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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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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 7-T fMRI study we have identified for the first time the neural correlates of the spatial representations emerging from the combination of the two dimensions. The direct comparison between the different spatial representations revealed a bilateral fronto-parietal network, mainly right sided, that was more involved in the egocentric categorical representations. A right fronto-parietal circuitry was specialized for egocentric coordinate representations. A bilateral occipital network was more involved in the 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 the allocentric coordinate representations. The fact that some areas were more involved in a spatial representation than in others reveals how our brain builds adaptive spatial representations in order to effectively react to specific environmental needs and task demands. © 2019 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: frames of references, spatial relations, 7-T fMRI, fronto-parietal network, occipital lobe.

Effective processing of visuo-spatial information is essential for human interaction 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/posi-

tions 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 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 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 limited to visuo-motor actions alone, but may also play a role in other domains (perception, language communication, memory; Burgess, 2006).

Another vital distinction for visuo-spatial processing concerns the quality or "grain" of the spatial relations between the elements of 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 the level of metric detail (coordinate spatial relations (SRs)) or by means of non-metric specifications (categorical SRs). There is sufficient evidence to consider it 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; Baciu et al., 1999; Slotnick and Moo, 2006; van der Ham et al., 2009; 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 lie not only at the level of stimulus encoding (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 non-metric 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 specifying a FoR. That is, while the former determines 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 coordinate and categorical SRs have been attributed by Milner and Goodale (1995, 2008) to 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 according to 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 according to 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 underlie functionally different daily tasks. Importantly, this observation has already received support by various behavioral studies. Ruotolo et al. (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, no study has examined whether these four basic spatial representations show different patterns of neural activations. Results addressing this question will greatly advance our understanding of the cerebral architecture of visuo-spatial 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); and if 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-T MRI scanner while participants performed the visuo-perceptual judgments. Because of small slice thickness, and restricted number of attainable slices within a workable TR (repetition time), the field of view was limited, among others excluding the vast majority of the temporal lobe and the orbitofrontal cortex. 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 reveal that egocentric processing is mainly supported by Fronto-Parietal areas, with more right-sided or left-sided activations in the 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 again more right-sided or left-sided activations in the 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).

EXPERIMENTAL PROCEDURES

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 × length: $0.1° × 0.4°$; 24 bits RGB color coding: 255, 255, 255; luminance 249 cd/m^2) placed below a white horizontal bar (width × length: $0.1° × 4.7°$; 24 bits RGB color coding: 255, 255, 255; luminance 249 cd/m^2) or below a gray horizontal bar (24 bits color 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 Fig. 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.

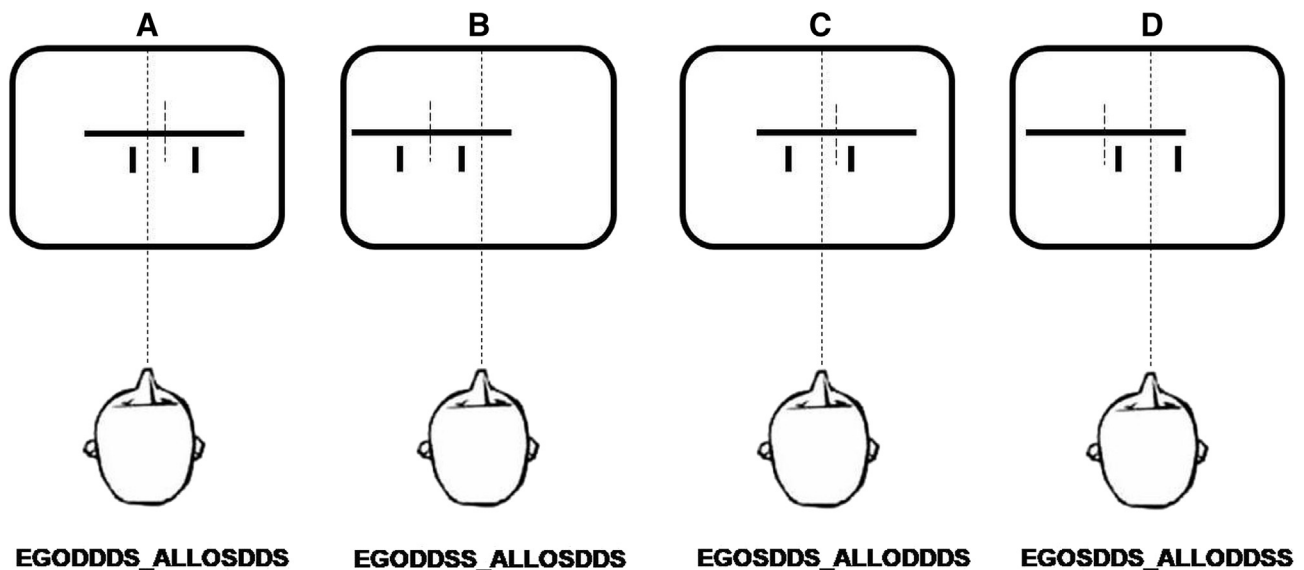| A	B	C	D
EGODDDS_ALLOSDDS	EGODDSS_ALLOSDDS	EGOSDDS_ALLODDDS	EGOSDDS_ALLODDSS

Fig. 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). Panel A illustrates vertical bars at different distances and on difference sides with respect to the body, but at same distance and on different sides with respect to the horizontal line; panel B illustrates vertical bars at different distances and on same side with respect to the body, but at same distance and on different sides with respect to the horizontal line; panel C illustrates vertical bars at same distance and on different sides with respect to the body, but at different distances and on difference sides with respect to the horizontal line; panel D illustrates vertical bars at same distance and on different sides with respect to body, but at different distances and on same side with respect to the horizontal line.

