# A Penny for Your Thoughts! Patterns of fMRI Activity Reveal the Content and the Spatial Topography of Visual Mental Images

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**Abstract:** Visual mental imagery is a complex process that may be influenced by the content of mental images. Neuropsychological evidence from patients with hemineglect suggests that in the imagery domain environments and objects may be represented separately and may be selectively affected by brain lesions. In the present study, we used functional magnetic resonance imaging (fMRI) to assess the possibility of neural segregation among mental images depicting parts of an object, of an environment (imagined from a first-person perspective), and of a geographical map, using both a mass univariate and a multivariate approach. Data show that different brain areas are involved in different types of mental images. Imagining an environment relies mainly on regions known to be involved in navigational skills, such as the retrosplenial complex and parahippocampal gyrus, whereas imagining a geographical map mainly requires activation of the left angular gyrus, known to be involved in the representation of categorical relations. Imagining a familiar object mainly requires activation of parietal areas involved in visual space analysis in both the imagery and the perceptual domain. We also found that the pattern of activity in most of these areas specifically codes for the spatial arrangement of the parts of the mental image. Our results clearly demonstrate a functional neural segregation for different contents of mental images and suggest that visuospatial information is coded by different patterns of activity in brain areas involved in visual mental imagery. *Hum Brain Mapp 00:000–000, 2014.* © 2014 Wiley Periodicals, Inc.

**Key words:** functional magnetic resonance imaging; multivariate pattern analysis; visuo-spatial mental imagery; imagery; topological images; nontopological images

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# INTRODUCTION

Visual mental imagery arises when perceptual information is accessed from memory, giving rise to the experience of "seeing with the mind's eye" [Farah, 1989; Kosslyn, 1980]. In the last two decades, several studies explored the thin boundary line between visual perception and visual mental imagery and raised some important issues [Ganis et al., 2004]. One of the major issues comes from neuroimaging studies which found that different brain areas are activated during visual mental imagery

tasks depending on the content of the image. In fact, imagining a face, an object, or a place produces activations in different brain areas [Ishai et al., 2000]: imagining a face leads to activation of a brain area known to be related to face perception (i.e., the fusiform face area, FFA), whereas imagining a scene leads to activation of a brain area known to be related to place and scene perception (i.e., the parahippocampal place area, PPA) [O'Craven and Kanwisher, 2000]. Furthermore, neuropsychological evidence from patients affected by hemineglect, a pervasive disorder of space representation that may also affect imaginal space, shows that in the imagery domain environments and objects can be selectively affected by brain lesions [Grossi et al. 1989; Guariglia et al., 2013; Ortigue et al. 2003; Palermo et al. 2010; Piccardi et al., 2008].

Guariglia and Pizzamiglio [2006, 2007] proposed a functional model of space mental representation by distinguishing between "topological" and "nontopological" images. The former are defined as mental representations of stimuli in which it is possible to navigate (e.g., landscapes, squares, rooms), while the latter are defined as representations of objects or visuo-spatial displays that can be observed or manipulated but not navigated (e.g., a desk, an object, a picture, a movie). A recent study by Guariglia and coworkers [2013] demonstrated that imagery neglect is more frequent for topological than for nontopological images and is not as rare as initially reported [Bartolomeo et al., 1994]. Hemineglect for topological images might specifically affect mental representations involved in building environmental cognitive maps or transforming egocentric into allocentric representations and vice versa [Burgess et al., 2001; Guariglia et al., 2005; Palermo et al., 2012b]. Additional clinical dissociations seem to be present in clinical case reports of topological images. Indeed, Rode et al. [2004] described a patient who suffered from severe imagery neglect when he had to imagine the map of France but not when he had to list as many French towns as possible.

The behavioral double dissociation strongly suggests not only that two different types of mental images exist processed by different cognitive systems but also that these distinct systems have different neural correlates. However, to our knowledge, there are no systematic anatomical studies investigating the different neural substrates of diverse clinical representational neglect manifestations [review in Salvato et al., 2014]. Indeed, this may be due to methodological difficulties in recruiting a sufficiently high number of patients affected by selective disorders. As most of the brain damaged individuals may show large lesions it may be very difficult to identify brain areas selectively involved in processing one specific type of mental images in not large samples. Interestingly, data coming from neurological patients are often in contrast with data concerning imagery-related cerebral activation in healthy participants [Salvato et al., 2014]. For example, functional neuroimaging studies on healthy participants often report bilateral activation during mental imagery tasks, suggesting a role of both hemispheres in visual imagery [Formisano et al., 2002; Sack et al., 2002; Sack et al., 2005;

Trojano et al. 2000]. Both functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) evidence converge in demonstrating a critical role of the bilateral parietal lobe in processing visuo-spatial mental images, especially regarding objects. Sack and coworkers hypothesized the existence of an interhemispheric compensatory process [Sack et al., 2005] in visuo-spatial mental imagery, with the left parietal lobe predominant in generating mental images and the right parietal lobe specialized in the spatial comparison of the imagined content.

Furthermore, several studies demonstrated a pattern of hemispheric specialization in both perceptual and imagery domains [Kosslyn et al. 1989, 1995; Laeng et al. 1994; Palermo et al., 2008]. In particular, the left-hemisphere specialization for language makes it more suitable for processing categorical spatial relations, whereas the prominent role of the right hemisphere in visuospatial and navigational abilities makes it more suitable for processing coordinate spatial relations [Kosslyn et al., 1989]. It has been hypothesized that categorical and coordinate spatial relations are two strategies of space representation for arranging mental images [Kosslyn, 1987; Kosslyn et al., 1995]. In categorical processing, judgments have to be made about the relative position of the components of a visual stimulus, and in coordinate processing absolute distances have to be calibrated between the components of a visual stimulus [Rybash et al., 1992]. Palermo et al. [2012a] found that people rely only on categorical processing to generate a mental image of a common object but require both coordinate and categorical spatial relations to generate mental images with navigational content.

Even if several studies assessed the neural underpinnings of generating and processing mental images, to our knowledge none of these directly compare topological and nontopological mental images and the effect of the visuospatial properties of the generated images. In the light of the previous neuropsychological and functional neuroimaging evidence [Ganis et al. 2004], it could be of interest to test whether different topological and nontopological mental images tap on different processes and/or different neural networks. Our recent study [Boccia et al. 2014aa) suggests a further subdivision of topological images into those which include the mental visualization of graphical representations (i.e., paper maps) of environments (hereafter called geographical topological images) and those which include the mental visualization of environments as they appear when looking at them during real or virtual navigation (hereafter called navigational topological images). Data also showed that categorical and coordinate spatial representations were differently required in generating and using these two different kinds of topological mental images (i.e., geographical vs. navigational) and nontopological mental images. Namely, nontopological images of an object (i.e., a clock) and topological geographical images (i.e., the map of Italy) were mainly processed as common objects (through categorical spatial relations), whereas topological navigational images (i.e., the campus)

were mainly processed as familiar navigational objects (through coordinate spatial relations).

These results suggest that topological navigational mental images are processed by a specific system, which is very likely involved in representing space for navigational purposes and is involved in the development and use of cognitive maps, whereas geographical images, which are graphical representations of the world, are processed by a different system that is also involved in imagining nontopological images.

