

# Neural Interaction between Spatial Domain and Spatial Reference Frame in Parietal–Occipital Junction

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## Abstract

■ On the basis of double dissociations in clinical symptoms of patients with unilateral visuospatial neglect, neuropsychological research distinguishes between different spatial domains (near vs. far) and different spatial reference frames (egocentric vs. allocentric). In this fMRI study, we investigated the neural interaction between spatial domains and spatial reference frames by constructing a virtual three-dimensional world and asking participants to perform either allocentric or egocentric judgments on an object located in either near or far space. Our results suggest that the parietal–occipital junction (POJ) not only shows a preference for near-space processing but is also involved in the neural interaction between spatial domains and spatial reference frames. Two dissociable streams of visual processing exist in the human brain: a ventral perception-related stream and a dorsal action-related stream. Consistent with the perception–

action model, both far-space processing and allocentric judgments draw upon the ventral stream whereas both near-space processing and egocentric judgments draw upon the dorsal stream. POJ showed higher neural activity during allocentric judgments (ventral) in near space (dorsal) and egocentric judgments (dorsal) in far space (ventral) as compared with egocentric judgments (dorsal) in near space (dorsal) and allocentric judgments (ventral) in far space (ventral). Because representations in the dorsal and ventral streams need to interact during allocentric judgments (ventral) in near space (dorsal) and egocentric judgments (dorsal) in far space (ventral), our results imply that POJ is involved in the neural interaction between the two streams. Further evidence for the suggested role of POJ as a neural interface between the dorsal and ventral streams is provided by functional connectivity analysis. ■

## INTRODUCTION

Cortical processing of visual information is dissociated in (at least) two neural streams: an occipital-temporal (ventral) stream and an occipital-parietal (dorsal) stream (Ungerleider & Mishkin, 1982). The ventral stream subserves visual awareness of object properties, whereas the dorsal stream guides manual actions to those objects. This perception–action model is based on evidence from a patient (referred to as DF) with a bilateral lesion of the ventral stream in the occipital–temporal cortex. Although the patient suffered from a strong visual form agnosia, that is, a deficit in recognizing the form of visual objects and identifying them, visually guided actions toward the same objects were unimpaired (Milner & Goodale, 1995; Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991).

On the basis of the perception–action model, it has been suggested that attending to space within (near space) and beyond (far space) arm’s reach is subserved by distinct brain circuits (Berti & Frassinetti, 2000; Previc, 1990, 1998; Vuilleumier, Valenza, Mayer, Reverdin, & Landis,

1998; Mennemeier, Wertman, & Heilman, 1992; Halligan & Marshall, 1991; Heilman, Bowers, & Shelton, 1990). Because an individual can directly act on and manipulate objects in near space, the dorsal stream is implicated in near-space processing. By contrast, because no direct actions can be implemented in far space, the ventral stream is involved in the conscious perception of objects in far space. However, we could show that both a perceptual (line bisection judgment) and an action (manual line bisection) task implicated the dorsal stream in near space, whereas both of them implicated the ventral stream in far space (Weiss, Marshall, Zilles, & Fink, 2003). These results suggest that the differential activations in the dorsal/ventral stream associated with near space and far space processing do not depend on task demands per se (i.e., action vs. perception; Pitzalis, Di Russo, Spinelli, & Zoccolotti, 2001). Rather, a crucial factor underlying the functional dissociation between the ventral and dorsal stream may be related to the selection of an appropriate reference frame (Bruno, 2001). In the brain, an object can be represented either within an egocentric reference frame (i.e., relative to the body or body effectors of the observer) or within an allocentric reference frame (i.e., relative to another object or the surroundings independent of the observer). Egocentric representations are readily encoded in the dorsal stream as sensorimotor representations (Andersen &

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Buneo, 2002; Cohen & Andersen, 2002; Andersen, Snyder, Bradley, & Xing, 1997). Allocentric representations are encoded in the ventral stream as perceptual representations (James, Culham, Humphrey, Milner, & Goodale, 2003; James, Humphrey, Gati, Menon, & Goodale, 2002; Georges-Francois, Rolls, & Robertson, 1999; Rolls, 1999). In a previous neuropsychological study, the aforementioned patient DF was asked to perform both a perceptual task and a motor task based on either allocentric or egocentric information (Schenk, 2006). DF's performance was preserved both in the perceptual and motor tasks when the tasks were performed relative to the egocentric reference frame. In contrast, DF's performance was impaired in both types of tasks when the tasks were performed relative to the allocentric reference frame. These data suggest that the crucial factors determining DF's performance may be the spatial reference frame (i.e., allocentric vs. egocentric) rather than the task demand (i.e., perception vs. action).

Taken together, previous studies suggest that the anatomically specified dorsal and ventral visual streams differentially support near and far space processing or allocentric and egocentric reference frame, respectively. It remains unclear, however, how the different dimensions interact. This issue is important because to successfully cope with our three-dimensional environment we need to effectively integrate object information in near and far space into egocentric or allocentric reference frames, depending on the task at hand. Evidence from previous neuropsychological studies also implies that spatial domains (near vs. far space) may differentially influence allocentric versus egocentric judgments. For example, unilateral visuospatial neglect, that is, egocentric deficits, can selectively impair allocentric representations during line bisection tasks either in near or far space (Berti, Smania, & Allport, 2001; Berti & Frassinetti, 2000; Vuilleumier et al., 1998; Cowey, Small, & Ellis, 1994; Halligan & Marshall, 1991). Therefore, the current study was specifically designed to address the neural interaction between spatial domains and spatial reference frames.

To this end, we measured BOLD responses by fMRI while healthy participants performed allocentric or egocentric visuospatial judgments on a three-dimensional object, which was presented via stereo goggles either in (virtual) near space or (virtual) far space. During allocentric judgments in far space ("Far\_ALLO") and egocentric judgments in near space ("Near\_EGO"), participants were required to process information represented commonly either in the ventral or the dorsal stream. In contrast, during allocentric judgments in near space ("Near\_ALLO") and egocentric judgments in far space ("Far\_EGO"), successful task performance relied on efficient information integration between the ventral and dorsal streams because neural representations subserving spatial domains and spatial reference frames were differently coded in the ventral and dorsal streams. The analysis of the fMRI data thus specifically aimed at the interaction term of the factorial design, that is, "(Near\_ALLO vs. Near\_EGO) vs. (Far\_ALLO vs. Far\_EGO)."

