

# Route and survey processing of topographical memory during navigation

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**Abstract** We investigated the characteristics of route and survey processing of a unique complex virtual environment both at the behavioral and brain levels. Prior to fMRI scanning, participants were trained to follow a route and to learn the spatial relationships between several places, acquiring both route and survey knowledge from a ground-level perspective. During scanning, snapshots of the environment were presented, and participants were required to either indicate the direction to take to follow the route (route task), or to locate unseen targets (survey task). Data suggest

that route and survey processing are mainly supported by a common occipito-fronto-parieto-temporal neural network. Our results are consistent with those gathered in studies concerning the neural bases of route versus survey knowledge acquired either from different perspectives or in different environments. However, rather than arguing for a clear distinction between route and survey processing, “mixed” strategies are likely to be involved when both types of encoding take place in the same environment.

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## Introduction

It is well-known that navigation in large-scale environments may rely on two types of mental representations, generally termed as route versus survey knowledge. The nature and properties of these representations have been intensively investigated in humans (e.g., Siegel & White, 1975; Thorndyke & Hayes-Roth, 1982; Rossano, West, Robertson, Wayne, & Chase, 1999; Foo, Warren, Duchon, & Tarr, 2005; Newman et al., 2007), and although the terminology has evolved, the route–survey dichotomy is still valid. Route knowledge consists in the memory trace of the sequence of places and landmarks encountered and of the turns performed along a route. Survey knowledge corresponds to a complex representation of the layout of an environment in which the spatial relationships between places or landmarks are explicitly expressed.

In humans, spatial knowledge may be acquired from different sources of information, with navigation (ground-level encoding) and map examination (aerial encoding) being the most common. The possibility that spatial knowledge resulting from ground-level and aerial encoding perspectives may reflect distinct properties has been investigated in several studies (e.g., Presson & Hazelrigg,

1984; Taylor, Naylor, & Chechile, 1999; Thorndyke & Hayes-Roth, 1982). For instance, Thorndyke and Hayes-Roth (1982) showed that with moderate exposure route distance estimates were better than straight-line distance estimates after navigation (route knowledge), whereas straight-line distance estimates were better than route distance estimates after examining a map (survey knowledge). However, differences between spatial knowledge acquired from ground-level or aerial perspectives tend to vanish with extensive exposure (e.g., Thorndyke & Hayes-Roth, 1982).

Besides the classical means for acquiring spatial knowledge, the use of virtual environments, which can provide a realistic and vivid visual-spatial experience and allow a large amount of environmental stimuli to be controlled, represent a useful tool for investigating spatial memory and navigation in humans (e.g., Péruch & Gaunet, 1998; Tarr & Warren, 2002). In particular, virtual environments allow experimenters to simulate navigation from ground-level or/and aerial perspectives in comparable dynamic situations, and to investigate the encoding or/and the retrieval of route or/and survey spatial knowledge.

Although the route-survey dichotomy has never been questioned, the co-existence or even interaction of route versus survey types of spatial knowledge have been suggested on the basis of behavioral data and models (e.g., Montello, 1998). Newman et al. (2007) proposed that landmark knowledge (necessary for route navigation) and survey knowledge can be acquired in parallel, with interactions occurring between both types of knowledge. Wolbers and Büchel (2005) highlighted the difficulty to dissociate route from survey knowledge acquisition in the absence of specific instructions. Moreover, some studies have shown that during navigation some metric information may be acquired very early as a component of both types of spatial knowledge (e.g., Ishikawa & Montello, 2006; Buchner & Jansen-Osmann, 2008). While the distinction between route and survey knowledge remains important, it is not clear-cut for many reasons. Finally, in addition to the probable entanglement of both types of spatial knowledge due to parallel acquisition, the existence of individual differences in skills and strategies may produce variable behaviors (e.g., Allen, Kirasic, Dobson, Long, & Beck, 1996; Waller, 2000; Ishikawa & Montello, 2006).

Several neuroimaging studies on spatial navigation support the route-survey dichotomy. In Wolbers et al. experiments (Wolbers, Weiller, & Büchel, 2004; Wolbers & Büchel, 2005), fMRI scanning occurred while participants learned an unfamiliar virtual environment from a ground-level perspective (movie of a trip along a fixed route). In subsequent scanning sessions, while standing in front of a landmark building participants indicated the direction of another landmark building which was not visible; the distance between pairs of landmark buildings was kept

constant. At the behavioral level, the authors made the distinction between the acquisition of route and survey knowledge as follows: route learners would show a better performance on direct than on close or remote pairs of landmarks, while survey learners would show no difference in performance between any kind of pairs of landmarks. Imaging data showed that the increase of route knowledge was correlated with an increase of activation of the posterior inferior parietal cortex, while the increase of survey knowledge was correlated with an increase of activation of the right retrosplenial cortex. The left hippocampus was involved in survey encoding and was prominent during the initial encoding phase, but its activation decreased with the improvement of the global performance. With respect to retrieval, in a PET study by Mellet et al. (2000a), participants had to mentally navigate within an environment that was learned either by actual navigation or from map examination. The authors found right hippocampal activation in both groups. The parahippocampal gyrus was activated bilaterally in the actual “navigation” group, suggesting that it is involved when the environment incorporates route information and includes landmarks. This interpretation was later confirmed by Janzen and van Turenout (2004). In an experiment by Hartley, Maguire, Spiers, and Burgess (2003), participants repeatedly followed a route in a virtual environment (route encoding) and freely explored another environment (survey encoding) from a ground-level perspective. During subsequent fMRI scanning, they were required both to replicate the previously over-learned route (route-following task) and to reach as directly as possible a target building in the freely explored environment (way-finding task). In addition to the activation of distinct networks of areas corresponding to each encoding condition, an analysis of between-participant performance revealed that with good survey navigators the left hippocampus was activated during the survey condition and the head of the caudate nucleus during the route condition. These data in humans are strikingly in accordance with animal studies showing the involvement of the hippocampus and caudate nucleus in map and route behaviors, respectively (O’Keefe & Nadel, 1978; Thinus-Blanc, 1996).

However, other data reveal that in some cases, the route-survey dichotomy is not so clear-cut. For instance, in Shelton and Gabrieli’s experiment (2002), during fMRI scanning participants explored a virtual environment from a ground-level perspective (route encoding) and another environment from a global perspective (survey encoding). Both types of encoding activated a common network of areas, while survey encoding recruited a specialized subset of areas within the overall area activated by route encoding. Some areas classically attributed to survey processing (e.g., parahippocampal gyri, precuneus and retrosplenial cortex) showed activation only in the route condition. As suggested

by the authors, these data speak against a clear distinction between route and survey processing.