It has, however, been highlighted that both navigational and non-navigational mental images can be defined according to egocentric and allocentric frame of references [Pizzamiglio et al., 1998], depending on the task requirement. Egocentric frame of reference involves the ability to locate objects with reference to one's own body, whereas allocentric coordinates determine where something lies in the world regardless of one's position. It is very difficult to establish whether allocentric or egocentric frame of references make the difference in mentally representing navigational and geographical images. This is especially true in the case of geographical maps, which also provide navigational information [Boccia et al., 2014a].

In the present study, we aimed at testing the hypothesis that different topological (navigational and geographical) and nontopological mental images tap on different neural networks, by using fMRI. Furthermore, we examined for the first time the spatial distribution of these classes of mental images in the brain, by means of a multivariate approach, with emphasis on the spatial properties of the generated mental images. The results of such a study, other than shedding more light upon neural processing of visuo-spatial mental imagery, could be useful to better understand the mechanism underlying the space representation, but it could also help to clarify the nature and the origin of representational neglect [Salvato et al., 2014].

First, we set out to explore whether different brain areas subtend different categories of topological and nontopological mental images. We also directly tested whether geographical and navigational topological images tap on different neural substrates. Second, we investigated whether activity patterns in these brain regions contain visuospatial information about mental images using multivariate analysis. For this purpose, we developed an fMRI event-related paradigm to directly determine whether there are specific adaptation effects for different categories of mental images: a familiar navigational place (i.e., a campus), a familiar geographical space (i.e., the map of Italy), and a familiar object (i.e., a clock). Thus, we directly tested the neural representation of different content of mental images using both a mass univariate and a multivariate approach, that is, an information-based approach aimed at identifying a perceptual representation or cognitive state on the basis of multivoxel regional fMRI signals [Kriegeskorte and Bandettini, 2007]. The first approach explores *where* in the brain mental images are coded and the second one directly tests *which* type of information is coded there.

## MATERIALS AND METHOD

### Participants

Participants included 15 healthy right-handed individuals (mean age: 24.67 and SD: 2.16; seven women) who had no history of neurological or psychiatric disorders. All were third year college students at the Sapienza University of Rome and, thus, were very familiar with the campus. Campus knowledge was assessed with a preliminary questionnaire in which participants were asked to locate the campus landmarks on an outline map (mean *landmark knowledge* of university campus 83.11%; SD 16.50%). We also assessed participants' geographical knowledge with a preliminary questionnaire in which they were asked to select the geographical area (i.e. northwest, northeast, southwest or southeast) of a group of Italian cities (mean knowledge about Italian cities 90.00%; DS 16.33%). Geographical knowledge did not differ from campus knowledge ($t = 1.02$; $P = $ n.s.). All participants gave their written informed consent to participate in the study. The study was designed in accordance with the principles of the Declaration of Helsinki and was approved by the local ethical committee of IRCCS Fondazione Santa Lucia of Rome.

### Stimuli and Imagery Task

To test the hypothesis that different brain areas code for different categories of mental images, we developed our set of stimuli according to three main dimensions: *topological-navigational images* about a familiar environment (i.e., the campus: Fig. 1A), *topological-geographical images* (i.e., the map of Italy: Fig. 1B), and *nontopological images about a familiar object* (i.e., the clock: Fig. 1C). For each category, we chose eight target items to be imagined; thus, the resulting set of stimuli included (a) eight landmarks on the campus, whose position is identified by the black circles in Figure 1A (Department of Literature, Department of Mathematics, Department of Chemistry, Orthopedics Clinic, Institute of Hygiene, Chapel, Department of Political Science, Department of Law); (b) eight Italian cities, identified by the black circles in Figure 1B (Bolzano, Trieste, Lecce, Foggia, Salerno, Frosinone, Alessandria, Cuneo); and (c) eight times on the clockface, identified by the eight hour pointers in Figure 1C (01:00, 02:00, 04:00, 05:00, 07:00, 08:00, 10:00, 11:00).

Participants were given written instructions about what to imagine (see Fig. 1D): either the name of a campus landmark, or the name of an Italian city or an hour. Participants were instructed to imagine the corresponding landmark/city/hour and its spatial position within the campus/map/clock as vividly as possible. For the campus condition, they should imagine where the landmark was located relative to an imagery standpoint situated in front of the statue of Minerva, which is located at the centre of the campus (red circle in Fig. 1B).

For all the three categories, the eight items were placed so that there were two items in each of four spatial
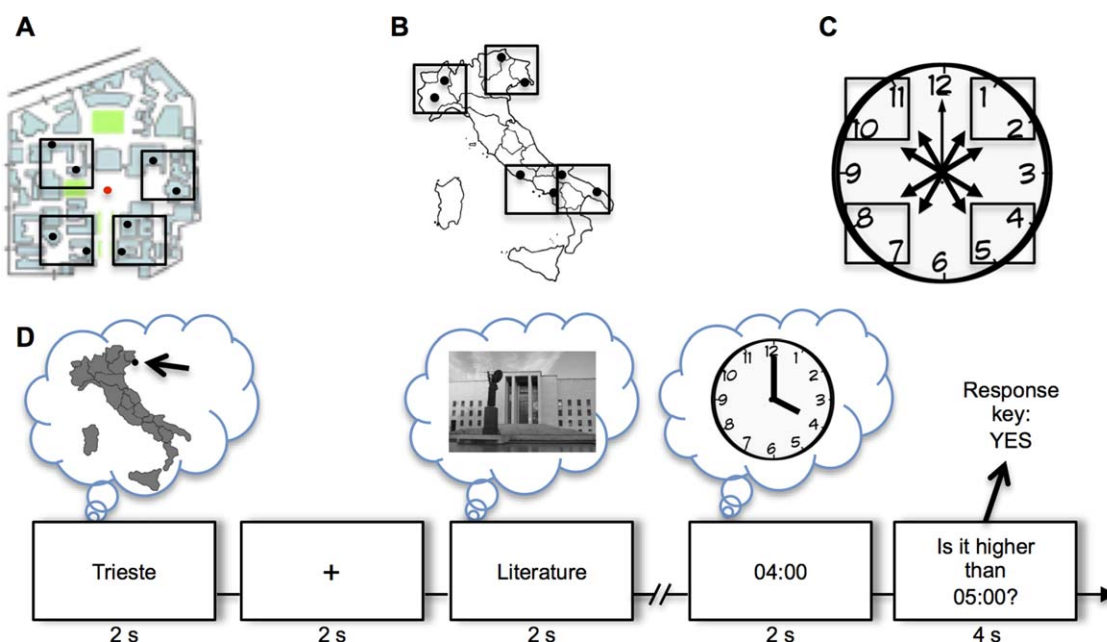
**Figure 1.**

Stimuli and task. **A**: Map of the campus indicating the eight landmarks to be imagined (black circles) and the imaginary standpoint (red circle). **B**: Map of Italy indicating the eight cities to be imagined (black circles). **C**: A clock indicating the 8 hours to be imagined. The black rectangles in **A–C** show the spatial subdivision of the eight items in four quadrants. **D**: Experimental trials and timeline (see text for details). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

quadrants, which corresponded, for the campus, to the directions "left ahead," "right ahead," "left behind," and "right behind" the imaginary standpoint (see black rectangles in Fig. 1A); for the map of Italy, to "north west," "north east," "south west," and "south east" (see black rectangles in Fig. 1B); for the clock, to "left top," "right top," "left bottom," and "right bottom" (see black rectangles in Fig. 1C). The subdivision in quadrants was used to attempt at demonstrating that neural representations contain information about the spatial location of the imagined item (see more below).