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), 2 mm and 6 mm, 8 mm, and 12 mm. So, in all trials, judgments 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 × 6 metric levels × 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).

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 "Discussion" 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 7-T 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 gray fixation cross (width × length: 0.1° × 0.4°; 24 bits color coding RGB: 63, 63, 63; luminance 17.1 cd/m^2) at the center of the screen. Participants were instructed to fixate the fixation cross for 1000 ms (1 s); next the cross disappeared, and they had to maintain ocular fixation at the center of the black screen for other 1000 ms. Afterwards, one of the stimuli was presented for 200 ms, and participants had 2000 ms (2 s) to give the response. This procedure was very similar to that used by Neggers et al. (2005, 2006) and by Ruotolo et al. (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 movements was used and results showed that participants were able to prevent eye movements on 95% of the trials (as also found by Posner et al., 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 s). 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 included 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
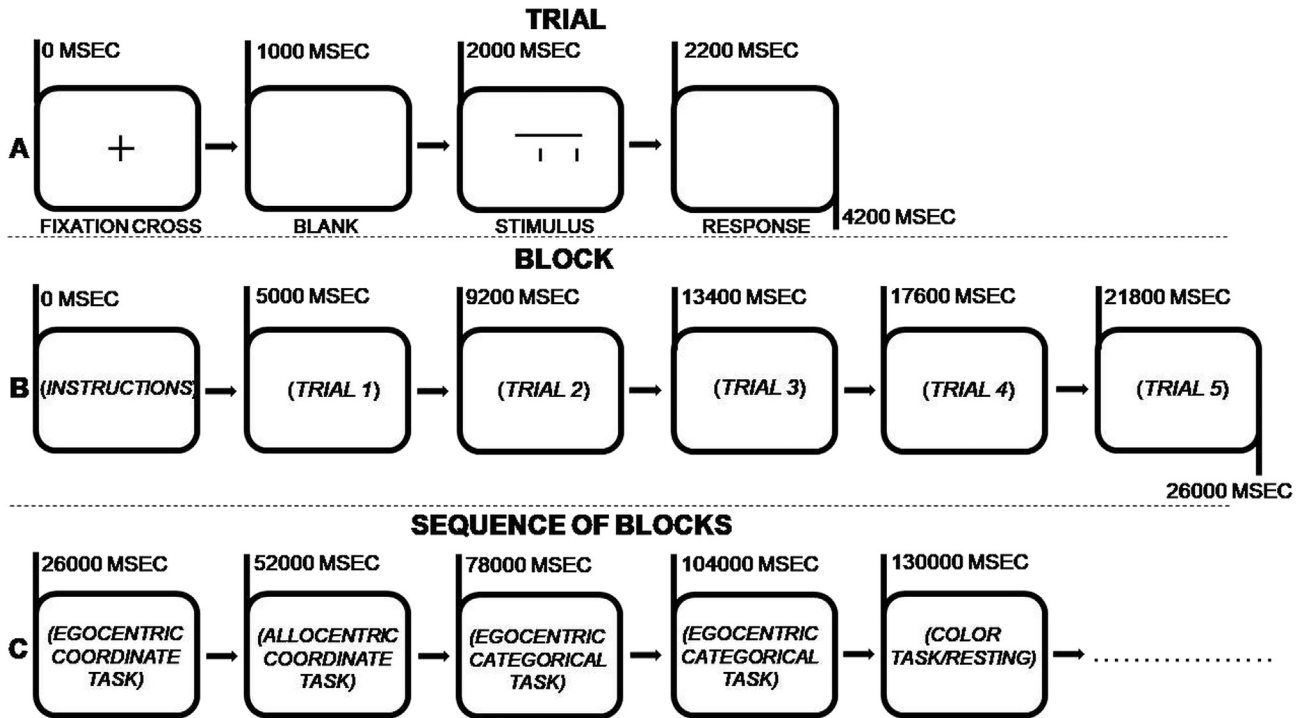
Fig. 2. Trial, Block, and Sequence. The figure shows an example of trial (A), block (B), and sequence (C). (A) Each trial started with a fixation cross (1000 ms), followed by a blank screen and after 1 s a stimulus was presented for 200 ms. Participants had 2 s to provide the answer. (B) Each block started with the instructions. Instructions were presented for 5 s. 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.

created by randomizing the sequence of blocks. For an example of a trial, block and sequence and their time duration see Fig. 2. Finally, the sequences were organized in five scanning sessions, four sessions contained four sequences and one session contained three sequences. The order of the sequences was randomized for each participant. The total duration of the tasks was 45 min and 50 s.

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 et al., 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 (Tables 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 in relation to each other and performed t tests on these data.

Table 1. Regions activated by the egocentric categorical with respect to allocentric categorical task. Areas marked with an asterisk were significant after correction for multiple comparisons. See Fig. 7 for the location of the significant ROIs* on the inflated cortical surface of one of the included subjects.

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 (Sup. part)*	**R**	**3.78**	**0.00113**
	Precentral sulcus (Sup. part)*	**L**	**2.89**	**0.00623**
	Precentral sulcus (Inf. part)*	**R**	**3.49**	**0.00196**
	Precentral sulcus (Inf. 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.

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.

Table 2. Regions activated by the allocentric categorical with respect to egocentric categorical task. Areas marked with an asterisk were significant after correction for multiple comparisons. See Fig. 7 for the location of the significant ROIs* on the inflated cortical surface of one of the included subjects.

