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RAPID COMMUNICATION

Neural Correlates of Topographic Mental Exploration: The Impact of Route versus Survey Perspective Learning

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There are two major sources of information to build a topographic representation of an environment, namely actual navigation within the environment (route perspective) and map learning (survey perspective). The aim of the present work was to use positron emission tomography (PET) to compare the neural substrate of the topographic representation built from these two modes. One group of subjects performed a mental exploration task in an environment learned from actual navigation (mental navigation task). Another group of subjects performed exploration in the same environment learned from a map (mental map task). A right hippocampal activation common to both mental navigation and mental map tasks was evidenced and may correspond the neural substrate of a "dual-perspective" representation. The parahippocampal gyrus was additionally activated bilaterally during mental navigation only. These results suggest that the right hippocampus involvement would be sufficient when the representation incorporates essentially survey information while the bilateral parahippocampal gyrus would be involved when the environment incorporates route information and includes "object" landmarks. The activation of a parietofrontal network composed of the intraparietal sulcus, the superior frontal sulcus, the middle frontal gyrus, and the pre-SMA was observed in common for both mental navigation and mental map and is likely to reflect the spatial mental imagery components of the tasks. © 2000 Academic Press

Key Words: **spatial mental imagery; route perspective; survey perspective; parieto-frontal network; hippocampus; parahippocampus; positron emission tomography.**

INTRODUCTION

Mental exploration constitutes a type of spatial mental imagery, which allows one to activate the representation of a previously perceived environment and to move mentally from a point to another while no visual input is present. To build such a spatial representation, people acquire information from different ways, e.g., by actually navigating in the environment (information is then acquired in an egocentric or "route" perspective) or by learning maps (information is acquired in an exocentric or "survey" perspective). The issue whether the topographic representation built from either route perspective or survey learning exhibited distinct or similar properties has been addressed by several studies (Thorndyke and Hayes-Roth, 1982; Taylor and Tversky, 1992; Ferguson and Hegarty, 1994; Schneider and Taylor, 1999; Taylor *et al.*, 1999). These behavioral data provide discrepant results and it remains unclear whether perspective is maintained in memory. Some studies have compared the representation of environments built from text descriptions in survey perspective, text descriptions in route perspective, or memorization of maps and found no effect of the perspective learning on subject's performance in a task testing their memory of the spatial organization of the environment (Taylor and Tversky, 1992). This supports that survey or route description may result in topographic representations that share properties.

On the other hand, other studies found an effect of the perspective learning on the properties of the topographic representation built from either text descriptions (Schneider and Taylor, 1999) or visual experience (Thorndyke and Hayes-Roth, 1982; Taylor *et al.*, 1999). For example, route distance estimations are more accurate than Euclidean distance estimations when information has been initially acquired by actual navigation, while the reverse pattern is observed when the spatial information has been encoded through survey learning (Thorndyke and Hayes-Roth, 1982). In the same vein, survey-learning subjects make more errors

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when judging orientation than when estimating of location landmarks belonging to the environment learned. On the opposite, route-learning subjects judge orientation more accurately than they judge landmark location. The structure of the topographic representation seems therefore in part constrained by the route or survey perspective in which spatial information is acquired.

Previous neuroimaging studies have investigated the neural substrate of navigation and studies explored either encoding (Maguire *et al.*, 1996, 1998a; Aguirre *et al.*, 1996) or retrieval (Maguire *et al.*, 1997, 1998b; Ghaëm *et al.*, 1997; Aguirre and D'Esposito, 1997) of topographical knowledge. In most of these studies, the environment was learned in route perspective, but the built representation was assumed to use both survey and route information (for example, see Maguire *et al.* (1997, 1998a). It thus appears that while the neural substrate of both encoding and retrieval of topographic information has been studied, the effect of the learning perspective on the neural structures involved in the retrieval and utilization of the topographic representation has, to our knowledge, never been considered.

In the present work, we compared the neural basis of spatial knowledge derived from two typical sources of spatial information, namely actual navigation and map learning. Since, the topographic representations built from either route or map visual learning have been shown to exhibit some distinctive behavioral features, we hypothesized that the neural network engaged in the activation of the representation would differ according to the perspective in which the topographic information has been acquired. We also expected neural structures common to both perspectives reflecting features shared by the two types of representation. In order to test this hypothesis, we used positron emission tomography (PET) to compare the pattern of activation in two groups of subjects during the mental exploration of the same environment that was learned in two different ways: either from actual navigation or from a map. Unlike most of the neuroimaging studies, our exploration tasks were performed in absence of any visual input and thus included a strong component of spatial mental imagery. This make our tasks very close to the natural activity of way finding. Actually, finding one's way requires most of the time to mentally simulate a route or to inspect a mental map of the environment, and thus strongly calls for spatial mental imagery.

In the following, "mental navigation" will refer to the mental exploration of a representation learned from an actual walk in the environment (Study 1), and "mental map" will refer to the mental exploration of a representation learned from a map (Study 2). The two tasks will be jointly named "mental exploration tasks."

MATERIALS AND METHODS

Because it was important to use exactly the same environment for both route and survey learning, we chose a multistudy design. The constitution of two distinct groups of subjects for the two types of learning was crucial to ascertain that the subjects learned the environment in one perspective only.

Study 1: Mental Navigation

The mental navigation task is part of a previous work published elsewhere (Ghaëm *et al.*, 1997). Data have been fully reanalyzed in order to be included in a multistudy design (See data analysis section).

Subjects

Five healthy right-handed male volunteers (20–22 years old) participated in this study. All were free from nervous disease or injury and had no abnormalities on their T1-weighted magnetic resonance images (MRI). In order to ensure optimal homogeneity of the sample of the subjects with respect to their imagery abilities, subjects were selected as high visuospatial imagers on the basis of their scores on the Minnesota Paper Form Board (MPFB) and on the Mental Rotations Test (MRT); all subjects scored beyond the 75th percentile of a population of 100 male subjects.

