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NEURAL CORRELATES OF EGOCENTRIC AND ALLOCENTRIC FRAMES OF REFERENCE COMBINED WITH METRIC AND NON-METRIC SPATIAL RELATIONS

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The authors declare no competing financial interests

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Abstract

Spatial relations (SRs: coordinate/metric vs categorical/non metric) and frames of reference (FoRs: egocentric/body vs allocentric/external element) represent the building blocks underlying any spatial representation. In the present 7T fMRI study we identified for the first time the neural correlates of the spatial representations emerging from the combination of the two dimensions. A bilateral fronto-parietal network, more right sided, supported egocentric categorical representations. A right fronto-parietal circuitry was specialized for egocentric coordinate representations. A bilateral occipital network supported allocentric categorical representations. Finally, a smaller part of this bilateral network (i.e. Calcarine Sulcus and Lingual Gyrus), along with the right supramarginal and inferior frontal gyri, supported allocentric coordinate representations. The selective and overlapping neural activations reveals how our brain builds adaptive spatial representations in order to effectively react to specific environmental needs and task demands.

Keywords: frames of references, spatial relations, 7-tesla fMRI, fronto-parietal network, occipital lobe

Effective processing of visuo-spatial information is essential for how humans interact with the environment. This processing is characterized by the definition of a frame of reference (FoR), that is a ground object, or unit, to which places/positions can be referred (e.g. Paillard 1991; Klatzky 1998; Majid et al. 2004). We can encode positions either with respect to our body (*egocentric* FoR), or with respect to the external environment (*allocentric* FoR) (Postma and Koenderink 2017). A huge amount of behavioral and neurofunctional research work supports the distinction between egocentric and allocentric frames of reference by showing that the two FoRs can be differently influenced by several factors (e.g. age, gender, familiarity, kind of stimuli, response modality, etc.) (for relevant reviews: Burgess, 2006; Galati et al. 2010) and are supported by partially distinct neural networks (Galati et al. 2000; Committeri et al. 2004; Neggers et al. 2006; but see also: Driver and Pouget, 2000; Deneve and Pouget, 2003). Specifically, fMRI studies, using a variety of tasks, have revealed bilateral activity in fronto-parietal areas (i.e. inferior frontal gyrus, intraparietal sulcus, superior parietal lobule, and precuneus; more right-sided for egocentric) and (especially for allocentric) hippocampal formation and lingual gyrus (Galati et al. 2000; Committeri et al. 2004; Neggers et al. 2006; Zaehle et al. 2007; Thaler and Goodale 2011; Chen et al. 2014). In their original "two-streams hypothesis" Milner and Goodale (1995, 2008) argued that egocentric FoRs, supported by the dorsal stream, are useful for motor action, whereas the allocentric FoRs, supported by the ventral stream, are more useful for recognition (de Haan and Cowey 2011). Other lines of research have suggested that egocentric referencing is not just limited to visuo-motor actions but may play a role in other domains as well (perception, language communication, memory; Burgess, 2006).

Another distinction that is vital to visuospatial processing involves the quality or "grain" of the spatial relations between elements in the outside world (e.g. Kosslyn 1987). In one of his most cited works, Stephen Kosslyn (1987) has pointed out that spatial relations can be encoded at a level of metric detail (*coordinate* spatial relations (SRs)) or by means of non-metric specifications (*categorical* SRs). Sufficient evidence exists for it to be considered a clear binary, and lateralized distinction (for relevant reviews of behavioral, PET, fMRI, MEG, EEG, and TMS studies supporting this distinction, see: Jager and Postma 2003; Kosslyn 2006; van der Ham et al. 2014). For example, fMRI studies have shown increased activity in frontal areas and inferior parietal areas (specifically in the inferior frontal and angular gyrus; Slotnick and Moo 2006; van der Ham et al. 2009; Baciu et al. 1999; Amorapanth et al. 2010), more left-sided for categorical encoding and more right-sided for coordinate encoding. Furthermore, the difference between coordinate and categorical SRs would not only lie at the stimulus encoding level (distance estimations vs. categorization) but also in the kind of functions they support. According to Kosslyn (2006), metric spatial information (e.g. distances estimation/comparison) is used for motor actions, whereas nonmetric spatial information offers a more abstract, global and invariant spatial code (e.g. right/left, above/below) supporting memorization and scene/object recognition.

Central to the current study is how SRs and FoRs connect. It obviously goes without saying that, at least at a conceptual level, there is interdependency between SRs and FoRs: it is not possible to encode any spatial relation without having specified a FoR. That is, while the former specifies the grain of the spatial relation, the latter defines the point of reference to anchor it. Furthermore, functions similar to those attributed by Kosslyn (2006) to the coordinate and categorical SRs have been attributed by Milner and Goodale (1995, 2008) to the egocentric and allocentric FoRs respectively. This functional similarity between SRs and FoRs is probably due to their adaptive purposes. Action necessarily, but not exclusively, requires coordinate SRs and an egocentric perspective. For example, we need the exact distance between our hand and a mug to reach and grasp it. In contrast, recognition processes more strongly require categorical SRs and an allocentric

FoR. We recognize a mug as different from a bucket also by the position of the handle: the handle is on the top of the bucket but on the right/left side of the mug. In turn, other daily tasks could require a different combination of FoRs and SRs. For example, we need to compare metric distances between different places (i.e. allocentric coordinate representation) to decide the shortest pathway to follow, and we commonly use egocentric categorical representations to describe a place or to provide road information (e.g. "you will find the church on your right, then follow the street sign you will see above you" and so on….). These examples clearly show that specific combinations of SRs and FoRs support functionally different daily tasks. Importantly, this observation has already received support by various behavioral studies. Ruotolo and co-authors (2015; 2016) have shown that a task with motor characteristics (i.e. immediate action/pointing towards manipulable objects) facilitates metric judgments according to the body position (i.e. egocentric coordinate judgments), whereas a task with non-motor characteristics (i.e. memory based verbal responses about spatial location of non-manipulable objects) facilitates categorical judgments among elements of a configuration (i.e. allocentric categorical judgments). Finally, the combination of motor and non-motor features tends to favor the other two spatial combinations.

The foregoing results suggest that at least at behavioral level we can distinguish between four types of spatial representations: egocentric coordinate, allocentric coordinate, egocentric categorical, and allocentric categorical. However, as far as we know to the present day no study has examined whether these four basic spatial representations are supported by either overlapping, partially overlapping or by completely different neural networks. Results addressing this question will greatly advance our understanding of the cerebral architecture of visuospatial processing.

In the current study, participants perceived two vertical bars below a horizontal bar and were asked to judge if the two vertical bars were at same distance with respect to their own body midline (*egocentric coordinate task*) or with respect to the midline of the horizontal bar (*allocentric* *coordinate task*). In the categorical conditions participants had to decide whether the two vertical bars were on the same side with respect to their body midline (*egocentric categorical task*) or on the same side with respect to the midline of the horizontal bar (*allocentric categorical task*). In brief, the visual input (i.e. the stimuli) was exactly the same in all conditions, only the instructions guiding the decisions to be made and the corresponding spatial coding differed.

Images of brain activity were acquired through a 7-tesla MRI scanner while participants performed the visuo-perceptual judgments. In order to exploit the high spatial resolution of the 7 tesla scanner, MRI data acquisition was performed with partial brain coverage, thereby excluding the vast majority of the temporal lobe. On the basis of previous literature (Kosslyn 2006; Milner and Goodale 2008; and fMRI studies reported above), we hypothesized that the direct comparison between egocentric and allocentric conditions would have revealed that egocentric processing is mainly supported by fronto-parietal areas, with activations more right sided or left sided in presence of coordinate (ECO) or categorical (ECA) judgments respectively. Instead, allocentric processing should involve the lingual gyrus and probably some other occipital areas responsible of the visuo-spatial analysis of the external world (Kamps et al., 2016), with activations more right sided or left sided in presence of coordinate (ACO) or categorical (ACA) SRs respectively. However, since coordinate and categorical spatial relations have often been found supported by parietal areas (Galati et al., 2000; Committeri et al., 2004), it is possible that some parietal areas will be recruited during allocentric processing, especially during ACO processing due to the possible functional role of coordinate SRs in action-oriented tasks (Kosslyn, 2006).

Materials and Methods

Participants

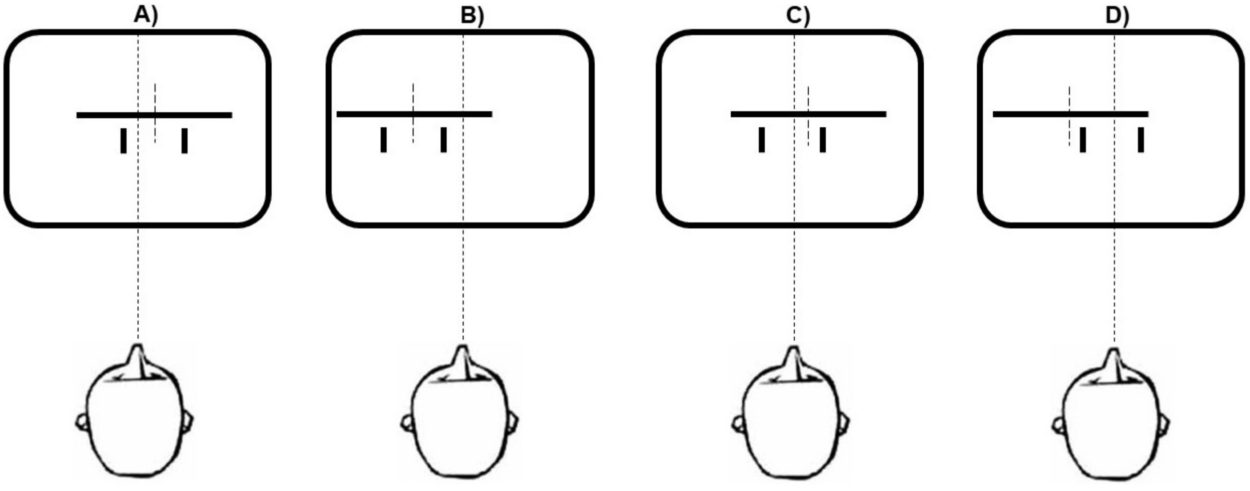
14 healthy participants (8 women, mean age 24, range 19-35) gave their written informed consent to participate in the experiment, whose procedures were approved by the ethics committee of the UMCU (University Medical Center Utrecht). All participants had normal vision and were right handed, as assessed by the Edinburgh Inventory (Oldfield 1971) (EHI score > 0.5).