## METHODS

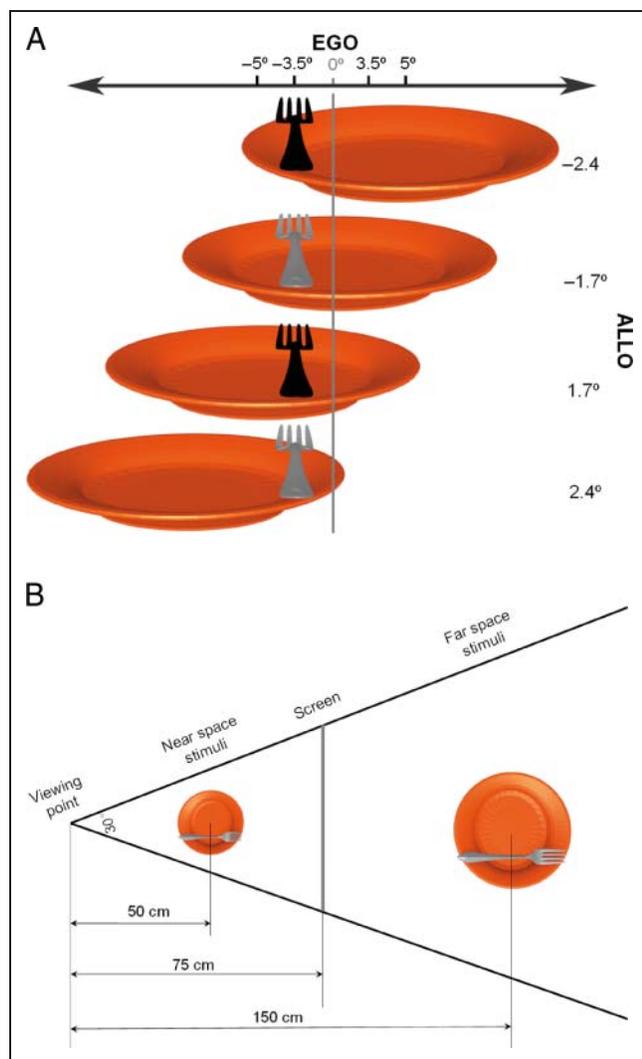
### Participants

Nineteen healthy volunteers (12 women and 7 men,  $24 \pm 3$  years old) participated in the study. They were all right-handed and had normal color vision and visual acuity. None of them had a history of neurological or psychiatric disorders. All participants gave informed consent before the experiment in accordance with the Helsinki Declaration and the study was approved by the local ethics committee.

### Apparatus, Stimuli, and Experimental Setup

A goggle-based MR-compatible system (VisuaStim Digital, Resonance Technologies, Northridge, CA) provided two separate VGA with digital dual video inputs for stereoscopic display, each with a resolution of 800 (horizontal)  $\times$  600 (vertical) pixels at 60 Hz refresh rate. The horizontal extent of the field of view was 30°. The default viewing distance was 75 cm. The dual-display stereoscopic video, with 0.5 mega pixel resolution in a 0.25 square area, yielded 3-D images by delivering slightly disparate images to each eye (binocular disparity).

To make the study ecologically more meaningful, we used a familiar but virtual tool (a fork) as the target stimulus. The virtual display in each trial contained two 3-D objects: a fork on the top of a round orange plate (Figure 1A). The 3-D objects were generated by Blender (free open source 3-D content creation software, www.blender.org), exported as DirectX files, and presented on a gray background by custom-made Presentation scripts (Presentation Software package, Neurobehavioral Systems, Inc., Albany, CA). The diameter of the plate was 15° of visual angle, and the nearer end of the fork was 2.5° of visual angle. There were two possible luminance values for the color of the fork: 64, 64, 64 or 192, 192, 192 (24 bits red, green, blue [RGB] color coding; Figure 1A). The allocentric locations of the fork (with respect to the midsagittal of the plate) and the egocentric locations of the fork (with respect to the midsagittal of the participants) were orthogonally varied (Figure 1A). Therefore, there were 4 (allocentric locations)  $\times$  4 (egocentric locations)  $\times$  2 (luminance of the fork: high and low) = 32 types of stimuli. These stimuli were presented either in near or far space (Figure 1B). In the near space condition, the 3-D objects popped out of the default screen of the goggles, and the distance from the center of the plate to the participants' eyes was 50 cm (Figure 1B). For the far space condition, the objects appeared behind the default screen and were 150 cm away from the participants' eyes. The different target distances were simulated by adjusting binocular disparity. The near and far space stimuli were presented at the same height ( $y = 0$ , at the level of the eyes) and tilted by 13° toward the participants (Figure 1A). Retinotopic sizes of the objects and visual angles of the egocentric and allocentric distances were both matched for near and far space.



**Figure 1.** The combination of spatial domains (near vs. far) and spatial reference frames (allocentric vs. egocentric) in this study. (A) Experimental stimuli. Three-dimensional visual stimuli consisted of a fork (with two levels of luminance) intersecting an orange plate. The fork could appear at one of four egocentric positions. For each of the four egocentric locations of the fork ( $-5^\circ$ ,  $-3.5^\circ$ ,  $3.5^\circ$ ,  $5^\circ$ ), the location of the plate was varied independently around the fork, using four possible allocentric positions ( $-2.4^\circ$ ,  $-1.7^\circ$ ,  $1.7^\circ$ ,  $2.4^\circ$ ). The visual angles of the eccentricities for the corresponding egocentric (EGO) and allocentric (ALLO) positions are given on top and on the right side of the figure, respectively. (B) A top view of the virtual three-dimensional setting. The stimuli in near and far space were matched in visual angle. The horizontal visual angle of the default screen of the goggles is  $30^\circ$ . The default distance from the observer to the default screen is 75 cm. The near space stimuli pop out of the default screen and were positioned 50 cm from the observer. The far space stimuli were presented behind the default screen and were 150 cm away from the observer.

### Experimental Design and Tasks

Participants were asked to perform three types of task on the identical set of stimuli. In the allocentric judgment task (ALLO), participants were asked to judge whether the fork was on the left or the right side of the plate. Participants were asked to press a button on the left (for left)

or right (for right) side of a response pad. In the egocentric judgment task (EGO), participants were asked to judge whether the fork was on the left or the right side of the midsagittal of their own body. Participants were asked to press a button on the left (for left) or right (for right) side of a response pad. In the high-level baseline (HLB) task (i.e., nonspatial luminance discrimination tasks), participants were asked to discriminate whether the fork had a high or low luminance. For this purpose, participants were familiarized with the two levels of luminance of the fork before scanning. Participants were asked to press one button for high luminance and the other button for low luminance. The mapping between the levels of luminance and the response buttons was counterbalanced across participants. In the middle of the scanning session, an instruction (6 sec) was displayed asking participants to switch hands. Nine participants switched from left hand to right hand in the middle of the scanning and vice versa for the other 10 participants. For both hands, participants were required to use their index fingers and middle fingers to press one of the two buttons on the left or the right side of the response pad. Before the fMRI experiment, all participants completed a training session of 15 min with a slightly different setting (shutter glasses) outside the scanner to familiarize them with the tasks and the experimental setup.