PET Methodology and Task Design

(a) Learning and training phase: Learning. The day before the PET scanning, the subjects walked within an environment (a park) they had never seen before. The learning phase included three repetitions of the same walk within the park. The first walk was guided by the experimenter. The subjects were instructed to memorize the route they covered including the direction changes (Fig. 1, left). Furthermore, during this first walk, seven landmarks were pointed out and named by the experimenter (see Fig. 1A, left). During the second and third walks, the subjects had to follow the first route they learned and name the landmarks they met, under the experimenter's control.

Training. The day after learning, three to four hours before the PET scanning, subjects were trained to the mental navigation task proper. The names of two landmarks (e.g., "gas station," "phone box") belonging to the environment were presented through earphones to indicate the route segment that the subject had to mentally simulate. The subject was instructed to recall the visual and sensory-motor mental images of his walk in a route perspective along the path segment. Three sessions of training including five segments delivered in different orders were performed. The length of the path segments varied from 48 to 172 m.

(b) PET procedure. Six sequential measurements of the normalized regional cerebral blood flow (NrCBF) were obtained from each subject on an ECAT 953B/31 PET camera (time acquisition: 80 s), replicating a series of three experimental conditions presented in randomized order. All conditions were performed eyes closed in total darkness, a black and opaque cloth covering the whole camera. For the purpose of the present study, two conditions only were included: A rest condition and a mental navigation task. In the rest condition subjects were eyes closed in total darkness. The second task was the mental navigation task described above in the training section, namely mentally follow the path between two landmarks verbally delivered and press a key when the second landmark was reached. Five different segments, randomly delivered, were used during each replication of the mental navigation condition.

The duration of the mental navigation along each segment was recorded. In order to monitor the spontaneous eye movements executed during the two conditions, horizontal electroculograms (EOG) were recorded for each subject using surface electrodes placed at the outer canthi and at the right ear as a reference.

Study 2: Mental Map

Subjects

Six healthy right-handed male volunteers (age: 19–25 years) selected for their high spatial imagery ability participated in this study. All were free from nervous disease or injury and had no abnormalities on their T1-weighted magnetic resonance images (MRI).

PET Methodology and Task Design

(a) Learning and training phase: Learning. The day before PET scanning, the subjects were taught the map thanks to eight slides projected on a blank screen. The map to learn represented the park described above and included seven colored dots that were linked by paths (Fig. 1, left). The dots were located at the same place than the landmarks belonging to the actual environment. The final size of the map was length: 1.64 m, width: 1 m and viewing angle: 25° × 15°. The first slide represented the whole map, including the seven colored dots. The subjects were told to examine the map during 3 min in order to memorize it. The next seven slides represented the whole map with a single dot, each slide showing one of the seven dots. Each slide was presented during 5 s and the name of the corresponding dot was said by the experimenter. The learning phase was completed by a last presentation of the whole map including the seven dots during 3 min, as in the initial phase. Note that there was no explicit instruction to scan along the paths during the learning phase.

To ensure that the subjects had accurately memorized the map, they were required to pin point each dot location on a slide of a blank map at the end of the learning phase.

Training. The day after the learning, three to four hours before the PET scanning, subjects were trained in the mental map task proper. Eyes closed, they had to visualize the map as accurately as possible including the seven dots, they were then given through earphones the name of two colored dots (e.g., “red,” “blue”) and had then to imagine a laser dot following the path segment drawn on the original map between the two dots. Once the second dot was reached, the subjects had to press a button with their right index, this action releasing the auditory delivery of a second pair of dots. Two sessions of training including segments delivered in a different order were performed. The length of the path segments varied from 15 to 198 cm on the map corresponding in the actual environment to a length varying from 48 to 574 m.

(b) PET Procedure

Four to six sequential measurements (time acquisition: 90 s) of NrCBF were obtained from each subject on an ECAT Exact HR+ PET camera, replicating two or three times a series of two experimental conditions presented in randomized order (Due to technical problems, the PET camera did not start during some of the acquisition resulting in missing replications in some subjects). All conditions were performed eyes closed in total darkness, a black and opaque cloth covering the whole camera.

In the rest condition, subjects were eyes closed in total darkness. The second task was the mental map task described above in the training section, namely mentally follow the path between two dots auditorily delivered and press a key when the second dot was reached. Fourteen different segments, randomly delivered, were used during each mental map conditions. The duration of the mental scan along each segment was recorded.

In order to monitor the spontaneous eye movements executed during both conditions, horizontal electroculograms (EOG) were recorded for each subject using surface electrodes placed at the outer canthi and at the right ear as a reference. The EOG system can detect saccades superior to a one degree of visual angle and was calibrated before each condition. All EOG records were analyzed by computer using a dedicated software (SAMO), which detects saccadic components and quantifies the amplitude and frequency of spontaneous saccadic eye movements.

Data Analysis

In order to be included in the analysis, all the scans from the two studies were processed using the same procedure which induced a reanalysis of the CBF data for the mental navigation study (Study 1). After automatic realignment (AIR) (Woods *et al.*, 1997), the original brain images were transformed into the standard stereotactic Talairach space using the MNI template (Friston *et al.*, 1995a). The camera used in the mental navigation group have a smaller field of view than the one used in the mental map group. This results in a final volume common to both groups extending in z direction from +63 mm to −27 mm from AC/PC line in the most anterior part of the brain to +67 mm to −14 mm in its most posterior part. It thus included hippocampal and parahippocampal regions. The images were smoothed using a Gaussian filter of 12 mm FWHM leading to a final smoothness of 15 mm FWHM. The rCBF was normalized within and between subjects using a proportional model. The comparisons across conditions were made by way of t statistics. Statistical parametric maps corresponding to comparisons between conditions and between studies were generated with the 1999 version of SPM (Friston *et al.*, 1995b). Simple comparisons within each study concerned mental navigation versus rest for Study 1 (Table 1) and mental map versus rest for Study 2 (Table 1). For each comparison, the voxel amplitude t map was transformed in a Z volume that was thresholded at $P < 0.001$ (uncorrected for multiple comparisons).