Stimuli

Stimuli were back-projected on a transparent screen (width: 25°) placed on top of the transmit coil using a projector that was placed outside the scanner room. The participant viewed the screen through a mirror and prism glasses. Stimuli were displayed on a black background and were generated using the Presentation Software package by Neurobehavioral Systems Inc. The stimuli were presented around the vertical meridian of the screen (0° reference). Each stimulus consisted of two vertical white target bars (width X length: 0.1° X 0.4°; 24 bits RGB colour coding: 255, 255, 255; luminance 249 cd/m^2) placed below a white horizontal bar (width X length: 0.1° X 4.7°; 24 bits RGB colour coding: 255, 255, 255; luminance 249 cd/m^2) or below a grey horizontal bar (24 bits colour coding RGB: 63, 63, 63; luminance 17.1 cd/m^2).

The two vertical bars could be positioned at the same distance (SD) but on different sides (DS) with respect to the body-midline (EgoSDDS), at the same distance but on different sides with respect to the center of the horizontal bar (AlloSDDS), at a different distance (DD) and on different sides with respect to the body-midline (EgoDDDS), at a different distance and on different sides with respect to the center of the horizontal bar (AlloDDDS), at a different distance but on the same side (SS) with respect to the body midline (EgoDDSS), at a different distance but on the same side with respect to the horizontal bar (AlloDDSS) (see Figure 1). The stimuli were built up by following some constraints: a) When the two vertical bars were at the same distance with respect to the body midline they were at different distances with respect to the horizontal bar; b) When the two vertical bars were at different distances with respect to the body midline they were at the same distance with respect to the horizontal bar; c) When the two vertical bars were on the same side with respect to the body midline they were on different sides with respect to the horizontal bar; d) When the two vertical bars were on different sides with respect to the body midline they were on the same side with respect to the horizontal bar.

As a consequence, four kinds of stimuli configurations were obtained: EgoDDDS_AlloSDDS, EgoSDDS_AlloDDDS, EgoDDSS_AlloSDDS, EgoSDDS_AlloDDSS. Stimuli were initially built up by placing the two vertical bars at different distances and on different sides with respect to the body midline or to the horizontal bar. A total of six metric levels were chosen: 4 mm, 6 mm, 8 mm, 10 mm, 12 mm, 14 mm. Each metric level was obtained by placing the two vertical bars in four different positions with respect to the egocentric or allocentric reference point. For example, a metric level of 4 mm in DDDS configurations could be obtained by placing one of the two vertical bars at 6 mm and the other at 10 mm on different sides with respect to the reference point. Instead, the other three positions of the two vertical bars could be: 4 mm (on the Left) and 8 mm (on the Right), 2mm and 6mm, 8mm, and 12mm. So, in all trials, judgements about the position of the two vertical bars were based on a metric difference of 4 mm. By following the same logic, metric levels of 6, 8, 10, 12, and 14 mm were obtained. A total of 48 stimuli were obtained (2 reference points X 6 metric levels X 4 vertical bars). Furthermore, in order to get the same metric levels for the other configurations, either the horizontal bar or the entire stimulus was displaced. In the egocentric condition, for each egocentric position of the two vertical bars, the center of the horizontal bar could appear rightmost or leftmost, with respect to the center of the screen. The amount of displacement created the same metric levels as indicated above. In this way the target positions with respect to the body midline remained the same, but irrelevant allocentric information—that is, the center of the horizontal bar—varied. Instead, in the allocentric condition the entire stimulus configuration could be rightmost or leftmost with respect to the center of the screen. Therefore, the allocentric positions of the two vertical bars remained the same, but irrelevant egocentric information—that is, the position of the target with respect to the extension of the body midline—varied. This procedure ensured an independent variation of ego- and allocentric stimulus coordinates. In sum a total of 96 stimuli were obtained. Importantly, in half of the stimuli the horizontal bar had the same luminance as the vertical bar, in the other half it was reduced (see above for the description).



EGODDDS_ALLOSDDS EGODDSS_ALLOSDDS EGOSDDS_ALLODDDS EGOSDDS_ALLODDSS

Figure 1. Stimuli Configuration. The figure shows an example for each of the four kinds of stimuli configuration. To make the example easier to follow, the stimuli have been enlarged with respect to original dimensions. The two vertical bars can be positioned at the same distance (SD) but on different sides (DS) with respect to the body-midline (EGOSDDS), at the same distance but on different sides with respect to the center of the horizontal bar (ALLOSDDS), at a different distance (DD) and on different sides with respect to the body-midline (EGODDDS), at a different distance and on different sides with respect to the center of the horizontal bar (ALLODDDS), at a different distance but on the same side (SS) with respect to the body midline (EGODDSS), at a different distance but on the same side with respect to the horizontal bar (ALLODDSS).

Cognitive tasks

Participants observed the stimulus and were instructed to give one of four types of spatial judgments: a) were the two vertical bars at the same distance with respect to your body midline? (egocentric coordinate task); b) were the two vertical bars on the same side with respect to your body midline? (egocentric categorical task); c) were the two vertical bars at the same distance with respect to the center of the horizontal bar? (allocentric coordinate task); d) were the two vertical bars on the same side with respect to the center of the horizontal bar? (allocentric categorical task).

So, the visual stimuli were always the same it was the spatial coding instruction that changed. Furthermore, in some blocks participants were required to indicate if the two vertical bars had the same luminance as the horizontal bar (color task; please note that the data from this condition were analyzed but not reported due to the reasons indicated in the "Limitations" section of the current manuscript). Finally, participants were required to fixate on a fixation cross without giving any kind of response during the resting period.

Apparatus

High resolution functional data were acquired using a Philips 7T scanner (Best, Netherlands) in combination with a 32-channel receive head coil (Nova Medical, MA, USA). Head motion inside the scanner was minimized using foam padding, and subjects wore earplugs for noise-cancellation.

Procedure

Each stimulus corresponded to a trial. A trial started with the presentation of a grey fixation cross (width X length: 0.1° X 0.4°; 24 bits colour coding RGB: 63, 63, 63; luminance 17.1 cd/m^2) at the centre of the screen. Participants were instructed to fixate the fixation cross for 1000 msec (one second); next the cross disappeared, and they had to maintain ocular fixation at the center of the black screen for other 1000 msec. Afterwards, one of the stimuli was presented for 200 msec (two hundred milliseconds), and participants had 2000 msec (two seconds) to give the response. This procedure was very similar to that used by Neggers and colleagues (2005, 2006) and by Ruotolo and colleagues (2011b). In these studies, and in a pilot experiment aimed at selecting stimuli for the current one, it was verified that participants were able to maintain their gaze at the center of the screen for the time requested for each trial and each stimulus received just one saccade. In addition, it is important to highlight that participants were explicitly told that the projection of their body midline was aligned with the fixation cross. This was made to prevent possible difficulties for participants in establishing their egocentric reference. Furthermore, data from the above mentioned studies assured us that participants were able to keep their egocentric reference even when the fixation cross disappeared. Specifically, in the pilot study an infrared camera monitoring participants' eye movement was used and results showed that participants were able to prevent eye movements on 95% of the trials (as also found by Posner, Nissen, and Odgen, 1978).

The 96 stimuli were first randomized and then organized in 19 blocks (18 blocks contained five stimuli each and one block six stimuli). The same blocks were used for all the spatial tasks. This resulted in 19 blocks for Egocentric Coordinate judgments, 19 blocks for Egocentric Categorical judgments, 19 blocks for Allocentric Coordinate judgments, 19 blocks for Allocentric Categorical judgments. 9 blocks were used for the Color task, and 9 were used for rest (passive fixation). The length of the resting block was the same as of the tasks (i.e. 26 seconds). Resting blocks were included as in a pilot study participants reported that the switching from one task to another was too demanding. Blocks were organized in sequences. Each sequence comprised one block that was repeated five times, each for a different spatial judgment and for the color/resting condition. A sequence never contained the same task twice. The sequences were created by randomizing the sequence of blocks. For an example of a trial, block and sequence and their temporal duration see Figure 2. Finally, the sequences were organized in five scanning sessions, 4 sessions contained 4 sequences and 1 session contained 3 sequences. The order of the sequences was randomized for each participant. The total duration of the tasks was 45 minutes and 50 seconds.