Some brain studies have demonstrated a caudate–hippocampal distinction, while others suggest the importance of the parietal–mesial temporal interaction. There may be methodological reasons for this diversity, such as the use of more or less sensitive imagery methods, the fact that scanning was performed either during encoding or retrieval, and the mode of encoding (from navigation in ground-level or aerial perspective, or from map examination). Moreover, the existence of different within-group and within-subject spontaneous strategies may also account for the observed differences across the literature (Shelton & Gabrieli, 2004; Etchamendy & Bohbot, 2007). But these different outcomes may also be due to the fact that the process of construction of spatial knowledge might not be serial and separate as assumed (e.g., Siegel & White, 1975), but might be achieved spontaneously by a parallel route and survey processing (e.g., Montello, 1998; Newman et al., 2007).

In most of the studies conducted so far, route and survey processing have been investigated in two different environments or with two different groups of participants, one for each kind of spatial processing (Shelton & Gabrieli, 2002; Hartley et al., 2003; Wolbers et al., 2004; Wolbers & Büchel, 2005). This methodological choice reduces the risk of interference between the two types of knowledge and thus corresponds to the most suitable means to highlight the two distinct networks involved in route and survey processing, respectively. However, in the case of interactions between route and survey processing, a comprehensive approach should also consider actual situations of navigation in large-scale environments. Indeed, in everyday life, people usually build route and/or survey spatial knowledge from navigation in the same environment (e.g., Thorndyke & Hayes-Roth, 1982; Ruddle, Payne, & Jones, 1997), and mostly along the same paths. In such conditions, it is possible that mental representations incorporating both route and survey properties may be more common.

In the present study, participants acquired route and survey knowledge from a ground-level perspective in a unique complex virtual environment prior to fMRI scanning. Brain activations recorded during subsequent route and survey tasks were compared to those recorded during a spatial perception task carried out in another environment (baseline task). The goals of the study were first, to assess the emergence of both route and survey processing from navigation in the same environment; and second, to examine the common brain areas involved in both route and survey processing. We expected our results to distinguish between two possible alternatives. First, on the basis of navigation in the same environment, participants develop and use two separate

and different mental representations. In such a case, distinct brain networks should be activated. Second, on the basis of the same “entry” (first-person view), participants construct a mixed mental representation sustained by a common network of brain structures. The use of one environment might lead to the construction of a common basis of data in which the pieces of useful information would be selected according to the task to be performed. In such a case, this mixed representation would combine, in a single entity, route and survey information. The brain networks activated in each testing condition should overlap, combining those brain areas usually involved in route processing and the ones involved in survey processing.

## Materials and methods

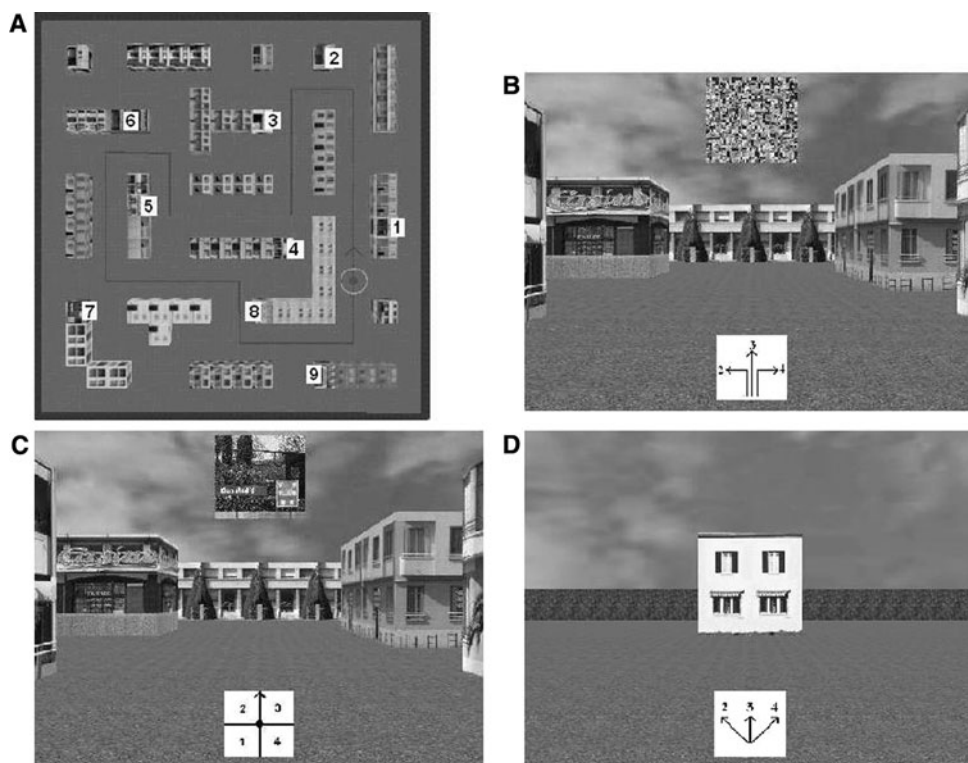
### Participants

The participants were 16 men (graduate and undergraduate students). They were all right-handed and free of any known neurological disease. Their ages ranged from 19 to 34 ( $M = 21.2 \pm 6.6$ ). All participants were paid and were unaware of the real purpose of the study. Informed written consent in accordance with the local medical ethics committee was obtained in all cases.

### Stimulus material

The experiment comprised four phases: practice, encoding, retrieval (performed during scanning), and post-scanning. Two virtual environments were built with a commercially available software (WorldViz Vizard) that displays a first-person point of view in a three-dimensional, fully textured environment. The first environment, used for the practice phase, was composed of four buildings with regular grids of streets. The main environment was a small virtual town (a 130-m sided square limited by a fence) composed of 21 “residential” buildings, mostly without distinctive signs, again with regular grids of streets. Nine other “landmark” buildings were characterized by a specific sign (hotel, bank, car park, car-dealer, pharmacy, supermarket, travel agency, wine shop, and restaurant). For the route-encoding phase, a film of a counterclockwise round trip along a fixed route was recorded. The trip started and terminated near the hotel. It comprised 7 left and 3 right turns and had an approximate length of 270 m (see Fig. 1a). The 9 landmark buildings were visible along the trip and mostly served as decision points. The film was displayed at a rate of approximately 60 frames per second and lasted about 80 s. Snapshots taken along the route from a first-person point of view on a ground-level perspective served as experimental stimuli.

**Fig. 1** **a** Top-view of the virtual environment with the buildings, including the landmarks (numbers 1 to 9), the route (continuous line), the starting and ending point (circle), and the direction followed (arrow). The map was never shown to the participants. **b** Example of route task in which participants indicate the direction to take at the next decision point in order to follow the route previously learned. **c** Example of survey task in which participants estimate, via a quadrant, the direction of an unseen target landmark (the image at the top of the screen) in relation to their current location in the environment. **d** Example of baseline task in which participants indicate the position of the building with respect to their body midline



## Procedure

### *Practice phase*

The participants were required to freely explore the practice environment in order to learn how to move with the computer keyboard. Translations (forwards/backwards with the up/down arrows) and rotations (leftwards/rightwards with the left/right arrows) could be produced only successively. A single push on a key produced one step of translation (7.5 m) or one step of rotation (90°) with a constant speed (about 5 m and 40° per second, respectively). A collision-detection algorithm constrained movement within the “streets”. After a few minutes of practice, all participants were able to move in the environment without any difficulty.