Between-study comparisons included (mental navigation − rest) versus (mental map − rest) and the reverse comparison, i.e. (mental map − rest) versus (mental navigation − rest) (Table 2, thresholded at $P < 0.001$, uncorrected for multiple comparisons). In order to avoid "false" activation due to deactivation in the second contrast, each interaction was masked by the main effect thresholded at 0.05 (for example (mental navigation − rest) versus (mental map − rest) was masked by mental navigation − rest).

Activations common to different contrasts were identified by conjunction analysis (Price and Friston, 1997). This analysis was performed to uncover the voxels that were activated in both mental map and mental navigation as compared to rest (Table 2). The threshold was set to $P < 0.001$ (uncorrected for multiple comparisons) for this conjunction analysis.

TABLE 1

Mental Navigation versus Rest and Mental Map versus Rest ($P < 0.001$)

Anatomical location of maximum voxel	Coordinates x	y	z	Z score
Mental navigation versus rest				
L. intraparietal sulcus/précuneus	−16	−66	54	5.4
L. occipito-parietal sulcus	−14	−56	20	3.9
L. occipito-parietal sulcus	−30	−64	6	3.5
R. occipito-parietal sulcus	24	−68	24	4.9
R. posterior cingulate gyrus	16	−56	12	4.0
Median superior frontal gyrus	10	10	48	4.1
L. precentral/superior frontal sulcus	−26	−2	56	3.5
R. precentral/superior frontal sulcus	36	−8	52	3.4
R. middle frontal gyrus	30	46	24	3.2
R. parahippocampal gyrus	28	−24	−22	3.2
L. parahippocampal gyrus	−34	−38	−8	3.2
Mental map versus rest				
L. intraparietal sulcus/précuneus	−8	−72	54	4.6
L. intraparietal sulcus	−22	−68	54	3.3
R. intraparietal sulcus/precuneus	16	−72	52	3.3
Median superior frontal gyrus	−6	2	54	4.0
Median superior frontal gyrus	0	10	46	3.6
L. precentral/superior frontal sulcus	−20	−4	64	3.2
R. precentral/superior frontal sulcus	38	−4	54	3.2
R. middle frontal gyrus	34	38	30	4.5
R. superior frontal sulcus	32	54	16	3.3
L. superior temporal gyrus	−64	−24	8	4.2
R. superior temporal gyrus	62	−20	6	4.1
R. middle temporal sulcus	56	−42	12	3.5
R. hippocampus	30	−12	−18	2.9*
R. supramarginal gyrus	48	−44	24	3.4
L. lenticular nucleus	−18	16	0	3.4
L. anterior insula	−24	28	8	3.3
R. lenticular nucleus	26	24	8	3.2

Note. Foci of significant normalized regional cerebral blood flow (NrCBF) increases when mental navigation (upper part) and mental map task (lower part) were compared to the rest conditions. The data, based, respectively, on five and six subjects are local maxima detected with SPM software. Within these regions, the anatomical localization of the maximum Z scores of the voxel is given on the basis of the MNI template, using the stereotactic coordinates of the Talairach space in mm (R., right; L., left).

RESULTS

Behavioral Results

Eye Movements Analysis

Mental navigation. The amplitude of horizontal saccadic eye movements was significantly higher (mean difference 1.1° ± 0.4°, $P = 0.003$, $n = 5$, post hoc t test) during the mental navigation task than during the rest condition. Note that although significant, the difference in amplitude was only of 1° (which is the minimum angle detected by our EOG system) and no significant difference was observed for the frequency of saccades between the two conditions.

Mental map. The mean amplitude of spontaneous horizontal saccadic eye movements during both the rest and the mental map conditions were 4.7 ± 0.4° (mean ± SD) and 6.2 ± 3.5°, respectively. No significant difference between these two conditions was observed in terms of either amplitude or frequency (post hoc paired t test, $P = 0.84$ and $P = 0.82$, respectively).

TABLE 2

Conjunction and Comparison of Mental Map and Mental Navigation

	Coordinates			
Anatomical location of max. voxel	x	y	z	Z score
Conjunction of mental navigation and mental map				
L. intraparietal sulcus/précuneus	−10	−70	54	6.6
L. intraparietal sulcus	−22	−68	54	5.1
R. intraparietal sulcus	22	−70	48	4.3
R. superior occipital gyrus	40	−78	28	3.5
Median superior frontal gyrus	2	12	46	5.3
L. precentral/superior frontal sulcus	−22	−4	54	4.9
L. precentral sulcus	−34	−4	54	3.9
R. precentral/superior frontal sulcus	38	−4	52	4.7
R. middle frontal gyrus	32	46	24	4.9
R. medial frontal gyrus	20	48	−10	4.0
L. lenticular nucleus/anterior insula	−30	14	4	4.4
R. lenticular nucleus	26	16	2	3.2
R. hippocampus	26	−20	−18	3.4
L. superior temporal gyrus	−66	−20	2	4.0
R. middle temporal gyrus	64	−36	−14	3.4
Mental navigation vs mental map				
R. occipito-parietal sulcus/cuneus	24	−70	24	4.8
L. intraparietal sulcus/precuneus	−18	−60	54	3.2
L. posterior cingulate gyrus	−12	−46	28	3.4
L. inferior frontal sulcus	−52	16	30	3.2
R. parahippocampal gyrus	32	−20	−26	2.7*
L. parahippocampal gyrus	−28	−36	−18	3.1
Mental map vs mental navigation				
R. precentral gyrus	64	8	16	4.4
R. superior temporal gyrus	52	−12	10	4.3
R. superior temporal gyrus	62	−18	6	4.0
R. Heschl gyrus	44	−4	8	3.7

Note. Upper part: Conjunction analysis revealing foci of significant NrCBF increases common to mental navigation and mental map tasks as compared to rest. Middle part: Foci of significant difference between mental navigation and mental map tasks. $^*P = 0.002$ uncorrected. Lower part: Foci of significant difference between mental navigation and mental map tasks. (See Table 1 legend for details.)