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
	Post. Lateral sulcus *	**R**	**3.23**	**0.00330**
	Subcentral gyrus and sulcus *	**R**	**3.22**	**0.00335**
	Inf part of sulcus of Insula	R	2.43	0.01513
	Inf part of sulcus of Insula	L	1.98	0.03476
	Long Insular gyrus	R	2.37	0.01696
	Post-Ventr p. of the cingulate gyrus	R	2.31	0.01899
	Post-Ventr p. of the cingulate gyrus	L	2.38	0.01678
	Post-Dors p. of the cingulate gyrus	L	1.78	0.04893

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. See Fig. 7 for the location of the significant ROIs* on the inflated cortical surface of one of the included subjects.

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.

We also checked for lateralization of the mean signal of each hemisphere (i.e. the average activity of the ROIs of right and left hemisphere emerging from each contrast), 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 × 4 contrasts: 180 + 45 left ROIs × 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 = .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 (see Figs. 4 and 6). 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

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. See Fig. 7 for the location of the significant ROIs* on the inflated cortical surface of one of the included subjects.

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
	Precentral sulcus (Inf. part)	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. See Fig. 7 for the location of the significant ROIs* on the inflated cortical surface of one of the included subjects.

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**
	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.

the coregistration, obtaining coregistered GLM maps. The co-registered maps were then spatially smoothed using a Gaussian kernel (sigma = 1 mm), 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 $p < .05$, uncorrected, with a minimum cluster size of 50 contiguous voxels. Results are projected over the reconstructed surface of the template brain.

Finally, in order to localize the ROIs with a statistically significant increased activity the inflated cortical surface of one of the included subjects was used (see Fig. 7).

RESULTS

Behavioral results: accuracy and response times

Behavioral data were successfully collected from all the 14 scanned participants while performing the task in the scanner. Mean accuracy was well above chance level for all judgments: 70% (sd: 0.14) for Egocentric Coordinate judgments, 80% (sd: 0.14) for Egocentric Categorical judgments, 86% (sd: 0.11) for Allocentric Coordinate judgments, 83% (sd: 0.09) for Allocentric Categorical judgements. Results from the repeated measures ANOVA (2×2: Egocentric/Allocentric × Coordinate/Categorical) showed that egocentric coordinate judgments were significantly less accurate than all other judgments, $F(3, 39) = 10.34$, $p < .00005$, $\eta_p^2 = 0.44$; post-hoc: Bonferroni. No significant differences were found for

response times, $F < 1$, (738.24 ms (sd: 73.71) for egocentric coordinate judgments; 723.22 ms (sd: 79.04) for egocentric categorical judgments; 730.89 ms (sd: 95.37) for allocentric coordinate judgments; 755.33 ms (sd: 90.77) for allocentric categorical judgments).

FMRI RESULTS

Differences between frames of reference (FoRs) within each spatial relation (SR)

Egocentric vs allocentric categorical judgments
Results of the direct comparison between egocentric (egocentric minus allocentric) and allocentric (allocentric minus egocentric) FoRs within the categorical SRs are reported in Tables 1 and 2 respectively (corrected and uncorrected results). In general terms, we observed higher activation in frontal and parietal areas with ECA rather than ACA judgments and in occipital areas and interlobar fissures with ACA rather than ECA judgments (see Figs. 3 and 4). In more specific terms, starting from the frontal lobe the ECA judgments showed higher activity in the right Superior Frontal gyrus and sulcus, and in the Middle Frontal gyrus. Moreover, a bilateral higher activity in the Inferior Frontal gyrus (triangular part) and sulcus, and in the Precentral sulcus (inferior and superior part) was also observed. Moving to the parietal lobe, ECA judgments showed higher activity bilaterally in the Supramarginal gyrus, in the Intraparietal sulcus and Angular gyrus, and only in the right hemisphere
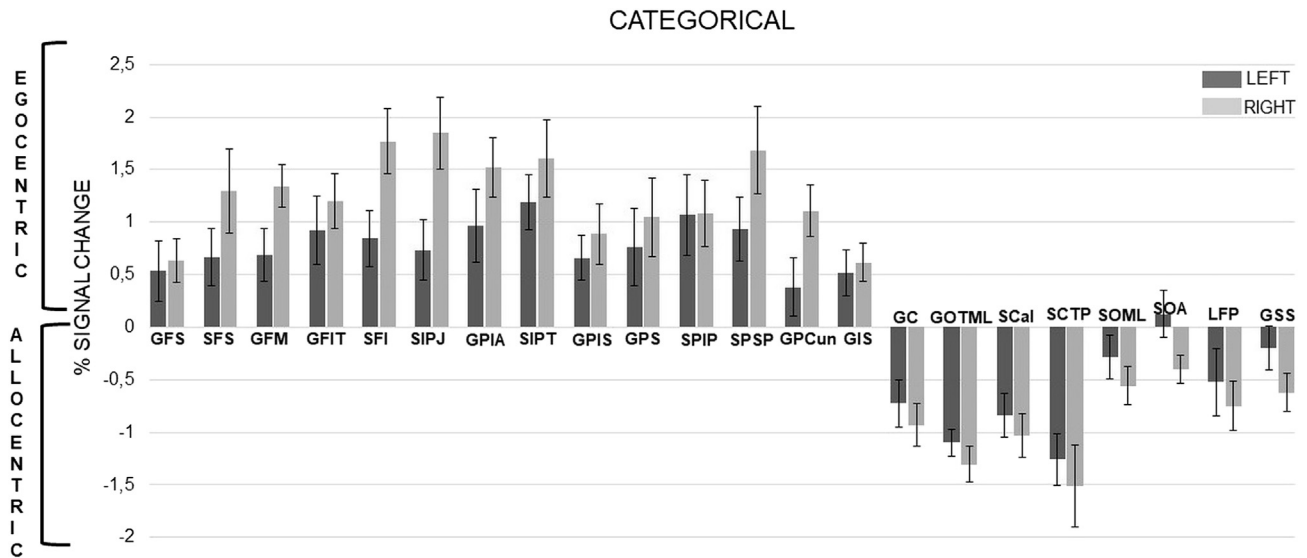
CATEGORICAL

