to interact with performance accuracy across groups. We computed mean deviation of estimates from actual directions separately for vectors to the left ($N = 3$), the right ($N = 4$), or the top or bottom ($N = 3$) of the reference landmark (i.e., the center of the page). We then ran an ANOVA on mean deviation of estimates with Group (left-damaged patients, right-damaged patients) and Vector Direction (left, right, top or bottom) as factors. As expected, the effect of Vector Direction was not significant ($p = .68$), nor did it interact significantly with Group ($p = .73$).

**Landmark sequencing (egocentric).** The ANCOVA on percent correct revealed no significant effect of Group, $F(1, 14) = 1.14$, $p = .30$, $\eta^2 = .08$; age ($p = .78$); education ($p = .92$); or experience with Toronto ($p = .84$). Despite the nonsignificant effect of Group in the ANCOVA analysis, individual *t* tests highlighted impaired performance in three of the seven patients (patients A.S., 1022, and 1047). Because two out of the three patients with left parietal lesions were impaired, whereas only one of the four patients with right parietal lesions was, we tested the possibility that the side of lesion had an impact on patients' performance. We therefore compared the performance of patients with left and right lesions with that of the controls separately. Whereas the performance of patients with right lesions ($M = .85$) was not significantly different from that of the controls' ($p = .74$), differences in performance between patients with left lesions ($M = .76$)

and controls ($M = .89$) approached significance (Mann–Whitney $U = 6.5$, $p = .08$).

**Route navigation (egocentric).** The ANCOVA on percent correct revealed a significant effect of Group, $F(1, 14) = 13.16$, $p < .005$, $\eta^2 = .41$, whereas there was no significant effect of the covariates ($p > .13$ in all cases). Individual *t* test analyses revealed impaired performance in five of the seven patients (patients 1050, A.S., P.K., 1047, 1022). In particular, all three patients with left lesions were impaired, whereas only two of the four patients with right lesions were. We therefore tested the possibility that the side of lesion had an impact on performance. We compared the performance of patients with left and right lesions separately with that of controls. We found that both patients with left lesions ($M = .43$, Mann–Whitney $U = 0$, $p < .01$) and patients with right lesions ($M = .58$, Mann–Whitney $U = 7.5$, $p < .05$) were significantly impaired compared with the controls ($M = .79$).

***Error analysis.*** In normal controls, the few errors made in the route task involved taking the blocked route. In patients, errors could involve (a) taking the blocked route (47% of cases); (b) giving up before reaching the goal location (25% of cases), which was often accompanied by complaints such as “I cannot visualize a map of the streets in this area” and “This region is too small to be visualized”; or (c) making “inconclusive detours” (21% of cases), such as making a couple of turns and being back in the same place, and making long detours and then forgetting the goal destination. Although taking the blocked route denotes the typical failure of egocentric navigation (i.e., individuals cannot navigate if not by relying on overlearned, allocentric relations between relevant landmarks), the other two types of errors may shed light on additional factors contributing to patients’ deficits.

Specifically, narratives such as “I cannot visualize a map of the streets in this area” might suggest that patients’ problems planning a route through Toronto depended on a deficit in recalling a detailed map of the area upon which to operate. To investigate this hypothesis, we reran the ANCOVA including the number of streets and landmarks reported in the map drawing task as two additional regressors. We found that the effect of Group on route navigation performance remained significant even when map drawing performance was factored out, $F(1, 14) = 5.96$, $p < .05$, $\eta^2 = .27$. Neither the number of streets ($p = .37$) nor the number of landmarks ($p = .52$) reported on the map had a significant effect on route navigation. Indeed, of the five patients who had impaired performance in this task, only two had additional deficits in map drawing (patients 1022 and 1047).