Debriefing of the Subjects

Within the five subjects of the navigation group four reported that they did not use a mental map strategy to mentally navigate but instead used a route perspective.

Within the six subjects of the map group, all rated the map mental image as accurate and reported that they actually follow the instructions they were given before the experiment (imagine a laser dot following the path segment drawn on the original map between the two dots).

Chronometric Data Analysis

The much longer reaction times we reported in the mental navigation group compared to the mental map group (respectively, 43.9 ± 14.0 and 7.4 ± 1.4 s) reinforce the assumption that the two tasks were actually different and that the subjects used a different perspective in the two tasks.

In each study, a correlation was computed between the time (averaged across subjects) spent to cover the different route segments. This correlation took into account only the route segments for which all subjects provided responses (respectively, $n = 5$ for the mental navigation group, and $n = 9$ for the mental map group).

Mental navigation. A positive correlation was evidenced between time and distance: the longer the distance between two landmarks was, the longer the subjects took to mentally cover the route between the landmarks (Fig. 1A, right; $r = 0.92$, $P = 0.025$, $n = 5$).

Mental map. A positive correlation was also found between time and distance in the mental map group (Fig. 1B, right; $r = 0.91$, $P = 0.006$, $n = 9$).

Note that because the average time spent to cover the route segments was longer in the mental navigation than in the mental map group, more pairs of landmarks were delivered to the survey than to the route group (about 11 for the survey subjects versus three for mental navigation subjects).

Pet Results

Mental Navigation versus Rest (Table 1; Fig. 2A)

The reanalysis of the present contrast using the MNI template revealed activation of the same set of cortical regions previously reported (Ghaëm *et al.*, 1997). Note, however, that the coordinates of activation may differ from this earlier report because the template used for the spatial normalization was different and the procedures used to compute the present normalization were more accurate. This can result in a different anatomical localization for some foci. Some other foci are no more present in the results because they just failed to reach the significance level in the new analysis (L. dorsolateral prefrontal cortex, Z score = 2.9, and L. middle occipital gyrus, Z score = 3.0).

An activation of the left intraparietal sulcus extended medially to the left precuneus. Within the medial part of the occipital lobe, an activation of occipitoparietal sulcus was bilaterally detected extending forward to the right posterior cingulate cortex. The median frontal region corresponding to the pre-SMA was also activated as well as the bilateral superior frontal sulcus near the intersection with the precentral sulcus. An activation located in the right middle frontal gyrus was also detected.

A bilateral activation was detected in the medial part of the temporal lobe (Fig. 2A). On the right side, it was located in the depth of the posterior collateral sulcus, at a level that corresponds to the limit between entorhinal and parahippocampal cortex (Bohbot *et al.*,

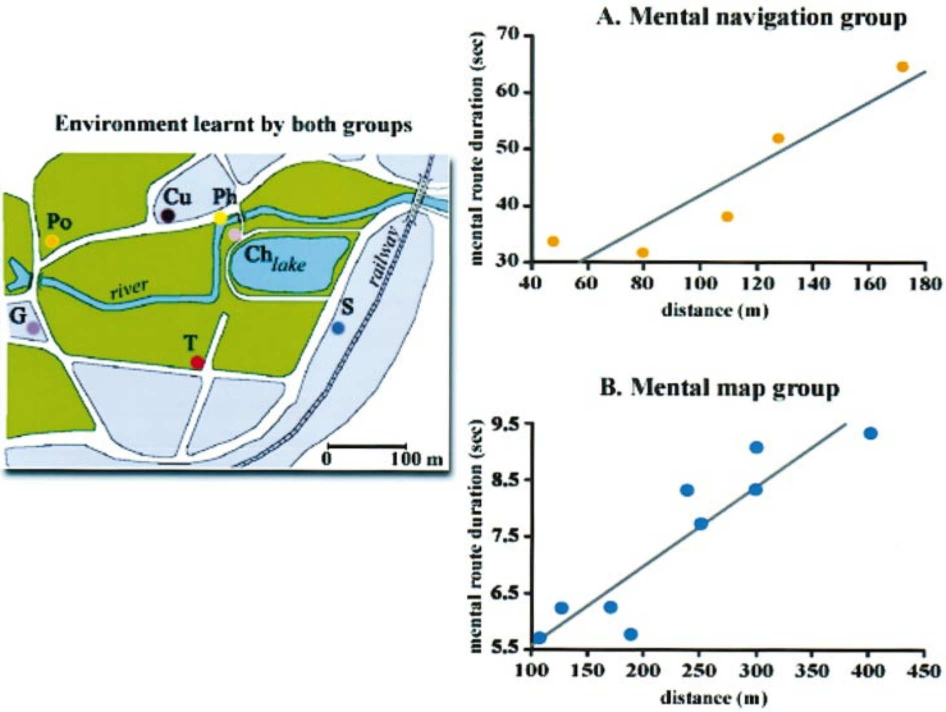

FIG. 1. Left: Environment learned by both mental navigation and mental map groups. In the mental navigation group learning was performed from an actual navigation within the environment including actual landmarks (T, tower; G, gas station; Po, portal; Cu, cubes; Ph, phone box; Ch, chalet; S, statue). In the mental map group learning was performed with a map of this environment and included colored dots. Note that the environment to be learned was the same in both groups and that the dot locations were the same as locations of the actual landmarks. Right: (A) Linear regression analysis between mental navigation duration and route segments length. (B) Linear regression analysis between mental map exploration duration and route segments length. In each group the regression was computed between average response times and segment lengths for the segments to which all subjects provided a response.

1998). On the left side, the activation was in a more posterior location and corresponds to the parahippocampal cortex. A slight CBF increase occurred in the right hippocampus that did not reach significance because of a strong interindividual variability.