### *Route-knowledge encoding*

The participants were shown the film recorded in the main environment three times. They were required to concentrate on the route features and were told that following the third presentation, they would have to interactively reproduce the route two times without mistakes. During reproduction of the route it was only possible to move forward. If the participants made a mistake they were put back to the previous correct location, from which they were allowed to continue along the route. If they made a second (or third) mistake they were shown the film a fourth (or fifth) time before

trying again to reproduce the entire route. This phase terminated after two consecutive correct reproductions of the route.

### *Survey-knowledge encoding*

The participants were required to move interactively for 10 min along the previously learned route in the main environment. Their exploration was not completely free, since although they could move in both directions (forward and backward) and rotate on-site, their movements were restricted to the route. As they had to concentrate on the spatial layout, and in particular on the arrangement of the landmark buildings, they were encouraged to rotate from different locations in order to see the landmarks from multiple perspectives. Following learning, they were placed at different locations along the route and requested to point toward the target landmarks that they could not see from their current location. If their average pointing error was greater than 25°, they had to learn again for 10 min before performing a new series of estimates.

### *Scanning phase*

Scanning took place immediately after the encoding phase, when both route- and survey-knowledge criteria had been reached by each participant. Before entering the machine, the participants were given the instructions and practiced with a 4-key antimagnetic keyboard. The stimuli were

projected on a screen, which the participants viewed through a mirror. Each participant was presented with three types of tasks: route, survey, and spatial perception (baseline). In the route task, the participants were shown a snapshot of the main environment, from which they had to indicate the direction to take at the next decision point in order to follow the route. At the top of the screen, a scrambled image of the same size and luminance of the images used in all tasks was presented. At the bottom of the screen a scheme was shown, reminding participants of the possible responses (turn left, go ahead, and turn right) and the corresponding three keys to press (see Fig. 1b). Following their response, participants were presented for 250 ms with an empty gray screen and were then placed at a different location in the environment for the next trial. In the survey task, participants were presented with a snapshot of the main environment, from which they had to estimate the direction of a target landmark in relation to their current location in the environment. At the top of the screen an image of the front of the target building was presented. At the bottom, a scheme was shown reminding participants of the available responses (in front to the left, in front to the right, behind to the left, and behind to the right) and the corresponding four keys to press (see Fig. 1c). Following the response, and after 250 ms of blank gray screen, the participants were immediately placed at a different location in the environment for the next trial. In both route and survey tasks, the snapshots were taken from the perspective that had been provided by following the route. The route task was supposed to mainly reactivate the spatial-temporal associations between consecutive landmarks along the previously learned route, while the survey task was supposed to be more cognitively demanding since it required additional spatial processing. Last, in the baseline task, the participants were presented with a snapshot of the practice environment showing a single building (see Fig. 1d). The participants had to indicate the position of this building with respect to their body midline. At the bottom of the image a scheme was shown reminding them of the available responses (left, center, and right) and the corresponding three keys to press. Following the response, and after 250 ms of blank gray screen, the building was re-positioned for the next trial. As in Aguirre and D'Esposito (1997), the presentation of stimuli was self-paced in each condition. This choice was justified by the existence of individual differences in the processing of spatial information. In such conditions, fixing a time limit for each stimulus might be stressful and could favor random responses. Allowing free expression of route or survey processing during scanning was considered as important as the number of successful trials.

Scanning started with anatomical acquisition (15 min). The participants then performed the behavioral task during

six successive runs. Each run was 236-s long and consisted of six 20-s epochs for the behavioral task (two epochs per type of task), with an inter-epoch interval ranging randomly from 16 to 18 s. The inter-epoch intervals consisted of a 12-s period of blank screen, followed by a 3-s period of task cueing, and finally with a still-blank screen lasting randomly 1–3 s. The task-cueing period was intended to inform the participants about the type of subsequent type of task. They were presented with an image associated with each specific task: an empty square for the baseline task, a scrambled image for the route task, and the front of a landmark building for the survey task. The orders of presentation of the tasks were pseudo-randomly counterbalanced so that their combination was different in each run. In each epoch, the number of stimuli presented depended on the participant's response times. Visual stimulation was synchronized with signal acquisition (using LabView software for the presentation of the stimuli). The participants received no feedback regarding their performance.

#### *fMRI data acquisition*

Imaging was performed using a 3T whole-body imager MEDSPEC 30/80 AVANCE (Bruker). High-resolution structural T1-weighted images were acquired for all participants to be used for anatomical localization ( $1 \times 0.75 \times 1.22$  mm). The anatomical slices covered the whole brain, missing the lower part of the cerebellum, and were acquired parallel to the anterior commissure–posterior commissure (AC–PC) plane. The functional images were acquired using a T2\*-weighted echo-planar sequence at 24 axial slices (repetition time = 2 s, interleaved acquisition, slice thickness: 3 mm, inter-slice gap: 1 mm,  $64 \times 64$  matrix of  $3 \times 3$  mm voxels). Statistical parametric mapping software was used for image processing and analysis (SPM2 - Wellcome Department of Imaging Neuroscience, London, UK). The functional images were interpolated in time in order to correct phase advance during volume acquisition, and realigned to the first image of each run. In order to compute multi-participant analysis, the anatomical references and the realigned functional images of all participants were transformed to a common standard space using the Montreal Neurological Institute (MNI) template. The functional data were then spatially smoothed (3D Gaussian kernel:  $6 \times 6 \times 6$  mm) and temporally filtered using a 120-s period high-pass filter and a Gaussian low-pass filter with 4 mm of full width at half maximum (FWHM).

#### *Post-scanning phase*

After leaving the machine, the participants were debriefed and required to draw on a blank A4 sheet of paper the arrangement of landmark buildings and the route followed.

These sketch maps were individually compared to the real layout of the environment with a bi-dimensional regression analysis (Giraudo & Pailhous, 1994; Friedman & Kohler, 2003; Tobler, 1994). The basic principle of this method is to compute the difference between two spatial configurations, the first corresponding to the actual locations of the landmark buildings and the second to their estimates by the participants. Several parameters are computed, including a bi-dimensional correlation coefficient which expresses the global agreement between the real layout and each sketch map. In addition, a cartographic visualization illustrates the level of inaccuracy of the sketch maps.

