Functional Dissociations Within Posterior Parietal Cortex During Scene Integration and Viewpoint Changes

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The posterior parietal cortex (PPC) is an anatomically heterogeneous brain region implicated in a wide range of cognitive operations, including egocentric spatial processing and both short- and long-term memory. Here, we report functional specificities of cytoarchitectonically defined subregions of PPC during the processing of scenes across changes in viewpoint. Participants \( n = 16 \) saw photographs of familiar and unfamiliar places while undergoing functional magnetic resonance imaging (fMRI). On each trial, 4 viewpoints of the same place were presented, with either a plausible sequence of viewpoints (SEQ) or a scrambled order (SCRA). Distinct response profiles were observed within PPC. Area 7A showed increased activity for SEQ versus SCRA order, regardless of place familiarity, whereas the rostral inferior parietal lobule showed preferential increases for unfamiliar versus familiar places in SEQ series. In contrast, more posterior subregions in both superior and inferior PPC exhibited increases for familiar versus unfamiliar places at the end of the sequence, regardless of order. The data highlight the distinctive contribution of several subregions of PPC during the processing of scenes, with specific cortical areas involved in the progressive integration of spatial information across viewpoint changes, and others involved in the retrieval and maintenance of scene information in memory.

Keywords: egocentric processing, functional MRI, memory, prediction, scene perception

Introduction

Orienting ourselves in space is a fundamental ability subserving navigation and memory. Although inspecting what stands “in front” of us can inform about our current location and facing direction, we usually look “around” us to search for confirmatory cues or to find our way to destination (Spiers and Maguire 2007a; Christal 2013). During these changes in perspective, past and current viewpoints combine, generating an internal representation in memory upon which what is expected to be seen at the next head turn can be predicted. Several studies on scene analysis and recognition have brought precious insights about brain mechanisms implicated in these abilities (Spiers and Maguire 2007a; Epstein 2008; Vann et al. 2009; Epstein and Vass 2014), pointing to a crucial contribution of the posterior parahippocampal gyrus (PPHG; Epstein and Kanwisher 1998) as well as the retropolential complex (RSC; a functionally defined region comprising the retropolential cortex proper, the adjacent posterior cingulate, plus their extension posteriorly to the parieto-occipital fissure; see Epstein 2008). However, several other brain areas are also engaged during the processing of scene and perspective information, but their exact role remains to be specified. In particular, separate lines of research implicate the posterior parietal cortex (PPC) in the representation of egocentric space (bilateral or right PPC, see Spiers and Maguire 2007a for review), as well as in short and long-term episodic memory (bilateral or left PPC, see Naghavi and Nyberg 2005; Wagner et al. 2005 for reviews; Cabeza et al. 2008). How these processes interact for the integration of successive viewpoints during scene recognition has not been formally investigated. In the present study, we specifically aimed at clarifying the role of the PPC in processing scene information across changes in perspective and its relation to spatial memory processes.

Facing direction and location information are represented in a distributed set of structures in both parietal and medial temporal lobe (MTL) areas, including RSC and the hippocampal/parahippocampal gyrus complex (Epstein 2008; Yoder et al. 2011; Christal 2013; Vass and Epstein 2013). Most recent studies have focused on the MTL and medial parietal areas, highlighting distinctive properties of the RSC and PPHG during scene processing and recognition (Epstein 2008; Park and Chun 2009; Park et al. 2010; Dilks et al. 2011; Harel et al. 2013; Sulpizio et al. 2013; Epstein and Vass 2014). Specifically, the PPHG appears involved in the coding of local elements within scenes (Epstein 2008; Epstein and Vass 2014), the discrimination of changes in perspective (Epstein et al. 2003; Park and Chun 2009), and mental imagery about scenes (O’Craven and Kanwisher 2000; Mégervand et al. 2014). Conversely, the RSC is considered to mediate the integration of viewpoints into a ‘panoramic’ representation (Park and Chun 2009), the coding of heading direction (Aguirre and D’Esposito 1999; Rosenbaum et al. 2004; Sulpizio et al. 2013), and the inference of spatial information beyond the immediate field of view (Epstein and Higgins 2007; Epstein 2008; Park and Chun 2009). In addition, the latter region is particularly sensitive to place “familiarity” (Epstein, Higgins, et al. 2007; Epstein, Parker, et al. 2007; Spiers and Maguire 2007a), and encodes stable features of the environment (Auger et al. 2012; Auger and Maguire 2013).

Complementing visual recognition, computations related to the viewer’s perspective take place in the lateral PPC (e.g., Farrell and Robertson 2000; Karnath 1994; Maguire et al. 1998; Schindler and Bartels 2013; Vallar et al. 1999; Vogele and Fink 2003; Weniger et al. 2009). In humans, both superior and inferior aspects of the parietal cortex appear critically involved. Activity in the tempo-parietal junction (TPJ)/inferior parietal lobule (IPL) correlates with rotations of the body during a mental imagery task (Schwabe et al. 2009; Schindler and Bartels 2013), as well as with heading accuracy during virtual navigation in a familiar environment (Maguire et al. 1998). In the superior parietal cortex (SPC), activity of area 7 varies according to the egocentric direction of target locations (Spiers and Maguire 2007b). In addition, lesion in SPC leads to egocentric disorientation (Stark et al. 1996; Aguirre and D’Esposito...
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1999; Wilson et al. 2005; Ciaramelli et al. 2010), possibly by preventing the update of heading position (Seubert et al. 2008). Finally, a recent study suggested a ventral/dorsal dissociation within parietal cortex consistent with a specialization for detecting spatial change and scene novelty, respectively (Howard et al. 2013). Nonetheless, it is still poorly understood how distinct functional subdivision in PPC contributes to spatial cognition and scene integration across viewpoints.