Fig. 3. The figure represents percentage of signal change for egocentric (on the top) and allocentric (on the bottom) judgments for the ROIs emerging from the comparison between ECA and ACA judgments (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 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; **SOA** = Anterior occipital sulcus and preoccipital notch; **LFP** = Posterior ramus (or segment) of the lateral sulcus (or fissure); **GSS** = Subcentral gyrus (central operculum) and sulcus.
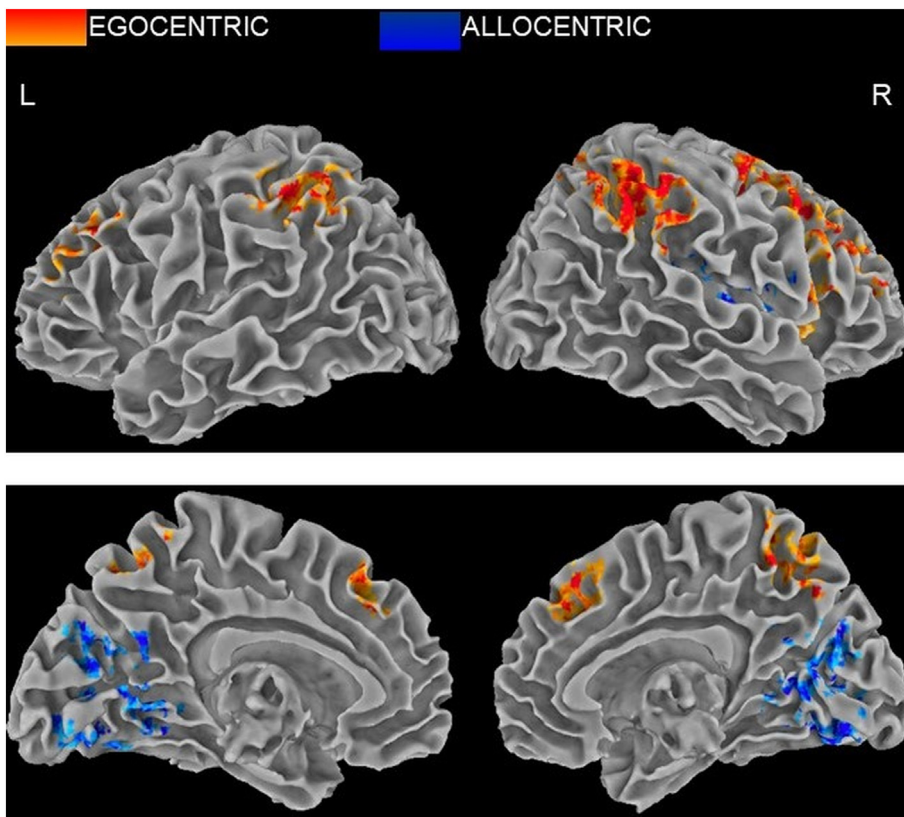
Fig. 4. The Figure shows higher bilateral activity in fronto-parietal areas for ECA coding (in red-orange) with respect to ACA coding (in blue) and higher bilateral activity in occipital areas for ACA compared to ECA judgments. Images of the brain have been obtained by averaging the results of all participants, 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.

in the Superior Parietal gyrus, Sulcus Intermedius primus (of Jensen) and Precuneus. Finally, a higher activity in the right Short Insular gyrus was found (see Fig. 3). Regarding ACA judgments, we specifically observed higher bilateral activity in the Calcarine sulcus, Posterior Transverse Collateral sulcus, Cuneus and Lingual gyrus with respect to the egocentric categorical judgments. Higher activity only in the right hemisphere was observed in Anterior and Middle Occipital sulci, posterior Lateral sulcus, and Subcentral gyrus (see Figs. 3 and 4).