### *fMRI data analysis*

Several analyses were performed on the data. First, a general linear fixed-effect model was applied to estimate the parameters for each task. There was one regressor for each task with a basic function of box-car type, convolved with a hemodynamic response function, and one regressor to model each cueing task period (preceding each epoch). The resulting set of voxel values for each contrast (see below) constituted a statistical parametric map of the  $T$  statistic. Second, the contrast images were subjected to a one-sample  $T$  test that treated subjects as random effects. The following contrasts were used: (1) route task versus baseline; (2) survey task versus baseline; (3) route versus survey task; and (4) survey versus route task. For all these comparisons, family wise error (FWE) rate at  $p < 0.05$  corrected for multiple comparisons was used and a spatial extent threshold of  $k \geq 5$  voxels. Correction was based on the entire search volume. Third, activations common to different contrasts were identified by a conjunction analysis (Price & Friston, 1997). This analysis was performed to uncover the voxels that were activated in both route and survey tasks as compared to the baseline task (FWE rate at  $p < 0.05$  corrected for multiple comparisons). For all these analyses, the resulting set of voxel values for each contrast constituted a statistical parametric map of the  $T$  statistic. Activated voxels surviving this threshold were superimposed on the standard MNI brain in order to identify the anatomical regions. To allow precise mapping of the regions, peak activations and sub-peaks arising from the different contrasts were tabulated. Fourth, in order to identify patterns of activation that could differentiate between tasks, data were subjected to a multivariate pattern classification analysis (e.g., Bray, Chang, & Hoefl, 2009). For this purpose, we used a software based on a modified Principal Component Analysis that performs voxel-wise scaled subprofile modeling (SSM, see Ma, Tang, Spetsieris, Dhawan, & Eidelberg, 2007). The typical workflow was as follows: preprocessing (standard general linear model), extraction of a pattern (linear combination of principal components that could discriminate

between the two tasks), and supervised learning algorithm. As it is the rule, to be sure to not analyze noise as signal, only components with more than 5% of the variance were used in the composition of the discriminating pattern; the linear combination must represent at least 10% of the total variance, and the significance for classification must have a  $p < 0.001$  (see Ma et al., 2007). Finally, we examined the functional connectivity (FC) of five regions of interest (ROIs), selected on the basis of peaks of activation observed in the previous analyses and of theoretical issues: bilateral parahippocampal gyrus/posterior hippocampus, bilateral posterior cingulate, and right superior parietal lobe. FC (Friston, Frith, Liddle, & Frackowiak, 1993; Horwitz, 2003) was computed only considering the signal time-course in each kind of task, taking into account the hemodynamic delay. The ROIs' signal was extracted with MARSBAR (Brett, Anton, Valabrègue, & Poline, 2002), a plug-in for SPM, for 5-mm radius spherical regions. Using RESTing-state fMRI data analysis toolkit (REST, by Song Xiaowei, <http://resting-fmri.sourceforge.net>), the voxel-wise FC and the correlation matrix for the five ROIs' time-courses in the different types of tasks were computed. Several nuisance factors, such as the global signal, the cerebrospinal fluid signal, and the white matter signal were inserted as covariates of non-interest as suggested by some recent studies (e.g., Zhang et al., 2008). The correlation maps were transformed in  $Z$ -maps with the Fisher transformation. In order to look at FC group differences between tasks, these maps were inserted in a second level analysis (two sample  $t$  tests, false discovery rate at  $p < 0.05$ , cluster  $> 10$  voxels). From the correlation matrix of the five ROIs, the correlations different from zero were computed for the group (one sample  $t$  tests,  $p < 0.05$ ), and among these the correlations differing between route and survey tasks (two sample  $t$  tests,  $p < 0.05$ ).

## **Results**

### Behavioral data

#### *Encoding phase*

About 10 min were needed to reach the route-encoding criterion, with an average of 2.12 trials (SD = 0.34). About 30 min were needed to reach the survey-encoding criterion, with an average of 2.50 route explorations (SD = 0.73), and an average pointing error of 15.75° (SD = 4.47°).

#### *Scanning phase*

The mean percentage of correct responses in each kind of task was 83.68% (SD = 14.74) for route tasks, 56.05%

(SD = 15.06) for survey tasks, and 94.48% (SD = 1.14) for baseline tasks. Performance was significantly superior to chance level ( $p < 0.001$  for all tasks; chance level: 33% for route and baseline tasks, 25% for survey tasks). A  $t$  test for dependent samples was performed on route and survey data corrected for guessing, with task (route versus survey) as a factor. The  $t$  test revealed a significant effect of task,  $t(15) = 4.999$ ,  $p < 0.001$ , with higher performance on route than on survey tasks. The mean number of responses given during an epoch (20 s) for each task were 9.41 (SD = 1.95) for route, 4.75 (SD = 1.30) for survey, and 23.08 (SD = 2.01) for the baseline. A  $t$  test for dependent samples revealed a significant effect of task (route versus survey),  $t(15) = 12.02$ ,  $p < 0.001$ , with a larger number of responses on route than on survey tasks.

#### *Post-scanning phase*

The analysis of the sketch maps indicated that the mean bi-dimensional correlation coefficient was 0.882 (SD = 0.082), showing that spatial knowledge remained reliable even after the scanning phase. All participants drew the landmark buildings and the route followed, but without revealing any systematic preferential order.

#### *Spontaneous strategies during the scanning phase*

In a further analysis, we wanted to ascertain that the participants did use survey knowledge when performing the survey tasks during scanning. If so, their response times should not relate to the route distances (here expressed as the number of turns, highly correlated with route distances,  $r = 0.94$ ,  $df = 50$ ,  $p < 0.001$ ) between their current location and the target landmark. For each participant performing the survey tasks, the correlation between the response times and the number of turns was computed during scanning. A positive correlation would suggest that participants had followed a route strategy even when the test and target locations are close to each other in Euclidian terms but remote in terms of the route travelled (for instance, as with the pair of landmarks 4 and 9, see Fig. 1a). Almost all individual correlations were non-significant, suggesting that participants had not merely used route knowledge while performing the survey tasks. There was only one significant correlation ( $r = 0.31$ ,  $df = 50$ ,  $p < 0.05$ ), suggesting that this participant may have used route knowledge while performing the survey tasks. Interestingly, this participant reached a high performance level (82.5% for the survey tasks). Another participant reached the same performance level during scanning (82.2% for the survey tasks) but without significant correlation between his response times and the number of turns between landmarks ( $r = 0.042$ ), suggesting the probable use of a survey strategy. Both participants had an

equivalent learning performance (2 trials for reaching the route knowledge and 3 trials for reaching the survey knowledge criteria) and scored high in the route tasks performed during scanning (respectively 91% and 87%). However, their respective sketch maps drawn after scanning were quite different (see Fig. 2). The participant whose correlation between response times and number of turns was significant showed the most distorted of the group. This is coherent with the absence of accurate survey knowledge and with the use of a route strategy in the survey task. On the contrary, the map drawn by the participant whose correlation was not significant was quite accurate, which is compatible with the actual use of survey knowledge in the survey task. Thus, these data suggest that participants successfully implemented different strategies during the survey tasks. They also show that a high level of performance in survey tasks may be underpinned by either survey or route strategies.