On the other hand, making inconclusive detours around the relevant landmarks may indicate that patients tended to avoid certain types of streets. It has been shown that patients with representational neglect following PPC lesions may lose access to (or neglect) the turns on the left side of a path (Bisiach et al., 1993), or the landmarks on the left side of a square (Bisiach & Luzzatti, 1978), despite retained knowledge of the same environments. Although our patients did not suffer from neglect, we conducted an additional analysis to determine whether their problems in navigating interacted with the type of turns (left vs. right) needed across trials. For each trial performed correctly by normal controls, we computed the mean number of left and right turns it involved. We then grouped the 11 routes according to whether in normal controls they mainly involved left turns (i.e., number of left turns greater than number of right turns; $N = 5$) or right turns (i.e., number of left turns less than number of right turns; $N = 6$). Finally, we ran an ANOVA on performance accuracy with Group (left-damaged patients, right-damaged patients) and Route Turns (left turns, right turns) as factors. As expected, Route Turns did not have a significant impact on route navigation ($p = .51$), nor did it interact significantly with Group ($p = .21$).

***First- versus third-person report.*** At the end of the route task, participants were asked whether they had lived the simulated navigation episodes from a first-person perspective or from a third-person perspective. Data were not available for one of the controls. Significantly fewer patients (four of seven) than controls (11 of 11) reported having adopted a first-person perspective during navigation ($\chi^2 = 5.66$, $p < .05$).

***Reexperiencing report.*** Participants were additionally asked whether they had experienced the simulated navigation episodes as vivid and rich in detail. Data were not available for one of the controls. Significantly fewer patients (one of seven) than controls (nine of 11) described their navigation episodes as vivid experiences ($\chi^2 = 7.90$, $p < .005$). When asked to describe the subjective experience of simulated navigation in the route task, controls reported numerous perceptual details (e.g., “I have imagined the buildings along the streets in their actual colors,” “The streets I was traveling through were as crowded as they normally are”), emotional details (e.g., “I was concerned that the route I had thought about was not allowed if traveling by car”), and, more rarely, proprioceptive details (e.g., “Turning left actually felt like that”). Patients rarely reported such vivid impressions. When directly interrogated on the presence of specific details, for example, by providing examples of normal controls’ reports, they admitted that “something like that actually occurred, but for such a brief time that it did not really constitute an experience.” The patients reported the imagined episodes as being very brief, “flashes of episodes.”

## Discussion

Consistent with our predictions, compared with the controls, all patients showed impaired performance in route navigation, and left-damaged patients also showed weak performance in landmark sequencing, suggesting an impairment in egocentric components of remote spatial memory. In contrast, all patients performed normally on most allocentric tasks, including distance judgments and proximity judgments. Although power is always a concern when reporting null effects in small groups, the observed effect sizes suggest that performance differences between patients and controls in allocentric tasks were indeed negligible (e.g., effect sizes of Group on proximity judgments and distance judgments were 1% and 0.4%, respectively), whereas those in egocentric navigation were substantial (41%). Importantly, patients did not report experiencing the environment as fully as controls, nor did they report taking a first-person perspective when performing their tasks, further suggesting an egocentric deficit affecting remote spatial memory in PPC patients. Consistent with the fact that patients did not suffer from neglect, deficits were found to be independent of competition for attention from the right side of an internal representation.

Additional impairments exhibited by patients included drawing a detailed map of downtown Toronto and computing directional vectors with respect to it. Both tasks require recalling a considerable amount of spatial information to operate on it. It is possible, then, that a deficit in recall of spatial information due to PPC damage compromised patients' performance on the two tasks. Consistently, deficits in spatial map drawing and vector mapping were related to one another. We elaborate more on this point in the General Discussion.