Mental Map versus Rest (Table 1; Fig. 2B)

The intraparietal sulcus was bilaterally activated, the activation extending medially to the precuneus. In the frontal lobe, a median frontal region anterior to the VAC plane was significantly activated and corresponded to the anterior part of supplementary motor area (pre-SMA). The superior frontal sulcus presented a bilateral activation located at the intersection with the precentral sulcus. An activation was also detected in the right middle frontal gyrus.

The superior temporal cortex was activated bilaterally in the vicinity of Heschl's gyrus and extended in the right hemisphere within the superior temporal sulcus and the right supramarginal gyrus.

At a subcortical level, the lenticular nucleus presented a bilateral CBF increase extending to the anterior insula on the left side.

During mental map, the right medial temporal presented an activation that just failed to reach the 0.001 threshold of significance ($P = 0.002$) while the left medial temporal lobe was clearly not activated. This right sided activation was located in the hippocampus, within the uncal sulcus (Fig. 2B). Note that, as shown on the histograms (Fig. 2B), the CBF slightly increased in this region during mental navigation.

Conjunction of Mental Navigation and Mental Map (Table 2, Fig. 2C)

This analysis revealed the regions which presented a similar activation in both mental navigation and mental map tasks. At the parietal level, it included bilaterally the intraparietal sulcus and the precuneus. In the frontal lobe, common activations were observed in the pre-SMA and in the superior frontal sulcus at the intersection with the precentral sulcus.

Additional common activation was detected in the right middle frontal gyrus and bilaterally in the lenticular nucleus extending leftward to the anterior insula.

Finally, the temporal cortex presented an activation located in the superior temporal gyrus on the left side and in the middle temporal gyrus on the right side.

In the medial part of the temporal lobe, an activation was detected that straddled the right hippocampus and the adjacent enthorhinal cortex.

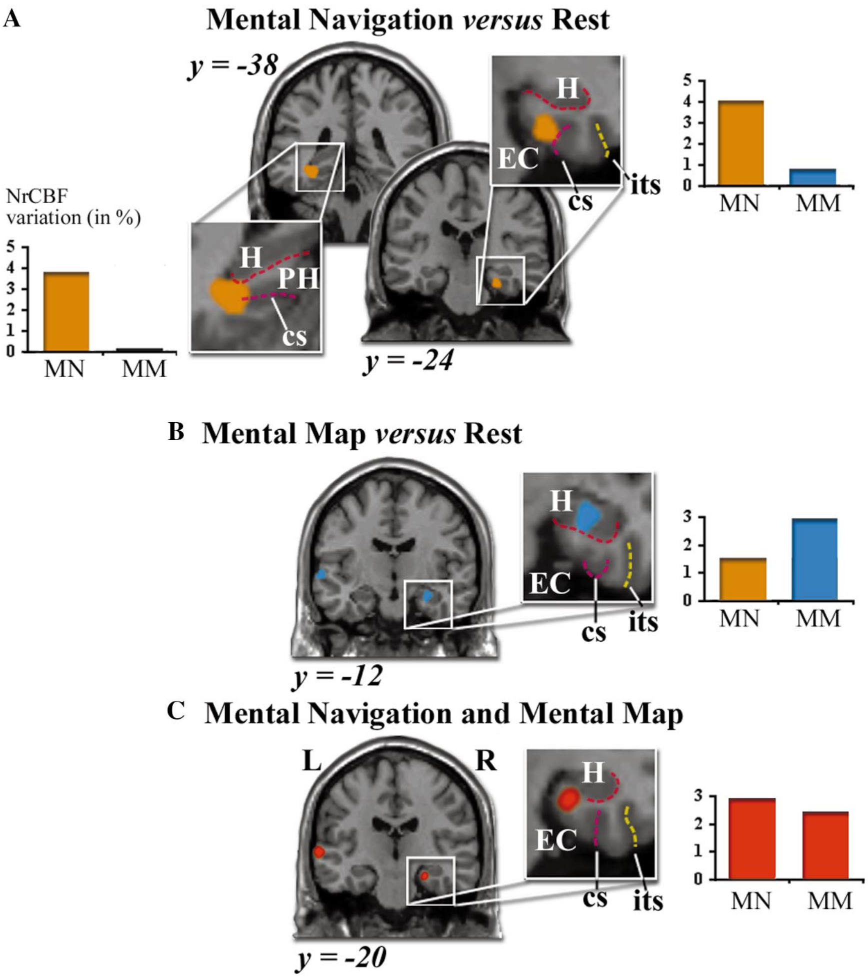

FIG. 2. (A) Middle: Statistical parametric map (SPM) revealing the bilateral activation clusters in the parahippocampus when subjects mentally explore the environment previously learned by actual navigation. Left and right: Adjusted CBF differences in the left and right parahippocampus corresponding to the two contrasts described above. This illustrates the specificity of the parahippocampal activation during the mental navigation task. (B) Left: SPM revealing the activation cluster in the right hippocampus when subjects mentally explored the map previously learned. The volume was thresholded at $P < 0.005$ (not corrected for multiple comparisons) and projected on a coronal view of the MNI template. Right: Adjusted CBF difference in the hippocampus corresponding to the two contrasts: MM, mental map versus rest; MN, mental navigation versus rest. (C) Left SPM revealing the right hippocampal area activated in both mental navigation and mental map tasks (conjunction analysis). Right: Adjusted CBF differences in the right hippocampus corresponding to the two contrasts described above. H, hippocampus; EC, entorhinal cortex; cs, collateral sulcus; its, inferior temporal sulcus.

Mental Navigation versus Mental Map (Table 2)

This contrast revealed an activation in the occipito-parietal sulcus at the border of the medial part of the occipital lobe (cuneus) and the medial part of the parietal lobe (precuneus). An activation in the middle occipital gyrus was also detected in the direct comparison.

Left-sided CBF differences were also observed in the inferior frontal gyrus (*pars triangularis*) and in the posterior cingulate cortex. In the medial temporal lobe, the left parahippocampal cortex presented a significant activation while a trend toward significance was present in the right homologous area ($P = 0.004$).