Therefore, the fMRI design was a 2 (spatial domains: near vs. far)  $\times$  3 (tasks: ALLO, EGO, and HLB) block design. Participants, accordingly, alternated between six types of experimental blocks (conditions). Each condition began with a 3-sec visual instruction, informing the participants of the type of task in the following block. The target presentation time during each trial was 150 msec. Such a short stimulus-on time was chosen to minimize eye movements. We chose not to use a central fixation in our virtual three-dimensional display for the following reason: If a central fixation cross had been presented throughout the experiment, participants could have used the position of the central fixation rather than their midsagittal, as a reference frame to perform the egocentric task. Participants were required to keep their gaze straightforward and converge toward the frontal plane in which the near space or far space stimuli appeared during near space blocks or far space blocks, respectively. The importance of not moving their eyes (i.e., maintaining their gaze stable), especially during the presentation of the behaviorally relevant target in each trial, was repeatedly emphasized. The duration of each trial was 1650 msec. Per block 10 trials were presented, resulting in a block duration of 16.5 sec. There were eight repetitions for each of the six block types. To further maximize the statistical power of the block design, the intertrial interval between events within each block was not jittered. Therefore, location effects induced by the four different allocentric and egocentric locations couldn't be analyzed as this would require event-related analysis methods.

## Eye Movement Monitoring

Because the 3-D goggles used during the MRI experiment covered the whole area of the eyes and hence prevented eye tracking in the MR scanner, we performed an additional eye tracking experiment outside the MR scanner. For this behavioral experiment, 2-D pictures of the experimental stimuli in real, rather than virtual, near and far spaces were presented. A new group of 13 healthy adult participants (seven women and six men,  $20 \pm 1.5$  years old) were recruited with the same screening criteria as those in the fMRI study. Except for the stimulus presentation, the experimental paradigm, stimuli, and timing were identical as those in the scanner.

Eye position was monitored with the EyeLink 1000 system (SR Research, Mississauga, Ontario, Canada) at a sampling rate of 1000 Hz. Participants were seated, and a steady head position was maintained with the aid of chin and forehead rests. Eye movement data were recorded from the right eye. For each participant, before the experiment, a 9-point calibration procedure was performed for near and far displays, respectively, to map the eye positions to screen coordinates. Eye movement data were analyzed to test whether the participants could keep their gaze straight-forward within the central area during allocentric and egocentric judgments in near and far spaces. Artifacts related to blinking were filtered out. A central quadratic area, whose height and width were both  $3^\circ$  of visual angle, served as an ROI for both near and far displays. For each of the four experimental conditions, the ratio between the overall time that participants kept their gaze within this ROI and the presentation duration of the target during each trial (150 msec) was calculated.

## Data Acquisition and Preprocessing

A 3-T Siemens Trio (Erlangen, Germany) system with a standard head coil was used to obtain T2\*-weighted EPIs with BOLD contrast (matrix size =  $64 \times 64$ , voxel size =  $3.1 \times 3.1 \times 3.0$  mm<sup>3</sup>). Thirty-six transversal slices of 3-mm thickness that covered the whole brain were acquired sequentially with a 0.3-mm gap (repetition time = 2.2 sec, echo time = 30 msec, field of view = 220 mm, flip angle =  $90^\circ$ ). There was one run of functional scanning, which was 16.5 min (450 EPI volumes). The first five volumes were discarded to allow for T1 equilibration effects. Additional high-resolution anatomical images (voxel size =  $1 \times 1 \times 1$  mm<sup>3</sup>) were acquired using a standard T1-weighted 3-D MPRAGE sequence.

Data were preprocessed with Statistical Parametric Mapping software SPM8 (Wellcome Department of Imaging Neuroscience, London, [www.fil.ion.ucl.ac.uk](http://www.fil.ion.ucl.ac.uk)). Images were realigned to the first volume to correct for interscan head movements. Then the mean EPI image of each subject was computed and spatially normalized to the Montreal Neurological Institute (MNI) single-subject template using the “unified segmentation” function in SPM8. This algorithm is based on a probabilistic framework that

enables image registration, tissue classification and bias correction to be combined within the same generative model. The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move individual data into the space of the MNI tissue probability maps, were then combined with the deformation field transforming between the latter and the MNI single subject template. The ensuing deformation was subsequently applied to individual EPI volumes. All images were thus transformed into standard MNI space and resampled to  $2 \times 2 \times 2$  mm<sup>3</sup> voxel size. The data were then smoothed with a Gaussian kernel of 8 mm FWHM to accommodate intersubject anatomical variability.

## Statistical Analysis of Imaging Data

Data were analyzed employing a general linear model as implemented in SPM8. At the first level, the general linear model was used to construct a multiple regression design matrix that included the six experimental conditions, that is, “Near\_ALLO,” “Near\_EGO,” “Near\_HLB,” “Far\_ALLO,” “Far\_EGO,” and “Far\_HLB.” Each condition was modeled by a boxcar reference vector (16.5 sec) convolved with a canonical synthetic hemodynamic response function. Additionally, all instructions and the six head movement parameters derived from the realignment procedure were included as covariates of no interest. Task blocks, in which participants did not adhere to the task instructions (error rates within such blocks were above 60%), were separately modeled as another regressor of no interest. This occurred in 2 of the 19 participants who each misperformed in one of a total of 48 task blocks. Data were highpass-filtered at 1/128 Hz. Parameter estimates were subsequently calculated for each voxel using weighted least squares to provide maximum likelihood estimators based on the temporal autocorrelation of the data. No global scaling was applied. For each participant, simple main effects for each of the six experimental conditions were computed. The six first-level individual contrast images were then fed into a  $1 \times 6$  within-participants ANOVA at the second group level employing a random-effects model (flexible factorial design in SPM8 including an additional factor modeling the subject means). In the modeling of variance components, we allowed for violations of sphericity by modeling nonindependence across parameter estimates from the same subject and allowing unequal variances both between conditions and participants using the standard implementation in SPM8. We were especially interested in the main effect of Spatial Domain [“(Near\_ALLO + Near\_EGO + Near\_HLB) > (Far\_ALLO + Far\_EGO + Far\_HLB)” and vice versa], the main effect of Spatial Reference Frames [“(Near\_ALLO + Far\_ALLO) > (Near\_EGO + Far\_EGO)” and vice versa], and the interactions between Spatial Domains and Spatial Reference Frames [“(Near\_ALLO > Near\_EGO) > (Far\_ALLO > Far\_EGO)” and vice versa]. Areas of activation were identified as significant only if they passed a conservative threshold of  $p < .001$ , corrected for

multiple comparisons at the cluster level with an underlying voxel level of  $p < .001$  (uncorrected; Poline, Worsley, Evans, & Friston, 1997). For the conjunction analysis, the conjunction null hypothesis, instead of the global null hypothesis, was tested as implemented in SPM8 (Friston, Penny, & Glaser, 2005; Nichols, Brett, Andersson, Wager, & Poline, 2005). Because the main focus of our study was on the differential activations between experimental conditions, we first extracted the absolute parameter estimates in the significantly activated brain regions and then calculated the differential parameter estimates (i.e., differential beta values between experimental conditions). The differential parameter estimates are shown as a function of the experimental conditions involved in specific SPMs.