Egocentric vs allocentric coordinate judgments

Results of the direct comparison between egocentric (egocentric minus allocentric) and allocentric (allocentric minus egocentric) FoRs within the coordinate SRs are reported in Table 3. In general terms, ECO judgments led to a higher activation mainly in frontal and parietal areas, while ACO judgments led to a higher activation in occipital areas (see Figs. 5 and 6). As regards ECO judgments, starting
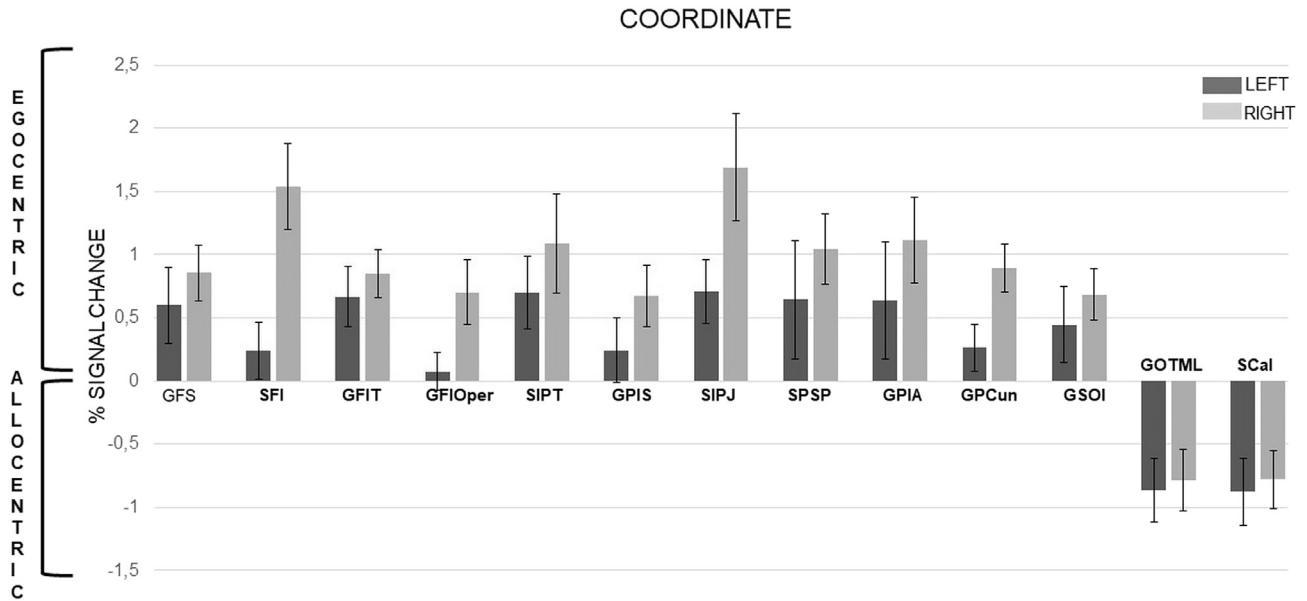
Fig. 5. The figure represents percent of signal change for egocentric (on the top) and allocentric (on the bottom) judgments for the ROIs emerging from the comparison between ECO and ACO judgements (starting from the frontal lobe on the left to the occipital pole on the right side of the graph). **GFS =** 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 and transverse parietal sulci; **GPIS =** Supramarginal gyrus; **SIPJ =** Sulcus intermedius primus (of Jensen); **SPSP =** Superior part of the precentral 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.
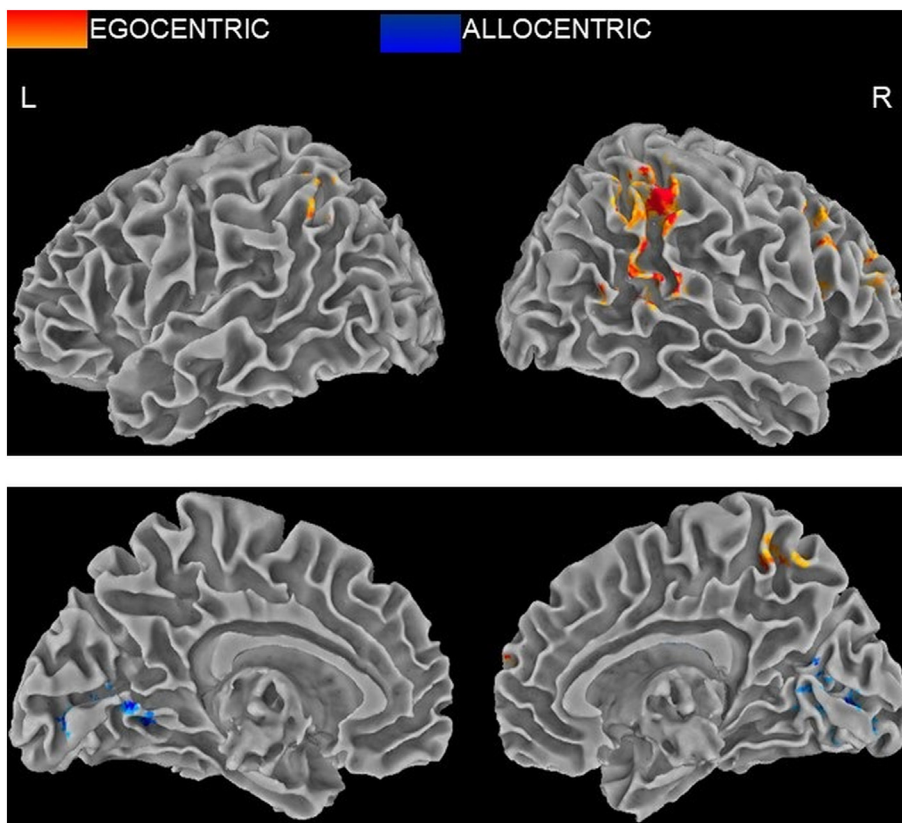
Fig. 6. The Figure shows higher right activity in fronto-parietal areas for ECO (in red-orange) as compared to ACO judgments (in blue), and higher bilateral activity in occipital areas for ACO as compared to ECO coding. Images of the brain have been obtained by averaging the results of all participants, 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.

from the frontal lobe a higher activity was found in the Superior Frontal gyrus, Inferior Frontal gyrus (opercular part) and sulcus, and in the Precentral sulcus (superior part) of the right hemisphere. Moreover, a higher bilateral activity in the Inferior Frontal gyrus (triangular part) and sulcus was observed. When zooming in on the parietal lobe, ECO judgments led to a higher activity in the right hemisphere in the Supramarginal gyrus, Intraparietal sulcus, Angular gyrus, Precuneus, and bilaterally in the Sulcus Intermedius Primus. Finally, a higher activity in the right Inferior Occipital gyrus was found (see Fig. 5). Regarding ACO judgments, we observed a higher bilateral activity in the Calcarine sulcus and in the Lingual gyrus (see Figs. 5 and 6).