## Experiment 2: Recognition of Toronto Landmarks

Although the PPC is not deemed to be necessary for landmark recognition (Aguirre & D'Esposito, 1999; Wilson et al., 2005), we ran a second experiment to exclude the possibility that patients had problems in route navigation because they were impaired at recalling the visual details of landmarks associated with relevant navigation instructions (e.g., go west at the red, round building). Participants were presented with a series of photographs of landmarks located in downtown Toronto, intermixed with structurally similar but unknown distractor landmarks from other North American cities. They had to recognize the Toronto landmarks among the foreign ones. To unveil potential subtle differences in memory for landmarks between patients and controls, we asked participants to express their degree of familiarity with the landmarks and the vividness of their memory for each landmark.

### Method

**Participants.** Six of the seven patients who had taken part in Experiment 1 also participated in Experiment 2. Patient 1022 was no longer available for testing. Patients had a mean age of 66.5 years (range: 48–88), a mean education of 13.5 years (range: 8–17), and a mean experience with downtown Toronto of 41.16 years (range: 5–88; see Tables 2 and 3 for individual patients' demographic and clinical data). A new group of healthy controls was recruited for the study. The control group comprised 12 individuals matched to the patients on mean age (67.5 years; range: 40–77), education (13.58 years; range: 12–17), and familiarity with downtown Toronto (40.25 years; range: 15–77; $p > .88$ in all cases). Participants were screened for clinically significant depression, alcohol and drug abuse, epilepsy, and any other known neurological conditions. All participants gave informed consent, and study procedures were approved by the ethics committees of Baycrest Hospital and York University.

**Materials and procedure.** Twenty color photographs of downtown Toronto landmarks and 20 photographs of landmarks structurally similar to those located in Toronto, but actually located in other Canadian and North American cities, were included. All photographs were taken from an unobstructed view and were digitally scanned and adjusted for luminance and contrast.

Experiment 2 took place about 2 months after Experiment 1. Participants were presented with the photograph stimuli, one at time, and for each stimulus, they were required to determine whether it was located in Toronto by pressing one of two buttons. There was no time limit for responding. For stimuli deemed to be located in Toronto, participants had to express two additional judgments. First, they had to rate the degree to which they were familiar with the stimulus, on a scale of 1 (*low familiarity*) to 7 (*high familiarity*; familiarity judgment). Familiarity was defined to participants as their level of knowledge of the landmark and the ease with which they recognized it. Moreover, for each stimulus recognized as from Toronto, participants had to judge whether they had a personal memory connected to that place, that is, if they could "go back in time and relive a detailed, personal episode that had happened at or near that location, or was somehow connected to it" (reexperiencing judgment).

**Statistical analyses.** The relevant variables were entered as dependent measures in a between-subjects ANOVA with Group (patients vs. controls) as factor. To control for the effect of age, education, and experience with downtown Toronto, we entered these variables as covariates in the ANCOVA.

### Results

Table 4 shows hit rates for Toronto landmarks, false-alarm rates to non-Toronto landmarks, and an accuracy score that was computed by subtracting false-alarm rates from hit rates. The table also shows mean familiarity levels for correctly recognized stimuli, as well as the proportion of correctly recognized stimuli attracting a reexperiencing judgment.

**Recognition accuracy.** The ANCOVA on accuracy scores revealed no significant effect of Group, $F(1, 13) = 1.26$, $p = .28$, $\eta^2 = .07$. Additionally, age ($p = .69$), education ($p = .93$), or experience with Toronto ($p = .72$) did not have a significant impact on performance.

**Familiarity judgment.** The ANCOVA on familiarity ratings for correctly recognized stimuli revealed no significant effect of Group, $F(1, 13) = 0.009$, $p = .92$, $\eta^2 = .0005$, or any of the covariates ($p > .18$ in all cases).

**Reexperiencing judgment.** The ANCOVA on the proportion of correctly recognized stimuli attracting a reexperiencing judgment revealed no significant effect of Group, $F(1, 13) = 0.34$, $p = .56$, $\eta^2 = .01$. It is interesting that age had a significant effect on performance ($\beta = -.76$, $p < .05$), such that older participants were less likely to report reexperiencing states at the view of Toronto landmarks than younger participants. Education ($p = .93$) and experience with Toronto ($p = .72$) had no influence on reexperiencing.