Another line of research has also consistently linked the PPC with working memory processes, orienting of attention, and episodic memory retrieval (Naghavi and Nyberg 2005; Wagner et al. 2005; Husain and Nachev 2007; Cabeza et al. 2008; Corbetta et al. 2008). Damage to the IPL leads to spatial neglect, a disorder of spatial awareness associated with deficits in attention and spatial working memory (Husain et al. 2001; Vuilleumier 2013). In addition, the PPC is involved in the online maintenance of information in short-term memory (Todd and Marois 2004; Edin et al. 2009), providing a putative neural basis upon which updating of scene representation across different viewpoints may take place (Byrne et al. 2007; Burgess 2008; Seubert et al. 2008; Wollbers et al. 2008). Finally, the PPC is consistently recruited during long-term memory retrieval (Naghavi and Nyberg 2005; Wagner et al. 2005; Cabeza et al. 2008) which might be related to the egocentric aspects of autobiographical representations (Wollbers et al. 2008; Freton et al. 2015) or the orientation of attention towards relevant information in memories (Cabeza et al. 2008; Corbetta et al. 2008). A posterior/anterior dissociation has been proposed to match the long-term/short-term memory retrieval dichotomy in the IPL (Elman et al. 2013). However, it remains to determine how these various properties of the PPC are engaged by the integration of scene information during serial changes in perspectives.

In sum, there is extensive evidence for the key involvement of a parieto-temporal network in scene processing and recognition (Spiers and Maguire 2007a; Burgess 2008; Kravitz et al. 2011). Nevertheless, how perceptual and memory processes interact in the PPC during the encoding or retrieval of a place representation is not well understood. Here, we therefore investigated how spatial memory and changes in perspective engage PPC activity when processing scenes across viewpoint changes. Pictures from the same place were presented in succession, either in a plausible sequential/overlapping order or in a random/nonoverlapping series of viewpoints. By comparing sequences (SEQ) of viewpoints presented in natural succession or scrambled order (SCRA), we could test for the role of PPC and other brain areas in the elaboration of coherent spatial representations of places integrating different views in a layout. In particular, this manipulation allowed us to examine the impact of sequence predictability on brain activity, based on within-trial, short-term memory (Enns and Lleras 2008). In addition, by comparing responses to familiar or novel places, we were able to determine how the spatial integration of viewpoints in these areas is modulated when their succession can be predicted based on short and/or long-term memory. A control condition with a succession of the same or different viewpoints is expected to show different activity during the beginning versus end of sequences in brain areas involved in the prediction of scene layouts based on an egocentrically coherent succession of viewpoints. Finally, areas involved in long-term episodic memory (preatial, temporal, RSC) should show increased activity for “familiar” compared with “unfamiliar” places, and more specifically, this effect should be more pronounced during the beginning of sequences for areas involved in place recognition, but more pronounced at the end of sequences for areas involved in memory retrieval processes.

Materials and Methods

Subjects
Participants were 16 adults (mean: 24.75 ± 4 years, 8 males) recruited through local advertisement among students of the University of Geneva. All but one were right-handed. History of neuropsychiatric, neurologic or sensory disorder, as well as substance abuse were part of the exclusion criteria, and assessed before the scanning session. All of them gave written informed consent prior to inclusion in the study, which has been approved by the local ethics committee. All were living in Geneva for at least 6 months.

fMRI Activation Task
Selection of Photographs
A few days before the fMRI session, each participant was asked to enumerate places he/she knew well in and around Geneva, as well as to describe some typical routes in the city taken several times each week. Descriptions were detailed and included street names. Photographs of familiar places on Google Street View were selected individually for each participant, according to the description of his/her typical routes, and then used as stimuli in the fMRI experiment. Unknown places from other cities were additionally selected to compare brain activity for familiar compared with unfamiliar places, and were identical for all the participants. All photographs were selected to obtain a series of 4 consecutive viewpoints, with an overlap of about 33% and a 45° rotation between 2 consecutive pictures.

Activation Task
We used an incidental categorization task, which required no explicit recognition abilities. Color photographs of places were presented in series of 4, shown each in turn during 2 s at the center of the screen (Fig. 1). Each picture of a given series consisted of a different viewpoint of the same place, which was either familiar or unfamiliar to the participant (FAM and UNFAM conditions, respectively). After each series, he/she had to indicate whether the places shown in the photographs were “lively” or “calm” (e.g., in terms of potential noise, traffic jam, or people crowding) as with a place of reference (which were 2 familiar locations in the city center, given as a reference to all participants). In addition to personal familiarity with places, we manipulated the succession of the viewpoints within each series of 4 pictures. In the “Sequential order” series (SEQ condition), the sequence of 4 pictures mimicked a point of view similar to one turning gradually his head from left to right or the reverse; that is, it was possible to predict the
upcoming picture, based on the previous ones of the same series (A-B-C-D or D-C-B-A order). Alternatively, in the "Scrambled order" series (SCRA condition), pictures were presented in a non-progressive order such that the upcoming picture was unpredictable (B-D-A-C or C-A-D-B order). In addition, we included 2 unfamiliar control conditions, one in which the same picture was repeated 4 times within a series ("repeated" condition), the other in which all pictures of a series were from different places ("different" condition). The categorical judgment was given by pressing one of 2 buttons of a response box. There were 20 trials per condition.

**Postscan Recognition Procedure**

After scanning, participants were submitted to a self-paced surprise place recognition test. All photographs of the familiar places were presented again and they had to indicate the name and/or the location of the place shown. A place was considered as "recognized" whenever either its name or its localization was correctly retrieved. The number of correct recognition was high and reached 97% on average (range: 88–100%).