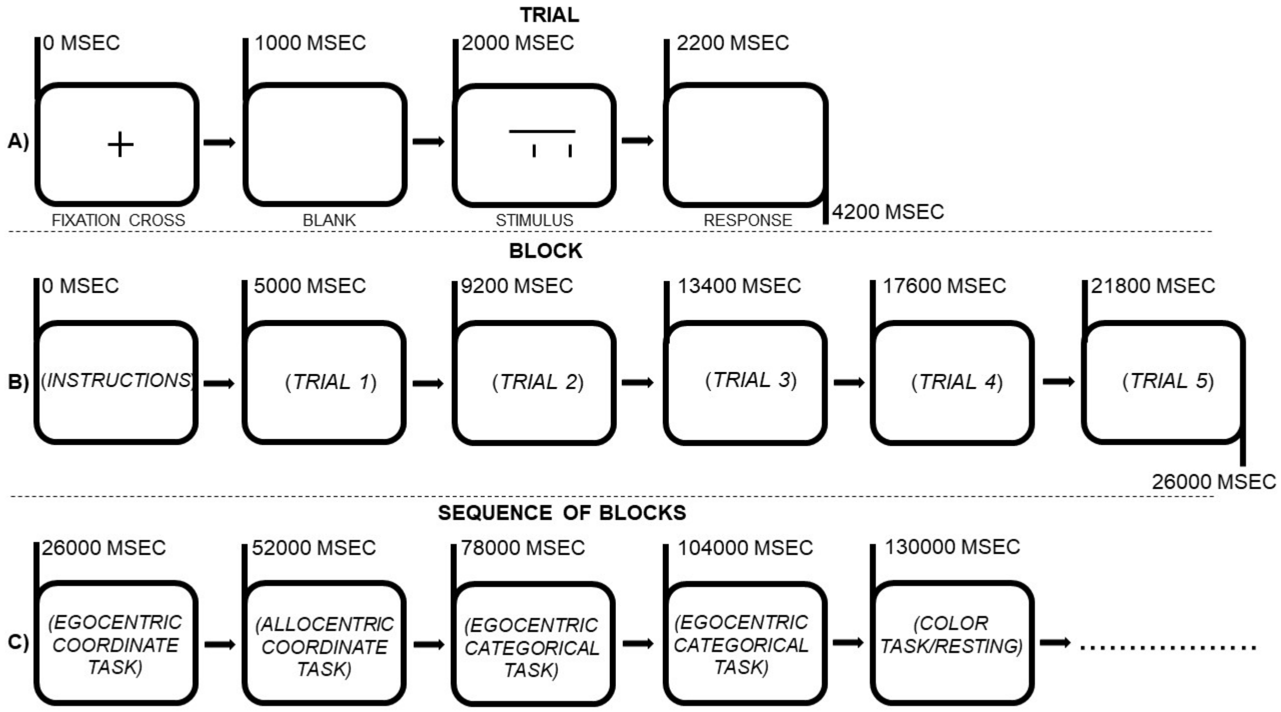


Figure 2. Trial, Block, and Sequence. The figure shows an example of trial (a), block (b), and sequence (c); a) each trial started with a fixation cross (1000 msec), followed by a blank screen and after 1 second a stimulus was presented for 200 milliseconds. Participants had 2 seconds to provide the answer; b) each block started with the instructions. Instructions were presented for 5 seconds. The following instructions could appear: BODY SIDE (egocentric categorical task); BODY DISTANCE (egocentric coordinate task); BAR SIDE (allocentric categorical task); BAR DISTANCE (allocentric coordinate task). After this, five trials were presented: c) each sequence included the four spatial tasks and the color or the resting block.

Image Processing and Analysis

Structural images

The T1 image was corrected for field inhomogeneities by dividing the T1 weighted image by the proton density image (van de Moortele 2009). A surface reconstruction was made based on the T1-weighted image using the Freesurfer pipeline (Fischl et al. 2002). Freesurfer's automatic parcellation of cortical and subcortical areas was included in the pipeline, which resulted in 45 regions of interest (Destrieux et al., 2010) for each subject. The only exclusion criteria adopted for the rest of the areas (29) was that they were not well detected due to the partial brain coverage during the acquisition phase (e.g. orbitofrontal and mainly temporal areas). This parcellation method uses geometric information derived from the individual cortical model in addition to neuroanatomical convention.

Functional images

All functional images were spatially preprocessed using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/). The preprocessing entailed the realignment of all functional scans to the mean functional scan, slice time correction, and coregistration. The T1 image was coregistered to the functional volume space using an affine transformation with normalized mutual information as cost function. The T1 image and the parcellation were interpolated on the functional space using nearest neighbor interpolation.

Statistical analysis

A first level-statistical analysis was performed using SPM12. A design matrix was constructed using separate factors for each spatial task and the control task. The design was estimated resulting in a regressor coefficient for each voxel and each factor in the design matrix. Subsequently, we calculated the mean regressor coefficients for every ROI, which were used for the second level analysis. All the analyses were performed on the spatially un-smoothed data in the original, single-subject space.

Two separate contrasts on categorical (Table 1 and 2) and coordinate (Table 3) SRs were calculated in order to estimate which regions were more active during egocentric compared to allocentric spatial judgments and vice-versa. Similarly, two separate contrasts on egocentric (Table 4) and allocentric judgments (Table 5) were performed to reveal brain activity underlying categorical and coordinate SRs. In other words, we computed the mean signal for each spatial condition relative to each other and performed paired t tests on these data.

For each ROI, one-sample t-tests were performed to determine if the change in Blood Oxygenation Level Dependent (BOLD) signal (expressed by beta values) was significantly different from 0. Outliers, identified by Thompson's tau technique (1985), with an opposite sign with respect to the average of the group were removed. These data corresponded to 2.7% of the entire dataset.

We also checked for lateralization of the mean signal of each hemisphere (i.e. the average activity of all selected ROIs of right and left hemisphere separately), and determined if the activity differed from zero. Results of the latter check are reported in a separate subparagraph.

Since a total of 360 t-tests were carried out (45 right ROIs x 4 contrasts: 180 + 45 left ROIs x 4 contrasts: 180), we decided to control for Type I errors by adjusting the alpha level with the False Discovery Rate control method (Benjamini and Hochberg, 1995) with q= 0.05.

ROIs with increased activity in both right and left hemispheres (at least p = 0.0085 *corrected*) are indicated as "bilateral activity".

Only for the purpose of visualization, we projected the most relevant T-maps on the MNI surface template. It is important to note that the following steps have been followed only to visualize the data in a standardized space. Single-subject GLM maps, defined in the original single-subject space, were projected into the standard template space, inverting the affine transform derived from the coregistration, obtaining coregistered GLM maps. The co-registered maps were then spatially smoothed using a Gaussian kernel (sigma=1mm), and for each voxel and T map, we tested whether the mean T-stat across all our participants differed significantly from zero. The resulting T-maps are reported thresholded at p<0.05, uncorrected, with a minimum cluster size of 50 contiguous voxels. Results are projected over the reconstructed surface of the template brain.

Results

Behavioral results: Accuracy and Response Times. Behavioural data were successfully collected from all the 14 scanned participants while performing the task in the scanner. Mean accuracy was well above chance for all judgments: 70% (sd: .14) for Egocentric Coordinate judgments, 80% (sd: .14) for Egocentric Categorical judgments, 86% (sd: .11) for Allocentric Coordinate judgments, 83% (sd: .09) for Allocentric Categorical judgements. Results from the repeated measures ANOVA (2X2: Egocentric/Allocentric X Coordinate/Categorical) showed that egocentric coordinate judgments were significantly less accurate than all other judgments, F(3, 39)=10.34, $p < .00005$, $\eta_p^2 = .44$; post-hoc: Bonferroni. No significant differences were found for response times, F<1, (738.24 msec (sd: 73.71) for egocentric coordinate judgments; 723.22 msec (sd: 79.04) for egocentric categorical judgments; 730.89 msec (sd: 95.37) for allocentric coordinate judgments; 755.33 msec (sd: 90.77) for allocentric categorical judgments.

fMRI results

Frames of Reference (FoRs).

Egocentric vs Allocentric categorical judgments. Results of the direct comparison between egocentric (egocentric minus allocentric) and allocentric (allocentric minus egocentric) FoRs are reported in Tables 1 and 2 respectively. In general terms, we observed increased activation in frontal and parietal areas with egocentric judgements, and in occipital areas and interlobar fissures with allocentric judgments (see Figure 4). In more specific terms, starting from the frontal lobe the egocentric judgments increased the activity in the right Superior Frontal Gyrus and Sulcus, and in the Middle Frontal Gyrus. Moreover, a bilateral increased activity in the Inferior Frontal Gyrus (triangular part) and Sulcus, and in the Precentral Sulcus (inferior and superior part) was also observed. Moving on the parietal lobe, egocentric judgments increased the activity bilaterally in the Supramarginal Gyrus, in the Intraparietal sulcus and Angular gyrus, and only in the right hemisphere in the Superior Parietal Gyrus, Sulcus Intermedius (of Jensen) and Precuneus. Finally, increased activity in the right Short Insular Gyrus was found (see Figure 3). Regarding allocentric judgments, we specifically observed increased bilateral activity in the Calcarine Sulcus, Posterior Transverse Collateral Sulcus, Cuneus and Lingual Gyrus. Increased activity only in the right hemisphere was observed in Anterior and Middle Occipital Sulcus, Lateral Sulcus, Subcentral Gyrus and Long Insular Gyrus (see Figure 3).