Differences between spatial relations (SRs) within each frame of reference (FoR)

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 ECO 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 ECA 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 ACO judgments, we observed an increased activity in the right Supramarginal gyrus and Inferior Frontal gyrus (Triangular part). As regards ACA 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 ($\alpha_{critical}$ = 0.012). As regards categorical relations, egocentric judgments showed a significant (*corrected) higher activation in a total of 14 brain areas of which seven were on both sides and seven were on the right side (ECA > ACA: see Table 1), while allocentric judgments showed higher activations in eight brain areas of which four were on both sides and four were on the right side (see Table 2). In both cases, the average of the activities of these areas 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) showed higher activations in 11 brain areas of which nine were on the right side and two were on both sides (see Table 3) but the average of the activities of these areas 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 showed higher activations in 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 ECO 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) showed higher activations only in right brain areas but the effects did not survive the corrections for multiple comparisons. The categorical judgments (ECA > ECO) showed a significant higher activation in 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, ACO judgments showed significant higher activation in two right areas and the average of the activities of these areas differed from zero only on the right (ACO right t = 3.14 p = .0039 df = 13; ACO left t = 0.35 p =

.36 df = 13). ACA judgments showed increased activation in two bilateral areas, one area on the left side and four areas on the right side, and the average of the activities of these areas 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 activities by exploring the neural correlates of egocentric and allocentric FoRs, combined with coordinate and categorical SRs.

Below we discuss the distinct brain areas more activated when adopting 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 areas in frontal and parietal lobes were more active in egocentric (ECA) than allocentric (ACA) processing. These results are in line with previous literature showing that a parieto-frontal premotor network, bilateral but more active on the right side, is usually associated with spatial localization according to the body midsagittal plane (Vallar et al., 1999; Galati et al., 2000, 2001). Importantly, the comparison between egocentric and allocentric frames combined with coordinate relations demonstrated that a subpart of this right fronto-parietal-network supports more the processing of metric spatial information linked to the body (ECO) than metric spatial information linked to an external reference (ACO) (see the following sections). In turn, bilateral activity mainly in the occipital lobe supported allocentric processing (ACA) more than egocentric processing (ECA). This is consistent with previous studies of spatial localization according to external objects (Galati et al., 2000; Committeri et al., 2004). Finally, the direct comparison between allocentric and egocentric coordinate judgments showed that a subpart of these areas supported ACO processing more than ECO processing.

