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Role of the human retrosplenial cortex/parieto-occipital sulcus in perspective priming

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ABSTRACT

The ability to imagine the world from a different viewpoint is a fundamental competence for spatial reorientation and for imagining what another individual sees in the environment. Here, we investigated the neural bases of such an ability using functional magnetic resonance imaging. Healthy participants detected target displacements across consecutive views of a familiar virtual room, either from the perspective of an avatar (primed condition) or in the absence of such a prime (unprimed condition). In the primed condition, the perspective at test always corresponded to the avatar's perspective, while in the unprimed condition it was randomly chosen as 0, 45 or 135 deg of viewpoint rotation. We observed a behavioral advantage in performing a perspective transformation during the primed condition as compared to an equivalent amount of unprimed perspective change. Although many cortical regions (dorsal parietal, parieto-temporo-occipital junction, precuneus and retrosplenial cortex/parieto-occipital sulcus or RSC/POS) were involved in encoding and retrieving target location from different perspectives and were modulated by the amount of viewpoint rotation, the RSC/POS was the only area showing decreased activity in the primed as compared to the unprimed condition, suggesting that this region anticipates the upcoming perspective change. The retrosplenial cortex/parieto-occipital sulcus appears to play a special role in the allocentric coding of heading directions.

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Introduction

Human ability to recognize scenes from different perspectives is a fundamental competence in every day life. It allows, for instance, to remember spatial locations despite intervening changes in the point of view and ensures to keep oriented in a large-scale space.

This ability has been experimentally measured by asking observers to study a scene from a given perspective, and then, after a true, imagined, or virtual self displacement, to detect whether a given object has been moved, or to point to a memorized location (Diwadkar and McNamara, 1997; Simons and Wang, 1998, 1999; Wang and Simons, 1999; Mou and McNamara, 2002; Amorim, 2003; Schmidt et al., 2007; Lambrey et al., 2008, 2011; Sulpizio et al., 2013; Montefinese et al., in press). Behaviorally, these experiments support the existence of view-dependent representations by showing a chronometric relationship between reaction times (RTs) and amount of perspective rotation. Such a viewpoint dependency is partially abolished when a prior mental transformation on the scene is allowed in advance, for example by using a priming paradigm in which the next perspective is primed by an avatar (Amorim, 2003; Lambrey et al., 2008; Sulpizio et al., 2015).

Concerning the neural correlates, previous imaging literature has demonstrated the involvement of a dorsal fronto-parietal network, and a specific recruitment of the lingual/parahippocampal gyrus and of the retrosplenial cortex/parieto-occipital sulcus during spatial updating of target locations from a shifted perspective (Committeri et al., 2004; Schmidt et al., 2007; Lambrey et al., 2011; Sulpizio et al., 2013; Zhang and Ekstrom, 2013; Dhindsa et al., 2014). In particular, two scene-selective regions have been identified within the posterior parahippocampal and anterior lingual/medial fusiform gyrus (the "parahippocampal place area" or PPA; Epstein and Kanwisher, 1998) and within the retrosplenial, posterior cingulate, and medial parietal cortex (the "retrosplenial complex" or RSC; Epstein, 2008). Lambrey et al. (2011) explored the neural bases of spatial updating of multiple object locations during imagined changes of the current perspective and during an equivalent amount of object rotation. The basic demand of encoding and retrieving the object locations produced the activation of a set of regions (medial, inferior, and superior parietal), which are often associated with spatial navigation (Maguire et al., 1998; Hartley et al., 2003; Iaria et al., 2007). The additional request of imagining the viewpoint rotation towards a virtual observer, as compared to the

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equivalent amount of object rotation, elicited activation in the RSC. Sulpizio et al. (2013) explored perceptive transformations relative to either an environmental or an object-based frame of reference. A selective recruitment of PPA and RSC was found both during memory encoding and when updating memorized locations after a viewpoint change, especially when the established reference frame included stable environmental features. They also found that fronto-parietal regions are involved in preparing and then implementing the update of egocentric coordinates, which is needed to compensate for viewpoint changes, but irrespective of the kind of frame of reference relative to which the perspective transformation is performed (Sulpizio et al., 2013). This interpretation is in line with the general idea of purely egocentric spatial maps in the parieto-frontal cortex (Berthoz, 1997; Kravitz et al., 2011), which get dynamically updated when the subject moves. These representations remain however transient, and the updating process alone would not allow the build-up of stable allocentric representations (see also Burgess, 2006; Byrne et al., 2007).