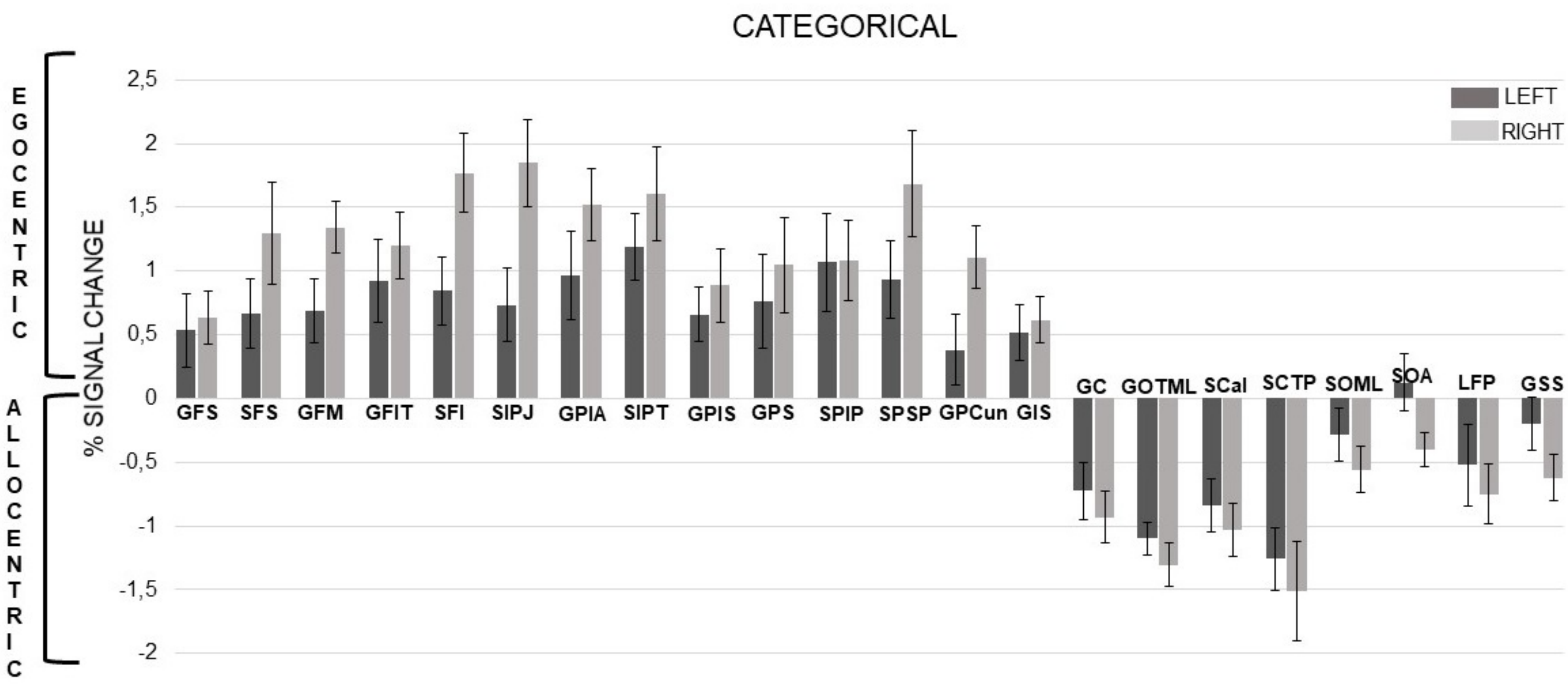


Figure 3. The figure represents percentage of signal change for egocentric (on the top) and allocentric (on the bottom) judgments for all the selected ROIs (starting from the frontal lobe on the left to the occipital pole on the right side of the graph). **GFS**= Superior frontal gyrus; **SFS**= Superior frontal sulcus; **GFM**= Middle frontal gyrus; **GFIT**= Triangular part of the inferior frontal gyrus; **SFI**= Inferior frontal sulcus; **SIPJ**= Sulcus intermedius primus (of Jensen); **GPIA**= Angular gyrus; **SIPT**=Intraparietal sulcus (interparietal sulcus) and transverse parietal sulci; **GPIS**= Supramarginal gyrus; **GPS**= Superior Parietal gyrus; **SPIP**= Inferior part of the precentral sulcus; **SPSP**= Superior part of the precentral sulcus; **GPCun**= Precuneus; **GIS**= short insular gyrus; **GC**= Cuneus; **GOTML**= Lingual gyrus, lingual part of the medial occipito-temporal gyrus; **SCal**= Calcarine sulcus; **SCTP**= Posterior transverse collateral sulcus; **SOML**= Middle occipital sulcus and lunatus sulcus; **SOA**= Anterior occipital sulcus and preoccipital notch (temporo-occipital incisure; **LFP**= Posterior ramus (or segment) of the lateral sulcus (or fissure); **GSS**= Subcentral gyrus (central operculum) and sulci

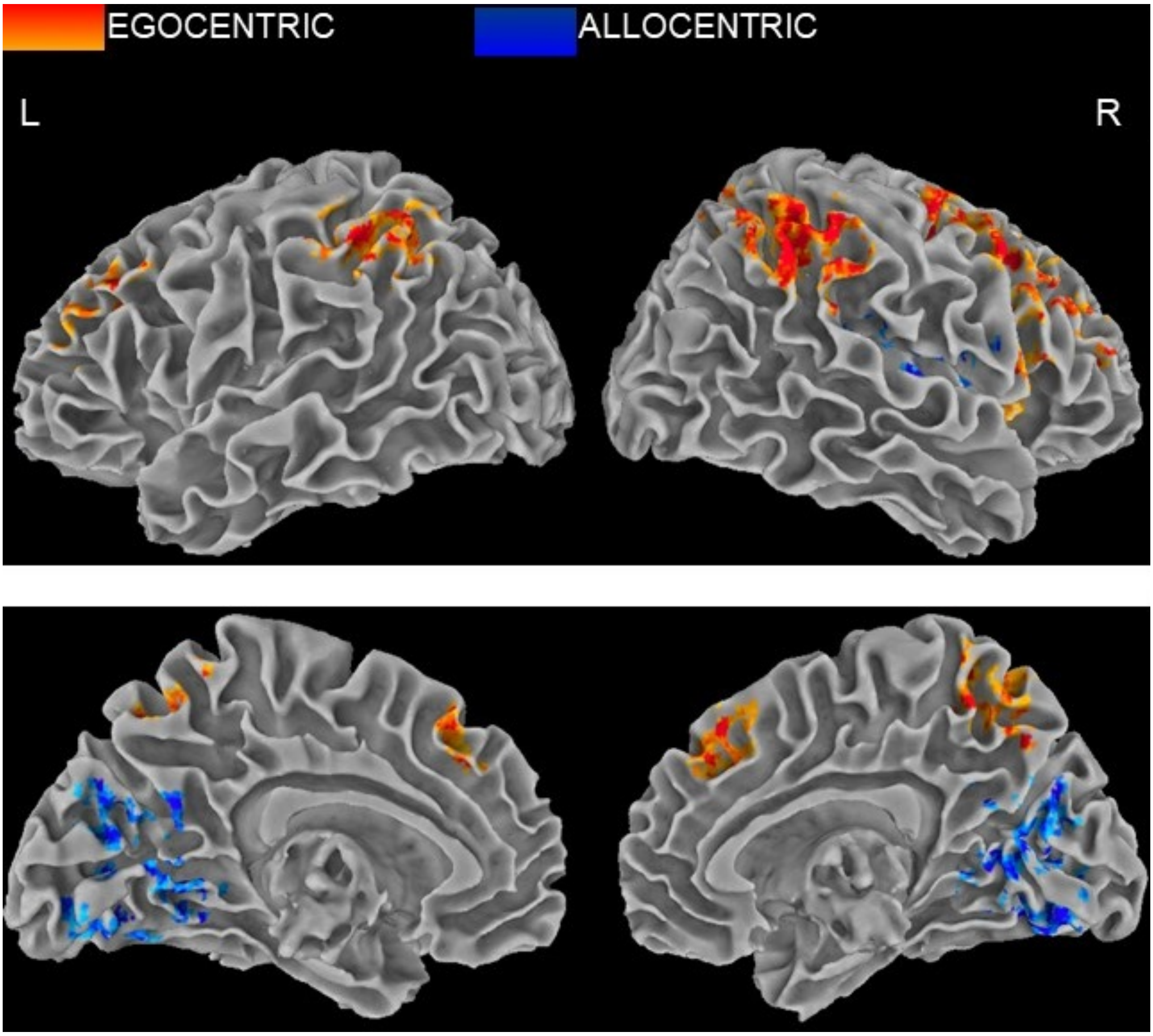


Figure 4. The Figure shows increased bilateral activity in fronto-parietal areas for ECA coding (in red-orange) and increased bilateral activity in occipital areas for ACA coding (in blue). Images of the brain and have been obtained by averaging the results of all participants, superimposed to MNI. The threshold of p is set to 0.05 (uncorrected) and with a minimum cluster size of 50 contiguous voxels. R= right; L= left.

Egocentric vs Allocentric coordinate judgments. Results of the direct comparison between egocentric (egocentric minus allocentric) and allocentric (allocentric minus egocentric) FoRs are reported in Tables 3. In general terms, egocentric judgments led to increased activation mainly in frontal and parietal areas, while allocentric judgments led to increased activation in occipital areas (See Figure 6). As regards egocentric judgments, starting from the frontal lobe an increased activity was found in the right hemisphere in the Superior Frontal Gyrus, Inferior Frontal Gyrus (opercular part) and Sulcus, and in the Precentral Sulcus (superior part). Moreover, a bilateral increased activity in the Inferior Frontal Gyrus (triangular part) and Sulcus was observed. When zooming in on the parietal lobe, egocentric judgments led to increased activity in the right hemisphere in the Supramarginal Gyrus, Intraparietal Sulcus, Angular Gyrus, Precuneus, and bilaterally in the Sulcus Intermedius Primus. Finally, an increased activity in the right Inferior Occipital Gyrus was found (see Figure 5). Regarding allocentric judgments, we observed an increased bilateral activity in the Calcarine Sulcus and in the Lingual Gyrus (see Figure 5).

