

# Multiple reference frames used by the human brain for spatial perception and memory

Gaspare Galati · Gina Pelle · Alain Berthoz ·  
Giorgia Committeri

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**Abstract** We review human functional neuroimaging studies that have explicitly investigated the reference frames used in different cortical regions for representing spatial locations of objects. Beyond the general distinction between “egocentric” and “allocentric” reference frames, we provide evidence for the selective involvement of the posterior parietal cortex and associated frontal regions in the specific process of egocentric localization of visual and somatosensory stimuli with respect to relevant body parts (“body referencing”). Similarly, parahippocampal and retrosplenial regions, together with specific parietal subregions such as the precuneus, are selectively involved in a specific form of allocentric representation in which object locations are encoded relative to enduring spatial features of a familiar environment (“environmental referencing”). We also present a novel functional magnetic resonance

imaging study showing that these regions are selectively activated, whenever a purely perceptual spatial task involves an object which maintains a stable location in space during the whole experiment, irrespective of its perceptual features and its orienting value as a landmark. This effect can be dissociated from the consequences of an explicit memory recall of landmark locations, a process that further engages the retrosplenial cortex.

**Keywords** Spatial reference frames · Functional neuroimaging · Egocentric · Allocentric · Parahippocampal place area · Retrosplenial cortex

## Introduction

The concept of reference frame is of core importance in the field of spatial perception and memory. A reference frame determines what kind of spatial location is represented, and how locations are specified within a spatial representation (McCloskey 2001). In recent years, it is often thought that humans and animals use two main classes of reference frames: egocentric and allocentric. However, humans and different animals use a variety of reference frames (Trullier et al. 1997). There are at least two reasons why this concept is so ubiquitous. First, animals live, move, and act in space, and manipulating spatial information is crucial for a variety of goals and cognitive abilities, thus, it is not surprising that many regions of the human cerebral cortex represent spatial properties (of objects, of the world, of our own body) and/or are organized as structured spatial maps of locations or features. We also know that different structures such as the parietal cortex, superior colliculus, hippocampus, and putamen, encode space in different frames and maybe even in different geometries (Tabareau et al. 2007).

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G. Galati (✉)  
Department of Psychology, Sapienza University, Rome, Italy  
e-mail: gaspare.galati@uniroma1.it

G. Galati  
Laboratory of Neuropsychology,  
Foundation Santa Lucia, Rome, Italy

G. Pelle · G. Committeri  
Department of Clinical Sciences and Bioimaging,  
University G. d’Annunzio, Chieti, Italy

G. Pelle · G. Committeri  
Institute for Advanced Biomedical Technologies,  
Foundation University G. d’Annunzio, Chieti, Italy

A. Berthoz  
Laboratoire de Physiologie de la Perception et de l’Action,  
CNRS, Collège de France, Paris, France

Second, much of the computational burden of manipulating spatial information involves decoding and merging different frames of reference. Sensory information which flows to our brain through sensory organs already comes organized into anatomically constrained reference frames (e.g., retinotopic and somatotopic for the visual and tactile systems, respectively), which are anchored to the body part where the sensory receptors are located. These intrinsic reference frames not only are different across sensory modalities, but also move relative to each other each time we move our eyes, head, or limbs, or whole body, thus raising the problem of conversion between different reference frames. The recent discovery that the brain also uses different, but combined geometries for both arm movements and locomotor navigation (Bennequin et al. 2009) also questions this problem in a new way.

In the following, we selectively review human functional neuroimaging studies that have explicitly investigated the reference frames used in different cortical regions for representing spatial locations of objects, and present some novel related experimental data.