The target items for the campus and Italy were chosen through a preliminary pilot study. We asked 17 college students at Sapienza University of Rome to mentally visualize the campus as if they were in front of the statue of Minerva and to describe what was on their left, right, in front, and in back of them. Then, we selected the most frequently reported exemplars. From this first step, the resulting set of stimuli included 15 exemplars. We then used these exemplars for a computerized experiment. We asked six college students to indicate whether the exemplar was on the left, the right, in front, or in back of them when they were walking toward the statue of Minerva, by using four buttons on the keypad. Accuracy was higher than 65% for all of the exemplars. Therefore, we selected exemplars according to their position on the campus so that there were two exemplars per quadrant. Similarly, we asked twelve participants to mentally visualize the map of Italy as if they were in

front of the map, and to indicate on a questionnaire where a set of 23 cities were located (i.e., in the north-west, north-east, south-west, or south-east). We then selected for each quadrant the two cities with the highest percentage of correct responses (always more than 75%).

### Procedure

We developed the fMRI event-related paradigm as a continuous carryover design [Aguirre, 2007]. This allowed us to estimate both the mean difference in neural activity between stimuli and the effect of one stimulus on another (i.e., carryover effect). Indeed, repeated exposure to a specific experimental condition results in the neural adaptation effect, which is a particular form of the carryover effect [Aguirre, 2007].

During five fMRI scans, stimuli were presented in an unbroken sequential manner in five serially balanced sequences in which each stimulus preceded and followed every other stimulus [Aguirre, 2007; Nonyane and Theobald, 2007]. Each category item was presented five times in each fMRI scan. Thus, each scan consisted of 120 experimental trials (*imagery trials*), plus 5 null trials and 9 *question trials*. With the exception of the question trials, which lasted 4 s, trials lasted 2 s and were followed by a fixation point of the same duration (Fig. 1D).

In imagery trials, as stated above, participants imagined the instructed landmark/city/hour and its spatial position

within the campus/map/clock. They were also advised that questions could appear randomly (*question trials*) and that they had to respond by using either of two buttons on the fMRI compatible keypad. Question trials were introduced to ensure that subject actually kept their attention and executed the imagination task. Nine questions appeared randomly and concerned the spatial position of the latest item with respect to another one presented in the question trial. For example, "Is it on the right of 08:00?" or "Is it further north than Salerno?" or "Is it on the right of the Law Department?"(Fig. 1D).

On average participants answered the question trials correctly 86.37% of the time (SD: 7.07%). Repeated measure analysis of variance (ANOVA) on participants' accuracy for the three categories (percentage of accuracy at the three categories: campus = 83.11%, SD = 14.00%; Italy = 87.56%, SD = 12.82%; clock = 88.44%, SD = 7.33%) failed to found any significant effect of the category ($F_{2,28} = 0.93$; $P = 0.41$).

## Image Acquisition

A Siemens Allegra scanner (Siemens Medical Systems, Erlangen, Germany), operating at 3 T and equipped for echo-planar imaging was used to acquire functional magnetic resonance images. Head movements were minimized with mild restraint and cushioning. Functional MRI images were acquired for the entire cortex using blood-oxygen-level dependent (BOLD) contrast imaging (30 slices, in-plane resolution = 3 × 3 mm$^2$, slice spacing = 4.5 mm, repetition time [TR] = 2 s, echo time [TE] = 30 ms, flip angle = 70 deg). For each scan, 277 fMR volumes were acquired. We also acquired a three-dimensional high-resolution T1-weighted structural image for each subject (Siemens MPRAGE, 176 slices, in-plane resolution = 0.5 × 0.5 mm$^2$, slice thickness = 1 mm, TR = 2 s, TE = 4.38 ms, flip angle = 8°).

## Data Preprocessing

Image analyses were performed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm). The first four volumes of each run were discarded to allow for T1 equilibration. All images were corrected for head movements (realignment) using the first volume as reference. The images of each participant were then coregistered onto their T1 image. Coregistered images were then normalized to the standard MNI-152 EPI template using the mean realigned image as a source. Images for univariate analysis were then spatially smoothed using an 8-mm full-width half-maximum isotropic Gaussian kernel. Multivariate pattern analysis (MVPA) was performed on unsmoothed images.

## Image Analysis: Univariate Analysis

Functional images were analyzed for each participant separately on a voxel-by-voxel basis, according to the general linear model. Separate regressors were included for each experimental condition (i.e., campus, Italy, clock,

question trials). The question trials were excluded from the group analysis that was performed on parameter estimate images that resulted from the individual models, treating the subject as a random factor. We first computed an omnibus F-contrast by comparing the imagery conditions (i.e., campus, Italy, clock) against the baseline. The resulting statistical parametric map was thresholded at $P < 0.005$, corrected for multiple comparisons using false discovery rate [Genovese et al. 2002] and a cluster size >20 voxels. For each subject and region we computed a regional estimate of the amplitude of the hemodynamic response in each experimental condition by entering a spatial average (across all voxels in the region) of the preprocessed time series into the individual general linear models. Then, regional hemodynamic responses were analyzed with a 3 × 24 ANOVA, with the three categories of content and the 24 resulting regions as independent variables. Then, we performed a 3 × 1 ANOVA in each region, with category of content as independent variable.

In a separate voxel-wise analysis we also modeled the category repetition: each trial was labelled both by its category and by its relationship with the category imagined in the previous trial (category repetition; category change), in order to assess neural adaptation effects due to the content of the mental images. The first trial of each fMRI session and first trial after each question trial were modeled as separate conditions and were not considered in the group analysis. Regional hemodynamic responses were analyzed with a 3 × 2 ANOVA, with category of content (i.e., campus, Italy and clock) and repetition (category repetition vs. category change) as independent variables.

## Image analysis: Multivariate Pattern Analysis

As a preliminary step for multivariate pattern analysis, we used a general linear model in which trials related to each of the 8 campus landmarks, of the 8 Italian cities and of the 8 hours were modelled by separate regressors, in order to estimate the magnitude of the response at each voxel for each imagined item. We thus extracted multi-voxel pattern of activity for each item in each of the regions that emerged as being involved in visuospatial mental imagery (as resulted from the F omnibus contrast). Multivariate pattern analyses were performed with a linear training classifier (Support Vector Machine, SVM) using libSVM [Chang & Ling 2011], using a leave-one-session-out cross-validation procedure. The most informative voxels were identified through recursive features elimination [De Martino et al. 2008]. For each classification analysis, we compared the between-subject distribution of classification accuracies with chance level (i.e., 0.5) by means of one-sample *t*-tests, applying Bonferroni's correction for multiple comparisons.