### Psychophysiological Interaction Analysis

Furthermore, we used the parietal–occipital junction (POJ) region (derived from the conjunction contrast “Near > Far”  $\cap$  “(Near\_ALLO > Near\_EGO) > (Far\_ALLO > Far\_EGO)”) as a source region to estimate the context-specific functional modulation of neural activity across the brain caused by the neural activity in POJ using psychophysiological interaction (PPI) analysis. PPI analysis allows for detecting regionally specific responses in one brain area in terms of the interaction between input from another brain region and a cognitive–sensory process (Friston et al., 1997). We used the neural activity in the POJ region as the physiological factor and the interaction contrast [i.e., “(Near\_ALLO > Near\_EGO) vs. (Far\_ALLO > Far\_EGO)”) as the psychological factor, respectively. For each subject, the conjunction between the main effect contrast “Near > Far” and the interaction contrast

“(Near\_ALLO > Near\_EGO) > (Far\_ALLO > Far\_EGO)” was first calculated at the individual level. Subsequently, each subject’s individual peak voxel was determined as the maximally activated voxel within a sphere of 16 mm radius (i.e., twice the smoothing kernel) around the coordinates of the peak voxel within POJ from the second level group analysis (MNI:  $-2, -78, 30$ ; Table 1C and Figure 6). Individual peak voxels from every subject ( $x = -1 \pm 8, y = -80 \pm 8, z = 32 \pm 7$ ) were located in the same anatomical structure. Next, POJ time series were extracted from a sphere of 4-mm radius (twice the voxel size) around the individual peak voxels (without deconvolution because of the block design). PPI analysis at the first individual level employed one regressor representing the extracted time series in the given ROI in POJ (the physiological variable), one regressor representing the psychological variable of interest, that is, “(Near\_ALLO > Near\_EGO) vs. (Far\_ALLO > Far\_EGO),” and a third regressor representing the cross product of the previous two (the PPI term). A SPM was calculated to reveal areas whose activation was predicted by the PPI term, with the physiological and the psychological regressors treated as confound variables. The PPI analysis was carried out for each participant and then entered into a random-effects group analysis ( $p < .001$ , corrected for multiple comparisons at cluster level with an underlying voxel threshold at  $p < .005$ , uncorrected).

## RESULTS

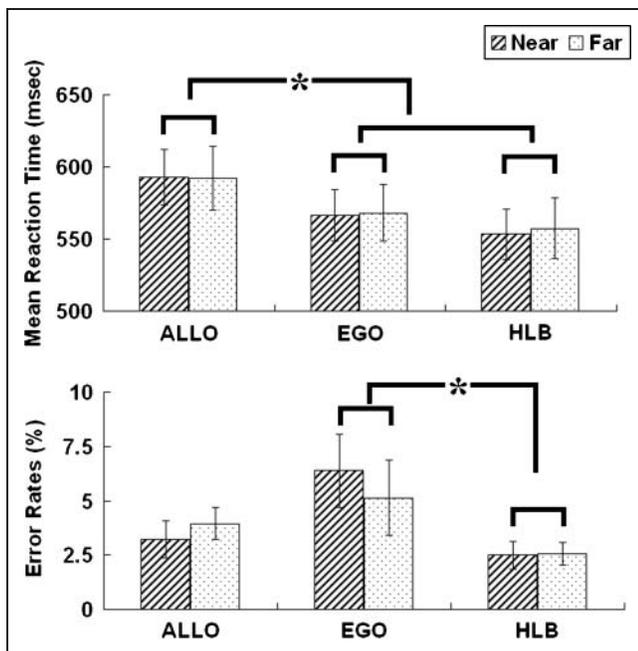
### Behavioral Parameters during fMRI Scanning

Mean RTs for correct trials and error rates (%) were entered into a 2 (spatial domains: near vs. far)  $\times$  3 (tasks: ALLO,

**Table 1.** Brain Regions Showing Significant Relative Increases of BOLD Response Associated with the Different Spatial Domains (Near and Far Space) and the Interaction between Spatial Domain and Reference Frame

Anatomical Region	Side	Cluster Peak (mm)	<i>t</i> Score	$k_E$ (Voxels)
<b>A. (Near_ALLO + Near_EGO + Near_HLB) &gt; (Far_ALLO + Far_EGO + Far_HLB)</b>				
Superior occipital gyrus	R	22, -86, 28	8.57	2906
	L	-10, -88, 34	7.57	
<b>B. (Near_ALLO &gt; Near_EGO) &gt; (Far_ALLO &gt; Far_EGO)</b>				
Superior parietal cortex (medial)	L	-4, -82, 48	5.31	2761
	L	-26, -48, 64	4.99	
	L	-2, -78, 30	4.50	
<b>C. “Near &gt; Far” <math>\cap</math> “(Near_ALLO &gt; Near_EGO) &gt; (Far_ALLO &gt; Far_EGO)”</b>				
POJ	L	-2, -78, 30	4.50	470
	L	-12, -82, 44	4.25	
	R	12, -82, 40	3.98	

The coordinates ( $x, y, z$ ) correspond to MNI coordinates. Displayed are the coordinates of the maximally activated voxel within a significant cluster as well as the coordinates of relevant local maxima within the cluster (*in italics*).



**Figure 2.** Behavioral results. Top: Mean RTs with SEs in the six experimental conditions. Bottom: The corresponding mean error rates with SEs.

EGO, and luminance discrimination as the nonspatial HLB) repeated-measures ANOVA, respectively (Figure 2). For RTs, the main effect of Task was the only significant effect,  $F(2, 36) = 11.18, p < .001$ , with participants responding significantly slower in allocentric tasks (mean  $\pm$  SE:  $592 \pm 20$  msec) than in egocentric ( $567 \pm 18$  msec) and HLB tasks ( $555 \pm 19$  msec), both  $p < .05$  (Bonferroni corrected; Figure 2, top). For error rates, the only significant effect

was also the main effect of Task,  $F(2, 36) = 4.06, p = .026$ , with participants making more errors in egocentric tasks ( $5.8 \pm 1.6\%$ ) than in HLB tasks ( $2.5 \pm 0.4\%$ ),  $p < .05$ , and there was no significant difference between allocentric ( $3.6 \pm 0.7\%$ ) and egocentric tasks (Bonferroni corrected; Figure 2, bottom). For both RTs and error rates, neither the main effect of Spatial Domain nor the interaction was significant (all  $F < 1$ ).