**fMRI Procedure**

**Equipment**

Participants were scanned during a single session of about 40 min. Data were acquired on a 3T MRI system (Trio TIM, Siemens, Germany) with a 12-channel head coil. Visual stimuli were back projected on a screen using E-prime (E-prime 1.0, Psychology Software Tools, Inc., Pittsburgh, PA, USA). Head movements were prevented using an ergonomic air head cushion. The responses were recorded with a button box (HH-2 × 4-C, Current Designs, Inc., USA).

**Scanning Protocol**

Whole-brain functional images were collected using a susceptibility weighted echo planar imaging (EPI) sequence (repetition time (TR)/echo time (TE) = 1810/30 ms; flip angle = 90 degrees; parallel imaging techniques (PAT) factor = 2; field of view (FOV) = 255 mm; matrix size = 64 × 64 pixels). Thirty-two transversal slices were acquired in an interleaved descending manner (slice thickness = 4 mm, interslice gap = 1 mm, voxel size = 4 mm isotropic). High-resolution anatomical images were acquired using a T1-weighted, 3D sequence (magnetization-prepared rapid gradient echo imaging (MP-RAGE); TR/inversion time (TI)/TE = 1900/900/2.32 ms; flip angle = 9°; voxel size = 0.9 mm isotropic; 256 × 256 × 192 voxels).

**Functional Data Analysis**

**Preprocessing**

Functional images were preprocessed and analyzed using a standard procedure implemented in Statistical Parametric Mapping (SPM8; Wellcome Trust Centre for NeuroImaging, London, UK). All volumes were first temporally realigned and resampled to the acquisition time of the middle slice. The data were then spatially realigned to the first slice. The anatomical volumes were spatially co-registered to the mean functional image resulting from spatial realignment. Functional images were then normalized to the Montreal Neurological Institute (MNI) EPI template, resampled to 3-mm isotropic voxels and smoothed with a Gaussian kernel (8-mm full-width at half-maximum).

**First-Level Analysis**

Because our aim was to identify brain responses as a function of the predictability of scenes based on their familiarity and sequence of presentation, our analysis focused on differential activations evoked in the first and second half of each trial, enabling us to compare repetition suppression and enhancement effects across the different conditions (e.g., Vannini et al. 2013). The first-level model for each participant included 2 regressors for each trial type, one corresponding to the first part of the sequence (pictures 1 and 2 = part 1), the other corresponding to the final part of the sequence (pictures 3 and 4 = part 2). This allowed investigating the effects of sensory/recognition processes (part 1) and prediction processes (part 2). This resulted in 12 regressors corresponding to the initial and last parts of the 6 possible trial types: UNFAM-SEQ1 and UNFAM-SEQ2, UNFAM-SCRA1 and UNFAM-SCRA2, FAM-SEQ1 and FAM-SEQ2, FAM-SCRA1 and FAM-SCRA2, DIFFERENT1 and DIFFERENT2, REPEAT1 and REPEAT2. In the familiar place condition, the analysis included only those trials for which the place was correctly located in the postscanning test (97%, see postscan

![Figure 1. Trial procedure.](http://cercor.oxfordjournals.org/)
recognition procedure). Familiar places that were not recognized during the postscan recognition test were entered into an additional regressor of no interest. The regressors were convolved to a canonical hemodynamic function. We added 6 other regressors to model head movements. A high-pass filter (cutoff = 128 s) and a first-order autoregressive function were applied to account for temporal autocorrelation. Statistical parametric maps (t-maps) were obtained by comparing each effect with baseline activation levels and then incorporated in the second-level group model.

Second-Level Analysis
Individual t-maps were entered into a full factorial design with 12 conditions (see above) to model the main effects (familiarity, sequence type, and trial part). Whole-brain analyses were performed on a voxel-wise basis with correction for multiple comparisons (P < 0.05 family-wise error (FWE) corrected, unless specified differently). We used the SPM8 (Wellcome Trust Centre for NeuroImaging) and Caret version 5.65 (http://www.sph.sc.edu/comd/caret). Brain surface renderings were created using SPM8 (Wellcome Trust Centre for NeuroImaging) and Caret version 5.65 (http://brainvis.wustl.edu).

ROI Analyses
Anatomical ROI. Because of our interest on the role of parietal cortex, we conducted more specific analyses on subregions of the SPC and the IPL (Fig. 2). These sub-ROIs were defined according to a cytoarchitectonic probabilistic atlas (Caspers et al. 2006; Caspers et al. 2008; Scherperjans, Hermann, et al. 2008; Caspers et al. 2013), based on the rationale that the distinct neuronal populations that compose and define subregions of SPC and IPL are likely to mediate different functions. Within the SPC, our ROI analyses concerned 3 subregions of area 7 (anterior area 7: 7A; medial area 7: 7M; posterior area 7: 7P). Area 7 has previously been related to egocentric coding during spatial movements. A high-pass filter (cutoff = 128 s) and a first-order autoregressive function were applied to account for temporal autocorrelation. Statistical parametric maps (t-maps) were obtained by comparing each effect with baseline activation levels and then incorporated in the second-level group model.

Figure 2. Anatomical regions of interests within posterior parietal cortex: rostral (PFop, PFr, PFcm), intermediate (PFm), and caudal part (PGa, PGp) of the inferior parietal lobule (IPL), and areas 7A, 7M, and 7P of the superior parietal cortex (SPC), overlaid on a lateral (left) and postero-medial (right) view of cortical surface (right hemisphere for illustration).

Results
Behavioral data
Response times on the categorization task were entered into a 2-way ANOVA (familiarity × sequence) for experimental conditions. There was a main effect of familiarity (F(1, 15) = 9.575, P < 0.01), reflecting faster response to familiar than unfamiliar places (681 and 762 ms, respectively). There was no other effect. The control condition was analyzed using a separate one-way ANOVA on “repeated” versus “different” pictures; subjects responded equally fast for the repeated and different place trials (780 and 755 ms, respectively; F(1, 15) = 0.31, P = 0.586).