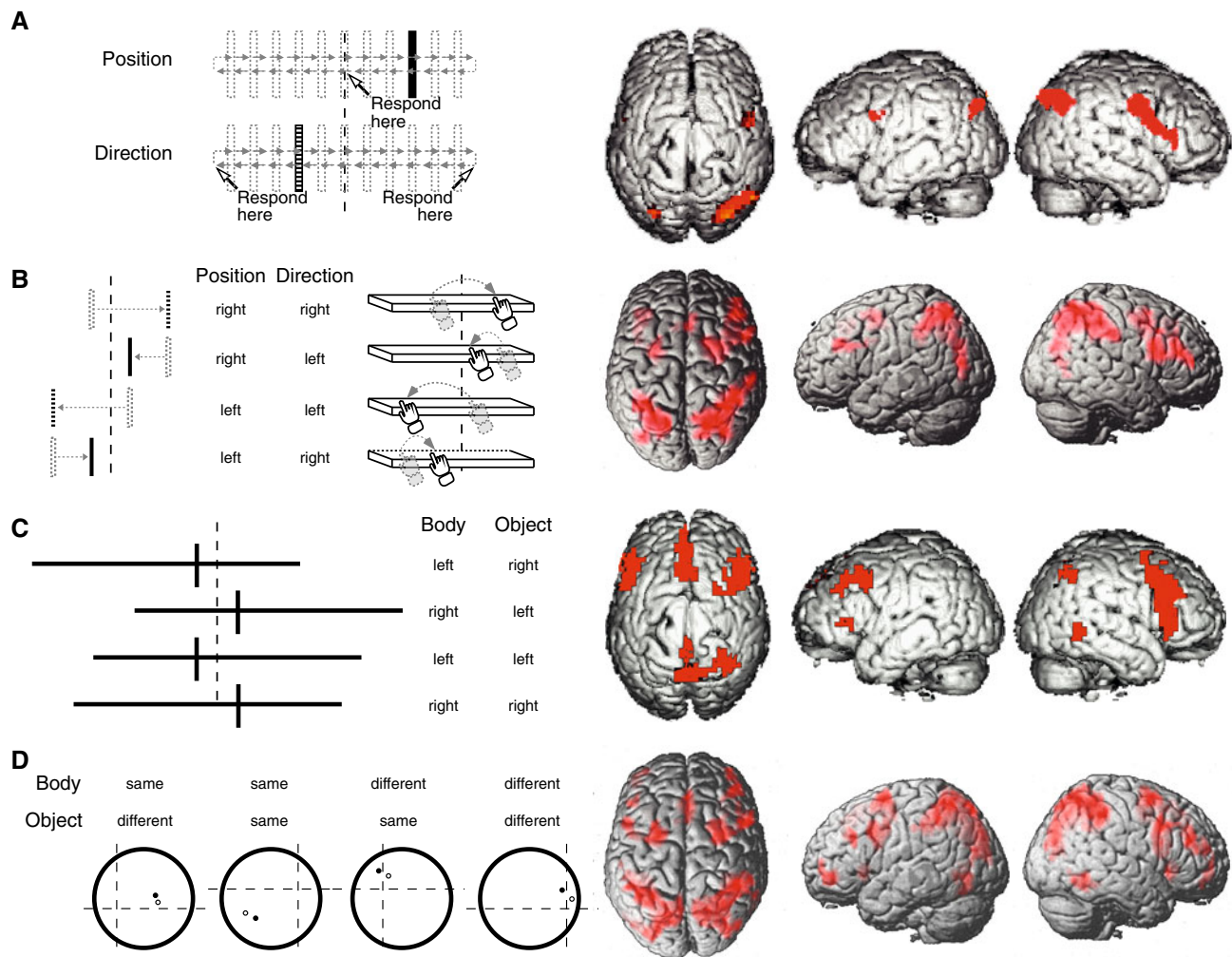
### Body referencing

Because locational information provided by sensory systems are intrinsically relative to the position in space of the respective sensory organs, conversion between the sensory reference frames needs to integrate a continuously updated representation of the relative position of the body segments, which may be formed on the basis of proprioceptive, vestibular, and motor signals. This dynamic postural model would serve as an “egocentric reference” and would correspond to the concept of “body schema”, which can be dated back to the beginning of the twentieth century (Head and Holmes 1911; Shildler 1935; Critchley 1953). Neuropsychological observations clarify the importance of internal representations based on egocentric reference frames and point to parieto-frontal cortical networks as the possible neural basis of such representations. For instance, spatial neglect is the neuropsychological syndrome which best represents the breakdown of egocentric spatial awareness in everyday life. Patients with spatial neglect fail to orient to and explore the portion of space contralateral to their cerebral lesion (typically the left side of space after right hemispheric lesions), even in the absence of primary sensory or motor deficits. The prevalent importance of body-centered frames in spatial neglect has been experimentally demonstrated in many ways and extensively reviewed elsewhere (Bisiach 1997; Vallar et al. 1997; Chokron 2003), and becomes immediately evident through two examples. The detection rate of visual targets in the left hemifield can increase following rotation of the patient’s trunk in the

leftward direction, while keeping retinal stimulation constant (Karnath et al. 1993). Similarly, the detection rate of tactile targets delivered on the left hand can increase if the left hand is shifted to the right of the trunk midline (Smania and Aglioti 1995). In both cases, stimuli are delivered at a constant location relative to intrinsic sensory (retinotopic and somatotopic) frames but in different body-relative locations, so these effects point to a special role of body-centered reference frames.

In a series of functional magnetic resonance imaging (fMRI) experiments (Vallar et al. 1999; Galati et al. 2000, 2001; Sepe et al. 2007), we searched for cortical regions involved in this body-referencing process, by asking healthy volunteers to manipulate spatial information in terms of body-centered coordinates. The rationale underlying these experiments relies on the classical principle of cognitive subtraction: subjects are shown identical visual stimuli under two conditions which differ in terms of the instructed task. One “egocentric” task explicitly required a perceptual spatial judgment which could not be solved through the use of sensory frames, but relied on a representation of the stimulus location relative to the subject’s body mid-sagittal plane. The control task, on the other hand, could be solved without explicitly representing body-centered stimulus locations. These studies are summarized in Fig. 1. The tasks were more or less directly inspired by the neglect literature: neglect patients show either a horizontal shift of the perceived position of the body mid-sagittal plane (e.g., Vallar et al. 1995; Karnath 1997; Richard et al. 2004; Kerkhoff et al. 2006; Saj et al. 2006), or an increased variance in body, but not object-centered spatial judgments (Pizzamiglio et al. 2000).

In two fMRI studies (Vallar et al. 1999; Galati et al. 2001), we compared a left–right judgment of stimulus location relative to the body mid-sagittal plane, with a left–right judgment about the direction of motion. In both studies, subjects tracked a horizontally moving bar and reported when it intersected their body midline. Because the subjects’ gaze smoothly followed the moving bar, its retinal position remained approximately constant across time, while its body-centered position systematically varied. Both studies provided evidence for the involvement of the posterior parietal and premotor cortex in computing body-centered locations. Activation was prominent in the right hemisphere, where it involved not only the superior parietal and posterior intraparietal cortex, but also the anterior part of the intraparietal and inferior parietal cortex. In the frontal lobe, the activation was also more extensive in the right hemisphere, especially for the ventral sector of the premotor cortex. In Galati et al. (2001), we compared the same visual body-centered task with a somatosensory equivalent, where the (unseen) participant’s hand was passively moved. Whenever the index