Mental Map versus Mental Navigation (Table 2)

This comparison showed that mental map induced greater right-sided CBF increase in the inferior part of the precentral sulcus and the superior temporal gyrus including Heschl's gyrus. This latter activation is likely to reflect that, as mentioned above, the frequency of auditory stimulation was more important in the mental map group than in the mental navigation group.

No activation of the right hippocampus was evidenced when contrasting mental navigation and mental map. This suggests, together with its activation in the conjunction analysis, that the right hippocampus plays a role in both mental navigation and mental map tasks.

DISCUSSION

The main purpose of the present study was to evidence the neural structures engaged in the utilization of a topographic representation that has been built from two different sources, actual navigation and map. It has recently been emphasized that acquiring the environment knowledge in a given perspective does not warrant that the subject will use the subsequent mental representation in the same perspective (Aguirre and D'Esposito, 1999). Numerous factors such as interindividual variability may constrain the "route" or "survey" perspective of their representation (Heft, 1979; Thorndyke and Hayes-Roth, 1982). Furthermore, it has been suggested that a representation in a route perspective may integrate spatial information of nonvisible parts of the environment (Thorndyke and Hayes-Roth, 1982). Moreover, the differences evidenced in the neural structure involved in the mental navigation and in the mental map tasks does not necessarily imply that the final representation was in a different perspective, but may reflect that the computations required to obtain the final representation used during the tasks were different. For these reasons, the differences in the neural structures engaged in our mental navigation and mental map tasks could be attributed either to the differences of the encoded material (e.g., 3-D versus 2-D), to the nature of the task (mental navigation in a subject-centered perspective versus mental map of a visually reconstructed map) or to both. However, the impossibility to disentangle these two sources of disparity is not conflicting with the question addressed in the present work: Does the way a person has learned an environment have an influence upon the patterns of activation during the utilization of the resulting topographic representation?

In the following sections, we will first discuss both the behavioral and anatomofunctional similarities evidenced between the two tasks, then we will focus on the anatomofunctional differences existing between these two tasks.

Similarities in Behavioral and Anatomo-Functional Results

Both the mental navigation and the mental map tasks required the recall of the spatial positions of items (i.e., landmarks, dots), the maintenance of the spatial relationships of the scenes, and the mental displacement from an item to another. The behavioral results reflected the common features of the two tasks: in both tasks we evidenced a positive correlation between times and distances. Such correlation is generally taken as reflecting the structural isomorphism between mental images and the configurations that they represent (Kosslyn *et al.*, 1978, see Cocude *et al.*, 1999, and Denis and Kosslyn, 1999, for a review). The present work shows that this isomorphism is preserved whether the topographic information has been acquired from survey or route perspective. Our findings strengthen the assumption that it is a general property of spatial mental images.

The similarities observed in the behavioral results were also expressed into the detection of a common set of regions similarly activated in both exploration tasks. These regions include the right hippocampus in the medial temporal lobe and a parietofrontal network that included four distinct regions.

1. Right Hippocampus

The right hippocampus was activated whatever the modality of topographic information encoding. The assumption that the hippocampus plays a key role in human navigation originates from electrophysiological and lesions studies in rodents (O'Keefe and Dostrovsky, 1971; Morris *et al.*, 1982). It has been proposed that the hippocampus maintains a cognitive map, providing a survey representation of the environment (O'Keefe and Nadel, 1978). The situation is less clear in humans. First, while hippocampal lesions may result in topographic disorientation, this trouble is accompanied by global episodic memory impairment (Vargha-Khadem *et al.*, 1997), which makes the specific role of hippocampus in navigation difficult to assess. A recent study has however reported a route learning impairment in seven subjects with right hippocampal lesion and emphasize the role of this region in spatial memories consolidation (Barrash *et al.*, 2000). On the other hand, parahippocampal lesions resulted more specifically in topographic disorientation suggesting that this region also plays a key role in human navigation (Habib and Sirigu, 1987; Barrash *et al.*, 2000; Bohbot *et al.*, 1998; Aguirre and D'Esposito, 1999). Second, neuroimaging studies have provided diverging results: some works using either encoding or retrieval navigational tasks reported an activation in the hippocampus proper (Maguire *et al.*, 1996, 1997, 1998b; Gron *et al.*, 2000), while some others did not (Aguirre *et al.*, 1996; Maguire *et al.*, 1998b; Aguirre and D'Esposito, 1997). The hippocampal activation reported here indicates that there exists an hippocampal region which is active during the recall of a topographic representation built from either route or survey information. If we assume that hippocampus would be the neural substrate of "cognitive maps," the present hippocampal activation could suggest that subjects have included some survey information in the representation initially acquired in a route perspective. This gives a support to the proposition that it may exist an intermediate representation between route or survey knowledge in which people may "look through" obstacles (Thorndyke and Hayes-Roth, 1982). This type of representation emphasizes that once the subjects have actually walked in the environment they have acquired information about parts of environment hidden by the obstacles and use a "survey knowledge from a perspective within" (Thorndyke and Hayes-Roth, 1982). The present hippocampal activation could reflect the use of such a "dual" representation.

2. ParietoFrontal Network

A parietofrontal network was activated whichever the way the spatial representation had been built and was thus neither dependent on the complexity of the material to learn (i.e., 2-D or 3-D), nor on the perspective in which the topographic information was acquired (here route or survey). This network included the bilateral intraparietal sulcus, the bilateral superior frontal sulcus, the right middle frontal gyrus and the pre-SMA. We postulate that this set of regions belongs to a network specialized in the processing of visuospatial information whenever the visual input is no longer present as it is the case in our two spatial imagery tasks. This network could reflect the spatial working memory processes required to maintain the mental image of the map or of the actual environment (Mellet *et al.*, 1998).

The first component of the network corresponds to the intraparietal sulcus. This structure is commonly involved during visuospatial attention (Corbetta *et al.*, 1998), spatial working memory (Smith *et al.*, 1996; Petit *et al.*, 1996), and spatial mental imagery (Mellet *et al.*, 1995, 1996, 2000). To our knowledge it has not yet been possible with functional imaging to dissociate between these different components in the intraparietal sulcus.