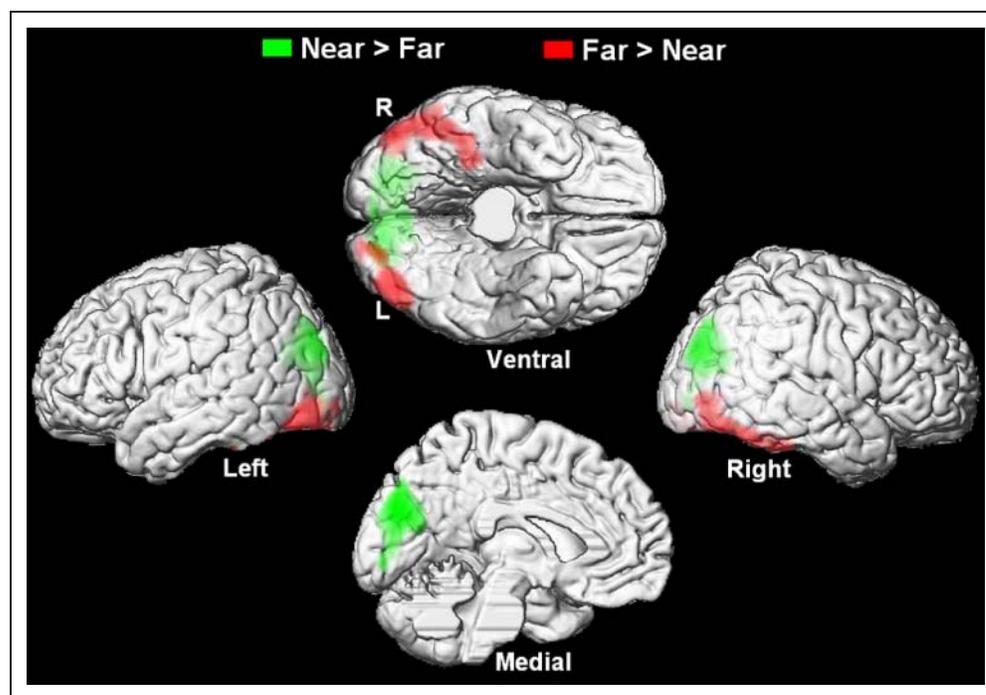
### Eye Movement Data

The average percentage of time that the participants maintained their gaze in the predefined center ROI ( $1.5^\circ$  visual angle around the center of the screen) during allocentric and egocentric judgments in near and far spaces was entered into a 2 (spatial domain: near vs. far)  $\times$  2 (tasks: ALLO vs. EGO) repeated-measures ANOVA (degrees of freedom corrected using a Greenhouse–Geisser correction). Neither the main effects of Spatial Domain and Tasks nor the interaction were significant (all  $F < 1$ ), indicating that the participants could keep their gaze in the central area equally well in the four experimental conditions (Near\_ALLO:  $96 \pm 1\%$ ; Near\_EGO:  $96 \pm 1\%$ ; Far\_ALLO:  $97 \pm 2\%$ ; Far\_EGO:  $97 \pm 1\%$ ).

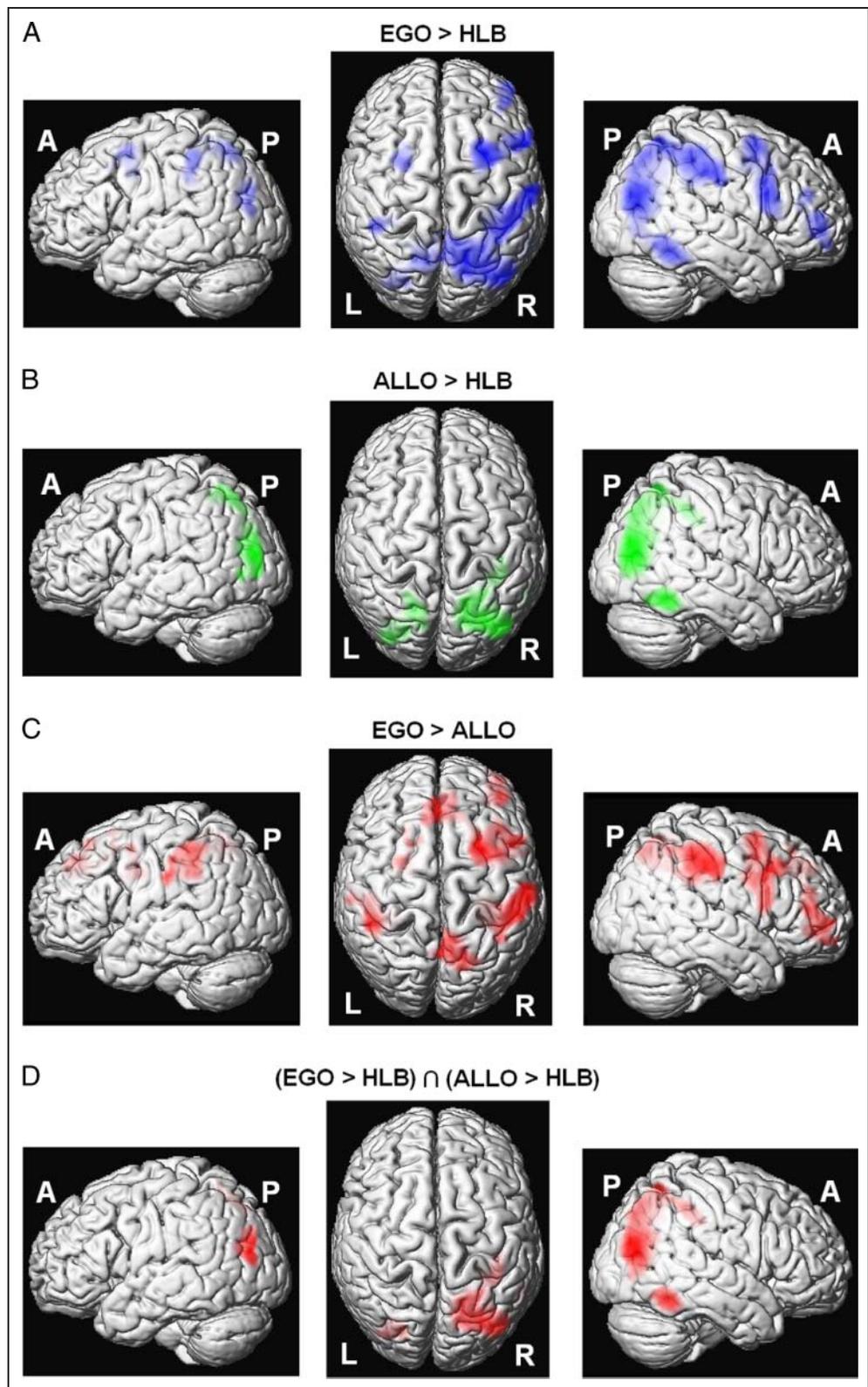
### Main Effect of Spatial Domain

We first identified brain regions associated with the processing of different spatial domains, that is, those regions which showed preferences for near space and far space processing. An extended activation cluster, including bilateral superior occipital gyrus and bilateral POJ, showed significantly higher neural activity in near than in far

**Figure 3.** Main effect of spatial domain. Bilateral superior occipital gyrus, including bilateral POJ, in the dorsal stream showed significantly higher neural activity during near space processing (green) compared with far space processing. Bilateral LOC in the ventral stream showed significantly higher neural activity during far space processing (red) compared with near space processing. For the purpose of display, threshold of the SPM in the later case (red) was set at  $p < .05$ , uncorrected at the voxel level, extent  $> 500$  voxels.