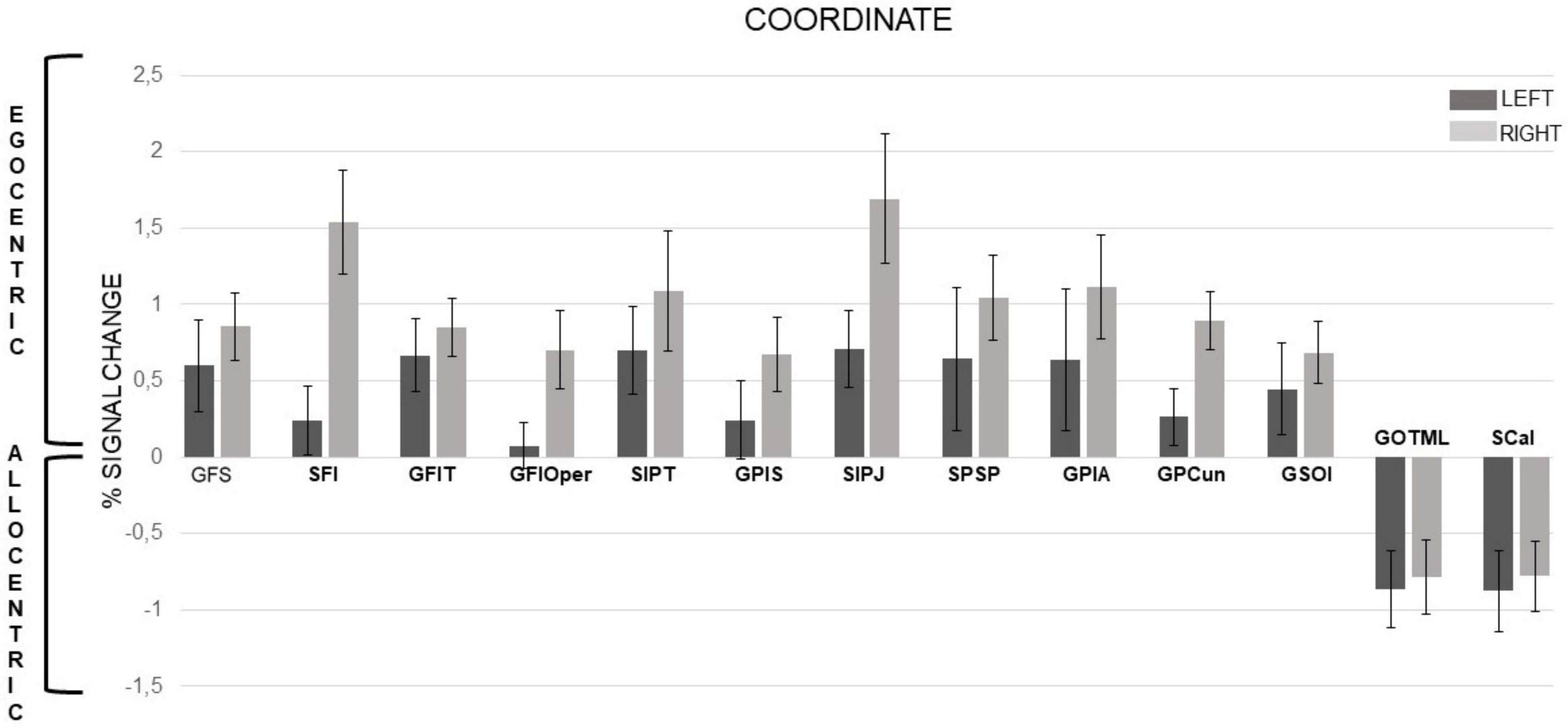


Figure 5. The figure represents percent of signal change for egocentric (on the top) and allocentric (on the bottom) judgments for all the selected ROIs (starting from the frontal lobe on the left to the occipital pole on the right side of the graph). **GFS=** Superior frontal gyrus; **SFI=** Inferior frontal sulcus; **GFIT=** Triangular part of the inferior frontal gyrus; **GFIOper=** Opercular part of the inferior frontal gyrus; **SIPT=**Intraparietal sulcus(interparietal sulcus) and transverse parietal sulci; **GPIS=** Supramarginal gyrus; **SIPJ=** Sulcus intermedius primus (of Jensen); **SPSP=** Superior part of theprecentral sulcus; **GPIA=** Angular gyrus; **GPCun**= Precuneus; **GSOI**= Inferior occipital gyrus (O3) and sulcus; **GOTML**= Lingual gyrus, lingual part of the medial occipito-temporal gyrus; **SCal**= Calcarine sulcus

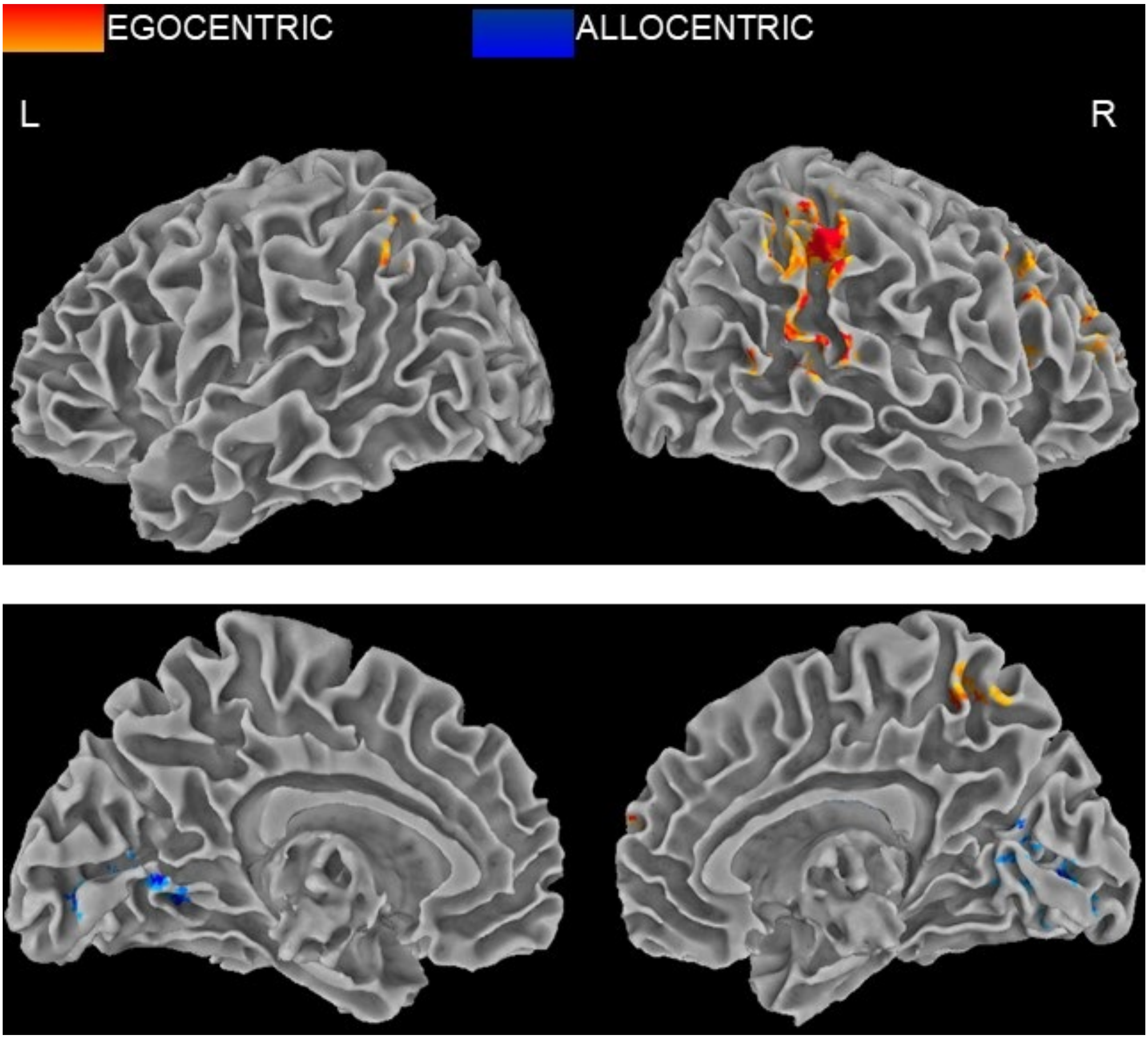


Figure 6. The Figure shows increased right activity in fronto-parietal areas for ECO coding (in red-orange) and increased bilateral activity in occipital areas for ACO coding (in blue). Images of the brain and have been obtained by averaging the results of all participants, superimposed to MNI. The threshold of p is set to 0.05 (uncorrected) and with a minimum cluster size of 50 contiguous voxels. R= right; L= left.

Spatial Relations (SRs).

Categorical vs Coordinate egocentric judgments. Results of contrasts between coordinate (coordinate minus categorical) and categorical (categorical minus coordinate) SRs within the egocentric reference frame are reported in Table 4. Regarding coordinate judgments, increased activity was observed only in the right hemisphere, but the effect was not statistically significant.

Instead, increased activity was found in the left Inferior Frontal Sulcus and the right Superior Frontal Sulcus for categorical judgments.

Categorical vs Coordinate allocentric judgments. Results of contrasts between coordinate (coordinate minus categorical) and categorical (categorical minus coordinate) SRs within the allocentric reference frame are reported in Table 5. As regards coordinate judgments, we observed an increased activity in the right Supramarginal Gyrus and Inferior Frontal Gyrus (Triangular part). As regards categorical judgments, increased bilateral activity was observed in the Posterior Transverse Collateral Sulcus and Posterior Lateral Sulcus. Moreover, categorical judgments activated the left Calcarine Sulcus and, on the right side, the Lingual Gyrus, Middle Occipital Sulcus, Occipital Pole and Central Sulcus.

Lateralization.

The contrasts between FoRs within each SR showed differential patterns of lateralization ($\alpha_{critical}$= .012). As regards categorical relations, egocentric judgments activated a total of 17 brain areas of which 7 on both sides and 10 on the right side (ECA > ACA: see Table 1), while allocentric judgements activated 10 brain areas of which 4 on both sides and 6 on the right side (see Table 2). In both cases, the average brain activities differed from zero for both sides (ECA right t= 5.35 p= .00006 df= 13; ECA left t= 3.30 p= .0028 df= 13; ACA right t= 5.67 p= .001 df= 13; ACA left t= 3.85 p = .001 df= 13). As regards coordinate relations, egocentric judgments (ECO > ACO) activated 11 brain areas of which 9 on the right side and 2 on both sides (see Table 3) but the average brain activities differed from zero only on the right side (ECO right t= 3.97 p= .0008 df= 13; ECO left t= 1.83 p= .045). Instead, allocentric judgments activated two bilateral areas (see Table 3) and the average brain activities differed from zero for both sides (ACO right t= 3.15 p= .0038 df= 13; ACO left t= 3.29 p= .0029). In sum, all combinations activated both hemispheres except the egocentric coordinate judgment that was essentially linked to the right hemisphere.

We now focus on the contrasts between SRs within each FoR. As regards egocentric frames, coordinate judgments (ECO >ECA) activated only right brain areas but the effects did not survive the corrections for multiple comparisons. The categorical judgments (ECA>ECO) significantly activated one area on the right and one area on the left; three areas on the left side were also activated but the effects did not survive the corrections. As regards allocentric frames, coordinate judgments significantly activated two right areas and the average right brain activities differed from zero (ACO right t= 3.14 p= .0039 df= 13; ACO left t= .35 p= .36 df= 13). Categorical judgments activated 2 bilateral areas, 1 area on the left side and 4 areas on the right side, and the average brain activities differed from zero for both sides (ACA right t= 3.84 p= .001 df= 13; ACA left t= 2.60 p= .011 df= 13). The overall pattern of results suggests that the categorical processing relies on bilateral areas while the coordinate processing seems more linked to the right side.