#### Hemodynamic responses

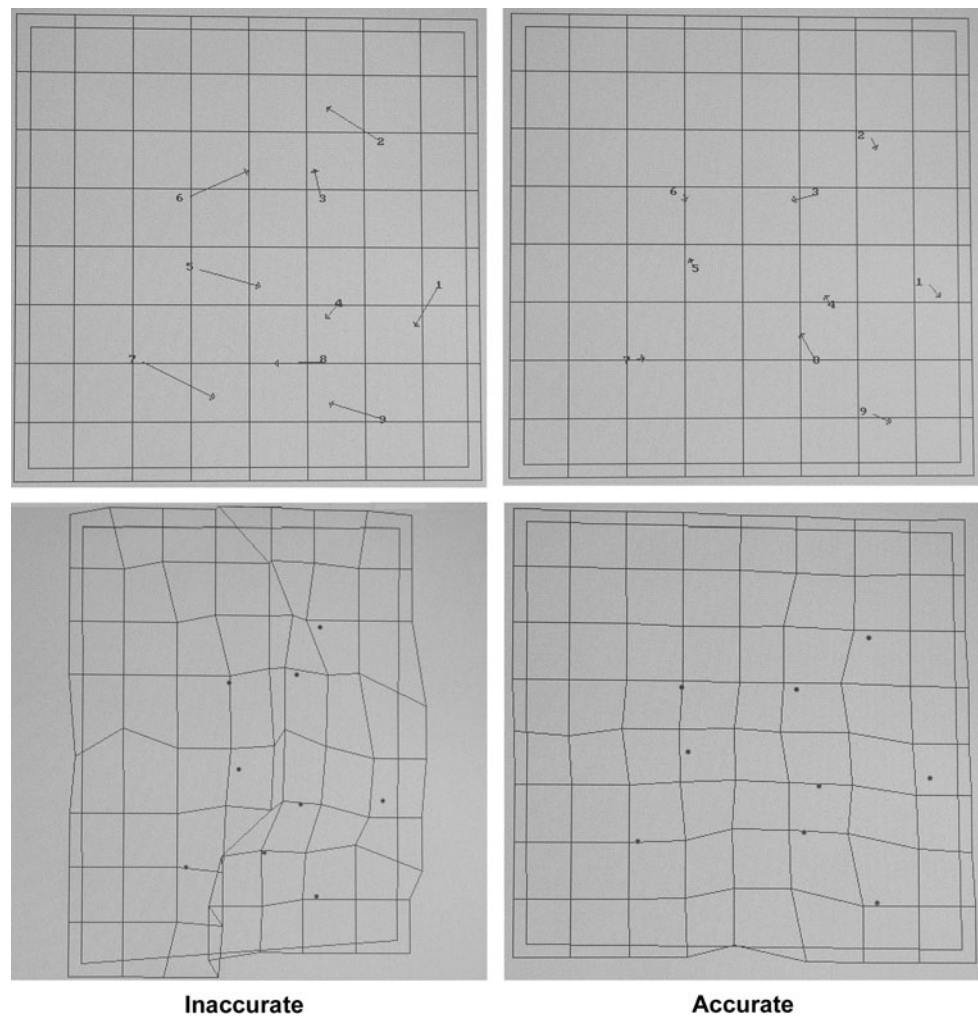
##### *Standard analysis*

We found statistically increased bold signal during route tasks, compared with the baseline in a distributed bilateral network containing the hippocampus and the posterior part of the parahippocampal gyrus, the posterior cingulate and retrosplenial cortex, the right precuneus, the right thalamus (pulvinar), and the left superior parietal gyrus (see Fig. 3; Table 1). Survey tasks compared with the baseline showed bilateral activations of the hippocampus/parahippocampal gyrus, the posterior cingulate and retrosplenial cortex, the precuneus, and an activation of the left lingual and fusiform gyri. In addition, in the standard analysis, route versus survey tasks showed activation in the middle cingulate gyrus, the superior temporal gyrus, the calcarine region, and the lingual gyrus. All the local maxima were located in the right hemisphere. Survey versus route tasks showed no supra-threshold activations.

##### *Conjunction analysis*

A conjunction analysis was computed, as we were mainly interested in the possibility that common structures were activated in both types of tasks (route and survey). The comparison of survey and route tasks versus baseline revealed at the parietal level a bilateral activation in the inferior and superior areas, in the angular gyrus and in the precuneus (see Fig. 4). In the frontal lobe, common activations were observed bilaterally in the middle and superior areas and in the SMA. The temporal cortex showed activations in the hippocampus bilaterally and in the right parahippocampal gyrus. The regions of the occipital cortex which were found to be activated bilaterally were the

**Fig. 2** Cartographic visualization of the sketch maps produced by the most inaccurate (*left*) and the most accurate (*right*) participants. The bi-dimensional correlation coefficients are 0.676 for the most inaccurate and 0.968 for the most accurate. *Top*, the *numbers* indicate the actual location of each landmark building; the *arrows* correspond to the location of each building as estimated by each participant. *Bottom*, the deformations of the maps are obtained after applying the local inaccuracies (i.e., the inaccuracy of each landmark building) to the whole surface (for more details see Giraudo & Pailhous, 1994)



middle superior and the lingual gyrus, the region around the calcarine fissure, and the right cuneus. The bilateral middle cingulate and the left anterior cingulate were also activated. In addition, other bilateral activations were found in the precentral regions, the insula, and in subcortical nuclei, such as the thalamus and the pallidum and, more importantly, in the left caudate nucleus.

#### *Multivariate pattern classification analysis*

We could not find any single or linear combination of principal components with more than 10% of the total variance that could discriminate between the two tasks with a  $p = 0.001$ . Thus, the outputs of the multivariate pattern classification analysis confirmed that the two tasks involved a very similar distributed pattern of brain activity.

#### *Functional connectivity analysis*

The findings of the functional connectivity analysis were in line with those of the previous analyses, i.e., they showed