Note that the selection of regions to be included in multivariate pattern analysis was derived by the omnibus contrast that included all experimental sessions (thus both those used for training the classifier and those used for

**TABLE I. Activation during visuo-spatial imagination**

| Region | Label | Hemisphere | $x$ | $y$ | $z$ | $F$ | Volume (mm³) |
|---|---|---|---|---|---|---|---|
| Angular gyrus | AG | L | −45 | −64 | 37 | 13.94 | 3,834 |
| Calcarine cortex | CC | L | −15 | −97 | −2 | 15.16 | 2,808 |
| | | R | 9 | −82 | 7 | 14.72 | 4,077 |
| Cuneus | CU | R | 3 | −76 | 28 | 12.78 | 1,242 |
| Fusiform gyrus | FG | L | −21 | −37 | −17 | 17.24 | 3,684 |
| | | R | 24 | −37 | −17 | 13.94 | 1,438 |
| Hippocampus | HC | R | 27 | −34 | −2 | 9.01 | 496 |
| Inferior frontal gyrus | IFG | L | −51 | 5 | 28 | 15.03 | 1,593 |
| | | R | 48 | −4 | 16 | 13.64 | 1,107 |
| Inferior parietal lobule | IPL | L | −39 | −43 | 49 | 20.13 | 4,806 |
| | | R | 42 | −40 | 49 | 16.24 | 3,834 |
| Inferior temporal lobe | ITL | R | 54 | −58 | −14 | 18.23 | 702 |
| Lingual gyrus | LG | L | −3 | −76 | 4 | 17.43 | 3,780 |
| Middle frontal gyrus | MFG | R | 30 | −4 | 52 | 11.49 | 1,242 |
| Middle/superior frontal gyrus | MFG_SFG | L | −24 | −4 | 49 | 20.97 | 5,238 |
| Middle occipital gyrus | MOG | R | 30 | −64 | 34 | 12.17 | 594 |
| Parahippocampal gyrus | PHG | L | −30 | −40 | −14 | 17.39 | 1,013 |
| | | R | 30 | −31 | −14 | 10.08 | 421 |
| Precentral/Postcentral gyrus | pCG_postCG | R | 39 | −22 | 61 | 12.82 | 1,512 |
| Precuneus | pCU | L | −3 | −79 | 46 | 15.23 | 1,674 |
| Retrosplenial cortex | RSC | L | −18 | −61 | 16 | 30.53 | 11,772 |
| | | R | 15 | −55 | 10 | 27.38 | 10,503 |
| Superior parietal lobule | SPL | L | −24 | −67 | 55 | 17.78 | 4,131 |
| | | R | 27 | −61 | 61 | 12.13 | 972 |

For each brain region showing activation during mental imagining condition, the table lists the label used in Figures 2–5 and throughout the text, the hemisphere, the MNI coordinates, the $F$-score ($P_{FDR} < 0.005$; cluster size > 20 voxels) and the region volume (mm³).

testing its accuracy). Although the use of both the training and the testing data sets for feature selection has been often discouraged because of potential overfitting and accuracy overestimation problems [e.g., Kriegeskorte et al. 2009], here feature selection was based on a criterion that was absolutely independent on the stimulus dimensions we tried to decode: selection on the basis of activation in the imagination task vs. the baseline yields in fact no risk of spuriously including voxels showing by chance some consistent differences between imagined categories or between imagined spatial positions (i.e., the two stimulus dimensions we tried to decode: see more below). However, as a control we also performed classification analyses on a couple of independently defined probabilistic regions of interest (ROIs), i.e., the PPA and the retrosplenial cortex (RSC). These were obtained by averaging individual functional ROIs from a separate group of 33 healthy participants who underwent a localizer fMRI experiment consisting in passive viewing of blocks of scenes vs. faces [described in Sulpizio et al., 2013, 2014; Tosoni et al., 2014].

We performed three sets of classification analyses. First, we assessed whether the activity patterns encoded the content of the mental images: to do so, we trained the classifier to decode the category of the content (i.e., campus, clock, map of Italy) from the activity pattern related to each imagined item. Second, we assessed whether the

activity patterns encoded the imagined spatial positions, i.e., the location of the landmark/city/pointer within the campus/map/clock in the generated mental images: to do so, we trained the classifier to decode (for each category separately) the quadrant the imagined item belonged to (see Fig. 1A–C). We also compared the classification accuracy for spatial positions across the three categories by means of a 3 × 1 ANOVA. Third, we tested whether the neural encoding of the imagined spatial locations generalized across the three categories: to do so, we trained the classifier to decode the quadrant from items of a given category and tested whether it was able to decode the quadrant from items of each of the two other categories. This was done for all possible category combinations.

## RESULTS

### Regions Involved in Visuospatial Mental Imagery

The first step of the analysis was aimed at obtaining a general picture of the cerebral regions involved in generating a mental image. An imagining-related activation was operationally defined within our experimental paradigm as an increase of the BOLD signal in the imagery condition (i.e., campus, Italy and clock) relative to the baseline. Thus, to identify regions involved in visuospatial mental imagery without considering differences among categories
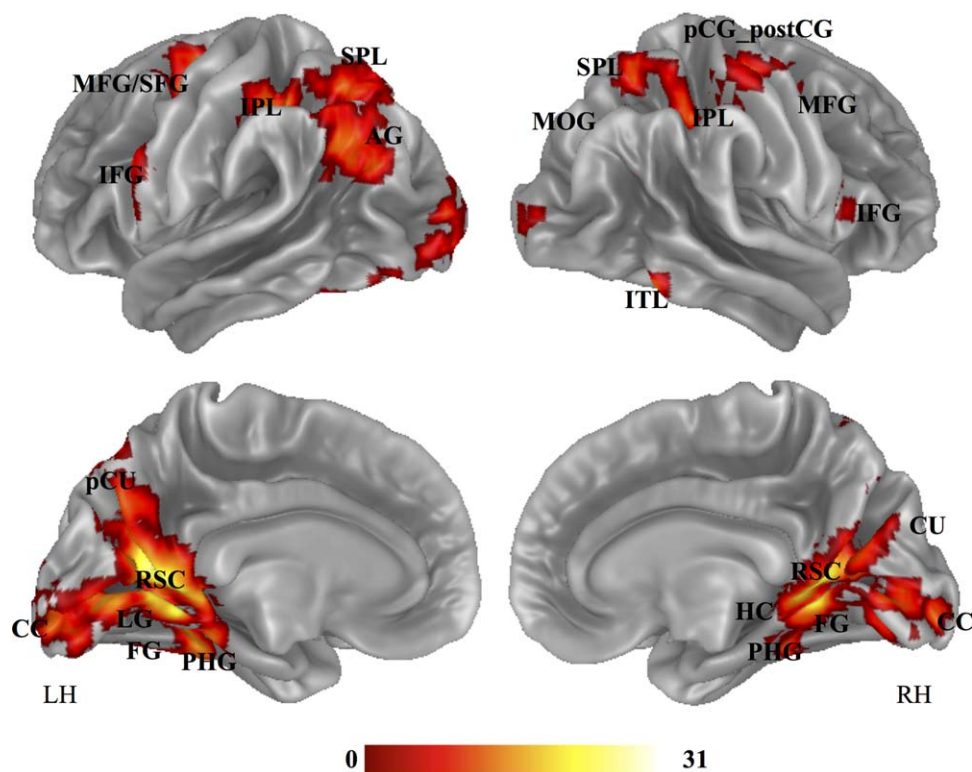
**Figure 2.**
Regions involved in visuospatial mental imagery. Regions involved in generating a mental image regardless of the category content. For region labels, see Table I. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

we performed an omnibus F-contrast by comparing imagery condition vs. baseline. This contrast revealed an extended bilateral network of imagery-related regions in the lateral and medial surface (Fig. 2), spanning from the occipital to the frontal lobe (p *FDR-corrected* < 0.005, cluster size > 20 voxels). Specifically, in the occipital lobe we found bilateral activations at the level of the calcarine cortex, lingual and fusiform gyri. Activations were also found bilaterally at the level of the posterior cingulate cortex and parieto-occipital sulcus, in the so-called retrosplenial complex [Epstein, 2008].