### Discussion

The results of Experiment 2 excluded memory problems for Toronto landmarks in patients with lesions in PPC. Not only did patients recognize as many landmarks as normal controls, they also reported similar feelings of familiarity and reexperiencing to the controls', suggesting an overlapping subjective experience associated with recognition of remote spatial information.

The absence of a deficit in reexperiencing in patients compared with controls contrasts with the results obtained in Experiment 1. One reason for the difference might be that in this experiment, participants were cued to reexperience a past event, whereas in Experiment 1 they were asked about concurrent experiences during mental navigation tasks only after the task was completed. The difference in the two tests corresponds to differences reported by Berryhill, Phuong, Picasso, Cabeza, and Olson (2007) in free and cued recall of autobiographical episodes in patients with bilateral PPC lesions. Though recollection did not occur spontaneously, it could be invoked upon instruction. We elaborate more on this point in the General Discussion.

## General Discussion

Models of spatial memory and navigation view the PPC as involved in coding environments within an egocentric coordinate system that allows for movement with respect to landmarks (Milner & Goodale, 1995). One important question for theories of remote spatial memory is whether the egocentric deficit following PPC lesions extends to remote memory representations acquired long ago. Aguirre and D'Esposito (1999) postulated that patients with PPC lesions might suffer from egocentric disorientation, a type of topographical disorientation attributable to a difficulty representing the relative location of objects (and landmarks) with respect to the self. This hypothesis predicts a specific pattern of difficulty with topographical tasks in patients with PPC lesions: Patients should be impaired at accessing egocentric mental views of places in familiar environments but show relatively preserved allocentric knowledge of the same environments. To test this prediction, we investigated remote spatial memory in patients with lesions in PPC and healthy individuals. Participants underwent a set of experimental tasks designed to simulate relatively higher demands on allocentric versus egocentric components of remote spatial memory (see Table 1). For four of the tasks, we had supporting behavioral and neuroimaging evidence regarding the preferred reference frame through which task performance was typically accomplished: allocentric for distance and proximity judgments, and egocentric for landmark sequencing and route navigation. Comparing PPC patients' performance between these two sets of tasks provided a unique opportunity to investigate the role of PPC in egocentric and allocentric navigation.

Consistent with our predictions, and in line with Aguirre and D'Esposito's (1999) theoretical framework, patients were normally able to perform distance and proximity judgments that, arguably, were based on intact allocentric, cognitive maps of topographical spaces. Patients' allocentric knowledge of downtown Toronto appeared preserved in many respects: Patients located landmarks on a sketch map of Toronto as precisely as controls and could determine their position in relation to other landmarks. Patients also proved able to recognize landmarks from downtown Toronto among structurally similar, yet never encountered, landmarks (see also Wilson et al., 2005), and the physical appearance of Toronto landmarks was reported as equally accessible and vivid by patients and controls. It is somewhat surprising that patients as a group were also able to perform correctly the landmark sequencing task, although a marginal deficit was detected in left-lesioned patients. This result was unexpected because healthy individuals commonly report accomplishing this task by adopting an egocentric, route-based strategy (Rosenbaum et al., 2004). One possibility is that although healthy controls commonly accomplish landmark sequencing by representing their own body position with respect to the relevant reference points, which confers the reported "egocentric flavor" to the task, the use of egocentric representations is not necessary to solve the task. When asked to judge whether city hall and the Eaton Centre are in the correct order if walking from west to east, for example, participants may imagine walking along Queen Street in that direction and seeing city hall appearing on their left, immediately followed by the Eaton Centre. This imaginary walk would allow them to arrive at the correct response (i.e., "yes"). A correct response, however, is also possible based on an allocentric map of Queen Street that specifies the relative position of the two landmarks along the west–east axis, without the need for lifelike navigation of downtown Toronto. Thus, intact knowledge of the invariant, geometrical relations between landmarks on a cognitive map may have supported patients' landmark sequencing performance. This result further confirms retained allocentric spatial knowledge after PPC lesions, but also suggests that patients should be impaired on tasks that tap egocentric processing more heavily, so that allocentric representations cannot entirely compensate for performance.