**Fig. 1** Summary of four different experiments implicating posterior parietal and frontal associative regions in body-centered spatial coding. *Left column* stimuli and paradigm. Stimuli are shown in *black*, *dotted lines* depict trajectories of moving stimuli, and *dashed lines* show the (unseen) position of the subject's body mid-sagittal plane. *Right column* activation resulting from the comparison of the egocentric position versus direction task (**a**, **b**), or the body- versus object-centered task (**c**, **d**), projected on top, lateral left, and lateral right views of a standard cortical surface. **a** Vallar et al. (1999): subjects reported when a vertical bar horizontally moving in darkness intersected the body mid-sagittal plane (position task) or when changed its direction (direction task). **b** Galati et al. (2001): in each trial, a vertical bar moved horizontally in darkness (visual modality *left column*) or the (unseen) right hand was passively moved in the horizontal direction (somatosensory

modality *right column*). Subjects reported the left–right body-centered position of the endpoint of the bar trajectory (visual position task), or of the point where the right index finger touched the table (somatosensory position task), or the direction of the last bar/hand movement (direction task). **c** Galati et al. (2000): subjects reported the left–right position of the vertical bar relative either to the body mid-sagittal plane (body-centered task) or to the midpoint of the horizontal line (object-centered task). **d** Sepe et al. (2007): subjects reported whether the two dots were in the same or in different quadrants, with quadrants defined either by egocentric primitives (the eye level, shown as a dashed horizontal line, and the body mid-sagittal plane: body-centered task) or by the principal axes of the enclosing circle (object-centered task). In another condition (not shown), subjects reported which of the two dots was closer to either the mid-sagittal plane or to the circle vertical axis

finger touched the table (see Fig. 1b, left panel), participants were asked to report the body-centered location of the point in space where the touch occurred. This task required to remap tactile stimulation from somatotopic to spatial, egocentric coordinates, while the visual task required a similar conversion from retinotopic to egocentric coordinates. The bilateral posterior parietal and premotor

cortex was consistently activated across the two modalities, and since no modality by task interaction was apparent in these regions, we concluded that they were commonly involved in building up body-centered spatial representations for both modalities.

In two further experiments (Galati et al. 2000; Sepe et al. 2007), we were able to compare the very same location

judgment task, performed either relative to the body mid-sagittal plane or to a peripheral visual reference. Galati et al. (2000) used a line bisection judgment task, while Sepe et al. (2007) used a two-dimensional task, with both a categorical and a metrical variant (Kosslyn 1987). In both studies, and in both variants of the two-dimensional task, activation in the parietal and frontal cortex, although also present for object-centered judgments, was stronger and more extensive for body-centered judgments (Fig. 1c, d, right panel, shows the direct contrast between body- and object-centered tasks). A preference of the parietal cortex for egocentric judgments has been also reported by Neggers et al. (2006).

The relationship of these data with the neglect literature is unclear. Most of the activation shown in Fig. 1 is in parieto-frontal regions far more dorsal than those structurally lesioned in spatial neglect, and pertains to the dorsal attentional system (Corbetta and Shulman 2002). However, this system is dysfunctional in acute neglect patients and its inter-hemispheric re-balancing in the chronic phase seems to correlate with the degree of functional recovery (Corbetta et al. 2005). Moreover, as observed above, the right hemispheric body-centered activation extends in the anteroventral parietal cortex and inferior frontal cortex, regions whose lesions have been associated with spatial neglect (see e.g., Committeri et al. 2007).

The main limitation of the previously reviewed studies relies in their simple, subtractive design: they show which regions participate in this process of body referencing of visuospatial and somatosensory information, but do not clarify the format of the resulting spatial representations. In recent years, phase-encoded fMRI paradigms, which allow to define a topographical relationship between the response of a particular voxel and the location of a stimulus (Engel et al. 1994; Sereno et al. 1995), have been used to demonstrate a number of topographical maps in the posterior parietal cortex (e.g., Swisher et al. 2007; reviewed in Silver and Kastner 2009). One single study (Sereno and Huang 2006), which has disentangled head-centered from purely retinotopical coordinates, has evidenced one small region of the posterior parietal cortex, whose phase maps, i.e., receptive field estimates, did not move with gaze and were consistent with head-centered maps of tactile stimuli applied to the face, as in the monkey ventral intraparietal area (Duhamel et al. 1997). However, in a related study (Gardner et al. 2008), in which a small set of screen locations were stimulated on the horizontal meridian while subjects fixated three different, horizontally arranged locations, no evidence for head-centered coding was found in any of twelve retinotopically defined areas in the occipital cortex (but see d'Avossa et al. 2007).

The ubiquitous prevalence of retinotopical codes can be reconciled with the involvement of parietal cortex in body

referencing: spatial coding in body-centered frames can be implemented through modulation of purely retinotopical maps by extra-retinal signals such as the position of the eye in the orbit or of the head on the trunk (Andersen et al. 1985; Cohen and Andersen 2002). These modulatory effects have been examined in a limited number of human neuroimaging studies. For example, during hand pointing using the contralateral hand, a pointing-selective region in the intraparietal sulcus showed a preference both for targets in the contralateral visual hemifield and for eye positions in the contralateral space (DeSouza et al. 2000). A tonic modulation of the hemodynamic signal by eye position has been found in V5 and V4/V8 even in the absence of any visual response (DeSouza et al. 2002). Head on trunk modulation has been demonstrated in the intraparietal sulcus, with higher responses during saccadic eye movements performed with the head turned in the contralateral direction (Brotchie et al. 2003).