The left precuneus and right cuneus were also activated during the imagery condition. At the level of the medial temporal lobe, we found bilateral activation of the parahippocampal gyrus and hippocampus. The right inferior temporal gyrus was also activated. At the level of the parietal lobe, we found bilateral activation of both the superior and inferior parietal lobule, at the level of the intraparietal sulcus and the left angular gyrus. We also found activations at the level of the bilateral middle frontal gyrus, left superior frontal gyrus, and right inferior frontal gyrus, as well as at the level of the right precentral and postcentral gyri.

The resulting 24 regions (Table I) were used in all further analyses. For univariate analyses, for each region and subject we computed a regional estimate of the amplitude of the hemodynamic response in each experimental condition. Multivariate analyses were performed on multivoxel patterns of estimated hemodynamic response amplitudes.

## Neural Segregation Among Different Categories of Mental Images

The analysis on the effect of the category of mental images on the regional BOLD signal yielded a significant region by category interaction effect ($F_{46,644}$= 29.049; $P < 0.001$), indicating that the category of imagined items had a differential impact across the selected regions. We, thus, assessed the effect of category on each region separately applying a Bonferroni correction for multiple comparisons.

With the exception of the left HC and the right precentral postcentral gyri, all regions showed a main effect of the category of mental images (Fig. 3A).

A set of regions, which encompassed the bilateral FG, PHG, RSC, and CC as well as the left LG, pCU, and right CU, was more highly activated when participants were imagining the campus (Fig. 3B–C) than the map of Italy and the clock. A subset of these regions, including bilateral
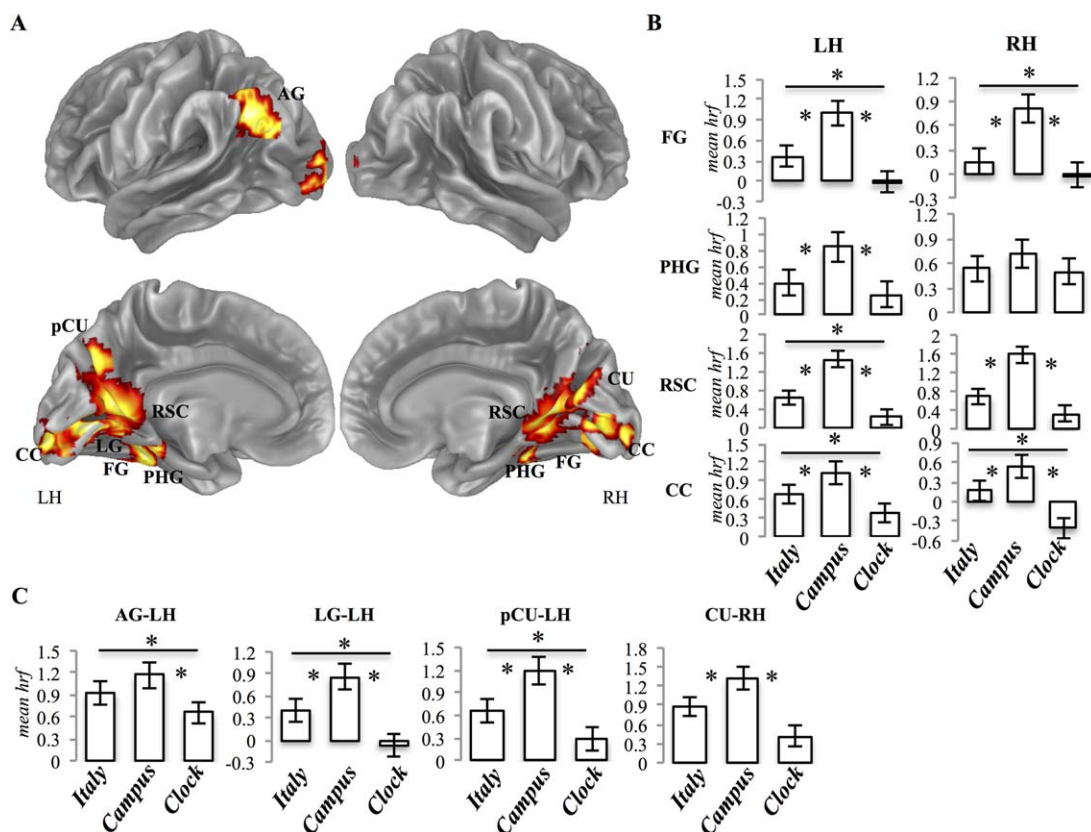
**Figure 3.**

Regions involved in generating mental images of familiar environments. **A**: Areas showing higher BOLD responses during the imagining of familiar environments. **B**: Percent BOLD signal change in bilateral FG, PHG, RSC and CC in relation to the three categories of mental images. **C**: Percent BOLD signal changes in the left AG, LG, pCU, and right CU in relation to the three categories of mental images. Left AG also shows increased activation for the map of Italy. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the FG and CC, right RSC, left LG, and pCU, was also more highly activated by imagining Italy than the clock. The left AG was more highly activated for both Italy and the campus (with no difference between them) than the clock.

On the other hand, a set of areas, including bilateral SPL, IPL, IFG and right ITL, MFG, and MOG, showed higher activation when participants were imagining the clock. Right IFG also showed higher activation for Italy than the campus, and the left MFG/SFG was equally more highly activated while imagining the campus and the clock than Italy (Fig. 4).