Imaging data
Main Effects in Whole-brain Analyses
To assess the general effect of scene familiarity, we compared the FAM versus UNFAM conditions independently of viewpoint order and trial part. This contrast (P < 0.05 FWE corrected; Table 1) revealed a widespread network similar to results from previous recognition memory studies (Spaniol et al. 2009; Rugg and Vilberg 2013), including activations in both inferior and medial parietal areas, RSC, medial prefrontal cortex, and visual occipital areas (Fig. 3). This network also strongly resembles the default mode network; familiar scenes were likely to favor the projection of oneself in a particular place, activating introspective processes and retrieval of
personal memories, which are key components of functions associated with the default mode network (e.g., Buckner et al. 2008 for review). There was no significant activation for the reverse contrast (UNFAM > FAM).

We also examined the main effect of sequence in scene viewpoints by comparing the SEQ versus SCRA conditions independently of familiarity and trial parts. This contrast revealed selective activations in superior PPC, hippocampus, antero-medial thalamus and anterior cingulate gyrus ($P < 0.005$ uncorrected; Supplementary Table 1). The reverse comparison showed no significant effect.

Finally, we looked at the main effect of within-trials time (part 1 vs. part 2) to reveal areas sensitive to repetition of place information across pictures, irrespective of familiarity and sequence type. First, pure repetition suppression effects unrelated to viewpoint manipulations were evaluated using the control condition with repeated places (part 1 > part 2 contrast, $P < 0.05$ FWE corrected), which showed significant decreases in bilateral PPHG/posterior fusiform (Supplementary Table 2), replicating previous data (e.g., Park and Chun 2009). Second, repetition enhancement effects were evaluated using the reverse comparison with repeated places (part 2 > part 1 contrast, $P < 0.01$ FWE corrected; Supplementary Table 2). This showed significant increases in visual (lingual, cuneus, and calcarine gyri), parietal (precuneus, supramarginal gyrus), temporal (middle temporal), cingulate (middle and anterior), and frontal cortices (inferior frontal gyrus). Then, to highlight brain areas involved in scene integration beyond unspecific visual or task-related effect (e.g., response anticipation), we performed the same contrast for within-trial time effects in the main experimental conditions (part 1 > part 2) but masked exclusively by the corresponding contrast for the different picture trials in the control condition (mask threshold $P = 0.05$ uncorrected). Repetition suppression in this comparison (part 1 > part 2 masked by the control different part 1 > different part 2) were only observed in the right fusiform/PPHG region ($P < 0.05$ FWE corrected; Supplementary Table 2). Conversely, the opposite contrast, testing for repetition enhancement across successive viewpoints (part 2 > part 1 masked by the control different part 2 > different part 1) were observed in bilateral SPC (precuneus, posterior cingulate area) and TPJ (supramarginal gyrus, superior and middle temporal gyrus), as well as thalamus, middle cingulate cortex, and inferior frontal areas ($P < 0.05$ FWE corrected; Supplementary Table 2).

Taken together, these whole-brain SPM results already point to dissociable effects not only between PPC and MTL (with predominantly increasing or decreasing activity over successive viewpoints, respectively), but also within PPC (with main effects of scene familiarity and sequence predominating in IPL and SPC, respectively).

### Table 1

<table>
<thead>
<tr>
<th>Region</th>
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</tr>
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</table>

L, Left; R, Right; RSC, retrosplenial complex; SPC, superior parietal cortex; IPC, inferior parietal cortex; PHG, parahippocampal gyrus; vmPFC, ventro-medial prefrontal cortex; TPJ, temporo-parietal junction.
Anatomical ROI Analysis in the Posterior Parietal Cortex

To clarify interactions between the main factors examined above, our whole-brain analysis was complemented by more specific analyses of anatomically defined ROIs in both the superior and inferior parietal cortices, as well as in the posteromedial and medial temporal areas. In all cases, repeated-measure ANOVAs were conducted on $\beta$ values averaged across all voxels in each ROI with the factors familiarity, sequence, time in the trial, and hemisphere, for the experimental and control conditions separately (see Materials and Methods).

**Superior parietal cortex.** Experimental conditions: All areas in SPC showed progressive increases with the successive scene views, and this effect was generally enhanced by familiarity for the most posterior areas 7P and 7M, but not the more anterior area 7A (Fig. 4).

For area 7A, there was an increase in activity from part 1 to part 2 within trials (main effect of time, $F_{1,15} = 6.252, P = 0.024$), but no significant effect or interaction involving familiarity. However, area 7A was the only region showing a main effect of sequence order, with higher activity for sequential than for scrambled viewpoints order ($F_{1,15} = 5.115, P = 0.039$). This effect was accompanied by a sequence × time × hemisphere interaction ($F_{1,15} = 6.135, P = 0.026$). Activity increased significantly within-trials for sequential trials in both the right ($t_{15} = 2.894, P = 0.011$) and left area 7A ($t_{15} = 2.58, P = 0.021$), whereas scrambled trials produced no significant increase on the right side ($t_{15} = 1.45, P = 0.173$) but marginal effects on the left ($t_{15} = 1.841, P = 0.085$). However, the pattern of predominant effects for sequential trials appeared globally symmetrical.

For area 7M, we found a similar increase of activity within trials (time effect: $F_{1,15} = 72.298, P < 0.001$). In addition, however, familiar places elicited much more activity than unfamiliar places in part 2 (+112%; $t_{15} = 3.977, P = 0.001$), while part 1 was similar for familiar and unfamiliar places ($t_{15} = 0.078, P = 0.939$), yielding a significant familiarity × time interaction ($F_{1,15} = 7.079, P = 0.018$; Fig. 4).