Discussion

The aim of this work was to advance our understanding of the neurocognitive architecture underlying fundamental visuo-spatial processing by exploring the neural correlates of egocentric and allocentric FoRs, combined with coordinate and categorical SRs.

Below we discuss the distinct brain areas that support the adoption of an egocentric or allocentric reference system, first during categorical and then during coordinate judgments. Subsequently, we focus on the direct comparison between categorical and coordinate judgments within the same reference system. Only areas with a statistically significant increased activity will be discussed (at least p = .00875).

Frames of reference

In general, the comparison between egocentric and allocentric frames combined with categorical relations showed that the egocentric processing is mainly supported by areas in frontal and parietal lobes. These results are in line with previous literature showing that a parieto–frontal premotor network, bilateral but more active on the right, is usually associated with spatial localization according to the body midsagittal plane (Vallar et al., 1999; Galati et al., 2000; Galati et al., 2001). Importantly, the comparison between egocentric and allocentric frames combined with coordinate relations demonstrated that only a subpart of this fronto-parietal-network on the right hemisphere supports the processing of metric spatial information related to the body (see the following sections). Instead, the comparison between allocentric and egocentric categorical judgments revealed that the allocentric processing was supported by bilateral activity mainly in the occipital lobe.This is consistent with previous studies of spatial localization according to external objects (Committeri et al., 2004; Galati et al., 2000). Finally, the direct comparison between egocentric and allocentric coordinate judgments showed that a subpart of these areas supported allocentric coordinate processing.

Now we focus on the specific contribution of brain areas in the different lobes involved in egocentric and allocentric FoRs.

Parietal Lobe. As regards the role of the parietal lobe in the egocentric categorical judgments, the results showed increased activity in the Superior Parietal Gyrus, the Sulcus Intermedius Primus (of Jensen), the Angular Gyrus, the Supramarginal Gyrus, the Intraparietal Gyrus and the Precuneus. The involvement of the Superior Parietal Gyrus confirms its key role in the egocentric processing (see also Galati et al. 2000; Committeri et al. 2004). Milner and Goodale (1995) and Simon and colleagues (2004) showed that visuospatial and manual tasks, which imply an egocentric encoding, activated more superior regions of the posterior parietal cortex. Lesions in these regions led to impairments in visually guided pointing and reaching tasks (e.g. in optic ataxia; Perenin 1997). We also found that the egocentric categorical combination engaged the Intraparietal Sulcus. The reason why the Intraparietal Sulcus is more involved in egocentric than allocentric judgments can be found in the numerous studies that have found it implicated in the encoding of peripersonal space

(Hyvärinen, 1981; Rizzolatti et al., 1981; Colby et al., 1993; Graziano and Gross, 1993) and in tasks requiring visuo-motor coordination of hand movements with respect to targets (Chaminade and Decety, 2002; Simon et al., 2002; Grefkes et al., 2004; Binkofski et al., 1998; Shikata et al., 2003; Frey et al., 2005).

As regards the Precuneus, it seems involved in egocentric disorders (Perenin and Vighetto, 1988; Levine et al., 1978; Ruggiero et al., 2014), probably due to its role in "maintaining one's bearing" (Hartley et al., 2003) during mental navigation in an environment learned from a route perspective (Mellet et al., 2000). Moreover, the Supramarginal Gyrus is probably more involved in egocentric than allocentric judgments because of its role in the interpretation of tactile information as well as in the perception of the space and location of the limbs (Naito et al., 2005; Goble et al., 2012; Ben-Shabat et al., 2015). Similarly, the bilateral activation of the Angular Gyrus is due to its involvement in memory retrieval, attention and spatial cognition, for example it would support the spatial analysis of external sensory information and the subsequent creation of internal mental representations (for review, see Sack 2009, Seghier, 2013). Remarkable is also the activation of the Sulcus Intermedius Primus (of Jensen) that divides the inferior parietal lobule into supramarginal (anterior) and angular (posterior) gyri. Jensen's sulcus runs, approximately perpendicular to the intraparietal sulcus, towards the temporal lobe (Destrieux et al., 2010). As far as we know, Brown and colleagues (Brown et al. 2004) report an anatomical anomaly of this area in the Turner syndrome, which entails visuo-spatial deficits, but without making any claims about its function. In our study this area was detected by the contrasts between egocentric and allocentric judgments for both categorical and coordinate relations. This may suggest a specific involvement in the encoding of spatial information in relation to the body rather than to external elements.

Finally, the comparison between egocentric and allocentric coordinate judgments revealed that all the above mentioned brain areas, with the exception of the Superior Parietal Gyrus, were significantly active mostly on the right hemisphere during egocentric coordinate judgments.

Frontal Lobe. The activity of the **frontal lobe** increased during egocentric rather than allocentric categorical tasks, and this is probably due to its role in attentional mechanisms in connection with the parietal lobe. Corbetta and colleagues (for reviews: Corbetta et al. 2008; Chica et al., 2013) have proposed the existence of two attentional networks: the Dorsal Attention Network (DAN) and Ventral Attention Network (VAN). The DAN is characterized by the Frontal Eye Fields (contained in the Precentral Sulcus; see Blanke et al., 2000; Grosbras et al., 2005), the Superior Parietal Gyrus and the Intraparietal Sulcus. This network supports endogenous processes such as attending to a stimulus at a certain location and preparing a subsequent motor response (Shulman et al., 1999; Corbetta et al., 2000; Rushworth et al., 2001). Instead the VAN, characterized by the Temporo-Parietal Junction, Middle and Inferior Frontal Gyrus, Anterior Insula and some parts of the inferior parietal lobe, works as an alerting system directing the attention to unattended or low-frequency events. As suggested by several authors, the DAN and VAN works together to direct attention towards task-relevant targets and filter out distracters (Rosen et al., 1999; Friedman-Hill et al., 2003; Hahn et al., 2006; Buschman and Miller, 2007; Weissman and Prado, 2012). In fact, during the egocentric tasks participants had to filter out the horizontal bar and focus their attention just on the two vertical bars related to their body-midline. This did not happen during the allocentric tasks where the stimulus had to be analyzed as a whole and no attentional filtering was necessary. Finally, even though the Superior Frontal Lobe is not included in the above mentioned attentional networks, it was found implicated in shifts of spatial attention (Yantis et al. 2002). Again, the comparison between egocentric and allocentric coordinate judgments revealed that all the above mentioned frontal areas, with the exception of the Middle Frontal Gyrus and the inferior part of the Precentral Sulcus, were significantly activated mainly on the right hemisphere during egocentric coordinate judgments.

Overall, Galati and colleagues (2000) suggested that the biological significance of this fronto-parietal network is "*probably related to the preparation of goal-directed movements (such as orienting the head and eyes towards an object, reaching, or grasping it), which require coding of the position of the target with respect to the motor effectors*". Results from the current study show that when the "*coding"* with respect to the body is of "metric" kind (i.e. egocentric coordinate judgments), only a subpart of this fronto-parietal network on the right hemisphere is specifically involved. This would confirm that the right, but not the left, hemisphere is particularly sensitive to metric spatial relations (Kosslyn 2006), especially when combined with an egocentric reference frame (Iachini et al. 2009).

Occipital Lobe. As regards the occipital lobe, the comparison between allocentric and egocentric categorical judgements showed that the allocentric ones increased the bilateral activation in the Cuneus, Lingual gyrus, Calcarine sulcus, and Posterior Transverse Collateral Sulcus. Furthermore, increased activation during allocentric categorical judgments was found in the right Anterior and Middle Occipital Sulcus. The involvement of the Cuneus, the Lingual gyrus and the Calcarine sulcus has already been shown in past studies. For example, Chen and colleagues (2014) found these brain areas more active when participants were required to adopt an allocentric rather than egocentric strategy to solve a reaching task. Moreover, the Lingual Gyrus seems to have a crucial role in the recognition of salient spatial stimuli since lesions in this area often cause ''landmark agnosia'' (i.e. inability to use salient environmental features for orientation; for a review: Aguirre and D'Esposito 1999). In fact, increased activity in the Lingual Gyrus, along with that in the parahippocampus, has been associated with the simple passive viewing of buildings/scenes (Aguirre et al. 1998; Epstein and Kanwisher 1998; Haxby et al. 1999). Similarly, the Middle Occipital Sulcus has been found to process the visuo-spatial features of the perceived scenes (Dumoulin et al., 2000, Wandell et al., 2007). Finally, two additional brain areas that were more active during allocentric than egocentric categorical judgments are the Anterior Occipital Sulcus and the Posterior Transverse Collateral Sulcus. The Anterior Occipital Sulcus originates in the preoccipital notch on the ventral margin of the hemisphere and marks the boundary between the temporal lobe rostrally and the occipital lobe caudally. Instead, the Posterior Transverse Collateral Sulcus is a branch of the medial occipito-temporal sulcus. These areas are parts of the occipito-temporal ventral stream of the brain (Milner and Goodale, 1995) and as such they could have a role in the allocentric spatial processing. Some authors suggest a strong relationship between the low-level visual information processed by these areas and that processed in the parahippocampus (Baldassano et al., 2013), which is involved in the processing of detailed spatial edges/structure of a scene (Rajimehr et al. 2011, Walther et al. 2011). Furthermore, it has been proposed that this occipito-temporal network would be responsible for the encoding of spatial information according to an external reference frame (Zaehle et al. 2007; Thaler and Goodale 2011; see also Milner and Goodale, 1995).