The second component is constituted by a bilateral region located in the depth of the superior frontal sulcus near its intersection with the precentral sulcus and labeled as Brodmann's area 6 (BA6) in the Talairach atlas (Talairach and Tournoux, 1988). This region has been reported activated in spatial working memory studies (Jonides *et al.*, 1993; Petit *et al.*, 1996) and in spatial mental imagery studies (Kawashima *et al.*, 1995; Mellet *et al.*, 1996). Its implication in the present study nicely fits with the fact that this area seems specifically involved in the period during which the visual input is no longer present and the spatial information has to be held on-line (Courtney *et al.*, 1998a). Although eye movements were not different from rest during mental map and differed by very small amplitude during mental navigation, we wanted to ascertain that the frontal activation described here was distinct from the frontal eye field (FEF). For this purpose, we displayed the activations reported in the present conjunction analysis together with those corresponding to the FEF and evidenced during the execution of self-paced saccades previously reported in a distinct group of six subjects (Petit *et al.*, 1996). Figure 3 shows that both patterns of activation were indeed different, the superior frontal activation being distinct and anterior to the FEF activation. This result is in agreement with those of a previous study which showed that the superior frontal activation elicited by a spatial working memory task was distinct and anterior from the one related to eye movements (Courtney *et al.*, 1998a, 1998b).

The third component is materialized by a frontal activation located in the right middle frontal gyrus labeled BA 9/46 in the Talairach atlas. This region appears less specifically spatial than the frontal BA 6. As a matter of fact, both object and spatial working memory studies reported an activation in this region (for a review see Smith and Jonides, 1997; Courtney *et al.*, 1998b). Although in the present study, it was activated in both mental exploration tasks, spatial by nature, further studies are required to characterize its role and its domain specificity in the frame of working memory processes.

The fourth component common to the two mental exploration tasks corresponds to the pre-SMA. This region has been functionally distinguished from the SMA in that it is involved in complex motor tasks as opposed to the SMA proper located posteriorely and involved in simpler motor tasks (Picard and Strick, 1996). In the present study, the subject had to press a button as soon as the dots or landmarks that terminated a segment was reached. It has recently been proposed that pre-SMA would be tightly linked to working memory, being involved in the preparation for selecting a motor response based on information held on-line (Petit *et al.*, 1998).

We suggest that this parietofrontal network constitutes the smallest set of regions necessary to deal with spatial representation including spatial working memory and spatial mental imagery. Neuroimaging studies have consistently reported an activation of this parietofrontal network during spatial imagery task performed in absence of any visual input (Roland *et al.*, 1987; Mellet *et al.*, 1995, 1996; Kawashima *et al.*, 1995). In a more general perspective, the parietofrontal system constitutes a large-scale distributed network that included a posterior "sensory" pole and an anterior "motor" pole. It has been suggested that this bipolar organization reflects a general frame for storage and retrieval of memories and give rise to the so-called "perception-action cycle" (Fuster, 1997, 1998). The present study provides further support to this view in demonstrating that a similar organization prevails for the neural substrate of spatial representation.

AnatomoFunctional Differences

The spatial representations the subjects reactivated in the two tasks differed according to the nature of their encoding. In the scanning task, the mental image