### Spatial updating

Because animals continuously move in space, the brain must either explicitly compensate for body movements and dynamically update egocentric spatial maps by incorporating information about body movements, or employ some alternative and more stable way of encoding spatial relationships that is invariant across body movements. The former alternative (dynamic spatial updating) is often studied by asking observers to encode the location of a stimulus and then to use the memorized information after a relevant body movement. A simple model is given by remapping of neuronal responses between receptive fields before saccades, which is observed in the macaque lateral intraparietal area (Duhamel et al. 1992). These neurons may start to fire when a saccade brings their receptive fields into a previously stimulated location, as if the trace of the stimulus location had been actively transferred from a retinotopic receptive field to another one, to compensate for the intervening eye movement (Duhamel et al. 1992). A similar phenomenon has been demonstrated in the human intraparietal cortex (Merriam et al. 2003). When a saccade brings the remembered location of a visual target from the retinotopically defined left to the right hemifield, activation in a parietal oculomotor region (Sereno et al. 2001) correspondingly shifts from the right to the left hemisphere, and vice versa (Medendorp et al. 2003). Similarly, activation shifts from one hemisphere to the other when a cue instructs to perform an eye movement in the direction opposite to the remembered location of a visual target (Medendorp et al. 2005). Responses to the remapped stimulus trace have been also demonstrated in the extrastriate cortex, especially in higher-order areas (Merriam et al. 2007).



Spatial updating most notably occurs during navigation, and contributes to maintain orientation and an accurate (egocentric) representations of object locations. As an alternative to “online” spatial updating, animals might explicitly build more stable representations of their surroundings based on stationary (allocentric) frames, and use these to update remembered spatial locations “offline” (Amorim et al. 1997). Although the concept of cognitive map (Tolman 1948; O’Keefe and Nadel 1978) and the existence of pure allocentric representations has been subject of intense debate (e.g., Bennett 1996), and it has been suggested that spatial memory is mostly supported by egocentric representations (Wang and Spelke 2002), there is strong neurophysiological evidence for allocentric representations at the single-neuron level (e.g., place cells: O’Keefe 1976; Ono et al. 1991; Ekstrom et al. 2003; head-direction cells: Taube 1998; grid cells: Hafting et al. 2005; spatial view cells: Rolls 1999). Indeed, both allocentric or “survey” strategies, based on the manipulation of map-like representations, and egocentric or “route” strategies, based on path integration or on sequences of stimulus–response associations, contribute to human navigation (Berthoz 1997; Maguire et al. 1998a; Burgess 2006). Behavioral data suggest that subjects spontaneously shift between the two strategies, or in some cases they may coexist and act in parallel (Amorim et al. 1997; Waller and Hodgson 2006; Iglói et al. 2009; Lafon et al. 2009).

Neuroimaging studies that have compared different navigational strategies have associated the hippocampus with allocentric strategies and the striatum with egocentric strategies (Maguire et al. 1998a; Hartley et al. 2003; Iaria et al. 2003), although the acquisition of a sequential egocentric strategy may also rely on the hippocampus (Ghaem et al. 1997; Mellet et al. 2000). More relevant for the issue of spatial updating are the studies which have examined memory for spatial location of an object across changes in point of view. Patients with hippocampal lesions are impaired in this task (Lambrey et al. 2008), which in healthy subjects activates the parahippocampal cortex proportionally to the amount of viewpoint change (Schmidt et al. 2007). The parahippocampal and retrosplenial cortex (RSC) are selectively involved in encoding object locations relative to fixed environmental landmarks and to retrieve them after a viewpoint change (Sulpizio et al. 2009; see also King et al. 2002).

In these tasks, subjects observe two consecutive snapshots of the same environment from different points of view and thus cannot obtain any form of “online” information from their own movement. Only one imaging study (Wolbers et al. 2008) examined brain activation in a situation where subjects actually perceived their own movement and could update the remembered location of target stimuli

“online” during virtual locomotion. In this situation, only activation of the precuneus was indicative of a process of spatial updating of memorized stimulus locations, since it increased with the number of targets whose memorized position had to be updated. Thus, it is possible that “online” and “offline” updating rely on different brain structures.

### **Allocentric reference frames and environmental referencing**

The term “allocentric” has assumed a very general meaning, and is used here to include any form of spatial representation where locations are encoded relative to reference points external to the holder of the representation. “Allocentric” is often considered as a synonym for “view-independent”, but not necessarily an allocentric representation is independent from the position and orientation of the observer. In the case of place and head-direction cells, for example, their firing does obviously depend on the position and orientation of the animal, respectively. They can however be qualified as allocentric because their receptive fields are anchored to a specific position in the enclosing environment.

In this general meaning, the term “allocentric” can be applied not only to stable reference frames useful for navigation, but also to local representations of relative, object-to-object spatial relationships. Local object-centered spatial referencing is involved during object-directed action like grasping (e.g., Patchay et al. 2006) and during object recognition, when the intrinsic spatial relationships between object parts have to be represented in an as abstract as possible code (but not necessarily in a completely view-independent manner, see Andresen et al. 2009). Object-centered encoding has been also described in the context of spatial attention, both in single-neuron recordings in behaving monkeys and in human patients with hemispatial neglect (Hillis and Rapp 1998; see Olson 2003, for a review). Hemineglect may indeed concern the contralesional side of individual objects, independent of their egocentric position (“object-based neglect”: Driver 1999). Recent neuroimaging studies (Shirani et al. 2009; Medina et al. 2009) have associated stimulus-based neglect (centered on the stimulus orientation relative to the observer rather than on the intrinsic, canonical object orientation) with the dysfunction of temporal regions of the ventral visual stream, whereas viewer-centered neglect depended on the integrity of dorsal visual stream regions.