## Neural Adaptation: Specific Carryover Effect for the Content of Mental Images

We developed our fMRI paradigm to test both the difference in neural activity among different categories of mental images and to assess the carryover effect due to category repetition. Thus, we assessed the carryover effect by means of a 3 × 2 ANOVA, with category of content and category repetition as independent variables. We found a main effect of category repetition, with a reduction of activation in repeated category trials, in the bilateral CC and the left LG. The reverse effect (increased activation following category repetition) was observed in the right IPL and the left superior and middle frontal gyrus. Importantly, we found a category by repetition interaction in several regions (Fig. 5), including the bilateral SPL and IPL and the right ITL on the lateral brain surface (Fig. 5A), and the bilateral RSC and right CC and FG on the medial brain surface (Fig. 5B). Such a result strongly suggests the existence of distinct patterns of adaptation for different categories of mental images. Post hoc pairwise comparisons showed that (a) the right CC as well as the bilateral RSC and the left SPL exhibited a reduction of activation for the repetition of the Italy category (Italy: category change > category repetition); (b) the bilateral IPL, the right ITL, and SPL exhibited an increase of activation for the repetition of the clock category (clock: category repetition > category change); and (c) the right RSC and
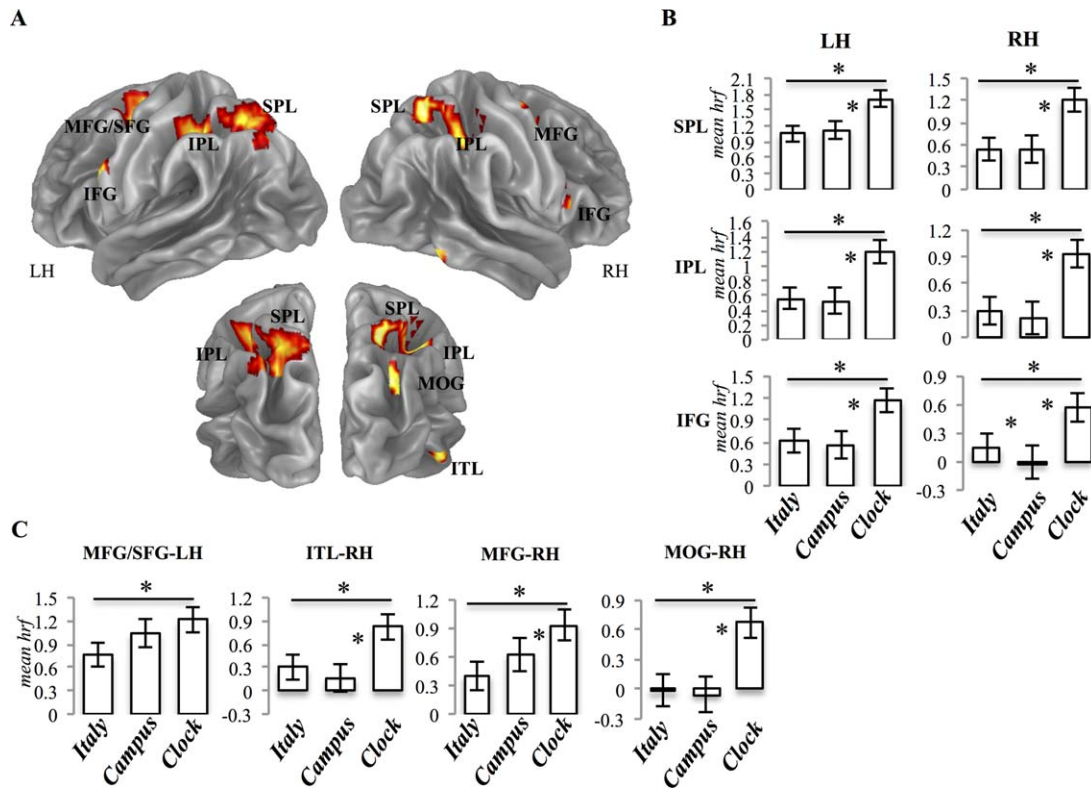
**Figure 4.**
Regions involved in generating mental images of familiar objects. **A**: Areas showing higher BOLD response during the imagining of a familiar object. **B**: Percent BOLD signal changes in bilateral SPL, IPL, and IFG in relation to the three categories of mental images. **C**: Percent BOLD signal changes in the left MFG/SFG and right ITL, MFG, and MO, in relation to the three categories of mental images. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

FG exhibited an increase of activation for the repetition of the campus category (campus: category repetition > category change).

## Multivariate Pattern Analysis: Decoding the Content and Spatial Locations of Mental Images

The first step of the MVPA was aimed at investigating whether the multivoxel pattern of activity in regions involved in visuospatial mental imagery encoded for the different content of mental images. All of the investigated regions allowed to decode the category of mental images (i.e. campus, map of Italy, clock) with supra-change accuracy, with the exception of the right HC, CU, and IFG and bilateral PHG. For more information about decoding accuracy, see Supporting Information Table S1.

Then, we asked whether the multivoxel pattern of activity of regions involved in visuospatial mental imagery encoded exemplar positions within the generated mental images, i.e., whether the classifier was able to decode the quadrant to which the imagined item belonged (see Fig. 1A–C for the definition of quadrants). We found that bilat-

eral CC, FG, IFG, IPL, RSC, as well as left AG, LG, MFG/ SFG, pCU, SPL, and right CU, MFG, pre- and post-central gyri encoded landmark spatial position on the campus. We also found that bilateral CC, FG, IPL, RSC, as well as left AG, LG, IFG, MFG/SFG, pCU, SPL and right ITL, CU, pre- and post-central gyri encoded the spatial position of cities on the map of Italy. Finally, we found that bilateral CC, FG, IPL, SPL, RSC, as well as left AG, LG, IFG, MFG/SFG, pCU, and right CU, pre- and post-central gyri encoded the spatial position of times on the clock (Table II).

We also tested differences in accuracy of decoding exemplar positions across categories and found that bilateral CC, right ITL, and left LG showed different patterns of accuracy in decoding spatial positions of exemplars in the three categories (Fig. 6). In detail, the bilateral CC and the left LG yielded higher classification accuracy for the spatial positions of landmarks on the campus, whereas the right ITL yielded higher classification accuracy for the spatial position of cities on the map of Italy.

Finally, we assessed whether the multi-voxel pattern of activity associated to different spatial positions in a given category allowed to decode positions for the other
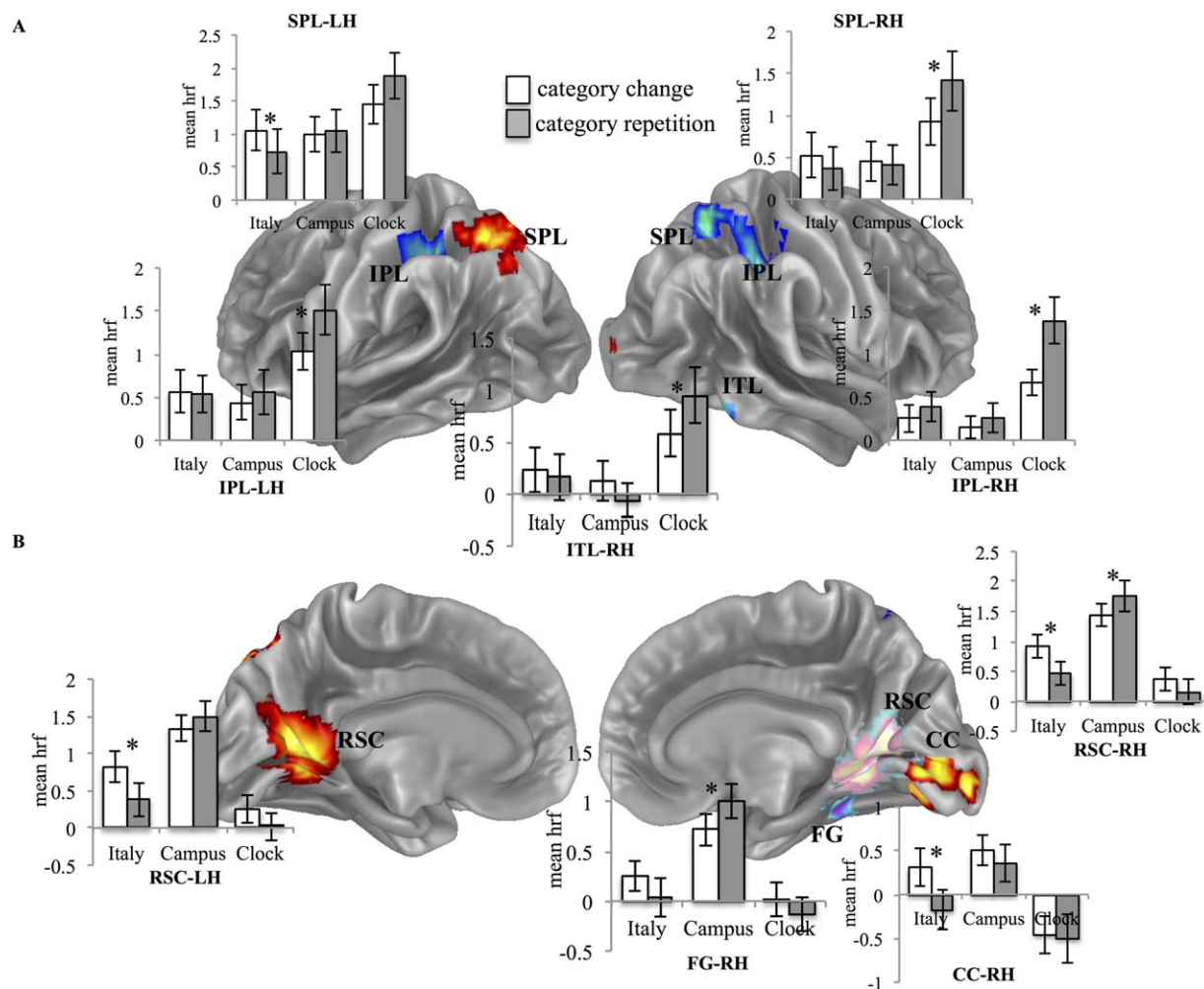
**Figure 5.**