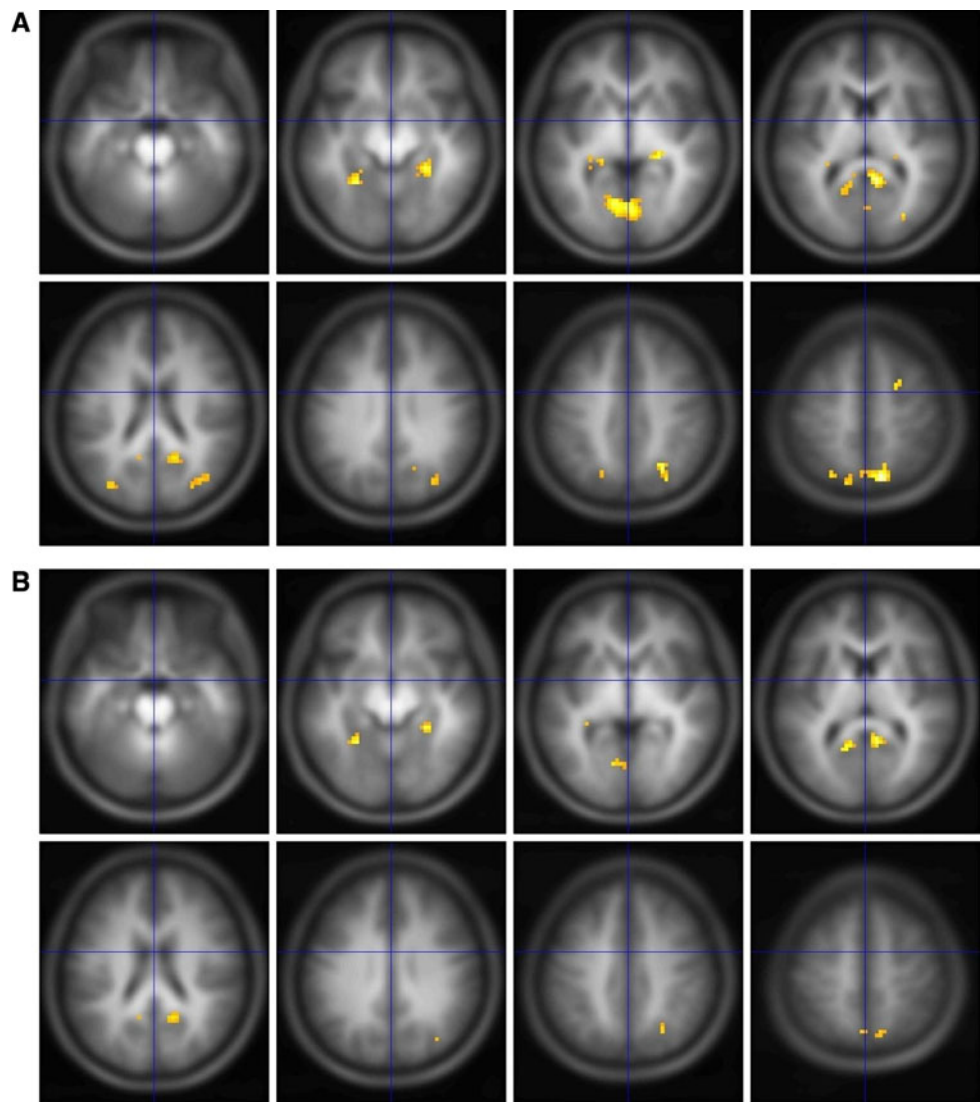
the implication of a globally similar network of regions in both types of tasks (see Fig. 5). Moreover, the analysis specified the nature and the strength of the interactions between regions of the selected network. First, all strong correlation coefficients ( $r > 0.10$ ) included the same subset of structures in both route and survey tasks: left parahippocampal gyrus/posterior hippocampus, left and right posterior cingulate, and right superior parietal lobe. Among these, the strongest co-activations included the posterior cingulate (bilaterally) and the parietal lobe. Second, there were notable differences of connectivity between route and survey tasks, with more and stronger co-activations in the route tasks for all pairs of regions (see Fig. 5c). Moreover, in the survey tasks the right parahippocampal gyrus/posterior hippocampus was not co-activated with another region.

#### *Individual analyses*

Finally, we observed the patterns of activations of the two participants who showed equivalent performance before and during scanning, but produced the most accurate and



**Fig. 3** Summary of activations from the group analysis. **a** Areas more activated in the route than in the baseline task. **b** Areas more activated in the survey than in the baseline task. Each panel (**a–b**) shows the mean normalized structural images of all subjects sliced at 10 mm intervals from  $z = 50$  to  $z = -20$ . For each contrast,  $p < 0.05$  corrected threshold and regions smaller than 5 voxels are not shown. The cross-hairs are at  $x = 0$ ,  $y = 0$  in each slide



the most inaccurate sketch maps at the end of the experiment. Their patterns of activation in the standard analyses did not reveal any difference in both tasks (route or survey versus baseline), except that in the survey tasks the participant whose sketch map was the most accurate presented some larger activations (occipital gyrus, hippocampus/parahippocampal gyrus) than the participant whose sketch map was the most inaccurate. However, most of the activations included the same structures and did not present particularities with reference to activations of the group.

## Discussion

The present study focused on the route and survey processing of the same environment at the behavioral and brain levels. This is a familiar situation in our everyday life. Indeed, we usually acquire both route and survey knowledge

(though at different levels of accuracy) while moving around in a given environment, and we progressively become more able to implement either type of processing according to the situation requirements. Several studies have pointed out distinct neural networks involved in the encoding/retrieval of route and survey knowledge using two different environments (and perspectives) but, as far as we know, there are no data concerning the explicit retrieval of route and survey knowledge of the same virtual environment learned from a ground-level perspective. Thus, we investigated the conditions of co-existence of route and survey processing as well as their corresponding patterns of brain activations.

At the behavioral level the data show that all participants reached the learning criteria in spite of somewhat drastic learning conditions (restriction of the displacements to a unique pathway in order to control the amount of available information in both types of tasks). Participants accurately

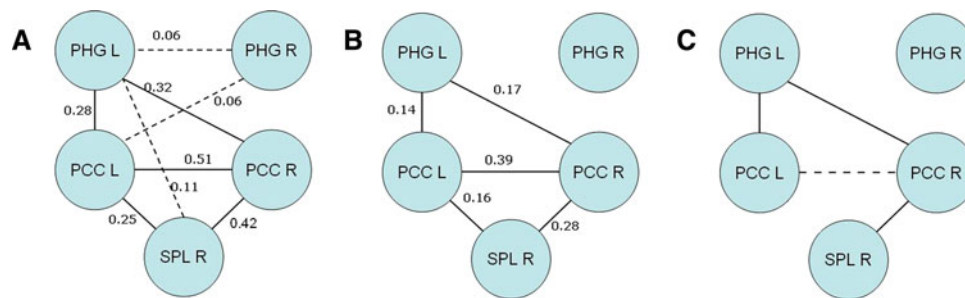
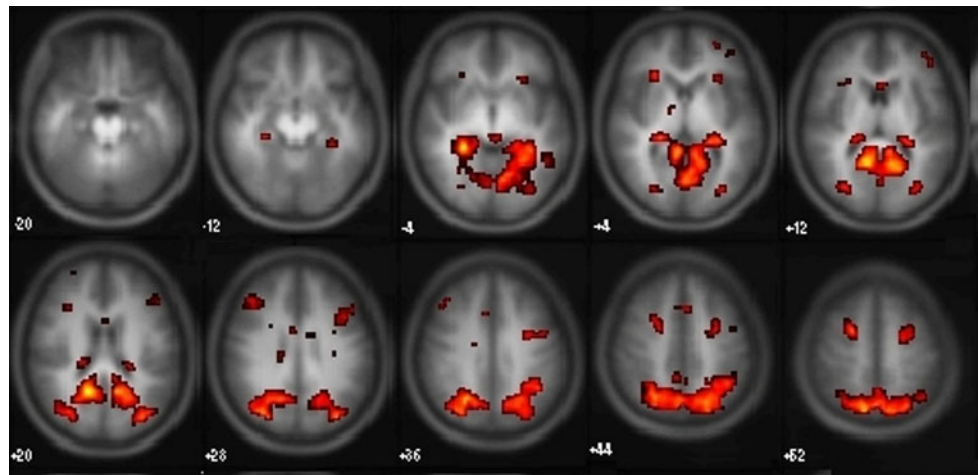
**Table 1** Areas of significant activations for the group analysis