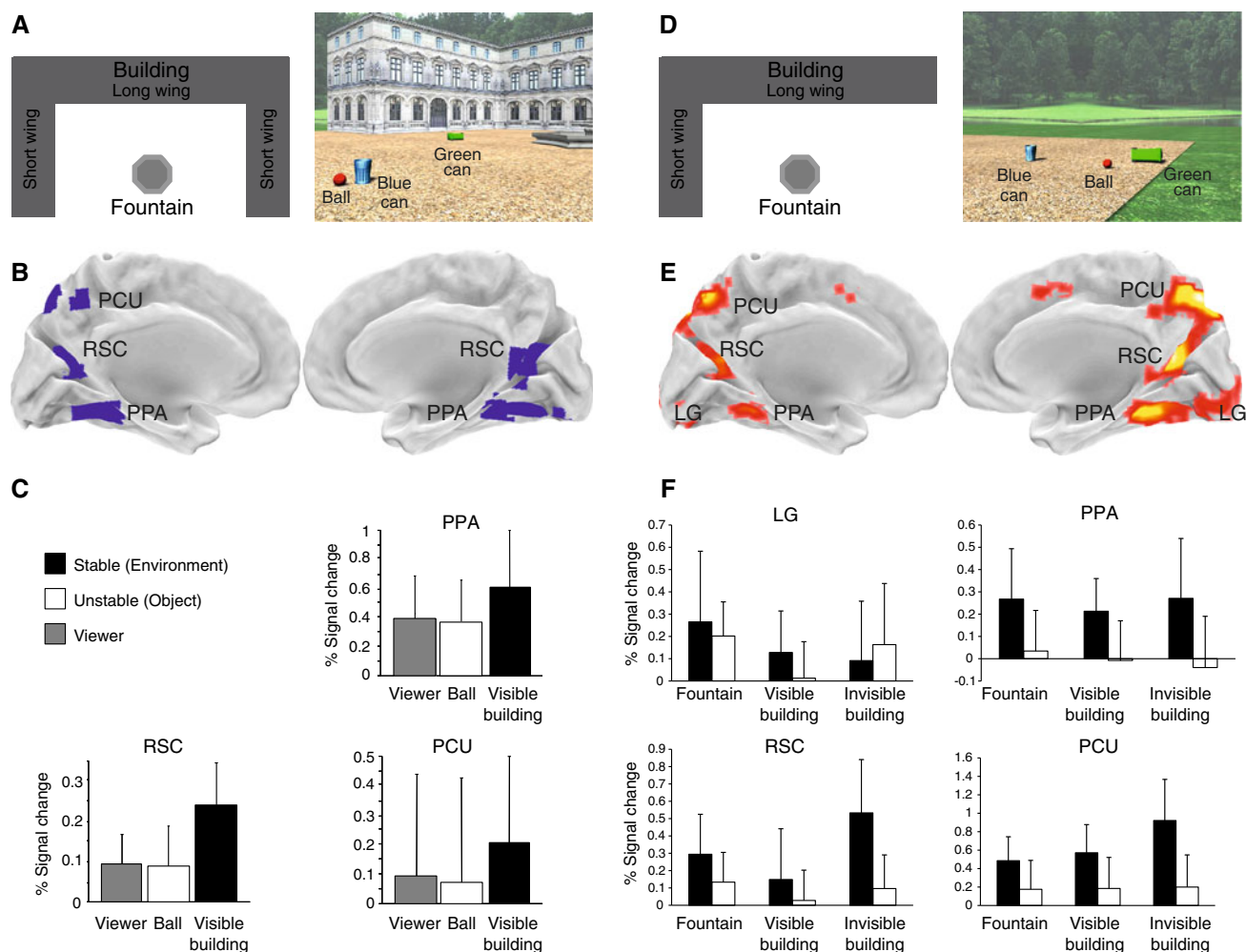
Although these data support the proposal that egocentric and allocentric spatial coding is subserved by dorsal and ventral visual stream, respectively (Milner and Goodale 1995), functional neuroimaging studies do not provide clear evidence for such dissociation. The activation pattern in

object-centered spatial tasks are similar to those reported for egocentric tasks (Fink et al. 1997; Honda et al. 1998; Fink et al. 2000; Galati et al. 2000; Neggers et al. 2006; Sepe et al. 2007). Studies which have directly compared egocentric and object-centered tasks (Galati et al. 2000; Sepe et al. 2007) have shown that object-centered computations activate a subset of parieto-frontal regions implicated in body referencing. Interactions between egocentric and object-centered reference frames also occurs in parieto-frontal regions (Fink et al. 2003).

Although the experimental evidence for a selective neural substrate of object-based representation is not consistent, in

the following, we will provide evidence for a selective neural substrate of environmental allocentric representations. In two fMRI studies (Fig. 2), we compared allocentric representations of enduring environmental features with allocentric representations of transient object-to-object relationships. These studies show that a set of medial parieto-temporal regions is selectively activated whenever a reference to the layout of a familiar environment or to a stable familiar landmark is implicitly required (see also Murphy et al. 2009).

In the first experiment (Committeri et al. 2004), we introduced an experimental paradigm allowing to assess the automatic and selective activation of environmental



**Fig. 2** Summary of two different experiments implicating the precuneus, parahippocampal and retrosplenial regions in environment-centered spatial coding. **a–c** Experiment by Committeri et al. (2004). **a** Map of the virtual environment and example of a stimulus. Subjects reported which of the two trash cans was closer to the observer (viewer frame), closer to the red ball (unstable or object frame), or closer to the long wing of the building (stable or environment frame). **b** Regions more activated in the environment than in the object and viewer frame, projected on the medial surfaces of the cerebral hemispheres. *PCU* precuneus, *RSC* retrosplenial cortex, *PPA* parahippocampal place area. **c** Averaged BOLD percent signal change across subjects and hemispheres in PPA, RSC, and PCU in the three experimental conditions.