Regions showing carry-over effects. **A**: Brain areas on the lateral surface showing carry-over effect. **B**: Brain areas on the medial surface showing carryover effect. Areas showing *attenuated* activation for repetition (category change > category repetition) for Italy are showed in red-to-yellow patches. Areas showing a *rebound* of activation for repetition (category repetition > category change) are showed in blue-to-light blue patches for clock and in light blue-to-violet patches for campus. The overlap between red-to-yellow and blue-to-violet patches at the level of the right RSC indicates the opposite effects for campus (category repetition > category change) and Italy (category change > category repetition). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

categories of mental images, thus testing whether spatial encoding generalized across the category of mental images. There was little evidence for such a generalization effect: we found a cross-decoding effect only for the multi-voxel pattern of activity of the left LG between the campus and the clock (average accuracy 52%).

Note that in many cases the achieved classification performances were quite low and only slightly above chance. The classifier performance may depend on many factors such as the number of features, i.e., the region size: however, what is important here is whether the achieved performance was significant, i.e., consistently above chance across subjects, which indicates that the given region actually contains information about the investigated stimulus dimension.

We also conducted the same multivariate analyses in two independently defined regions of interest (PPA and RSC). The results confirmed the main analysis: both the PPA and the RSC allowed to significantly decode exemplar positions in all three categories (see Supporting Information Fig. S1).

## DISCUSSION

The present study was aimed at testing whether different topological (navigational and geographical) and

**TABLE II. Accuracy of decoding of imagined spatial locations**

| Label | Hemisphere | Campus | | | Italy | | | Clock | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | P value | Mean | SD | P value | Mean | SD | P value |
| AG | L | 0.66 | 0.08 | <0.001 | 0.63 | 0.10 | <0.001 | 0.62 | 0.08 | <0.001 |
| CC | L | 0.72 | 0.08 | <0.001 | 0.65 | 0.10 | <0.001 | 0.64 | 0.08 | <0.001 |
| | R | 0.76 | 0.08 | <0.001 | 0.64 | 0.08 | <0.001 | 0.68 | 0.07 | <0.001 |
| CU | R | 0.76 | 0.08 | <0.001 | 0.64 | 0.08 | <0.001 | 0.68 | 0.07 | <0.001 |
| FG | L | 0.64 | 0.07 | <0.001 | 0.65 | 0.08 | <0.001 | 0.62 | 0.08 | <0.001 |
| | R | 0.56 | 0.06 | 0.001 | 0.56 | 0.05 | <0.001 | 0.62 | 0.04 | <0.001 |
| HC | R | 0.49 | 0.03 | n.s. | 0.49 | 0.05 | n.s. | 0.50 | 0.05 | n.s. |
| IFG | L | 0.56 | 0.06 | 0.001 | 0.59 | 0.06 | <0.001 | 0.59 | 0.06 | <0.001 |
| | R | 0.56 | 0.04 | <0.001 | 0.56 | 0.08 | <0.001 | 0.54 | 0.06 | n.s. |
| IPL | L | 0.66 | 0.08 | <0.001 | 0.67 | 0.07 | <0.001 | 0.64 | 0.07 | <0.001 |
| | R | 0.70 | 0.09 | <0.001 | 0.67 | 0.11 | <0.001 | 0.64 | 0.08 | <0.001 |
| ITL | R | 0.49 | 0.05 | n.s. | 0.55 | 0.04 | <0.001 | 0.54 | 0.06 | n.s. |
| LG | L | 0.72 | 0.09 | <0.001 | 0.64 | 0.09 | <0.001 | 0.65 | 0.08 | <0.001 |
| MFG | R | 0.57 | 0.06 | <0.001 | 0.54 | 0.06 | n.s. | 0.56 | 0.07 | n.s. |
| MFG/SFG | L | 0.67 | 0.07 | <0.001 | 0.70 | 0.06 | <0.001 | 0.67 | 0.06 | <0.001 |
| MOG | R | 0.51 | 0.03 | n.s. | 0.53 | 0.05 | n.s. | 0.53 | 0.06 | n.s. |
| PHG | L | 0.50 | 0.06 | n.s. | 0.53 | 0.04 | n.s. | 0.53 | 0.05 | n.s. |
| | R | 0.50 | 0.06 | n.s. | 0.48 | 0.05 | n.s. | 0.50 | 0.05 | n.s. |
| pCG/postCG | R | 0.55 | 0.05 | <0.001 | 0.58 | 0.04 | <0.001 | 0.56 | 0.06 | 0.001 |
| pCU | L | 0.56 | 0.05 | <0.001 | 0.57 | 0.06 | <0.001 | 0.57 | 0.07 | 0.001 |
| RSC | L | 0.71 | 0.07 | <0.001 | 0.71 | 0.10 | <0.001 | 0.67 | 0.10 | <0.001 |
| | R | 0.75 | 0.09 | <0.001 | 0.72 | 0.11 | <0.001 | 0.66 | 0.09 | <0.001 |
| SPL | L | 0.65 | 0.09 | <0.001 | 0.66 | 0.08 | <0.001 | 0.62 | 0.09 | <0.001 |
| | R | 0.55 | 0.06 | n.s. | 0.56 | 0.09 | n.s. | 0.56 | 0.04 | <0.001 |

For each brain region showing activation during mental imagining condition and for each imagined category, the table lists the accuracy of the classification of the imagined spatial locations into the four quadrants (mean and SD across subjects) and the corresponding significance.
n.s., not significant.

nontopological mental images tap on different neural networks and to explore the neural representation of visuo-spatial information.
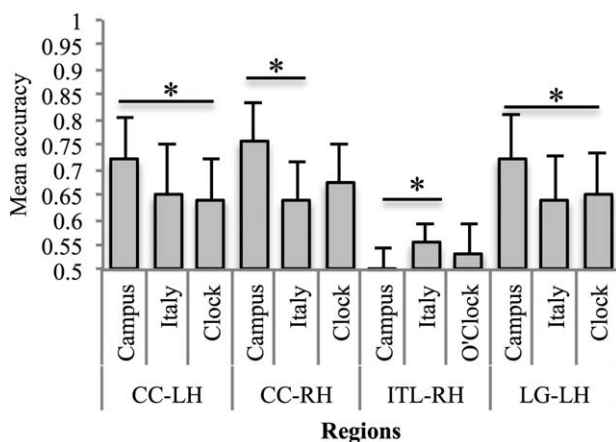


**Figure 6.**

Decoding spatial positions. Mean effect of category on mean accuracy of decoding spatial positions of category exemplars.