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

Parietal lobe

As regards the role of the parietal lobe in the ECA judgments, the results showed higher activation than the ACA judgments in the Superior Parietal gyrus, the Sulcus Intermedius Primus (of Jensen), the Angular gyrus, the Supramarginal gyrus, the Intraparietal sulcus and the Precuneus. The involvement of the Superior Parietal gyrus confirms its key role in the
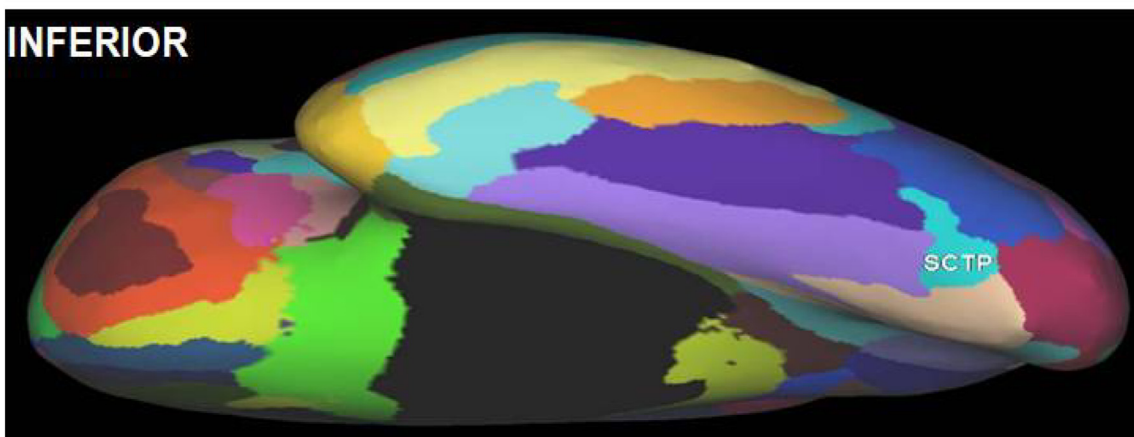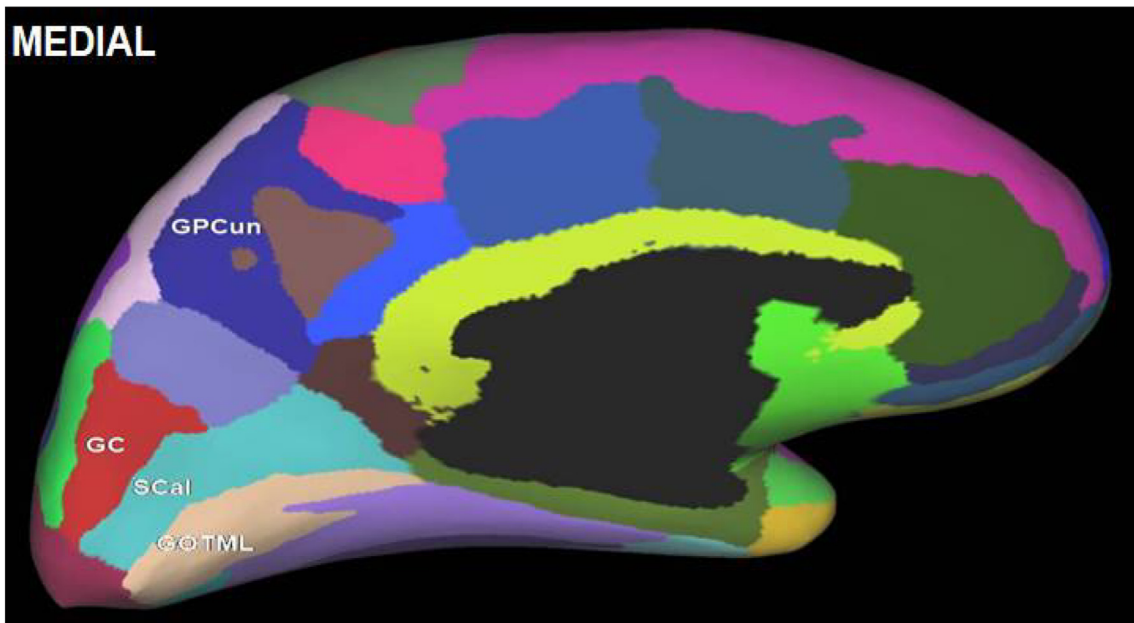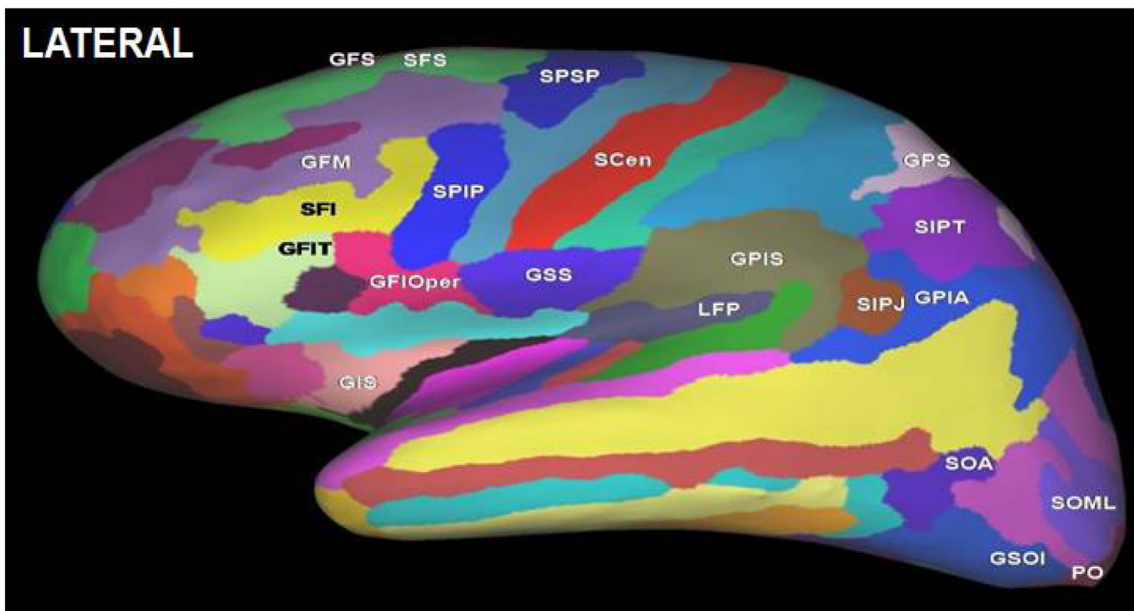
egocentric processing (see also Galati et al., 2000; Committeri et al., 2004). Milner and Goodale (1995) and Simon et al. (2004) showed that visuo-spatial and manual tasks, which imply egocentric encoding, activated more superior regions of the posterior parietal cortex. Lesions in these regions led 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 active in egocentric than allocentric judgments can be found in the numerous studies that have shown its involvement 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 (Binkofski et al., 1998; Chaminade and Decety, 2002; Simon et al., 2002; Shikata et al., 2003; Grefkes et al., 2004; Frey et al., 2005).

As regards the Precuneus, it seems involved in egocentric disorders (Levine et al., 1978; Perenin and Vighetto, 1988; 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 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 more 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 more significantly active in the right hemisphere during ECO than ACO judgments.

Frontal lobe

Frontal lobe activity was higher during egocentric 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 gyri, 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 work 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 stimuli 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 ECO judgments.