Areas of activation ( $p < 0.05$ , corrected)	Side	Brodmann area	MNI co-ordinates (x, y, z)	Voxel level (z-score)
<b>Route versus baseline tasks</b>				
Superior frontal gyrus	R	8	24, 6, 51	5.31
Superior parietal gyrus	L	7	-21, -69, 42	5.26
Precuneus	R	7	12, -69, 51	6.28
Posterior cingulate/retrosplenial cortex	R	29	9, -42, 18	4.97
	R	17	15, -54, 18	6.16
	L	30	-12, -54, 18	5.65
Superior occipital	R	7	27, -63, 39	5.82
Middle occipital	R	19	33, -75, 27	5.52
	L	19	-33, -78, 24	5.25
Calcarine cortex	L	17	-12, -51, 6	5.32
Lingual gyrus	R	18	-9, -69, -3	6.15
	L	37	-27, -51, -6	6.3
Post parahippocampal gyrus/hippocampus	R	37	27, -39, -9	5.89
	L	37	-33, -42, -3	4.94
	L	-	-21, -33, 0	5.15
Thalamus	R	-	21, -30, 3	5.63
Cerebellum	R	-	6, -45, 6	6.24
<b>Survey versus baseline tasks</b>				
Precuneus	R	7	3, -66, 48	4.96
	L	7	-3, -63, 54	5.05
Posterior cingulate/retrosplenial cortex	R	30	9, -51, 9	5.86
	L	30	-12, -54, 18	5.83
Superior occipital gyrus	R	7	27, -63, 36	5.15
Calcarine cortex	L	17	-15, -54, 9	5.42
Lingual gyrus	L	18	-9, -69, -3	5.73
Fusiform gyrus	L	37	-27, -51, -9	5.57
Post parahippocampal gyrus/hippocampus	R	37	27, -39, -6	6.24
	L	37	-36, -42, -3	5.11
<b>Route versus survey tasks</b>				
Middle cingulate gyrus	R	23	3, -21, 39	5.06
Superior temporal gyrus	R	48	60, -36, 24	5.51
Calcarine cortex	R	17	6, -78, 12	5.04
Lingual gyrus	R	18	21, -75, -3	5.35

reproduced the route and built up a survey-type mental representation with small angular errors (about  $15^\circ$ ) at the end of the learning phase. Survey learning appeared more complex than route learning as shown by the longer time needed to reach the learning criterion, the lower performance level and the longer response times during scanning. In order to ascertain that no route strategy was used in the survey tasks performed during scanning, we computed the correlations between the response times and the number of turns from the test points to the targets. No correlation was significant, except in one participant. The accuracy of sketch-maps drawn in the post-scanning phase (more than

one hour after initial learning) was excellent but it may have resulted from the memory of a combination of both route and survey features. The case of the participant who was suspected to use a route strategy to perform the survey tasks is particularly interesting. Indeed, the map that he drew was the least accurate of the group but his performance level during scanning was very high. While the behavioral data indicate that all the other participants followed the given instructions, this pattern suggests that different strategies can lead to successful comparable performance (Shelton & Gabrieli, 2004; Etchamendy & Bohbot, 2007).

**Fig. 4** Summary of activations from the conjunction analysis showing areas more activated in the route and survey tasks in comparison to the baseline task. The figure shows the mean normalized structural images of all subjects sliced at 8-mm intervals from  $z = 52$  to  $z = -20$



**Fig. 5** Functional connectivity between the five regions of interest: **a** route tasks, **b** survey tasks, and **c** route–survey comparison. On figures **a** and **b**, *full* and *dotted connecting lines* correspond, respectively to strong ( $r > 0.10$ ) and weak ( $r < 0.10$ ) correlation coefficients, all being significant. On figure **c**, *full* and *dotted connecting lines* correspond respectively to strong ( $p < 0.05$ ) and weak ( $p < 0.10$ ) significant differ-

ences of co-activation between route and survey tasks; co-activations are always stronger in the route than in the survey tasks. PHG L/R: parahippocampal gyrus/posterior hippocampus (*left and right*); PCC L/R: posterior cingulate (*left and right*); SPL R superior parietal lobe (*right*)

Although it is always difficult to presume the use of spatial strategies in individuals or groups, there are arguments against the single implementation of route knowledge in both types of tasks. First, reaching the criterion for survey encoding required more than simple route knowledge. Second, in the tasks performed during scanning, route knowledge was not sufficient to succeed in performing all the trials, in particular due to large distance variations. Third, as already seen, in survey tasks there was no correlation between the number of turns and the response times. Might participants have alternated between route and survey representations, depending on the task requirements? While there was no a priori reason and no enough time to do so within a block of trials of the same type of task (route or survey), alternating between blocks might have been possible since the type of task was indicated at the beginning of a block of trials. However, it remains difficult to explain how alternating representations could have produced different route/survey performance but similar route/survey activations (at least in terms of standard analyses). Furthermore, the possible implicit involvement of irrelevant representations (i.e., use of route representation in survey tasks, and

vice versa) cannot completely be excluded. This might have been possible with trials in which the target was located somewhere after the next turn along the route. However, such a situation occurred very seldom, several turns being involved in the large majority of trials (and their number not being a predictor of response times in the survey tasks). Since the two types of representations originated from a common encoding mode, they very likely shared common features. Thus, a more plausible explanation is that participants might have built up and used a mixed representation, composed for instance of “basic” route components and of additional survey components. Such an interpretation is in line with the idea of parallel learning, and shows how it may be difficult and artificial to dissociate, along the same journey, route, and survey knowledge acquisition. In a similar vein, even with explicit instructions for survey knowledge acquisition, Wolbers and Büchel (2005) could not exclude the possibility that their participants may have acquired some route knowledge as well.

At the brain level, the analyses revealed a similarity between route and survey tasks by reference to the baseline, with an activation of the posterior cingulate cortex

bilaterally and of the left hippocampus. The parahippocampal gyrus was activated in the survey tasks in the right hemisphere, while it was found to be activated bilaterally in the route tasks. Additionally, a peak of activity was observed in the right caudate nucleus in the route tasks. The most interesting result is the extensive occipito-fronto-parieto-temporal network implicated both in route and in survey tasks, together with areas usually specifically involved in route tasks, such as the SMA, the insula, and the caudate nucleus. Within this network, some structures are commonly associated with sub-processes necessary for performing route and survey tasks, such as visuo-spatial mental imagery, landmark processing, and transitions between egocentric and allocentric reference frames.