In line with this prediction, patients dramatically failed the route navigation task. Because producing a verbal description of a route between two landmarks usually is not a well-practiced behavior (Farrell, 1966), individuals typically resort to the egocentric simulation of an imaginary route between the two landmarks to produce the description (see also Ward et al., 1986). It is not surprising that participants in Rosenbaum et al. (2004) reported adopting an egocentric perspective while performing this task. Similarly, in the present study, virtually all control participants reported that navigation was experienced from a first-person (as opposed to third-person) perspective, and their descriptions appeared as vivid and rich in detail as a real-life experience. Patients with lesions in PPC could not perform the task normally and mentally arrived at the destination less frequently than control participants with similar preexperimental experience navigating in downtown Toronto. According to the patients themselves, they did not experience a first-person perspective during navigation and did not have feelings of reexperiencing during navigation as frequently as normal controls (see also Ally, Simons, McKeever, Peers, & Budson, 2008; Davidson et al., 2008; Simons, Peers, Mazuz, Berryhill, & Olson, 2009), suggesting that they were not processing remote spatial memories within an egocentric reference frame.

This finding is consistent with fMRI evidence. Rosenbaum et al. (2004), using the same tasks, showed that left superior-medial PPC was more strongly activated in participants as they performed tasks that they described as involving an egocentric, route-based strategy (i.e., landmark sequencing, route navigation) compared with tasks described as involving an allocentric, maplike strategy (see also Rosenbaum, Winocur, Grady, Ziegler, & Moscovitch, 2007). That left (as opposed to right) PPC mediated egocentric components of remote spatial memory in Rosenbaum et al. (2004) is in line with our finding that left-lesioned patients showed performance decrements in both route navigation and, though only marginally, landmark sequencing, a task for which egocentric navigation was, arguably, even less crucial than it was for route navigation. Moreover, Spiers and Maguire (2006) showed that, compared with coasting (i.e., navigating automatically without any directed thoughts), route planning was associated with consistent activity in the left superior PPC, and not the hippocampus as was previously thought, and that activity in PPC bilaterally coded the egocentric direction to the goal destination (Spiers & Maguire, 2007a). These activations were similar to the activations reported by Maguire and colleagues (Maguire et al., 1998; Maguire, Frackowiak, & Frith, 1997) when subjects mentally followed routes reconstructed through their knowledge of familiar environments.

How does PPC support egocentric mental views of places in a familiar environment? It does not seem that PPC stores long-term memories of these views, because neglect patients appear to retain knowledge of familiar routes, although they lose access to those on the left side of (representational) space when trying to retrieve spatial information from remote memory (Bisiach & Luzzatti, 1978). It is more likely that PPC supports processing and manipulation of spatial information retrieved from elsewhere in the brain (see Burgess, 2006; Moscovitch et al., 2005; Spiers & Maguire, 2006b). According to one prominent theory (Byrne, Becker, & Burgess, 2007), medial parietal regions around the precuneus provide egocentric access into medial-temporal-lobe-based long-term allocentric spatial memory to enable mental imagery, planning, and navigation (i.e., the parietal window). Access by the parietal window into allocentric representations is mediated by a transformation circuit, likely supported by posterior parietal and retrosplenial cortices, converting allocentric into egocentric representations (and vice versa; Burgess, 2006; Byrne et al., 2007).