**d–f** Novel experimental data presented in the main text. **d** Map of the virtual environment and example of a stimulus used in the invisible building condition. Subjects reported which of the two trash cans was closer to the ball (unstable or object frame) or (in separate sessions) to the fountain or building (stable frame). The building could be either visible (as in the example in **a**) or invisible (as in the example in **d**) from the current point of view. **e** Regions more activated in the stable than in the unstable frame for at least one condition (fountain, visible building, invisible building). *LG* lingual gyrus. **f** Averaged BOLD percent signal change across subjects and hemispheres in LG, PPA, RSC, and PCU in the experimental conditions

representations in a controlled situation. Our aim was to directly compare viewer-centered, object-centered, and environment-centered spatial coding of the same three-dimensional information. Subjects saw snapshots of a familiar virtual environment representing a square arena in a park, with some relevant landmarks such as a three-winged building and a fountain (Fig. 2a). Each snapshot included a partial view of the building and three additional objects: two target objects (garbage cans) and one reference object (a red ball). Subjects judged which of the two target objects was closer either to the observer (viewer frame), or to the reference object (object frame), or to the long wing of the building (environment frame). Importantly, the three reference frames were independently manipulated: in each trial, the observer's position was moved, and the position of the target and reference objects were independently changed with respect both to the observer and to the environment. This paradigm allowed not only to directly compare egocentric and allocentric reference frames, but also to explicitly test the idea of a possible differential neural substrate between environment-referenced allocentric representations, which include enduring spatial information about locations of landmarks, and object-referenced representations, which can use any set of objects as a spatial reference.

Two aspects of the results of this experiment are particularly important in the current context. First, posterior parietal and frontal regions which we had implicated in body referencing did not prefer the viewer frame, as one would expect if they were specialized for egocentric versus allocentric processing. Importantly, the viewer frame in this experiment does not require an explicit reference to any specific body part or to the position of the body in space, and can be solved in purely visual terms, without any form of remapping from retinal to body-centered coordinates. The preference of parieto-frontal regions for egocentric versus allocentric reference frames needs thus to be qualified: it should be restricted to the process of body referencing and may not be generically applied to any viewer-dependent representation or to any task requiring to assume a first-person perspective.

The second important aspect of the results is the selective involvement of a set of cortical regions in the environment frame (Fig. 2b, c). These included portions of the medial temporal cortex and adjacent anteromedial occipital lobe (lingual, fusiform, and posterior parahippocampal gyri), the RSC and the ventral parieto-occipital junction. The medial temporal cortex (hippocampus proper and parahippocampal gyrus) and the RSC respond during a variety of cognitive tasks involving navigation, learning and/or recall of environmental information (e.g., Aguirre et al. 1996; Aguirre and D'Esposito 1997; Ghaem et al. 1997; Maguire et al. 1997, 1998b; Mellet et al. 2000; Hartley et al. 2003; Rosenbaum et al. 2004; Wolbers and Büchel

2005; Iaria et al. 2007). However, note that our task did not require any form of topographical learning, since subjects were already familiar with the virtual environment before entering the scanner. Fusiform, lingual, and parahippocampal gyri, as well as the RSC are also activated during simple passive exposure to photographs of scenes, places and famous landmarks, as compared to objects (Aguirre et al. 1998; Epstein and Kanwisher 1998; Haxby et al. 1999; Sugiura et al. 2005). The “lingual landmark area” (Aguirre et al. 1998) seems to be involved in the recognition of stimuli with orienting value, and to be implicated in “landmark agnosia” (see Aguirre and D'Esposito 1999, for a review). The “parahippocampal place area” (PPA: Epstein and Kanwisher 1998) seems to be particularly implicated in the perception of the visuo-spatial structure of the local, immediate scene and on the selective discrimination of different views (Epstein et al. 2007; Park and Chun 2009), and has been associated with pure topographical disorientation (Habib and Sirigu 1987). Retrosplenial lesions, on the other hand, yield a kind of topographical disorientation, where patients cannot use well-recognized landmarks to find their way in familiar environments, as if they had lost their “heading” within the environment (Aguirre and D'Esposito 1999). This is in accordance with the discovery, in this region of the rat brain, of “head-direction cells”, which fire only when the animal maintains a certain heading or orientation within the environment (Chen et al. 1994). In the case of our experiment, however, an explanation in terms of passive exposure to environmental layouts cannot hold, as stimuli were exactly the same across conditions.

The dorsal precuneus and the posterior part of the inferior parietal lobule, near the temporo-parieto-occipital junction, also preferred the environment to the object and viewer frames. The precuneus, corresponding to monkey area PGM or 7m, participates to memory- and imagery-related processes (Fletcher et al. 1995), which are plausibly involved when recalling the visual scene in the environment-centered frame of reference. The precuneus is also responsive to optic flow inducing a strong sensation of self motion (e.g., Kovács et al. 2008), and during spatial updating of object coordinates (Wolbers et al. 2008). As for the temporo-parieto-occipital junction, it was found to be activated in several previous neuroimaging studies of orientation in large-scale space (e.g., Maguire et al. 1998b), and may correspond to the dorsal building-specific area described by Hasson et al. (2003).