**Figure 4.** Main effect of spatial reference frame. (A) Brain regions activated by egocentric judgments (EGO) as compared with the HLB task. (B) Brain regions activated by allocentric judgments (ALLO) as compared with the HLB task. (C) The parietal and frontal regions specifically activated by egocentric judgments as compared with allocentric judgments independent of spatial domain, that is, “(Near\_EGO + Far\_EGO) > (Near\_ALLO + Far\_ALLO).” (D) Brain regions commonly activated by both egocentric and allocentric judgments, as depicted by the conjunction analysis of the two contrasts “EGO > HLB (near and far space combined)” and “ALLO > HLB (near and far space combined).”



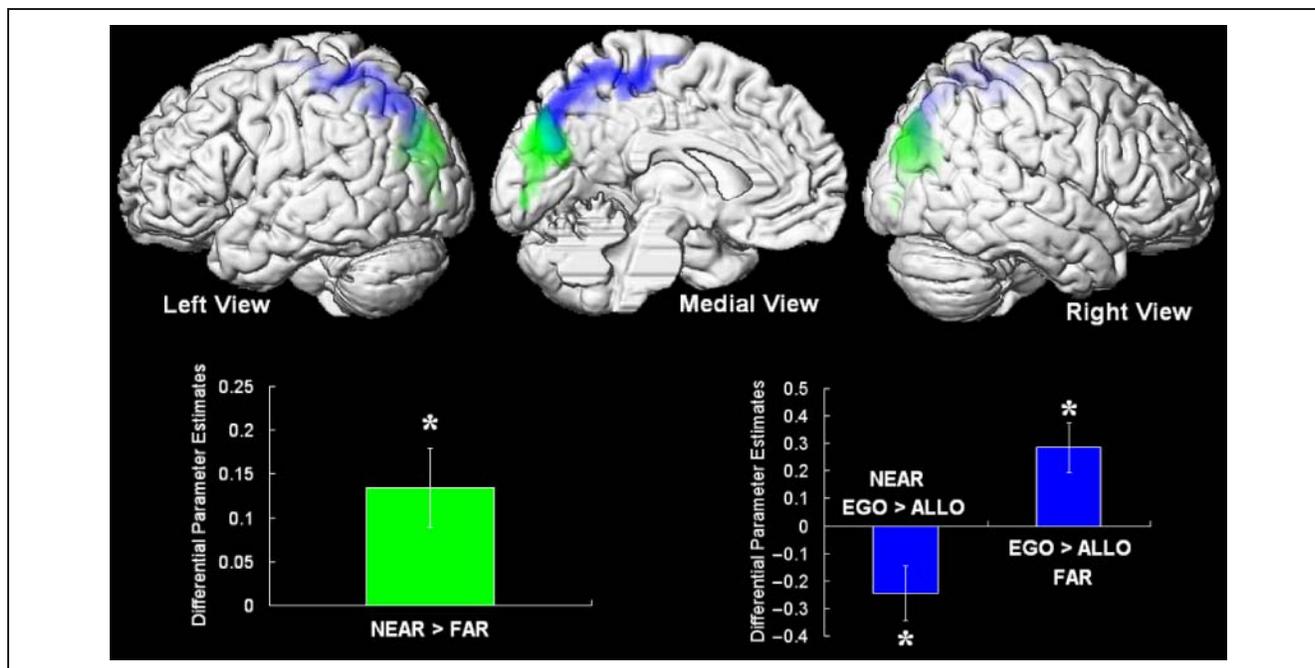
space (allocentric and egocentric judgment combined), that is, in the contrast “Near > Far” (allocentric and egocentric judgments combined; Figure 3 and Table 1A). For the reverse contrast, that is, “Far > Near,” no significant activation was observed at the threshold of  $p < .001$ , cor-

rected for multiple comparisons at the cluster level with an underlying voxel level of  $p < .001$  (uncorrected). However, because we had the clear a priori hypothesis that the ventral stream is involved in far space processing, we additionally performed a small volume correction

**Table 2.** Brain Regions Showing Significant Relative Increases of BOLD Response Associated with the Different Spatial Reference Frames (Egocentric and Allocentric Judgments)

<i>Anatomical Region</i>	<i>Side</i>	<i>Cluster Peak (mm)</i>	<i>t Score</i>	<i>k<sub>E</sub> (Voxels)</i>
<i>A. EGO &gt; HLB</i>				
Superior parietal cortex	R	18, -74, 54	9.79	6791
	<i>R</i>	<i>40, -80, 26</i>	<i>9.62</i>	
	<i>R</i>	<i>40, -36, 42</i>	<i>8.82</i>	
Inferior frontal gyrus	R	52, 10, 26	7.18	1928
	<i>R</i>	<i>28, 2, 60</i>	<i>6.65</i>	
Middle frontal gyrus	R	44, 44, 10	4.54	538
Superior frontal gyrus	L	-26, -2, 56	5.37	423
Inferior parietal cortex	L	-44, -44, 52	5.22	367
	<i>L</i>	<i>-38, -42, 40</i>	<i>4.84</i>	
Middle occipital gyrus	L	-28, -80, 30	4.65	418
<i>B. ALLO &gt; HLB</i>				
Middle occipital gyrus	R	40, -74, 16	7.86	2682
	<i>R</i>	<i>20, -74, 52</i>	<i>6.03</i>	
	<i>R</i>	<i>40, -38, 44</i>	<i>4.74</i>	
Inferior temporal gyrus	R	56, -56, -12	5.85	428
Middle occipital gyrus	L	-36, -86, 18	5.36	704
Superior parietal cortex	L	-22, -60, 58	4.60	389
<i>C. EGO &gt; ALLO</i>				
Postcentral gyrus	R	56, -26, 48	6.62	1714
	<i>R</i>	<i>36, -36, 40</i>	<i>6.08</i>	
	<i>R</i>	<i>50, -34, 56</i>	<i>5.91</i>	
Precuneus	R	8, -68, 60	5.79	1086
Precentral gyrus	R	36, 0, 34	5.73	2746
	<i>R</i>	<i>26, 8, 50</i>	<i>5.67</i>	
	<i>M</i>	<i>0, 34, 42</i>	<i>5.07</i>	
Middle frontal gyrus	R	36, 38, 16	4.73	748
Precentral gyrus	L	-26, -6, 40	4.60	410
Anterior IPS	L	-44, -44, 42	5.29	947
<i>D. (EGO &gt; HLB) ∩ (ALLO &gt; HLB)</i>				
Middle occipital gyrus	R	38, -78, 24	7.78	2475
	<i>R</i>	<i>20, -74, 52</i>	<i>6.03</i>	
	<i>R</i>	<i>42, -40, 46</i>	<i>4.66</i>	
Inferior temporal gyrus	R	56, -54, -12	5.81	348
Middle occipital gyrus	L	-28, -80, 26	4.27	339

The coordinates (*x, y, z*) correspond to MNI coordinates. Displayed are the coordinates of the maximally activated voxel within a significant cluster as well as the coordinates of relevant local maxima within the cluster (*in italics*).