Likewise, for area 7P, there was not only a general increase within trials (time effect: $F_{1,15} = 17.127, P < 0.001$), but again a significant interaction of familiarity × time ($F_{1,15} = 6.032, P = 0.027$; Fig. 4) reflecting greater responses to familiar than unfamiliar places in the second part of the trials only ($t_{15} = 4.299, P < 0.001$; first part: $t_{15} = 1.201, P = 0.248$). Unlike area 7M, however, the main effect of familiarity was also significant ($F_{1,15} = 6.049, P = 0.027$).

Control conditions: In area 7A, activity increased significantly within trials for repeated trials (+130%; $t_{15} = 2.458, P = 0.027$) but not different trials ($t_{15} = 0.807, P = 0.432$), yielding a condition × time interaction ($F_{1,15} = 5.016, P = 0.04$; Fig. 5). There was no other effect.

In areas 7M and 7P, activity increased within trials for both conditions (main effect of time: $F_{1,15} = 16.066, P = 0.001$; $F_{1,15} = 9.749, P = 0.007$, respectively). For area 7M, this increase was also greater for repeated (+146%; $t_{15} = 5.506, P < 0.001$) than different trials (+112%; $t_{15} = 2.458, P = 0.027$), yielding a condition × time interaction ($F_{1,15} = 7.362, P = 0.016$; Fig. 5). This was not the case for 7P ($F_{1,15} = 0.462, P = 0.507$).

Taken together, these data indicate that superior parietal areas were progressively recruited by the presentation of successive scene views, with distinct modulations by predictability in area 7A (due to sequential presentation or repetition) or by familiarity in areas 7M and 7P.

![Figure 4](http://cercor.oxfordjournals.org/) Normalized $\beta$ values across conditions in the superior parietal cortex: anterior (7A), middle (7M), and posterior (7P) part of area 7. UNFAM-SEQ: unfamiliar sequential order; UNFAM-SCRA: unfamiliar scramble order; FAM-SEQ: familiar sequential order; FAM-SCRA: familiar scramble order.
**Inferior parietal lobule.** Experimental conditions: Except for the most rostral ROI, the IPL areas showed similar patterns to areas 7M and 7P in SPC (Fig. 6). In rostral IPL (pooling areas PFop+PFt + PFcm), like other parietal ROIs, activity increased from part 1 to part 2 within trials ($F_{1,15}=31.526, P<0.001$). However, unlike all other parietal areas, responses were globally higher for unfamiliar than familiar places (by 41%; $F_{1,15}=12.074, P=0.003$). In addition, remarkably, there was a familiarity × sequence interaction ($F_{1,15}=5.786, P=0.03$) reflecting that such increase to unfamiliar places was significant only for the sequential order presentations (+48%; $t_{(15)}=6.38, P<0.001$), with no difference for scrambled presentations ($t_{(15)}=0.393$).

In the intermediate IPL (areas PF + PFm), activity also increased within trials ($F_{1,15}=26.932, P<0.001$). In addition, there was a significant modulation of these effects by familiarity. While familiar and unfamiliar places produced similar activations in the first part of the trials ($t_{(15)}=0.482, P=0.637$), there was a marked increase for familiar when compared with unfamiliar places in the second part of the trials (by 104%; $t_{(15)}=4.132, P<0.001$), leading to a significant familiarity × time interaction ($F_{1,15}=7.525, P=0.015$; Fig. 6).

Finally, in caudal IPL (areas PGa + PGp), activity globally increased within trials ($F_{1,15}=29.468, P<0.001$) and was higher for familiar than unfamiliar places ($F_{1,15}=32.311, P<0.001$). As in the preceding ROI, there was a significant familiarity × time interaction ($F_{1,15}=7.556, P=0.015$; Fig. 6). Activity was clearly higher for familiar than for unfamiliar trials in the second part of the trials (+85%, $t_{(15)}=7.813, P<0.001$), but only marginally so in the first part (+32%, $t_{(15)}=1.88, P=0.08$).

Control conditions: For both the rostral and intermediate IPL, there was a main effect of time within trials (part 2 > part 1; rostral: $F_{1,15}=20.741, P<0.001$; intermediate: $F_{1,15}=16.433, P=0.001$; see Fig. 5), as well as a main effect of repetition condition (repeated > different trials; rostral: $F_{1,15}=8.465, P=0.011$; intermediate: $F_{1,15}=40.222, P<0.001$). In both cases, these effects were accompanied by a significant condition × time interaction (rostral: $F_{1,16}=16.955, P<0.001$; intermediate: $F_{1,15}=35.862, P<0.001$), indicating much greater increases for repeated than different trials (Fig. 5).

For the caudal IPL, activity also globally increased within trials ($F_{1,15}=12.875, P=0.003$) but there was no significant difference between the repeated and different conditions ($F_{1,15}=0.976, P=0.339$) and no interaction ($F_{1,15}=2.171, P=0.161$).

To summarize, 2 main profiles were observed within IPL. First, in the caudal and intermediate portions, like in posterior and intermediate area 7, activity was higher for familiar compared with unfamiliar places in the final part of the series. Sequence order had no effect. In contrast, the rostral IPL showed a unique pattern of increased activation for unfamiliar than familiar places that arose only when the viewpoints succeeded each other in a sequential manner.

**ROI Analyses of Functionally Defined Place-selective Regions**

**Retrosplenial complex.** Experimental conditions: In accordance with the whole-brain analysis (see above), there was a marked effect of familiarity characterized by higher activity for familiar than unfamiliar places (+77%; $F_{1,15}=59.607, P<0.001$). On the other hand, activity tended to decrease within trials (main effect of time: $F_{1,15}=3.826, P=0.07$). Although marginally...
significantly, this effect is clearly opposite to the pattern observed in posterior parietal ROIs (Fig. 7). There was no other main effect or interaction. These data are consistent with previous findings highlighting the sensitivity of RSC to familiarity (Spiers and Maguire 2006; Epstein, Higgins, et al. 2007; Epstein, Parker, et al. 2007).