Many studies involving the processing of spatial mental images have found activation in the precuneus (e.g., Aguirre, Detre, Alsop, & D'Esposito, 1996; Maguire, Burke, Phillips, & Staunton, 1996; Ghaëm et al., 1997; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998). In the same way, the superior and middle occipital gyri are hypothesized (Mellet et al., 2000b) to be implicated in tasks requiring spatial mental imagery. The conjunction analysis also revealed the activation of the lingual gyrus. This region is hypothesized to be a crucial area for encoding and retrieving the visual image of topographical landmarks (Aguirre & D'Esposito, 1999). Furthermore, a right parahippocampal activation was observed both in route and in survey tasks. The posterior part of the parahippocampal gyrus is activated by the presentation of scenes in a three-dimensional space (Epstein & Kanwisher, 1998), in the mental evocation of landmarks (Maguire, Frackowiak, & Frith, 1997), and during navigation (Aguirre & D'Esposito, 1997; Maguire et al., 1998). Additionally, this area responds to the navigational relevance of landmarks at the decision points but not for other landmarks even though they are well or better remembered (Janzen & van Turenout, 2004).

Recently, Epstein, Parker, and Feiler (2007) showed that the posterior part of the parahippocampal gyrus (parahippocampal place area) and the retrosplenial cortex play distinct but complementary roles in place recognition. The former would primarily support perception of scenes, whereas the second would be involved in memory retrieval mechanisms that allow the scene to be localized within the whole environment. The observed recruitment of the inferior and superior parietal regions is believed to reflect the processing of information in egocentric reference frames (Galati, Committeri, Sanes, & Pizzamiglio, 2001; Halligan, Fink, Marshall, & Vallar, 2003) and more generally in spatial perception and movement in space (Mesulam, 1981; Posner, Walker, Friedrich, & Rafal, 1984). Indeed, during navigation tasks implying the use of a survey representation, allocentered information needs to be converted in an

egocentered reference frame in order to be implemented in actions. The left posterior cingulate cortex was also activated in route and in survey tasks. It is defined here (as in Epstein et al., 2007) as a functional region including the retrosplenial cortex (Brodmann's areas 29 and 30), the posterior cingulate (area 23), and extending posteriorly into the parietal-occipital sulcus/anterior calcarine region. In a review of neuroimaging and lesion studies concerning the cingulate cortex, Maguire (2001) highlighted its role in active spatial navigation. Activation of the retrosplenial cortex was reported in several studies in which participants were required to perform a virtual or mental navigation task (Hartley et al., 2003; Wolbers et al., 2004; Wolbers & Büchel, 2005). Importantly, this activation was found not only for tasks tapping survey processing but also for tasks probably more akin to route processing (Ghaëm et al., 1997). As this area is thought to be involved in the transformation of egocentric to allocentric knowledge (Maguire, 2001; Burgess, Maguire, Spiers, & O'Keefe, 2001) and vice versa (Iaria, Chen, Guariglia, Ptito, & Petrides, 2007), it could be expected to be activated by both route and survey processing.

Unlike the activation of the above-mentioned brain regions corresponding to the requirements of both route and survey tasks, an activation of the left hippocampus regardless of the type of processing was relatively unexpected. According to several studies, the hippocampus is mainly involved in survey processing (e.g., O'Keefe & Nadel, 1978; Nadel & Moscovitch, 1997; Hartley et al., 2003; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003), with a right predominance (see Burgess, Maguire, & O'Keefe, 2002, for review). In contrast, other studies have demonstrated a bilateral or even left-sided hippocampal involvement in spatial memory (Iaria et al., 2003; Incisa della Rocchetta et al., 2004). In addition, Shelton and Gabrieli (2002) found a robust activation of the medial bilateral temporal lobe including the posterior hippocampus during route encoding. A similar activation was observed by Mellet et al. (2000a) in a PET study during route retrieval. Thus, a possible complementary explanation for the left hippocampal activation in the present route and survey tasks is provided by several authors (Maguire et al., 1998; Burgess et al., 2001, 2002), who argue that the left hippocampus is involved in spatial episodic memory via retrieval of spatial context (the scene of the events) or in non-topographical memory (the sequence of events; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001).

A part of the network activated in the present study both in route and in survey tasks, including the precuneus, retrosplenial, parietal, and parahippocampal cortices, and the hippocampus in some studies, has been shown to be activated during navigation relying on survey knowledge in previous neuroimaging studies (for reviews see Burgess

et al., 2002, and subsequent papers, e.g., Shelton & Gabrieli 2002; Iaria et al., 2007). However, as discussed above, though classically associated with way-finding, the structures included in this network are likely to be implicated in route processing, too, because of their relatively non-specific spatial functions. This is the case for visual-spatial imagery, landmark processing, episodic memory, planning of real or imagined actions, and use of reference frames. In contrast, as far as we know, brain structures specifically activated by route processing, such as the SMA, the insula, and the caudate nucleus (except Hartley et al., 2003, for the later structure, see above), have never been shown to be activated during survey tasks. This pattern of data suggests that the brain areas, respectively involved in route processing and those involved in survey processing when distinct environments are used (or when learning takes place from different perspectives), are all activated when learning takes place in the same environment from a ground level perspective, regardless of the kind of processing. As suggested above, performing two different types of spatial processing within a same environment would activate a mixed representation combining route and survey information in a single entity.

The multivariate pattern classification analysis confirmed that a common distributed network of brain activity supported the two tasks. Bray et al. (2009) mentioned that multivariate pattern classification analyses may be limited because they do not explicitly model the shape of the neural response as it is the case with univariate general linear models. However, since they are sensitive to co-varying patterns of activity, these analyses are intrinsically linked to functional connectivity analyses, confirming that investigating the temporal dynamics may be crucial to understand the similarities and differences in the brain activation between situations.

In addition to these analyses, the functional connectivity analysis revealed the degree of co-activation between regions of the network. The fact that almost all these regions co-activated in one or both tasks confirms their importance for topographical processing. However, there were differences of connectivity between route and survey tasks: co-activations were stronger and more extended in the route tasks. These findings suggest that the regions of the selected network were activated in a more synchronous manner for route tasks than for survey tasks. In the language domain, Tivarus, Hillier, Schmalbrock, and Beversdorf (2008) have proposed that semantic tasks require greater interaction outside the language areas, as compared to phonological tasks. There is a tempting parallel in the present spatial domain: it is possible that route tasks activated to a greater extent the network of regions selected for the connectivity analyses, while survey tasks might have required interactions outside this network. Indeed, we cannot exclude a critical role of

additional regions not selected in the functional connectivity analysis but revealing activity in previous analyses. If this is true, such a difference could partly be due to the semantic components of survey knowledge (e.g., Tse et al., 2007). However, such considerations must be considered purely speculative at this point and require further study, in particular with a more detailed functional analysis.

In conclusion, this study is among the first to use the same environment for route and survey information retrieval. The data suggest that people construct mixed representations including elements of both route and survey knowledge. This hypothesis had been advanced not only in studies belonging to the field of cognitive psychology (e.g., Montello, 1998; Newman et al., 2007) but also in some functional neuroimaging studies (Mellet et al., 2000a; Shelton & Gabrieli, 2002; Hartley et al., 2003). Further behavioral and functional imagery studies are necessary to better support the present results.

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