A rather consistent complaint across patients during route navigation was that they had difficulties visualizing the streets in the relevant area and that their subjective experience of mental navigation was impoverished. It does not seem that PPC patients had a general deficit in visual imagery, that is, in the maintenance of or access to visual material. Indeed, as we already mentioned, the patients were able to use spatial imagery of a remotely formed cognitive map to perform accurate judgments about proximity and distance. As well, they were normally able to draw a clock and to imagine the position of the clock's hands at 12:45. Their complaint appeared to refer specifically to the type of immersive visual imagery required to form and maintain an egocentric representation (but see below). Such a deficit is consistent with an impairment in the parietal window, which is presumed to act as the "mind's eye," allowing the egocentric inspection of mental images (Burgess, Becker, King, & O'Keefe, 2001; Fletcher et al., 1995). The patients' complaint, however, is also consistent with a deficit in the transformation mechanisms that makes egocentric representations available to imagery. The fact that patients' lesions were in most cases lateral, and not medial, reinforces this possibility. Deficits in the parietal window, however, are difficult to dissociate from those affecting transformation mechanisms (see also Byrne et al., 2007). One possible way to distinguish the two deficits would be to test whether PPC patients are able to integrate egocentric views of newly learned locations into preexisting allocentric spatial knowledge.

Alternatively, the patients' problems with egocentric navigation might be due to an impairment in the cognitive processes operating on egocentric representations within the parietal window. As we discussed earlier, to drive navigation, egocentric representations have to be examined in visual imagery to enable actual or imagined movements, and manipulated to allow for mental exploration and spatial updating. It is presumed that one can attend sequentially to the spatial locations of items in imagery just as in perception, presumably via planned eye movements (see Postle, Idzikowski, Della Sala, Logie, & Baddeley, 2006). It has been proposed recently that overlapping attentional mechanisms operate when directing attention in space and within internal representations derived from memory (i.e., the attention-to-memory [AtoM] hypothesis; Cabeza et al., 2008; Ciaramelli et al., 2008). In perception, the superior PPC is implicated in directing top-down attention to relevant information, whereas the inferior PPC mediates the bottom-up attentional capture by salient information (Corbetta & Shulman, 2002). According to the AtoM hypothesis, superior and inferior PPC serve analogous roles in memory retrieval to those they play in attention: Superior PPC mediates the voluntary allocation of attentional resources to memory retrieval, whereas inferior PPC is associated with the bottom-up attentional capture by retrieved contents. It is possible, then, that although the results of Experiment 2 indicate that all patients were able to recognize the visual details of relevant landmarks, patients with lesions in the superior PPC did not use those landmarks as efficient cues to retrieve the navigation instructions with which they were associated. On the other hand, the same landmarks might not have automatically popped out in imagery in patients with inferior PPC lesions, who, as a result, navigated in a pathologically empty space. The latter deficit would correspond, in effect, to a deficit in spatial imagery but would be secondary to poor capture of bottom-up attention by (spatial) memory contents. Indeed, when reliving was probed with views of Toronto landmarks in Experiment 2, patients were able to imagine personal experiences connected to those landmarks.

This interpretation fits with evidence that patients with PPC lesions have memory problems that mirror their attentional problems. Berryhill et al. (2007; but see Davidson et al., 2008) found that patients with lesions in inferior PPC were impaired in spontaneous autobiographical recall but succeeded at recalling the same contents if probed by specific questions. Moreover, although unimpaired in recognition and source memory (Davidson et al., 2008; Simons et al., 2008, 2009), PPC patients may be extremely reluctant to judge recognized items as "remembered" and show low confidence in their memories (Simons et al., 2009). Together these findings support the hypothesis that, like percepts, memories do not capture attention automatically in patients with lesions in inferior PPC, leading to "neglect" of objectively available memory contents (Berryhill et al., 2007), or diminished recollective experience and confidence in less severe cases (Davidson et al., 2008; Simons et al., 2008; but see Simons et al., 2009, for an alternative interpretation). However, when attention is directed to memory in a top-down fashion, by instructions or cues, its contents are revealed (Berryhill et al., 2007). In this respect, it could be interesting to investigate whether deficits in egocentric navigation would disappear if subjects were explicitly instructed to adopt a first-person perspective or to attend to specific spatial features along the route.