In addition to a network of brain areas involved in visuo-spatial mental imagery spanning from the occipital to the frontal lobe (Fig. 2), our results show neural segregation among networks subtending different content of mental images. In fact, we found that different brain areas are involved in imagining a *topological-navigational image* (i.e., the campus), a *topological-geographical image* (i.e., the map of Italy), and a *non-topological image* (i.e., the clock). Specifically, we found that a set of brain regions (including the bilateral RSC and PHG) which are classically involved in perceiving and retrieving navigational scenes [Epstein et al. 2007], were more activated when participants were imagining a *familiar navigational space*. On the other hand, imagining *a topological-geographical space* activated a set of areas that partially overlapped with those involved in imagining a *familiar navigational space* (left AG) and *familiar object* (right IFG). Instead, imagining an object produced activation in a set of frontal (MFG and IFG), parietal (SPL and IPL), and occipital areas (right MOG). These areas were already reported to be involved in imagining objects in a previous study using a different mental imagery paradigm (Trojano et al., 2000). It has to be highlighted that parietal activation we found in imagining the clock may not be due to the mere effect of notation format (words vs.

digits), as notation formats were found to be processed in the right fusiform gyrus [Pinel et al., 1999], with this region more activated by digits than by number words.

These results deserve some consideration to understand the thin line between visual perception and visual mental imagery. First, we have to consider that the observed differences may not be due to a mere effect of familiarity. Actually, according to the Multiple Trace Theory [Moscovitch et al., 2005, 2006] a new trace is formed in the hippocampus every time a certain memory is recollected. As activity in hippocampal areas were found to be independent from the type of image to be mentally visualized and the amount of activation in this region did not change according to the content of the visual image, we can consider the episodic component not critical in determining the observed differences. We found that different brain areas were engaged in visuo-spatial mental imagery depending on the content of the mental images. This finding is sustained by neuropsychological evidence from patients with representational neglect [Guariglia et al. 2013], which demonstrated that in the imagery domain environments (i.e., topological mental images) and objects (i.e., nontopological mental images) can be represented separately and can be selectively affected by brain lesions. Furthermore, in the present study we assessed a never before investigated question about topological mental images: Does imagining a navigational space differ from imagining a geographical space? The description by Rode and coworkers [2004] of the case of a patient who was unable to imagine the map of France despite preserved geographical knowledge made it possible to hypothesize that geographical space is represented by specific processing in the brain, leaving unspecified whether or not the mental representation of geographical space overlaps that of navigational space. Our results demonstrate that geographical- and navigational-topological images are processed in the brain by two different systems, which are almost nonoverlapping. Indeed, it seems that the only area the two types of topological images share is the left AG, known to be involved in categorical spatial judgments [Amorapanth et al. 2010; Baciu et al., 1999; Trojano et al., 2006]. Imagining a familiar navigational space activates a set of areas frequently reported in fMRI human navigation studies [Boccia et al., 2014b], and imagining a geographical space leads to activation in areas selectively involved in categorical spatial judgments. On one hand, these results confirm that imagining landmarks within navigational space requires both categorical and coordinate spatial representations [Palermo et al., 2012a]. On the other hand, they suggest that imagining a geographical space primarily taps on a categorical spatial representation system. In other terms, topological-geographical mental images are expected to share only the categorical spatial representation system with topological-navigational mental images.

Furthermore, these results shed light on the contribution of RSC and PHG to human navigation. RSC and PHG (particularly the PPA) were recently found to be critical in modality-independent spatial computations [Wolbers et al. 2011]. As stated above, these areas are also crucial in topographical orientation, with separate but complementary roles in human navigation, namely, in the perception and localization of visual scenes [Epstein 2008; Hirshhorn et al. 2011]. Our results demonstrate that both of these areas and their contribution to human navigation are dissociated from visual input. Indeed, most of the studies investigating the role of RSC and PHG in human navigation have adopted visual tasks in which scenes or landmarks were presented. Our results suggest that RSC and PHG are engaged in processing navigational information regardless of the visuo-perceptual input [Ino et al. 2002]. Furthermore, this finding confirms how thin the line is between visual perception and visual mental imagery, because the PPA and RSC brain regions were strongly activated by both viewing navigational scenes [O'Craven and Kanwisher, 2000] and by imagining them.

Analysis of the carryover effects deserves some important considerations. Indeed, other than finding a main effect of repetition in the bilateral CC and the left LG, with a reduction of the activation for category repetition, we also found an increase of activity for the repetition in the right IPL and the left superior and middle frontal gyrus. This result is somewhat surprising, since basing on the previous literature [see for example, Epstein and Morgan, 2012] we expected to find a neural adaptation for the category repetition. This result is however in line with ERP results by Ganis and Schendan [2008], who found that visual mental imagery and perception produced opposite adaptation effects on early brain potentials, and thus demonstrated that different brain regions show different neural adaptation effect in the mental imagery domain. Nonetheless, our results also suggest that distinct patterns of adaptation subtend different categories of mental images. Indeed, while category repetition resulted in a suppression of neural signal (at the level of left SPL, right CC, bilateral RSC) in imaging geographical space, such as Italy, category repetition resulted in an enhancing of activation for both clock and campus in several brain areas (*campus*: right FG, right RSC; *clock*: bilateral IPL, right ITL, right SPL). These results not only suggest that different neural mechanisms underlie visual mental imagery and perception but also suggest that different neural mechanisms underlie different categories in the visual mental imagery domain. To the best of our knowledge, this is the first fMRI study comparing the adaptation effect of different categories of mental imagery and our results open the debate about the possibility of different adaptation effects in the imagery domain. Any other discussion about this effect may result largely speculative. Further investigations are needed to better understand these complex differences, by using well-designed and controlled paradigms, able to assess both perceptual and imagery domains.

For the first time, we directly assessed whether the multivoxel pattern of activity in these regions conveyed information about the visuo-spatial representation. All of the

investigated regions contained information about the content of mental images with the exception of the right HC, CU, and IFG and the bilateral PHG. This result confirms that the pattern of activity in the regions involved in visuospatial imagery encodes information about the content of the mental images generated.

Then, we explored the possibility that regions involved in visuospatial mental imagery contain information about the spatial arrangement of single parts (i.e., exemplars) of the mental image. We found that most of the investigated regions (see Table II) contained information about the position of the items, with differences among categories at the level of the bilateral CC, left LG, and right ITL (Fig. 6). Similar to what has been demonstrated for visual perception [Epstein and Morgan, 2012; Kay and Gallant, 2009], it is also possible to detect information about the features of mental images in the mental imagery domain. This is somewhat surprising because the participants did not see anything and were only asked to mentally visualize each stimulus. In fact, regardless of individual differences in generating mental images, contextual information was processed by a well-defined network of areas. This suggests that a dedicated brain network codes the visuospatial information necessary for retrieving perceptual information from memory and gives rise to the experience of "seeing with the mind's eye."

In conclusion, our results shed some light on the functional organization of the neural processes underlying visual mental imagery. First, they clearly demonstrate functional segregation among the brain networks underpinning human visual mental imagery for different content of mental images. Second, our results confirm that visual perception and visual mental imagery share a common network, particularly when imagining a navigational space and object. Imagining a geographical space requires activation of areas involved in both topological-navigational and non-topological mental images, demonstrating that imagining the map of Italy is different from representing a familiar space and representing an object, even if it partially shares a functional network with both of them. If visual mental imagery arises when we retrieve stored perceptual information from memory, imagining the map of Italy could be the thin line between perception/visual mental imagery and imagination, because we never really experience it except when it is possible to fly over it (i.e., the case of aviation pilots or astronauts), and we cannot retrieve real perceptual information about it from memory.

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