As happened for the egocentric coordinate judgments, the <u>allocentric coordinate</u> ones only activated a subpart (i.e. Calcarine sulcus and Lingual Gyrus) of the areas activated by the allocentric categorical judgments. This may lead to think that allocentric coordinate representations have more specific functions with respect to the allocentric categorical ones. The direct comparison between the two different allocentric judgements helps to clarify this point (see *Spatial Relations* section). What instead appeared from this comparison is an increased activation of the right Inferior Occipital Gyrus during egocentric, but not allocentric, coordinate judgments. The right occipital gyrus is usually indicated as the “occipital face areas” and it has been found more active when participants, had to discriminate between faces, that are body-related elements, and objects (Rossion et al., 2003). This explanation along with the fact that allocentric coordinate task involve less occipital areas might justify the increased activation of the inferior occipital gyrus during egocentric coordinate rather than categorical judgments.

Finally, some other areas result from the direct comparison between egocentric and allocentric reference frames. For example, the Short and the Long Insular Gyri were particularly active during egocentric and allocentric categorical judgments respectively. Ghaem and colleagues (1997) found that the insula was involved when participants imagined to navigate through a previously learned path. Therefore, it is possible to hypothesize about a distinct role of the Short Insular Gyrus in providing egocentric spatial information due to its connection to the frontal lobe and of the Long Insular Gyrus in providing allocentric spatial information due to its connection with temporo-parietal areas (Türe et al., 1999). Both egocentric and allocentric representations would then be both used during navigation (Burgess, 2006). Peculiar is also the increased activation observed in the right posterior part of the Lateral Sulcus and in right Subcentral Gyrus and Sulcus during allocentric rather than egocentric categorical judgments. The Lateral Sulcus separates the frontal and parietal lobes from the temporal lobe, whereas the Subcentral Gyrus, which may lie in the Lateral Sulcus (Petrides, 2014), is a U-shape gyrus that connects the pre- and postcentral gyri (Wagner et al., 2013). As far as we know, the Lateral Sulcus may contain, at least in monkeys, areas involved in spatial awareness and exploration (Grüsser et al., 1990; Chakraborty and Thier, 2000), whereas the Subcentral Gyrus is involved in the circuit of language (Gabrieli et al., 1998). This would suggest that these areas would specifically support attributions of verbal spatial categories (right-left) to external, not-body related, references. In fact, these areas are not present when egocentric and allocentric coordinate judgements are compared.

Spatial Relations.

Now we focus on the specific contribution of the brain areas involved in categorical and coordinate spatial relations within each frame of reference.

As regards the egocentric reference frame, coordinate relations led to increased activation in areas within the right hemisphere but no one survived the multiple testing correction procedure. Instead, categorical spatial relations mainly activated areas on the left side of the hemisphere and only one on the right hemisphere. However only the effects for the left Inferior Frontal Sulcus and right Superior Frontal Sulcus survived the multiple testing correction procedure. Overall, these results are in line with Kosslyn's suggestions (2006) that coordinate spatial relation are more right lateralized and categorical spatial relations more left lateralized Specifically, the involvement of the left Inferior Frontal Sulcus during categorical judgments could be due to its role in language functions (for a review: Costafreda et al. 2006). This finding would reinforce the idea that there is an innate link between categorical spatial relations and language (Kosslyn 2006). Instead, the increased activation in the Superior Frontal Sulcus could be due to the fact that during categorical judgments participants were required to shift their attention from one side of the screen to the other one to decide if the target bars were, or were not, on different sides (Yantis et al., 2002). This mechanism was probably less necessary during metric distance judgments.

As regards the allocentric reference frame, categorical judgments increased activation in areas of the occipital lobe (i.e. left Calarine Sulcus, right Lingual Gyrus, right Middle Occipital Sulcus, right Occipital Lobe and Posterior Transverse Collateral Sulcus bilaterally) and the posterior part of the Lateral Sulcus bilaterally. Moreover, categorical judgments activated the right Central Sulcus and the right Subcentral Gyrus and sulcus. This would suggest that allocentric categorical information is mainly processed in areas involved in the visuo-spatial analysis of scenes or object according to an external reference and involved in language processing (Subcentral gyrus and sulcus). Interestingly, the Central Sulcus is more involved during the processing of external, not body-related stimuli. Instead, coordinate spatial relations increased activity in the right Supramarginal Gyrus and in the right Inferior Frontal Gyrus. The Supramarginal gyrus, located inferiorly to the intra-parietal sulcus and in proximity to the Temporo-Parietal Junction, is crucially involved in judging the symmetry of bisected lines (Oliveri and Vallar 2009) and the location of a visual stimulus with respect to another object or the body (Galati et al 2000). Furthermore, the right Supramarginal Gyrus along with the

Inferior Frontal Gyrus is implied in tasks requiring strategic orienting of attention (Perry and Zeki 2000; Corbetta et al. 2008). In sum, this evidence indicates that distance judgments according to an external reference frame recruit a subpart of the brain areas involved in the egocentric coordinate judgments. Finally, in line with what happened during egocentric judgements, brain activity during coordinate as compared to categorical allocentric judgments increased significantly in the right, but not in the left, hemisphere. Instead, bilateral activity was again observed during categorical judgements.

In sum, the comparisons between egocentric and allocentric frames of reference on one side, and between categorical and coordinate spatial relations on the other side, seem to suggest distinct brain areas supporting the four kinds of spatial combinations. Specifically, the egocentric-categorical combination activated bilateral, but more right sided, parieto-frontal areas. This network could be involved in both planning and execution of actions by identifying the broad spatial category of a target in relation to our body (e.g. the cup is on my right). The left-side activity might suggest that this spatial attribute is mediated semantically (i.e. attribution of a spatial category). Instead, the egocentric coordinate combination involved only a part of this network and on the right hemisphere. This points out that, in line with what suggested by both Kosslyn (2006) and Milner and Goodale (1995), the metric encoding according to the body would play a specific role during the on-line control of immediate actions towards elements in space (e.g. reaching positions). The allocentric-categorical combination activated bilateral occipital and occipito-temporal areas. These areas are mainly devoted to recognition by analyzing more stable, object-object relations among elements in space. Processes involving body and action seem to not be rooted here. Finally, the allocentric-coordinate combination engaged bilateral occipital areas, the right supramarginal gyrus and the right inferior frontal gyrus. This would support the idea that the processing of the metric relations between elements in the environment is useful for action planning in our cluttered environments as well as recognition of fine details.

This pattern of results is in general in line with our hypotheses that these four spatial representations can be distinguished at a neural level.

Before concluding, it is important to address some critical issues. One might argue that differential fMRI activations between conditions could be due to different task difficulties, i.e. egocentric coordinate judgments were less accurate than other spatial judgments. However, some arguments may be brought against this issue. First, at behavioural level the four spatial judgments did not differ in terms of response time. This suggests that the number of processes/computations involved during the different spatial judgments was quite similar (Lohman, 1989). Instead, the low accuracy of egocentric coordinate judgments can be explained by the characteristics of the task. As already shown in previous studies, irrelevant allocentric cues (i.e. highly salient horizontal bar) may negatively affect egocentric coordinate judgments (e.g. Ruotolo et al. 2011b; Bridgeman et al. 1997, 2000; see Neggers et al., 2006; Liu et al., 2017). In our task, it is possible that the behavioral responses for "same" trials were affected by the target bars seen as illusorily displaced. However, when an egocentric coordinate task requires a visuo-motor rather than a visuo-perceptual response modality, the illusory effect disappears and the task becomes more accurate than its allocentric counterpart (Bruno et al., 2008; Bruno and Franz, 2009). Second, if egocentric coordinate judgments had been more difficult than others, they should have caused more increased brain activations. On the contrary, we found either no difference or even lower activation for egocentric coordinate (*less accurate*) than egocentric categorical (*more accurate*) judgments.

Another critical issue regards the fixation cross that participants could have used as an allocentric cue in the egocentric task. To prevent (or mitigate) this spurious effect a 1 second delay between fixation cross and stimulus presentation was added. This procedure has been commonly used in previous fMRI works about Egocentric and Allocentric FoRs (ex. Galati et al., 2000; Neggers et al., 2007) as well as in our behavioral studies (Ruotolo et al., 2011a,b). Even if the fixation cross played a role during the encoding phase we might speculate that this information has been eventually converted into a body-centred coordinate framework (see also Galati et al., 2001). In fact, our data clearly show the involvement of distinct brain areas during egocentric and allocentric judgments: fronto-parietal areas more active during egocentric judgments and occipital areas more active during allocentric judgments.

Conclusions

Our aim was to identify the neural correlates of four basic spatial representations resulting from the combination of FoRs and SRs. As a strength, the same set of visual stimuli was presented in the four spatial combinations and a 7 tesla MRI scanner was used. Only the instruction differed between conditions and dictated the specific way in which the stimuli had to be processed. The results show that different patterns of cerebral areas were recruited depending on the kind of spatial combination. However, a clearer and wider pattern was linked to the egocentric vs allocentric rather than coordinate vs categorical comparison. In an ideal hierarchy of basic spatial architecture, therefore, frames of reference should play a primary role over spatial relations (see Ruotolo et al. 2011a). Moreover, each spatial combination, which should be involved in different behavioral purposes, is correlated with a specific pattern of neural activations. This might suggest that the functional modulation of these neural activations is rooted in adaptive functions and obey to environmental needs.

Limitations of the current study

One of the limitations of this study is the partial coverage of the brain during the brain images acquisition phase. This has prevented the exploration of the temporal lobe, which is believed to support allocentric, but not egocentric, representations. According to the cognitive map theory (O'Keefe and Nadel 1978), the spatial relationships among the elements of a configuration are stored in the hippocampus.

A second limitation of this study refers to the fact that the use of egocentric coordinate representations was explored with a visual-perceptual judgment task that limited the accuracy of this type of judgment (see discussion section). Egocentric coordinate representations are indeed more useful for the on-line control of the movement (e.g. reaching for an object). Therefore, future studies are necessary in which the acquisition of brain activity is carried out while participants perform a reaching or pointing tasks in the four different spatial conditions.