**Figure 5.** POJ was involved both in the processing of near space and the interaction between spatial domains and spatial reference frames. Green: Main effect of Spatial Domains. Bilateral parietal–occipital cortex was specifically activated during near space processing (Near) as compared with far space processing (Far). Blue: The interaction between Spatial Domains and Spatial Reference Frames, that is, “(Near\_ALLO > Near\_EGO) > (Far\_ALLO > Far\_EGO),” activated an extended cluster around the medial superior parietal cortex. The POJ was activated both by near versus far space processing and by the interaction term as depicted by a conjunction analysis (the overlapping area between green and blue in the top middle). The parameter estimates in the maximally activated voxel within POJ ( $-2, -78, 30$ ) were significantly higher for near space processing than for far space processing (bottom left), that is, the main effect of Spatial Domain, and for allocentric judgments (than egocentric judgments) in near space, and for egocentric judgments (than allocentric judgments) in far space (bottom right), that is, the interaction between Spatial Domain and Spatial Reference Frame. The error bars represent the *SEs*. The asterisks indicate  $p < .05$ , corrected.

analysis within bilateral lateral occipital cortex (LOC), a key area of the ventral stream. The searching areas were two spheres centered upon  $\pm 41, -71, -10$ , with a radius of 12 mm. These Talairach coordinates were obtained from patient DF based on the lesions in bilateral LOC (James et al., 2003). Right (MNI:  $x = 50, y = -74, z = -14, Z = 3.5$ , eight voxels) and left (MNI:  $x = -46, y = -78, z = -14, Z = 3.39$ , eight voxels) LOC showed significantly higher neural activity during far space processing than during near space processing,  $p < .05$ , family-wise error correction at the voxel level (Figure 3).

### Main Effect of Spatial Reference Frame

We then identified the pattern of neural activity elicited by allocentric and egocentric judgments. As compared with HLB, egocentric judgments (Figure 4A and Table 2A) and allocentric judgments (Figure 4B and Table 2B) conjointly activated both the ventral stream in the right inferior temporal gyrus and the dorsal stream in the right middle occipital gyrus extending to the right superior parietal cortex, the right intraparietal sulcus (IPS), and the left middle occipital gyrus (Figure 4D and Table 2D). When compared with allocentric judgments (near and far space combined), egocentric judgments more strongly acti-

vated a dorsolateral fronto-parietal network including bilateral anterior IPS, bilateral precentral gyrus, bilateral anterior middle frontal gyrus, the right ventral pFC, and the right precuneus (Figure 4C and Table 2C). No significant activation was found in the reverse contrast.

### Neural Interaction between Spatial Domain and Spatial Reference Frame

The interaction term “(Near\_ALLO > Near\_EGO) > (Far\_ALLO > Far\_EGO)” revealed a left dorsomedial cluster located around the left precuneus extending dorsally to left superior parietal cortex and ventrally to left POJ (Figure 5, blue area at the top; Table 1B). No significant activations were found for the reverse interaction contrast.

To isolate brain regions that both showed preferences for near space processing and were involved in the interaction between Spatial Domains and Spatial Reference Frames, we performed a conjunction analysis between the main effect of spatial domains (“Near vs. Far space processing”) and the interaction between spatial domains and reference frames [“(Near\_ALLO > Near\_EGO) > (Far\_ALLO > Far\_EGO)”. The POJ was identified as the only brain region that both showed a significant preference for near space processing and was involved in the



reverse contrast, that is, “(Near\_EGO > Near\_ALLO) > (Far\_EGO > Far\_ALLO).”

## DISCUSSION

In the current fMRI study, we aimed at localizing the neural interaction between spatial domains (near vs. far) and spatial reference frames (egocentric vs. allocentric) by crossing the two factors. Before we discuss in detail the activation pattern observed in POJ, which implies an important role of POJ in integrating information from the ventral and dorsal streams, the main effects of spatial reference frames and spatial domains will be first summarized.

The bilateral activation of parietal and frontal regions in the dorsal stream (more extensive on the right hemisphere) during egocentric judgments as compared with allocentric judgments (Figure 4A) is consistent with results from previous imaging studies on spatial reference frames (Zaehle et al., 2007; Neggers, Van der Lubbe, Ramsey, & Postma, 2006; Committeri et al., 2004; Fink et al., 2003; Galati et al., 2000; Vallar et al., 1999; Fink, Dolan, Halligan, Marshall, & Frith, 1997). No significant activation was found during allocentric judgments compared with egocentric judgments. Because allocentric judgments in near (dorsal stream) and far (ventral stream) space were combined in the main effect contrast, neural activity in the dorsal and ventral stream could cancel out with each other, resulting in the null main effect of allocentric judgments.

The higher neural activity in bilateral LOC of the ventral stream in far space than in near space fits well with previous evidence suggesting the involvement of the ventral stream in far space processing (Weiss et al., 2000, 2003). The higher neural activity in the vicinity of bilateral superior occipital gyrus crossing the cuneus in near space than in far space also replicates previous results showing the preferences for near space processing in POJ (Quinlan & Culham, 2007; Weiss et al., 2000, 2003). Note that the current differential activations for near space processing in POJ were induced by egocentric and allocentric judgments on visual stimuli presented in a virtual three-dimensional environment within the MR scanner, while our previous PET data resulted from processing of line stimuli physically presented on screens at real distances of 0.7 m (near) or 1.7 m (far). These results are thus consistent with recent evidence showing comparative task performance during visual line bisection tasks in real and virtual environments (Gamberini, Seraglia, & Priftis, 2008).

It has been suggested that simply having one's gaze on a near versus far fixation point could induce activation in the human POJ (Quinlan & Culham, 2007). A recent single neuron recording study on awake monkeys also showed that a significant proportion of neurons in V6A displayed a stronger preference for processing targets in near space than in far space (Hadjidimitrakis et al., 2011). Because we instructed the participants to keep their gazes straight forward and converge toward the frontal plane in which

near or far space stimuli appeared in this study, one may argue that vergence, accommodation, and pupil size of the eyes may drive the higher neural activity in POJ during near space processing. Note, however, POJ in our study not only showed higher neural activity in near space processing but also showed differential activity with respect to allocentric and egocentric judgments in near versus far space. Because allocentric and egocentric judgments were first contrasted in near and far space, respectively, and then the products of the two contrasts were compared in the interaction contrast “(Near\_ALLO > Near\_EGO) > (Far\_ALLO > Far\_EGO),” the resulting neural interaction in POJ cannot be simply explained by the potentially differential oculomotor processes either between near and far spaces or between allocentric and egocentric judgments.