Recent neuroimaging evidence (Marchette et al., 2014; Sulpizio et al., 2014) supports the idea that RSC is part of a neural circuit supporting the neural representation of allocentric heading. We recently demonstrated that scene-selective regions are automatically recruited while participants view pictures taken from a specific location (place), view and heading within a familiar virtual environment, even in the absence of any explicit navigational demand. In particular, we found that the RSC is critical for combining place and view information, compatibly with the recent idea that this region anchors internal spatial representations to local topographical features, like an internal compass that represents one's heading/direction and updates this quantity as we move. Also Doeller et al. (2010) observed, within the RSC, neural adaption to absolute running directions in a navigational task. Evidence of how this internal compass is implemented at the neuronal level comes from previous neurophysiological experiments showing the existence, in the retrosplenial cortex of rodents, of "head-direction cells" which encode the animal's heading or orientation within the environment (Chen et al., 1994; Taube, 2007), independently from its location. Furthermore, neuropsychological results as well as theoretical models (Burgess, 2006; Byrne et al., 2007) support the idea that the RSC is crucial for the neural representation of heading directions. RSC lesions in humans lead to heading disorientation, a form of topographic disorientation in which patients are unable to derive directional information from landmarks they can recognize (Aguirre and D'Esposito, 1999) and, in some cases, to describe routes through maps of familiar places they can draw (Ino et al., 2007). Taken together, these pieces of evidence support a recent theoretical model (BBB model) suggesting that the RSC is part of a circuitry (transformation circuit) specialized in transforming the allocentric codes (mediated by the medial temporal lobe and suitable to build-up a stable allocentric/enduring representation of the environment) into egocentric codes (mediated by the posterior parietal cortex), and vice versa. A central prediction of the BBB model is that these transformations can be accomplished very simply if absolute heading direction is known in advance. As predicted by this model, the RSC should use head-direction information from the anterior thalamic nuclei to compensate for the rotational offset between egocentric and allocentric coordinates (Byrne et al., 2007).

In the present study, we aimed at testing this prediction by exploring spatial memory under different conditions of perspective transformations during an object location task. Specifically, we tested the idea that the retrosplenial head-direction system should be sensitive to upcoming perspective/heading changes. To this aim, we adapted a priming paradigm previously used to explore perspective taking abilities (Amorim et al., 2003; Sulpizio et al., 2015). We argued that a brain region sensitive to changes in head-direction should be sensitive to perspective priming, according to the idea that this region is involved in matching the stored perspective with the actual perspective on the scene (Lambrey et al., 2011; Sulpizio et al., 2013, 2014). We acquired functional magnetic resonance images while participants detected target displacements across consecutive views of a familiar virtual room, either from the perspective of an avatar (primed condition) or in the absence of such a prime (unprimed condition). Focusing on the comparison between primed and unprimed conditions during the test phase, allowing us to test the effect of anticipating the visual perspective on the scene, we predicted a particular involvement of the RSC. If the RSC encodes perceived heading direction (Baumann and Mattingley, 2010) and uses this information to transform the allocentric into an egocentric (head-centered) representation, the retrosplenial head-direction system should be advantaged by cueing the observer to be in a certain heading direction. We further hypothesized that fronto-parietal regions scale their activity with the amount of perspective rotation, according to the higher updating costs with increasing changes of perspective.

Materials and methods

Subjects

Fourteen neurologically normal volunteers (all males, mean age = 26.6 yrs, s.d = 3.2) participated to the fMRI study. All subjects were right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) (mean index = 0.7; s.d. = 0.2) and had normal or corrected-to-normal vision. The protocol was approved by the ethical committee of Fondazione Santa Lucia, Roma, and a written informed consent was obtained from each participant before starting the study.

Virtual environment and stimuli

We adopted the same environment used in Sulpizio et al., 2013, 2014, 2015. The virtual environment, representing an internal view of a square living room (Supplementary Fig. 1), was designed using 3Dstudio MAX 9 (Autodesk Inc, San Rafael, CA, USA). It included stable landmarks (distal cues) such as a door, windows and a fireplace, and unstable landmarks such as pieces of furniture arranged on a circular carpet in the center of the room. The furniture set was not informative of the task solving but was added to give the impression of a realistic living room.

In order to familiarize the subjects with the environment, we first presented a 52-s movie consisting of a 360 deg tour of the virtual room with only the stable landmarks. They were allowed to watch the movie until they were sure to be able to draw a sketch representing the survey perspective of the room. All subjects performed a maximum of 3 virtual tours and reproduced one correct map of the explored room (except for two subjects that correctly reproduced the map in a second time).

During the experiment, participants were shown different snapshots of the virtual environment. Each snapshot simulated a photograph of the environment taken with a 24-mm lens (74 by 59 deg simulated field of view) from one of eight different viewpoints. Each viewpoint corresponded to the position of a virtual camera (Supplementary Fig. 1). The different virtual cameras were distributed at 45 deg intervals along a circle whose center corresponded to the center of the virtual room. Each camera was directed towards the center of the room, where the furniture set was placed. Each snapshot also included a plant, used as the target object, which was located outside the carpet but quite close to it, in one of eight possible positions, distributed every 45 deg along a smaller concentric circle (Supplementary Fig. 1). The target position in both study and test pictures was never presented directly in front of the observer or directly behind the carpet and was presented half of the times on the left and the remaining half on the right of the observer (Fig. 1). Each snapshot depicted the virtual room so as to include the whole furniture set on the carpet, the target and some of the fixed cues on the walls. The five pieces of furniture were arranged in different configurations on the circular carpet stably located at the center of the room. In the study picture of the primed condition also

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