Control conditions: In line with general stimulus repetition effects, activity was lower on repeated trials relative to different trials ($F_{1,15} = 30.196$, $P < 0.001$; Fig. 5) and also tended to decrease within trials ($F_{1,15} = 4.153$, $P = 0.06$). The latter effect was significant for the repeated ($\sim 52\%$, $t_{15} = 2.299$, $P = 0.036$) but not for the different condition ($t_{15} = 1.436$, $P = 0.171$), yielding a marginally significant condition × time interaction ($F_{1,15} = 3.472$, $P = 0.082$).

Posterior parahippocampal gyrus. Experimental conditions: Activity was generally higher for familiar than unfamiliar places ($F_{1,15} = 18.986$, $P < 0.001$). There was no reliable within-trial effect of time ($F_{1,15} = 3.244$, $P = 0.092$), in line with previous data showing a lack of repetition adaptation in PPHG when different viewpoints of a same place succeed (Park and Chun 2009). However, there was a quadruple interaction of hemisphere × familiarity × sequence order × time ($F_{1,15} = 4.646$, $P = 0.048$, Fig. 7). When comparing conditions with paired t-tests for the left and right PPHG separately, we found that this interaction reflected different effects: one related to an influence of the time factor on familiarity, and one related to sequence order.

In the right PPHG, activity was higher for familiar than unfamiliar places in the first part of the trials regardless of sequence (familiar sequential > unfamiliar sequential: $t_{15} = 2.623$, $P = 0.019$; familiar scrambled > unfamiliar scrambled: $t_{15} = 3.792$, $P = 0.002$). There was no effect of familiarity in the second part (all $t$s < 1.722, all $P$s > 0.106; familiarity × time interaction: $F_{1,15} = 0.851$, $P = 0.058$). The left PPHG did not show these modulations by time or sequence. Familiar places always yielded more activity than unfamiliar places, irrespective of presentation order and trial part (part 1: familiar sequential > unfamiliar sequential: $t_{15} = 3.517$, $P = 0.003$; familiar scrambled > unfamiliar scrambled: $t_{15} = 2.813$, $P = 0.013$; part 2: familiar sequential > unfamiliar sequential: $t_{15} = 2.365$, $P = 0.032$; familiar scrambled > unfamiliar scrambled: $t_{15} = 2.332$, $P = 0.034$).

Finally, within-trial effects also differed as a function of sequence order, familiarity and hemisphere. Decreases for the second part of trials were more pronounced in the familiar scrambled than the unfamiliar scrambled conditions in the right PPHG ($t_{15} = 3.01$, $P = 0.009$) but not the left PPHG ($t_{15} = 1.045$, $P = 0.313$; hemisphere × familiarity interaction: $F_{1,15} = 7.823$, $P = 0.035$). In contrast, there was no difference between familiar and unfamiliar places viewed in a sequential manner in either left ($t = 0.388$, $P = 0.703$) or right PPHG ($t_{15} = 0.354$, $P = 0.728$).

Control conditions: As for RSC, activity level was reduced for repeated compared with different trials ($F_{1,15} = 40.977$, $P < 0.001$). Within-trial decreases (part 1 > part 2) were present for the repeated trials (by 40%, $t_{15} = 2.548$, $P = 0.022$) but not the different trials ($t_{15} = 0.166$, $P = 0.87$), yielding a significant condition × time interaction ($F_{1,15} = 8.524$, $P = 0.011$; Fig. 5) and replicating previous data (Park and Chun 2009).
Altogether, these data indicate a main effect of familiarity in both the first and last parts of the trials for the left PPHG, but in the first part of trials only for the right PPHG. In addition, in the right PPHG and for scrambled series, neural activity decreased much more for familiar than unfamiliar places in the course of the trials.

Discussion
In this study, we investigated the effect of familiarity and the spatio-temporal relationships across changes in viewpoints as they become integrated during scene processing. Our study focused on the role of PPC and scene-selective regions (PPHG and RSC) that have consistently been implicated in scene recognition. Our results reveal dissociable response profiles not only between PPC and other medial brain areas, but also within PPC itself.

Superior Parietal Cortex
All parietal areas showed increased activity from the first part to the second part of the trials, indicating a progressive recruitment with the succession of different viewpoints and thus providing direct evidence for an important role of PPC in the spatial integration of scene information. However, in area 7, 2 different types of response were observed. First, area 7A exhibited a unique profile as it was not significantly modulated by familiarity, unlike all other parietal areas, but instead strongly sensitive to the presentation order of viewpoints. Only area 7A, among all ROIs, showed a main effect of sequence order, with increasing activity for sequential but not scrambled presentations. Moreover, as would be expected, this sequence effect interacted with trial part because it was present only in the second half of trials, when scenes were seen after 2 viewpoints presented in a natural (plausible) succession. Furthermore, in the control conditions (with unknown scenes), neural activity increased within a trial only when the same viewpoint was repeated, again consistent with a progressive integration of information even without a perspective shift. Altogether, the data suggest that area 7A is involved in the building of egocentric representations of visuospatial layouts and navigationally relevant cues (Andersen and Buneo 2002), possibly also contributing to the formation of predictions across viewpoint changes. These results are consistent with evidence that the human SPC is critically involved in the coding of egocentric space and heading direction (e.g., Stark et al. 1996; Aguirre and D’Esposito 1999; Kravitz et al. 2011). Area 7A has also been implicated during motor sequences independently of the effectors (mouth or hand) used to reproduce motor actions (Heim et al. 2012), suggesting that this region may be capable of encoding the correct succession of movements associated with shifts in perspective and changes in viewpoint (see also Byrne et al. 2007). Other studies have also implicated the SPC in the short-term maintenance of information in working memory (Todd and Marois 2005; Edin et al. 2009; Christophel et al. 2012), which may constitute an important process enabling the integration of past and current viewpoints. Altogether, these data converge to indicate that a role of area 7A in coding visuospatial information across sequences and sustaining working memory for spatial layouts could provide an essential neural basis for the ability to integrate, over time, visual scene information into navigationally coherent representations.