A final limitation of this study could be the absence of a non-spatial control condition for the four spatial representations. As a matter of fact, even if a number of 6 blocks had been added in which participants had to judge the luminance of the stimuli, data from this condition are not reported. This was done because the luminance judgment seemed to work better as a control for the allocentric (both presumably processed by occipital and temporal areas) than for the egocentric judgments. Future studies are necessary to verify which of the areas found in the current study is specifically involved in spatial information processing rather than in the analysis of other characteristics of the presented stimuli.

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Table 1. Regions activated by the egocentric categorical with respect to allocentric categorical task and vice versa. Areas marked with an asterisk were significant after correction for multiple comparisons

Contrast	Regions	Right/Left	t-value	p-value
ECA > ACA	**Superior Frontal gyrus***	**R**	**2,88**	**0,00640**
	Superior Frontal gyrus	L	1,77	0,04982
	Superior Frontal sulcus*	**R**	**3,22**	**0,00336**
	Superior Frontal sulcus	L	2,38	0,01660
	Middle Frontal gyrus*	**R**	**6,14**	**0,00002**
	Middle Frontal gyrus	L	2,71	0,00898
	Middle Frontal sulcus	R	2,18	0,02374
	Inferior Frontal gyrus (Triang.)*	**R**	**4,52**	**0,00029**
	Inferior Frontal gyrus (Triang.)*	**L**	**2,82**	**0,00726**
	Inferior Frontal gyrus (Opercular)	R	2,31	0,01886
	Inferior Frontal sulcus*	**R**	**5,35**	**0,00007**
	Inferior Frontal sulcus*	**L**	**3,14**	**0,00388**
	Precentral sulcus (superior part)*	**R**	**3,78**	**0,00113**
	Precentral sulcus (superior part)*	**L**	**2,89**	**0,00623**
	Precentral sulcus (inferior part)*	**R**	**3,49**	**0,00196**
	Precentral sulcus (inferior part)*	**L**	**2,76**	**0,00802**
	Angular gyrus*	**R**	**5,03**	**0,00011**
	Angular gyrus*	**L**	**2,79**	**0,00766**
	Intraparietal sulcus*	**R**	**4,14**	**0,00058**
	Intraparietal sulcus*	**L**	**4,27**	**0,00045**
	Sulcus intermedius primus*	**R**	**5,42**	**0,00006**
	Sulcus intermedius primus	L	2,54	0,01240
	Supramarginal gyrus*	**R**	**3,04**	**0,00474**
	Supramarginal gyrus*	**L**	**3,18**	**0,00360**
	Superior Parietal gyrus*	**R**	**2,79**	**0,00760**
	Superior Parietal gyrus	L	2,05	0,03073
	Precuneus*	**R**	**4,25**	**0,00048**
	Middle occipital gyrus	R	1,95	0,03672
	Short insular gyrus*	**R**	**4,16**	**0,00061**

ECA= egocentric categorical; *ACA= allocentric categorical*

Table 2. Regions activated by the egocentric categorical with respect to allocentric categorical task and vice versa. Areas marked with an asterisk were significant after correction for multiple comparisons

Contrast	Regions	Right/Left	t-value	p-value
ACA > ECA	**Lingual gyrus***	**R**	**7,07**	**0,00000**
	Lingual gyrus*	**L**	**7,78**	**0,00000**
	Calcarine sulcus*	**R**	**4,78**	**0,00018**
	Calcarine sulcus*	**L**	**4,02**	**0,00072**
	Post. Trans. collateral sulcus*	**R**	**3,85**	**0,00100**
	Post. Trans. collateral sulcus*	**L**	**4,77**	**0,00018**
	Cuneus*	**R**	**4,31**	**0,00042**
	Cuneus*	**L**	**3,08**	**0,00439**
	Middle occipital sulcus*	**R**	**2,91**	**0,00610**
	Anterior occipital sulcus*	**R**	**2,85**	**0,00679**
	Occipital pole	R	2,38	0,01676
	Superior occipital gyrus	L	1,91	0,03616
				0,00330
	Post. Lateral sulcus *	**R**	**3,23**	
				0,00335
	Subcentral gyrus and sulcus *	**R**	**3,22**	
				0,01513
	Inf part of sulcus of Insula	R	2,43	0,03476
	Inf part of sulcus of Insula	L	1,98	**0,00045**
	Long Insular gyrus*	**R**	**5,42**	
				0,01899
	Post-Ventr p. of the cingulate gyrus	R	2,31	0,01678
	Post-Ventr p. of the cingulate gyrus	L	2,38	0,04893
	Post-Dors p. of the cingulate gyrus	L	1,78	

ECA= egocentric categorical; *ACA= allocentric categorical*

Table 3. Regions activated by the egocentric coordinate with respect to allocentric coordinate task and vice versa. Areas marked with an asterisk were significant after correction for multiple comparisons

Contrast	Regions	Right/Left	t value	p-value
ECO > ACO	**Inferior Frontal gyrus (Triang) ***	**R**	**4,45**	**0,00033**
	Inferior Frontal gyrus (Triang) *	**L**	**2,80**	**0,00751**
	Inferior Frontal sulcus*	**R**	**4,29**	**0,00044**
	Inferior Frontal gyrus (Operc) *	**R**	**2,73**	**0,00851**
	Superior Frontal gyrus*	**R**	**3,67**	**0,00140**
	Superior Frontal gyrus	L	1,91	0,03953
	Middle frontal gyrus	R	2,48	0,01370
	Precentral sulcus (Sup. Part.) *	**R**	**3,53**	**0,00184**
	Precentral sulcus (Inf. Part.)	R	2,16	0,02515
	Precentral gyrus	R	1,83	0,04535
	Central sulcus	R	1,80	0,04741
	Paracentral lobule and sulcus	R	1,84	0,04433
	Precuneus*	**R**	**4,13**	**0,00060**
	Sulcus intermedius primus*	**R**	**4,00**	**0,00075**
	Sulcus intermedius primus*	**L**	**2,81**	**0,00734**
	Angular gyrus*	**R**	**3,26**	**0,00308**
	Angular gyrus	L	2,03	0,03159
	Supramarginal gyrus*	**R**	**2,74**	**0,00842**
	Superior Parietal gyrus	R	2,62	0,01059
	Intraparietal sulcus*	**R**	**2,78**	**0,00788**
	Intraparietal sulcus	L	2,28	0,01997
	Inferior occipital gyrus*	**R**	**3,22**	**0,00338**
	Anterior occipital sulcus	R	1,85	0,04381
ACO > ECO	**Calcarine Sulcus***	**R**	**3,18**	**0,00356**
	Calcarine Sulcus*	**L**	**3,14**	**0,00390**
	Lingual Gyrus*	**R**	**3,21**	**0,00339**
	Lingual Gyrus*	**L**	**3,02**	**0,00487**
	Cuneus	R	2,34	0,01776
	Cuneus	L	2,16	0,02498
	Post. trans collateral sulcus	R	1,84	0,04401

ECO= egocentric coordinate; ACO= allocentric coordinate

Table 4. Regions activated by the egocentric coordinate with respect to egocentric categorical task and vice versa. Areas marked with an asterisk were significant after correction for multiple comparisons

Contrast	Regions	Right/Left	t value	p-value
ECO > ECA	Subcentral gyrus	R	2,39	0,01611
	Central sulcus	R	1,77	0,04974
	Lateral sulcus	R	1,85	0,04387
	Precentral gyrus	R	1,87	0,04193
ECA > ECO	**Inferior Frontal sulcus***	**L**	**4,31**	**0,00042**
	Superior Frontal sulcus*	**R**	**2,78**	**0,00779**
	Lateral Occipito-Temporal sulcus	L	2,22	0,02246
	Inferior part of the Precentral sulcus	L	1,88	0,04154
	Inferior frontal gyrus (Opercular)	L	1,87	0,04189

ECO= egocentric coordinate; ECA= egocentric categorical

Table 5. Regions activated by the allocentric coordinate with respect to allocentric categorical task and vice versa. Areas marked with an asterisk were significant after correction for multiple comparisons

Contrast	Regions	Right/Left	t value	p-value
ACO > ACA	**Supramarginal gyrus***	**R**	**3,40**	**0,00234**
	Supramarginal gyrus	L	2,46	0,01426
	Inferior Frontal gyrus (Triang)*	**R**	**2,83**	**0,00710**
	Short insular gyrus	L	2,38	0,01663
	Precentral sulcus (Inf. Part)	**R**	1,79	0,04813
	Precentral sulcus (Inf. Part)	L	1,81	0,04679
	Precentral sulcus (Sup. Part)	**R**	1,82	0,04591
ACA > ACO	Calcarine Sulcus	R	2,61	0,02500
	Calcarine Sulcus*	**L**	**3,63**	**0,00151**
	Lingual gyrus*	**R**	**3,34**	**0,00264**
	Lingual gyrus	L	**2,68**	**0,00944**
	Middle occipital sulcus *	**R**	**2,94**	**0,00573**
	Middle occipital sulcus	L	2,01	0,03271
	P. Transverse collateral sulcus*	**R**	**4,47**	**0,00016**
	P. Transverse collateral sulcus*	**L**	**4,82**	**0,00031**
	Occipital pole*	**R**	**2,94**	**0,00572**
	Post. Lateral sulcus*	**R**	**3,50**	**0,00124**
	Post. Lateral sulcus*	**L**	**3,74**	**0,00193**
	Occipital Anterior sulcus	**R**	2,25	0,02120
	Cuneus	**R**	2,13	0,02627
	Superior Occipital gyrus	**L**	1,99	0,03344
	Inferior occipital gyrus and sulcus	**L**	1,91	0,03914
	Central Sulcus*	**R**	**3,38**	**0,00243**
	Subcentral gyrus and sulcus*	**R**	**3,15**	**0,00384**
	Paracentral sulcus	R	1,89	0,04034
	Paracentral sulcus	L	2,63	0,01037
	Postcentral gyrus	R	2,07	0,02926
	Circular sulcus of the insula (Inf)	R	2,04	0,03082
	Circular sulcus of the insula (Inf)	L	1,83	0,04530
	Long insular gyrus	R	2,25	0,02118

ACO= allocentric coordinate; ACA= allocentric categorical