In this study, POJ was the only brain region that was conjointly activated by the main effect of near versus far space processing and by the interaction between spatial domains and spatial reference frames. The POJ region activated here was located in the POJ (Figure 5). This constitutes the anatomical locus of the putative human visual area V6A (Cavina-Pratesi et al., 2010; Luppino, Hamed, Gamberini, Matelli, & Galletti, 2005; Galletti, Fattori, Gamberini, & Kutz, 1999; Galletti, Fattori, Battaglini, Shipp, & Zeki, 1996). Recent electrophysiological and tract tracing studies in monkeys have pointed to the V6A as a crucial neural node during the process of transforming visual/perceptual information into sensorimotor representations. Functionally, the V6A complex contains both visual and sensorimotor cells (Gamberini, Galletti, Bosco, Breveglieri, & Fattori, 2011; Galletti et al., 2010; Breveglieri, Galletti, Gamberini, Passarelli, & Fattori, 2006; Galletti, Fattori, Kutz, & Battaglini, 1997). Anatomically, the V6A complex is located at the transition area between the somatic and peripheral visual representations in the cerebral cortex and is interconnected with several posterior parietal areas of the dorsal visual stream (Passarelli et al., 2011; Gamberini et al., 2009; Galletti et al., 2001; Shipp, Blanton, & Zeki, 1998; Zeki, 1986). Taken together prior studies suggest that the V6A complex is both functionally and anatomically specialized to feed (visual) perceptual information into the sensorimotor system.

In near space, POJ was more strongly activated by allocentric than by egocentric judgments. Once a target object is within near (i.e., reachable) space, not only its egocentric representations but also its allocentric representations are important with regard to guiding manual responses to it. For example, the aforementioned patient DF was unimpaired in grasping *per se* but showed deficits when grasping objects by placing her fingers in two or three circular holes whose locations were varied from trial to trial, that is, motor deficits specific to allocentric representations (Dijkerman, Milner, & Carey, 1998). These data suggest that this type of movements must be supported by an allocentric reference frame (see also Schenk, 2006). A recent

fMRI study on neural correlates underlying movements based on allocentric reference frames as compared with movements based on egocentric reference frames revealed that the former one implicated both bilateral LOC in the ventral stream and parietal–frontal regions in the dorsal stream (Thaler & Goodale, 2011). A question to be further answered is which region in the brain is responsible for transforming perceptual representations in bilateral LOC of the ventral stream to sensorimotor representations in the parietal–frontal regions of the dorsal stream. In this study, for target objects in near space, both egocentric and allocentric information needs to be transformed to sensorimotor representations to support potential manual actions. During egocentric judgments, participants associate external behavioral targets with their own body effectors. Egocentric positions of the targets are thus readily represented as high level sensorimotor representations in the parietal–frontal regions (Zaehle et al., 2007; Galati et al., 2000; Vallar et al., 1999). On the other hand, allocentric judgments, that is, assessing the position of an object relative to another object, draw upon perceptual representations in the ventral stream (Zaehle et al., 2007). Thus, when participants performed allocentric judgments on objects located in near space, the ventral perceptual representations, on which allocentric judgments are based, had to interact with the dorsal sensorimotor representations supporting near space processing. The higher neural activity in POJ during allocentric judgments in near space suggested that this interaction took place in POJ (Figure 5).

In far space, POJ was more strongly activated by egocentric than by allocentric judgments. When an object appears in far (unreachable, perceptual) space, its object properties are encoded in the ventral pathway as perceptual representations (Figure 3). Egocentric judgments in far space, however, associate distant objects with subjects' own body or body effectors, which requires activation of the sensorimotor representations in the dorsal stream. Therefore, the perceptual representations in the ventral stream, underlying far space processing, need to interact with the sensorimotor representations in the dorsal stream supporting egocentric judgments. Again, our data suggest that POJ was activated by this interaction (Figure 5). Growing evidence from neurophysiological and neuropsychological studies has shown that the active, purposeful use of a tool can extend the range of near space by changing both neural and behavioral responses (Legrand, Brozzoli, Rossetti, & Farne, 2007; Farne, Iriki, & Ladavas, 2005; Maravita, Husain, Clarke, & Driver, 2001; Berti & Frassinetti, 2000; Iriki, Tanaka, & Iwamura, 1996). Tools enable human beings (and some primates) to manipulate objects that would otherwise not be reachable by hand. The integration of vision and action during tool use, which allows us to reach and to manipulate objects in far space as if they were in near space, leads to a remapping of far space to near space. In the current study, POJ showed not only preferences for near space processing but also

higher neural activity during egocentric judgments in far space. One tempting speculation is that egocentric judgments in far space may play a similar role as tool-use does in functionally remapping far space to near space, probably by transforming perceptual representations of objects in far space to high level sensorimotor representations (Legrand et al., 2007; Farne et al., 2005; Maravita et al., 2001; Berti & Frassinetti, 2000; Iriki et al., 1996). Taken together, POJ showed higher neural activity whenever there was a necessity for the perceptual representations in the ventral stream and the sensorimotor representations in the dorsal stream to interact, that is, during allocentric judgments in near space and egocentric judgments in far space. This notion is further supported by the results from the functional connectivity analyses: POJ showed higher functional interactions with the left IPS both in “Near\_ALLO” and “Far\_EGO” conditions compared with “Near\_EGO” and “Far\_ALLO” conditions (Figure 6), implying that perceptual information may be transformed to sensorimotor presentations in the left IPS (Iriki et al., 1996) via POJ whenever there is a necessity to exchange information between the dorsal and ventral streams. Our functional connectivity data also fit well with previous anatomical data from tract tracing studies: the dorsal part of V6A, that is, V6Ad, has strong connections with the parietal areas where arm-reaching and grasping activities are represented (Gamberini et al., 2009).

Please note, in our study perceptual (allocentric and egocentric) tasks were performed both in near and far space. Because the differential involvement of dorsal/ventral streams in near/far space processing is commonly assumed to be associated with the fact that an object can be manually manipulated in near space, but not in far space, one may argue that given the setup in the MR scanner, participants may not have perceived the near space stimuli as reachable, and hence the dissociation between near and far space may not have been valid in our study. However, as pointed out by Milner and Goodale, the critical factor that controls the involvement of the dorsal/ventral stream is the underlying processes rather than the tasks (Milner & Goodale, 2008). Accordingly, evidence from our previous studies suggests that the dorsal/ventral streams are differentially involved in near/far space processing, irrespective of whether a perceptual or a motor task is performed (Weiss et al., 2003), indicating that stimuli falling in near and far space are differentially represented in the dorsal and ventral stream irrespective of the behavioral tasks performed on them.

To summarize, by asking subjects to perform allocentric and egocentric judgments either in near space or far space, we found that in addition to its role in near space processing (Quinlan & Culham, 2007; Weiss et al., 2003), POJ is activated whenever perceptual representations in the ventral stream have to interact with the sensorimotor representations in the dorsal stream. Thus, our data implicate POJ as the neural interface between the dorsal and the ventral streams.

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