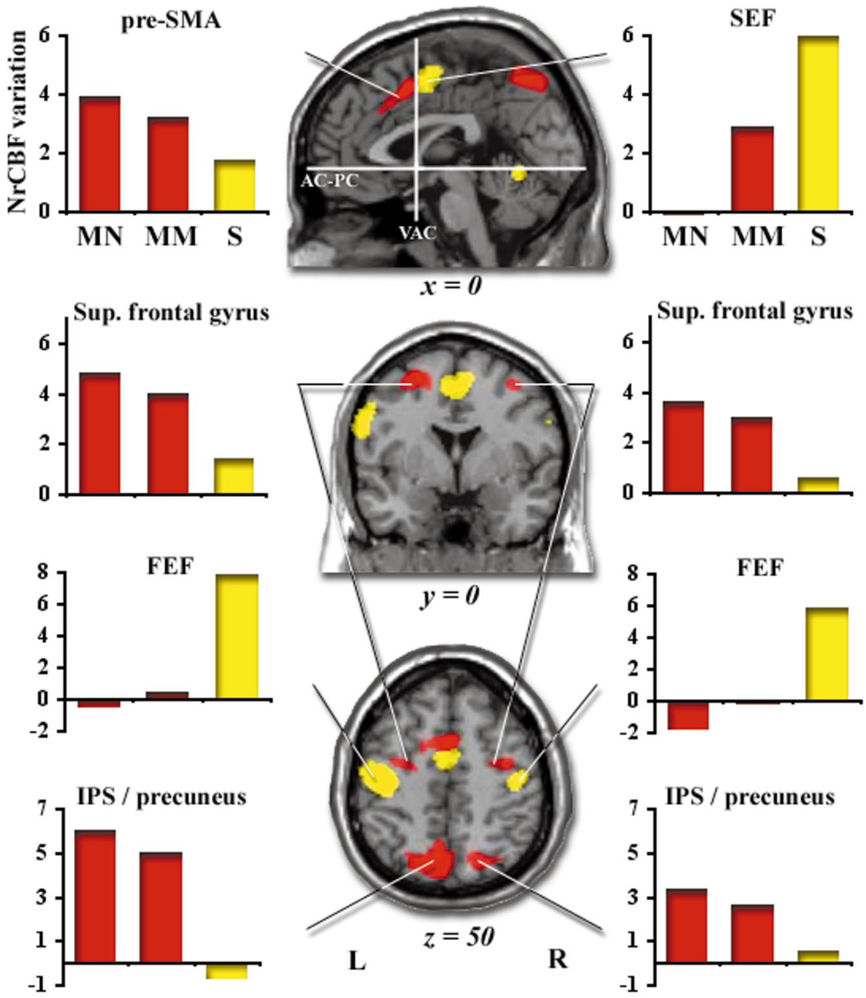

FIG. 3. In red: SPM revealing the activations shared by mental navigation and mental map compared to rest. This analysis uncovered a bilateral parietofrontal network including the intraparietal sulcus, the superior frontal sulcus, and the pre-SMA. In yellow: The activations elicited in a distinct group of subject by the execution of self-paced saccades (S) are shown in yellow. Note that the FEF are distinct and posterior to the superior frontal area activated in both mental exploration tasks The maximum voxel in the precentral/superior frontal activation in the conjunction analysis of both mental exploration tasks was 38, −4, 52 for the left frontal and −22, −4, 54 for the right frontal. The norm of the vector distance between FEF an frontal activation is thus 17 mm for the right and 24 mm for the left. This distance exceed the smoothness value and the foci can be considered as distinct. The supplementary eye field (SEF) part of the SMA proper was significantly activated in the self-paced saccades only (Petit *et al.*, 1996). The histograms represent the adjusted CBF differences observed during mental navigation (MN), mental map (MM), and self-paced saccades (S).

included a complete description of the map comprising the borders, the paths, and the dots in 2-D. In the navigation task, the mental image included only local views, excluding the landmarks that were not visible from the subject point of view. The route perspective thus required an additional computation to derive the shortest path to reach a given landmark.

1. Medial temporal lobe (MTL) activity in mental map and mental navigation. Although the right hippocampus was activated whatever the perspective in which the topographic information was encoded, differences related to the mode of learning were observed within the parahippocampal regions. Given that most of the studies of navigation reported bilateral activation of the parahippocampal gyrus (Aguirre *et al.*, 1996; Maguire *et al.*, 1998b; Aguirre and D'Esposito, 1997), it has been suggested that in humans, parahippocampal gyrus is crucial for navigation and spatial mapping (Aguirre *et al.*, 1998).

Our results confirm such a claim, but provide a new insight: MTL regions involved in the mental exploration may differ according to the perspective in which the environment was encoded. As a matter of fact, our results revealed an activation in the bilateral entorhinal/parahippocampal cortex when subject mentally explore an environment built from a route perspective, while these regions were not involved when the environment had been learned in a survey mode. This result is compatible with several propositions that have been made recently regarding the role of parahippocampal gyrus in topographical processes. It has been shown that the parahippocampal gyrus is active in the encoding of an environment when salient landmarks were present but not when landmarks were lacking (Maguire *et al.*, 1998a). In the present mental exploration tasks, real salient landmarks were used to mark limits in the mental navigation while only colored dots limited the segment to explore during mental map. This also fits with the bilateral parahippocampal activations reported during the mental evocations of salient landmarks (Maguire *et al.*, 1997). In addition, a recent work showed that the parahippocampal cortex is engaged in the passive viewing of local environment as compared to the passive viewing of objects (Epstein and Kanwisher, 1998). In the same vein, these regions had been involved in the retrieval of spatial relationships between objects (Owen *et al.*, 1996; Johnsrude *et al.*, 1999). Our results show that the parahippocampal cortex is also active when the environment is only mentally imaged and suggest that this region is a common neural substrate for viewing an environment and dealing with the mental image of this environment.

In summary, our results are compatible with a dissociation between the right hippocampus and the bilateral parahippocampal gyrus. Right hippocampus involvement would be sufficient when the representation incorporates essentially survey information. On the other hand, the bilateral parahippocampal gyrus would be additionally involved when the environment to mentally explore is a large-scale space, which incorporates route information and includes "object" landmarks. Note, however, that this result concerned an all-male sample of subjects. As a matter of fact, it has recently been emphasized that during navigation males take advantage of both landmarks and geometric configuration while female mainly rely on landmark (Maguire *et al.*, 1999). Given that one major difference between map and actual navigation learning concerned the nature of the landmarks the contrast between the navigation and the map group might have been different in a mixed gender or all-female sample (Grön *et al.*, 2000).

2. Differences between mental map and mental navigation in other regions. The posterior cingulate cortex was activated in the mental navigation condition and not in the mental map task. Interestingly this region has been consistently reported in previous neuroimaging works involving topographical tasks (Aguirre *et al.*, 1996; Maguire *et al.*, 1997, 1998a; Aguirre and D'Esposito, 1997). It has been suggested that this region contributes to the transformation of a route representation to a survey representation (Vogt *et al.*, 1992). As suggested in the introduction, it is likely that to reach parts of the environment that are not visible from an initial location, subjects have to derive survey information from the route knowledge they acquired. This is not the case for mental map, in which the topographic representation used includes by nature survey knowledge. In this framework, the specificity of the posterior cingulate contribution to the mental navigation task may reflect the transformation of route to survey knowledge required to perform the task.

The median occipitoparietal regions (cuneus and precuneus) were activated during the mental navigation task and not during the mental map task. During the mental exploration, the subjects generated visual images that resulted from actual navigation and thus perceived more detailed and realistic than the schematic map visualized during mental map. This occipitoparietal activation could be related to a richer and more vivid visual imagery activity during mental navigation than during mental map. However, this interpretation must be moderated because the occipitoparietal regions evidenced here appeared more medial and inferior than those reported in visuospatial imagery (Mellet *et al.*, 1995, 1996, 2000). Alternately, the occipitoparietal region reported in the present study is anatomically interposed between the parietal cortex and the posterior cingulate and may also contribute to the transformation of route coordinates into survey coordinates.

Conclusion

The present findings demonstrate the contribution of both common and distinct regions in the mental exploration of an environment learned in either route or survey perspective. A parietofrontal network involved in the general processing of spatial representations was activated in both mental exploration tasks together with a right hippocampal area that may subserve a cognitive map common to both types learning. The additional processes required to elaborate a cognitive map from a route knowledge expressed in the activation of additional regions including bilaterally parahippocampal gyrus for "object" landmarks processing.

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