The attentional hypothesis might also explain an unexpected finding of the present study. Although patients showed largely preserved allocentric knowledge in a variety of tasks, they were impaired on two tasks that were previously thought to be solved within an allocentric reference frame: spatial map drawing (see also Levine et al., 1985; Stark et al., 1996) and vector mapping (see also Seubert, Humphreys, Müller, & Gramann, 2008). One notable aspect of the patients' performance, especially those with inferior PPC lesions, was that their poor recall of landmarks on a map of downtown Toronto was observed along with preserved ability to place the same landmarks on the map upon request. Poor map drawing might then be the expression of a disproportionate deficit in spontaneous, compared with prompted, spatial memory retrieval, mirroring the already described deficit in the nonspatial domain (Berryhill et al., 2007). A deficit in recalling a map of Toronto, in turn, may have impaired patients' ability to compute vectors with respect to it. Indeed, when we controlled for deficits in map drawing, patients were no longer impaired on vector mapping. In addition, lesions in inferior compared with superior PPC resulted in a larger susceptibility to deficits in vector mapping, supporting the idea that vector mapping deficits may be secondary to poor bottom-up AtoM.

Yet, attentional deficits cannot fully account for impaired mental navigation. The patients remained impaired on route navigation even when controlling for deficits on map drawing, suggesting that additional problems interfered with egocentric navigation in PPC patients. We know that humans do not plan routes all at once (Wiener & Mallot, 2003), and therefore route navigation likely involves constant spatial updating of the unseen goal location while navigating. Online construction of updated egocentric representations (see Wolbers, Hegarty, Büchel, & Loomis, 2008) requires the integration of egocentric mental views with proprioceptive cues about locomotion and is likely to place demands on spatial WM. Although we did not test spatial WM in our patients, fMRI studies have shown that the PPC plays an important role in spatial WM (Jonides et al., 1993; Walter et al., 2003), and patients with lesions in PPC may be impaired on spatial WM tasks (Berryhill & Olson, 2008; Ferber & Dankert, 2006; Seubert et al., 2008; but see Piccardi, Bianchini, Zompanti, & Guariglia, 2008). It is possible, then, that poor spatial WM contributed to patients' deficits in route navigation. Additionally, PPC patients may have problems processing proprioceptive information that is necessary for spatial updating. Indeed, there is converging evidence that right PPC regions code for several aspects of self-processing, such as agency, self–other distinctions, and mental own-body imagery (e.g., Blanke & Arzy, 2005; Ruby & Decety, 2001). Activation in right TPJ has been reported during simulation of actions from a first-person compared with a third-person perspective (Ruby & Decety, 2001), and interference with this area in neurological patients may lead to the experience of disembodiment (Blanke, Ortigue, Landis, & Seeck, 2002). However, the observed tendency for left-sided lesions to produce greater deficits than right-sided ones, despite the tasks being spatial, is more consistent with an AtoM interpretation of the results.

The exact mechanism by which PPC damage disrupts egocentric access to remote spatial memory—that is, a deficit in the parietal window), the transformation circuit, or the attentional and WM processes operating on mental images in the parietal window—remains to be clarified in more specific, future research. For the time being, by using a variety of spatial memory tasks, we have shown that lesions to PPC impair egocentric navigation, while leaving performance on most tasks relying on allocentric components of remote spatial memory unaffected. These findings suggest that the PPC, especially on the left, is at the core of a system mediating retrieval of remote spatial memories within an egocentric framework that normally enables navigation as well as reexperiencing. Our results, however, show that the PPC is also implicated in specific aspects of allocentric navigation, possibly through the pivotal role it plays in supporting cognitive processes that are necessary for its normal expression, such as spontaneous retrieval.

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