Our proposal is that the selectivity of these regions for the environmental frame reflects the automatic activation of an enduring representation of the environment layout that occurs when processing the spatial location of objects that are permanently embedded in it. However, there are at least two alternative explanations that cannot be ruled out. First, distance estimation in the environment task may explicitly

require to mentally reconstruct the global environmental layout, because instructions require to locate the “long wing” of the building, which can only be recognized as such by means of its geometrical relationship with the short wings: although part of the long wing is always visible, the building is never visible in its entirety. Second, although the same stimuli were presented across conditions, allocation of visual attention to the building may exert a top-down modulation of activity in scene-selective or category-specific areas (Tong et al. 1998; O’Craven et al. 1999; Avidan et al. 2003). The building is also perceptually different from the red ball used as an unstable reference, is much bigger and more peripheral (see Hasson et al. 2003).

### Stability and enduring spatial representations: new experimental evidence

To disentangle between these alternative explanations, we designed a new fMRI experiment, which was performed on 11 healthy right-handed volunteers (7 females and 4 males; mean age 23 years; age range 20–29 years) on a Siemens Vision 1.5 T whole-body scanner operating at ITAB (Fondazione Università G. d’Annunzio, Chieti, Italy). Participants gave their written informed consent before being enrolled in the study, and experimental procedures received local ethics approval.

After familiarizing with a simplified version of the original virtual environment (see Fig. 2d), in three separate fMRI scans subjects alternated between (1) a “stable-frame” distance estimation task (determining which of the two garbage cans was closer to a stable environmental reference: see below); (2) an “unstable-frame” distance estimation task (determining which of the two garbage cans was closer to the red ball, whose position in space changed across trials); and (3) a non-spatial control task (indicating which of the two garbage cans was lying on the ground).

The stable frame varied across scans. One scan replicated the same design as in Committeri et al. (2004), with subjects using the long wing of the building as the reference object, which was always partially visible, such as in the example in Fig. 2a. In a second scan, subjects used the central circular fountain as the stable reference object. Unlike the building, which substantially contributes to define the geometrical layout of this particular environment, and has a peculiar shape, that may need to be explicitly considered to solve the task, the fountain does not define the geometrical structure of the surrounding layout in itself, but is a stable relevant landmark. It is embedded in a stable way in the environment and is perceptually salient, but, given its central position and its circular shape, is not a very informative landmark: it appears the same from any perspective, so it

does not help people to determine where they are in the arena. Furthermore, the fountain is always visible and subjects do not need to mentally reconstruct the overall environment layout to solve the task. It is also much smaller and less peripheral and in far space than the building, and in fact perceptually more similar to the red ball than to the building. In a third scan, to explicitly test for the idea that mental reconstruction of the environmental layout had a role in this paradigm, we forced mental reconstruction by presenting images where the building was never visible (see example in Fig. 2d). Here subjects again used the long wing of the building as the reference for distance judgment. This condition also tests for the importance of perceptual availability of the building: a hypothetical region with a selective response for buildings should be actually less activated in this condition.

Blood-oxygenation-level-dependent functional magnetic resonance images (Kwong et al. 1992) were acquired using gradient-echo echo-planar imaging with a standard quadrature head coil (26 contiguous axial slices, TR = 3.075 s, TE = 60 ms, flip angle = 90°, voxel size = 4 × 4 × 4 mm). In each scan, subjects performed eight 18-s blocks for each of the three alternating tasks in an interleaved order. Each block began with a 1.5-s written instruction, followed by a 1.5-s fixation cross, and comprised six 2.5-s trials, each composed by a 1-s snapshot of the environment and a 1.5-s fixation cross. After standard preprocessing procedures, a random-effects analysis was performed using SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London). Activations were thresholded at  $P < 0.05$ , corrected for multiple comparisons using false discovery rate (Genovese et al. 2002).

Regions more activated in at least one of the three stable frame conditions (fountain, visible building, and invisible building) relative to the corresponding unstable frame condition, are shown in Fig. 2e. Mean percent signal changes in these regions with respect to the non-spatial control condition, averaged across subjects and hemispheres, are plotted in Fig. 2f. A main effect of stability, with more activation for stable than unstable frames, was found in the bilateral PPA (left:  $F_{1,10} = 27.84$ ,  $P < 0.0005$ ; right:  $F_{1,10} = 46.83$ ;  $P < 0.0001$ ) and RSC (left:  $F_{1,10} = 7.54$ ,  $P < 0.05$ ; right:  $F_{1,10} = 31.96$ ;  $P < 0.0005$ ). Importantly, the bilateral RSC, but not the PPA, showed a significant stability by reference interaction (left:  $F_{2,20} = 17.04$ ,  $P < 0.0001$ ; right:  $F_{2,20} = 14.45$ ;  $P < 0.001$ ), due to a greater preference for stable frames in the invisible building condition than in the fountain (left:  $F_{1,10} = 33.28$ ,  $P < 0.0005$ ; right:  $F_{1,10} = 16.50$ ;  $P < 0.005$ ) and visible building conditions (left:  $F_{1,10} = 13.23$ ,  $P < 0.005$ ; right:  $F_{1,10} = 14.92$ ;  $P < 0.005$ ). The precuneus showed the same effects as the RSC, with a main effect of stability (left:  $F_{1,10} = 43.05$ ,  $P < 0.0001$ ; right:  $F_{1,10} = 61.34$ ;  $P < 0.0001$ ) and an



interaction due to a further specialization for the invisible building condition (left:  $F_{2,20} = 4.20$ ,  $P < 0.05$ ; right:  $F_{2,20} = 7.24$ ;  $P < 0.01$ ). Posterior to PPA, the left and marginally the right lingual gyrus also showed a significant stability by reference interaction (left:  $F_{2,20} = 3.78$ ,  $P < 0.05$ ; right:  $F_{2,20} = 3.11$ ;  $P = 0.064$ ), but in this case the advantage for stable versus unstable frames, which was present in the fountain and visible building condition, was abolished in the invisible building condition (interaction between visible and invisible conditions, left:  $F_{1,10} = 18.41$ ,  $P < 0.005$ ; right:  $F_{1,10} = 13.48$ ;  $P < 0.005$ ).