In marked contrast to 7A, the areas 7M and 7P showed a significant response to scene familiarity. This effect predominated in the second half of trials, but there was no effect of presentation sequence. This pattern suggests a progressive integration of scene information based on a comparison with long-term memory, rather than based on incoming visuospatial cues. It is also possible that increased attentional resources were allocated to the processing of familiar compared with unfamiliar scenes due to the recognition of places and their known content. This is in line with a role for the dorsal PPC in the top-down allocation of attention during memory retrieval processes (Cabeza et al. 2008; Summerfield et al. 2011), as opposed to the inferior PPC that would subside only bottom-up allocation processes. More generally, our data add to the emerging evidence for a major functional subdivision within SPC, between the more anterior (7A) and more posterior (7M/7P) cortical areas (Scheperjans, Eickhoff, et al. 2008; Bernier...
and Grafton 2010), by showing here that these regions subserve complementary processes in response to consecutive views of the same place.

**Inferior Parietal Lobule**

Again, in IPL, we found 2 different profiles of activations across subareas. First, unlike all other parietal regions, the rostral IPL responded more to unfamiliar than familiar places, specifically when the viewpoints were presented in a sequential as opposed to a scrambled order. This points to a unique role for the rostral IPL in the spatio-temporal grouping of discrete viewpoints into a coherent scene, but specifically when it is novel. Spatio-temporal grouping occurs for information presented across consecutive displays (e.g., Kramer and Yantis 1997; Alais and Lorenceau 2002), and is critically implicated in the experience of spatio-temporal continuities (Vuilleumier 2013). In accord with this, previous studies have more generally implicated the ventral IPL in the construction of Gestalt perceptions from visually or temporally discontinuous inputs (Battelli et al. 2007; Huberle and Karnath 2012; Zaretskaya et al. 2013), and in tasks requiring temporal order judgments (Davis et al. 2009; Roberts et al. 2012). Anterior IPL is also recruited whenever some spatio-temporal predictions are built from external cues, such as expecting particular events at particular locations or particular times (Assmus et al. 2005; Coull and Nobre 2008). The distinctive sensitivity of rostral IPL to unfamiliar places during sequential trials is consistent with such implicit visual prediction processes (Coull and Nobre 2008), because this effect did not result from the task demands (i.e., sequence order was irrelevant to the categorization task), nor from long-term memory retrieval (i.e., familiar places did not induce greater responses in sequential trials), but it solely depended on the availability of relevant visual information in short-term memory—in this case, the preceding unfamiliar viewpoints—and its comparison with new inputs (Enns and Lleras 2008). Supporting this interpretation, the rostral IPL also showed significant increases for repeated viewpoints of unfamiliar places in the control conditions, but not for different viewpoints where no predictions could be made. It has also been proposed that a subregion within IPL, around the posterior superior temporal sulcus/ventral supramarginal gyrus junction, subserves the ability to re-orient attention toward behaviorally relevant cues in the environment (Corbetta et al. 2008). To the extent that ecologically plausible series have a particular behavioral relevance, this attentional account would be consistent with our findings in rostral IPL. Taken together, these data indicate a general role of IPL in binding and/or controlling attention towards discontinuous events in time and space which could contribute to scene organization and navigation processes.

In contrast, the more posterior subregions in IPL (intermediate and caudal parts) showed only an effect of familiarity during the second half of trials (with increasing activity for known but not unknown places), similar to the profile of areas 7P and 7M. There was no sequence order effect. Several studies reported that the angular gyrus is engaged during memory recollection and its activity correlates with retrieval success (Spaniol et al. 2009 for review; Johnson et al. 2013). The distinct profiles of activity between the caudal/parietal and rostral IPL echoes similar distinctions previously made by attentional accounts of parietal functions. According to Corbetta et al. (2008), a different sensitivity to perceptual and mnemonic cues would be expected within IPL because its rostral sector is part of a ventral attention network enabling the re-orientation of attention toward behaviorally relevant cues, whereas its posterior sector in the angular gyrus is part of the default mode network favoring more internally driven, self-reflective activities. On the other hand, Cabeza et al. (2008) have proposed that monitoring the confidence about the oldness or novelty of an event may trigger attentional processes mediated by the IPL. Interestingly, Cabeza et al. (2008) raised the question of a possible anterior/posterior functional organization within the ventral parietal system according to the nature of the task or memory content. Our data provide new support for such segregation, with a sensitivity to familiar places in the most posterior regions likely to reflect long-term memory retrieval, and responses to unfamiliar places in anterior regions (during sequential presentation of viewpoints) likely to reflect perceptual encoding of visual-spatial cues. Taken together, these data therefore suggest that, like posterior area 7, IPL regions may contribute to the integration of visuo-spatial cues and/or distribution of attention in scenes based on information retrieved from memory, presumably contributing to the elaboration of a coherent representation of the environment in working memory.