Interestingly, Galati et al. (2000) suggest 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

Fig. 7. The figure shows the cortical parcellation according to Destrieux et al. (Neuroimage 2010, 53, 1–15) on the inflated cortical surface of one of the included subjects, with different colors representing the different ROIs. The ROIs with an increased activation (*see Table from 1 to 5) are marked with their respective labels: **GC** = Cuneus; **GFIOper =** Opercular part of the inferior frontal gyrus; **GFIT =** Triangular part of the inferior frontal gyrus; **GFM =** Middle frontal gyrus; **GFS =** Superior frontal gyrus; **GIS** = short insular gyrus; **GOTML** = Lingual gyrus, lingual part of the medial occipito-temporal gyrus; **GPCun** = Precuneus; **GPIA =** Angular gyrus; **GPIS =** Supramarginal gyrus; **GPS =** Superior Parietal gyrus; **GSOI** = Inferior occipital gyrus (O3) and sulcus; **GSS** = Subcentral gyrus and sulci; **LFP** = Posterior ramus (or segment) of the lateral sulcus (or fissure); **PO** = occipital pole; **SCal** = Calcarine sulcus; **SCen** = Central sulcus; **SCTP** = Posterior transverse collateral sulcus; **SFI =** Inferior frontal sulcus; **SFS** = Superior frontal sulcus; **SIPJ =** Sulcus intermedius primus (of Jensen); **SIPT** = Intraparietal sulcus(interparietal sulcus) and transverse parietal sulci; **SOA** = Anterior occipital sulcus; **SOML** = Middle occipital sulcus and lunatus; **SPIP** = Inferior part of the precentral sulcus; **SPSP =** Superior part of the precentral sulcus.

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 underlined categorical judgements showed that ACA judgments more than ECA judgments increased bilateral activation in the Cuneus, Lingual gyrus, Calcarine sulcus, and Posterior Transverse Collateral sulcus. Furthermore, ACA judgments provoked higher activation 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 et al. (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 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 would process the visuo-spatial features of the perceived scenes (Dumoulin et al., 2000; Wandell et al., 2007). Finally, two additional brain areas in the Anterior Occipital sulcus and the Posterior Transverse Collateral sulcus were more active during ACA than ECA judgments. The Anterior Occipital sulcus originates in the pre-occipital 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).

The comparison between egocentric and underlined allocentric coordinate judgements showed that ACO judgments activated a subpart (i.e. Calcarine sulcus and Lingual gyrus) of the areas activated by the ACA judgments. This may suggest that ACO representations have more specific functions with respect to the ACA ones. The direct comparison between the two different allocentric judgements helps to clarify this point (see *Spatial Relations* section). Moreover a higher activation of the right Inferior Occipital gyrus during ECO, but not ACO, judgments was observed. The right occipital gyrus is usually indicated as the "occipital face areas" and seems particularly active when participants have to discriminate between faces, i.e. body-related elements, and objects (Rossion et al., 2003). This explanation, along with the fact that the ACO task involves fewer occipital areas, might justify the higher activation of the inferior occipital gyrus during ECO than ECA judgments.

Finally, the direct comparison between egocentric and allocentric reference frames highlights the role of other areas. For example, the Short Insular gyrus was particularly active during ECA than ACA judgments. Ghaem et al. (1997) found that the Insula was involved when participants imagined navigating through a previously learned path. Therefore, it is possible to hypothesize a role of the Short Insular gyrus in providing egocentric spatial information due to its connection to the frontal lobe (Türe et al., 1999). Remarkable is also the higher activation observed in the right posterior part of the Lateral sulcus and in the right Subcentral gyrus and sulcus during ACA rather than ECA 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 might 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 specifically support attributions of verbal spatial categories (right–left) to external, not-body related, references. In fact, these areas are not present when ECO and ACO judgments 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 rather than categorical relations led to higher activation in areas within the right hemisphere, but no one survived the multiple testing correction procedure. Instead, categorical spatial relations compared to coordinate relations activated particularly 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 relations 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 higher 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 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 provoked higher activation than coordinate judgments 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, ACA showed higher activation than ACO judgments in the right Central sulcus and the right Subcentral gyrus and sulcus. This would suggest that compared to the ACO judgments, ACA information is more 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, ACO showed higher activity with respect to ACA relations in the right Supramarginal gyrus and in the right Inferior Frontal gyrus. The Supramarginal gyrus, located inferiorly to the intraparietal 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 (ACO) recruit a subpart of the brain areas involved in the ECO judgments. Finally, in line with what happened during egocentric judgements, brain activity during ACO as compared to ACA judgments increased significantly in the right, but not in the left, hemisphere. Instead, bilateral activity was again observed during ACA judgements.

Limitations of the current study

Before concluding, it is important to address some critical issues and limitations of the current study. A 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-s 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., 2006) 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 converted into a body-centered 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.

Another critical issue refers to the fact 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 behavioral 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. Bridgeman et al., 1997, 2000; see Neggers et al., 2006; Ruotolo et al., 2011b; 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). In addition, if egocentric coordinate judgments had been more difficult than others, they should have caused more 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. Admittedly, the fact that the use of egocentric coordinate representations was explored with a visual-perceptual judgment task can be considered a limitation of this study. 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 task in the four different spatial conditions.

Finally, two others limitations of this study need to be discussed. First, the partial coverage of the brain during the images acquisition phase 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. The second one refers to the absence of a non-spatial control condition for the four spatial representations. As a matter of fact, even though a number of six blocks had been added in which participants had to judge the luminance of the stimuli, data from this condition have not been reported. This was done for two main reasons. First, the luminance judgment was found to be too difficult for some participants. Second, 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 and as such could not work as a proper control. Future studies with low-level control tasks can shed light on areas of overlap between the four spatial representations.

Summary

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-T MRI scanner was used. Only the instruction differed between conditions and dictated the specific way in which the stimuli had to be processed. The comparisons between egocentric and allocentric frames of reference, on one side, and between categorical and coordinate spatial relations, on the other side, suggest that there are areas more involved in one combination than the others. Specifically, the egocentric–categorical combination showed higher bilateral activations, but more right sided, in 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. In line with what suggested by both Kosslyn (2006) and Milner and Goodale (1995), this points out that 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 showed higher activations in 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 involved 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. 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 is recruited for 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 obeys to environmental needs.

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