These results, besides merely confirming what reported by Committeri et al. (2004), provide two additional important observations. First, all regions showing enhanced activation for stable frames in the visible building condition, which directly replicates Committeri et al. (2004), show a comparable enhancement in the fountain condition, although the fountain is a relatively small object, has not a building-like appearance, does not contribute to define the geometrical structure of the environment, and has little orienting value. Furthermore, the fountain is always visible and subjects do not need to mentally reconstruct the overall environment layout to solve the task. The critical feature of the fountain is, however, that it is embedded in the environment in a stable way. This produces an automatic activation of the medial parietal and temporal cortex independently of the potential usefulness for spatial orientation of the information that the object provides.

Here, we propose “stability” as the critical factor in engaging this set of regions. Objects whose position is stable over time are normally associated with more global, invariant environmental representations. Stability is a prerequisite for spatial learning, i.e., for memorizing the locations of objects after repeated exposures, by associating them to other environmental features. Accordingly, rats learn to use landmarks to represent the location of a food reward only if landmarks maintain stable locations within a geometric frame of reference (Biegler and Morris 1993). Movable objects are instead not consistently associated with other environmental features over time and are not embedded into long-term environmental representations. These representations are automatically retrieved once subjects make use of geometrical information or landmarks, but not of objects that are perceived as unstable. Compatibly with this view, photographs of familiar buildings abstracted from their surroundings and placed on a white background lead to activation in the PPA and RSC more than unfamiliar buildings (Epstein et al. 1999; Epstein and Higgins 2007), probably because they are processed by subjects as partial scenes. These authors highlight that buildings are particular because they are prominent in defining the spatial structure of the surrounding environment, but here we show that these areas are engaged as well

by objects or landmarks that are not buildings and do not help to define the surrounding geometry, but are known to be stably part of it. This is the case even though these objects are not located at a decision point, useful for navigational purposes (Janzen and van Turenout 2004; Janzen 2006).

A second relevant aspect of the results is the difference between the visible and invisible building conditions. The RSC and the precuneus were more involved in the retrieval of a reference which was not actually visible, whereas PPA was not sensitive to the perceptual availability of the building. This is in accordance with the recent proposals of distinct and complementary roles for PPA and RSC in scene representation (Epstein and Higgins 2007; Park and Chun 2009): PPA would represent the visuospatial structure of the local scene and focus on selective discrimination of different views, whereas the RSC would support mechanisms of orientation within a wider environment (boundary extension) and allow the integration of different scenes under the same spatial context. Interestingly, the lingual gyrus posterior to PPA showed an opposite activation pattern, with a selectivity for stable frames only when landmarks were perceptually available. This pattern is consistent with the idea of a purely visual landmark-selective response (Aguirre et al. 1998).

## Conclusions

We have reviewed human functional neuroimaging studies, from our and other research groups, which have explicitly investigated the issue of which spatial reference frames are used for spatial computations in the human cerebral cortex.

Spatial frames of reference are traditionally classified into “egocentric” and “allocentric”, but we have shown that further qualification of these concepts is necessary when speaking about their neural basis. One particular form of egocentric reference frame comes from body referencing, i.e., the integration of spatial body knowledge (in the form of proprioceptive signals or motor efference copies) into visual and somatosensory maps, to produce representations of the location of a target stimulus with respect to relevant body parts. Converging evidence shows that the posterior parietal cortex and associated cortical fields in the premotor regions are the selective neural basis of this process, which is compatible, at the neuronal level, with a gross topographical organization in retinal coordinates. The posterior parietal cortex is not necessarily selective for any other form of “egocentric” frame, in the general meaning of a “viewer-dependent” representation or a “first-person” perspective.

Similarly, there are cortical regions selective for one particular form of allocentric reference frame, which are not simply selective for “allocentric” frames in the general

meaning of “viewer-independent” representations (which would include any form of “object-centered” encoding). This particular form of allocentric reference frame results from encoding the location of a target stimulus within a long-term cognitive representation of stable spatial features of a familiar environment. The novel fMRI study presented here, together with previous findings, indicates medial temporal regions, together with the RSC and the precuneus, as the selective neural basis of such process of environment-referencing.

Compatibly with two-system models of spatial memory (Berthoz 1997; Burgess 2006, 2008; Waller and Hodgson 2006), which would be simultaneously supported by both spatial updating of transient egocentric representations and by long-term enduring allocentric representations, we have shown that PPA and RSC are domain specific and selectively associated with global invariant spatial representations centered on stable features of the surrounding environment. The RSC is particularly involved when environmental information is not directly available to senses, and is localized within a wider imagined spatial context (comprising what is beyond the observer). In accordance with this, preliminary data from an fMRI study (Sulpizio et al. 2009) show that the RSC is selectively activated when a new environmental viewpoint must be registered to the memorized one, so that this region may play the pivotal role of interface between body and world centered reference frames. Interestingly, the use of our original perceptual paradigm in a pathological population of schizophrenic patients revealed that an egocentric reference frame is preserved, whereas adopting an allocentric frame and switching between egocentric and environment-centered frames are impaired (Landgraf et al. submitted). Perturbations in non-egocentric referencing and transferring efficiently between different referential systems might be the source of altered personal and social world comprehension in schizophrenia.

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