Interestingly though, the caudal and intermediate IPL differed somewhat in the control conditions. While activity increased within trials similarly for both conditions in the caudal IPL, there was a greater increase for repeated trials in the intermediate IPL. This difference in activity between the 2 regions when the successive pictures are identical, and thus become highly predictable in the course of a trial, suggests a functional dissociation related to working memory and/or expectation processes. This is in line with a functional distinction previously made between the angular and supramarginal gyrus, the former being implicated whenever attention orienting occurs, either exogenously or endogenously, the latter being more specifically dependent on working memory processes (Himmelbach et al. 2006; Mayer et al. 2010). As regards a role for expectation, the supramarginal, but not the angular gyrus, appears to track the subjective bias induced in memory about the likely nature of a to-be remembered target (O’Connor et al. 2010). Although further research is needed to clarify the exact nature of such dissociation within IPL, our results reveal that a similar functional specialization extends to the integration of successive viewpoints during scene processing. In line with this, structural connectivity and functional connectivity at rest points to a division of IPL into several clusters with distinct connectivity profiles, along the rostro-caudal axis, and such subdivisions accord with the parcellation into cytoarchitectonic components (Caspers et al. 2011; Mars et al. 2011; Ruschel et al. 2014; Wang et al. 2012). Lastly, even finer-grained specificities may exist within the caudal and intermediate IPL with, for instance, different connectivity profiles recently described for PGa and PGr (Uddin et al. 2010; Caspers et al. 2011; Mars et al. 2011; Wang et al. 2012). Altogether, structural and functional data converge to suggest that IPL can be subdivided into different subareas with different properties. Further investigation is required to evaluate their implication for spatial memory and viewpoint integration.

**Posterior Parahippocampal Gyrus**

There were 2 main findings in the PPHG, both presumably reflecting the same functional characteristics. First, like the other scene-selective ROI in RSC, bilateral PPHG showed globally
increased responses to familiar scenes. Moreover, particularly in the right PPHG, this familiarity effect predominated in the first half of the trial. This pattern is consistent with a recruitment of this region in the recognition of known landmarks (Landis et al. 1986; Aguirre and D’Esposito 1999; Takahashi and Kawamura 2002), which habituates with successive viewpoints of the same scene. Such habituation effects were also clearly observed for repeated images in the control conditions. This pattern highlights a perceptual role of PPHG in processing visual information from the scenes (e.g., Epstein 2008), which habituates when the same scene is recognized across successive views. Second, PPHG activity was differentially modulated by familiarity when viewpoints were presented in a scrambled or sequential order. In particular in the right PPHG and when the viewpoints did not appear sequentially, activation was more reduced in the second half of the trials for familiar than for unfamiliar places. In our paradigm, during sequential presentations, there was an overlap of about 30% of visual information between 2 consecutive pictures, making it clear that the different viewpoints were of the same place. In contrast, during scrambled presentations, there was no continuity between consecutive pictures. In this case, recognition of the same scene was possible only for familiar places, based on long-term memory. The fact that the PPHG is connected with both the PPC and the hippocampus (Kravitz et al. 2011) may explain its sensitivity to both sequence and familiarity, respectively. Furthermore, a predominance of sequence and order effects for the right PPHG (relative to the left) dovetails with the well-established predominance of the right MTL region in spatial navigation and topographic scene recognition (Landis et al. 1986; Aguirre and D’Esposito 1999; Takahashi and Kawamura 2002). Overall, our findings therefore accord with a general perceptual function of PPHG for the visual analysis of scene content (Epstein 2008; Park and Chun 2009).

Retrospenial Complex
Like PPHG, the RSC exhibited systematically greater responses to familiar than unfamiliar places, in line with previous results (Epstein, Higgins, et al. 2007; Epstein, Parker, et al. 2007) and intimate links of this region with the MTL memory systems (Vann et al. 2009). Unlike PPHG, however, this familiarity did not vary according to presentation order (sequential or scrambled) or time in the trial (first or second half). This adds to previous evidence that RSC preferentially reacts to specific place identities but not to particular viewpoints (Park and Chun 2009). For instance, it activates identically whether the left or right side of a scene is remembered, suggesting that the viewpoint or sensory content of the scene does not impact on activity during memory recognition (Park et al. 2010). Interestingly, in our experiment, we found that activity in RSC remained relatively stable when seeing different viewpoints of the same unfamiliar place (regardless of sequence order) or when seeing a succession of different unfamiliar places (i.e., different condition in control trials), whereas it was markedly reduced when identical viewpoints of an unfamiliar scene were repeated [i.e., repeated condition in control trials; see also (Park and Chun 2009; Morgan et al. 2011)]. If the RSC was strictly sensitive to abstract place identity, one may have expected similar decreases for changing and repeated viewpoints (at least in the second half of trials). This pattern indicates that RSC does encode viewpoint information in addition to perceptual information about familiar scenes. This also agrees with recent finding that the RSC encodes heading orientation signals, which is compatible with its role in both localization and orientation (Epstein and Vass 2014). More generally, these results supports the notion that RSC is involved in information exchanges between egocentric and allocentric representations in PPC and MTL systems, respectively (e.g., Byrne et al. 2007; Burgess 2008; Seubert et al. 2008; Wolbers et al. 2008).

Conclusions
Our work provides new insights into the functional role of key brain regions implicated in the representation of spatial scenes and highlights functional dissociations both within and between the ventral and dorsal cortical pathways. The most anterior portion of area 7 (7A) appears selectively involved in the integration of successive changes in plausible order, presumably contributing to the elaboration of coherent scenes in an egocentric perspective, irrespective of familiarity. More posterior regions in both area 7 and IPL appear to mediate spatial integration processes related to the retrieval of information in long-term memory, which may contribute to guide exploration and attention in familiar environments. Finally, the most rostral portion of IPL seems preferentially involved in the spatiotemporal binding of consecutive views, presumably held in working memory and contributing to build representations of novel scenes. On the other hand, we show distinct response profiles for medial brain regions in PPHG and RSC, which appear primarily engaged by perceptual visual information necessary for the recognition of familiar places. Altogether, our novel findings shed light on the multiple contributions of the PPC to the representation of spatial scenes, within more extended parieto-temporal networks implicated in place recognition and navigation.

Supplementary Material
Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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References


