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Effects of shifting perspective of the self: An fMRI study

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When looking to our reflection, or moving a video-game character, we see our own movement preformed by an agent which is physically separated from our body. Yet, we consider the agent to be ourself. Using fMRI, we sought to explore the neural underpinnings of *disembodiment,* the cognitive mechanism under which the properties of the self are projected away from the boundaries of one's own body towards an external entity. Seventeen participants watched a video-game in which three players threw each other a ball. Subjects' key-press could either be synchronous or asynchronous with one of the players' action (TASK: Agency vs. Control). The game was shown from one of four viewpoints which could either be fixed or change every trial (VIEWS: Fixed vs. Changeable). Consistent with previous studies, the left insula was activated when the agent's movements were synchronous with those of the participants (main effect of TASK, $p < 0.05$, SVC). The analysis of the interaction TASK * VIEWS revealed activation ($p < 0.05$, corrected) of the right parieto-temporal-occipital (PTO) junction when the agent whose movements were synchronous to the participants was processed in a spatial position each time different with respect to the preceding trials. Our findings implicate the right PTO junction in assigning one's own movements to an agent which is physically independent of oneself. They also suggest that the ability to *disembody*, and thereby *objectify,* bodily or mental states concerning the self is common to all experimental paradigms which led to an activation of the PTO junction.

Keywords: Agency; Disembodiment; Self-objectification; Temporo-parietal junction; Theory of mind

Introduction

In the last years the study of the neural underpinnings of self-processing has become an increasingly prominent issue in cognitive neuroscience. Recent studies have investigated the ability of perceiving an *embodied* self, that is perceiving oneself as constrained within the boundaries of one's physical body (e.g., pointing the gaze towards the ground and looking at one's own feet). David et al. (2006), for instance, had participants face a video-game like display in which fictional players were throwing each other a ball, and carry out an agency task in which their key-presses triggered the movement of one of the players, which could be perceived from either first-person or third-person view. They found that seeing one's own action from a first-person view elicited an activation of the left cingulate and the left superior frontal cortex.

A large number of both neurophysiological and neuropsychological studies have investigated the neural correlates of *disembodiment*, the cognitive ability to project properties of the self outside the boundaries of one's own body, and as a consequence to process an external entity as an *objectified* (or *disembodied*) self. An extended right hemisphere network, including the inferior parietal lobule, the supramarginal gyrus, the inferior frontal gyrus, and the inferior occipital gyrus, was found to be involved in perceiving either their own face (Keenan et al., 2001; Sugiura et al., 2000), or the digital morph between their own face and a gender-matched familiar face of another individuals (Uddin et al., 2005). Similar results came from the study of autoscopic phenomena (e.g. Blanke and Mohr, 2005; Brugger, 2002), in which subjects report of viewing their own body in a position which is separated from the observer. These hallucinations can be induced by epilepsy over regions in the right temporal cortex (Devinsky et al., 1989), as well as by electrical stimulation over the right temporo-parietal junction (Blanke et al., 2002).

The neural correlates of processing *disembodiment* were also described by neurophysiological studies in which macaques were trained to use a tool even though they never exhibit such ability in the wild life (e.g., Iriki, 2006; Maravita and Iriki, 2004). Iriki and

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colleagues had macaques reach a piece of food which was placed either outside their arm reach space (e.g. Iriki et al., 1996), or within their arm reach but occluded from their direct sight (Iriki et al., 2001). In both conditions, macaques could reach the food (thus overcoming their body limits) by means of external features, such as a rake for extending their own reach (Iriki et al., 1996), or a video displaying the position of the food with respect to their moving arms from a non-egocentric point of view (Iriki et al., 2001). The authors found that macaques can be trained to make productive use of the tool or the images displayed; this newly acquired skill is associated with the emergence of cortico-cortical connections between neurons in the intraparietal sulcus (IPS – typically responding to visual stimuli in the peri-personal space – e.g., Duhamel et al., 1998) and temporo-parietal junction (Hihara et al., 2006). Mastering tool-use skills requires the ability to project one's own motor intention towards an external object, the tool. It has been suggested that the involvement of both the temporo-parietal complex in the human brain for observations, such autoscopic phenomena, and homologous regions in the monkey brain for the emergence of tool-use skills, is suggestive of this part of the brain being recruited whenever properties of the self are externalized towards an external entity (namely whenever *disembodiment* occurs, which in turn leads subject, based on the equivalence between the external tool and own body, to regard its own body as an external object, namely *self-objectification*; see Hihara et al., 2006, and Iriki, 2006, for a more detailed comment about this topic).

In the present study we aimed at further specifying the neural mechanisms involved in *disembodiment*. We designed an fMRI experiment in which, similarly to the paradigm employed by David et al. (2006), participants faced a video-game like display in which fictional players were throwing each other a ball. Participants were engaged in an Agency task in which their key-presses were synchronous with the movement's onset of one of the players, which in turn represented the self. In a control condition, participants' key-presses were instead unrelated to the action of the players in the video-game. At variance with David et al.'s (2006) in which participants experienced an *embodied* self, described as perceiving their own action from a first-person view, the key condition of the present study was that participants experienced a *disembodied* self, described as perceiving their own action from third party's views. Moreover, in one experimental condition the players were displayed from a point of view which varied every trial, thus appearing each time misaligned with respect to the proceeding trial, whereas in a control condition the points of view were instead fixed. Thus, employing the Agency (but not the Control) task under Changeable (but not Fixed) views would require, at each trial, reassigning the player which we consider to be ourself towards a different position in the outside space that is labeling a new agent as the self. Based on the existing findings we hypothesized that the analysis of this condition would reveal increased neural activity in the right hemisphere over and around the temporo-parietal junction.

Materials and methods

Participants

Seventeen subjects (eight females) participated in the study. None of the participants had any history of neurological or psychiatric illness. Written informed consent was obtained from all subjects. The study was approved in advance by the RIKEN Functional MRI Safety and Ethics Committee and conducted in accordance with the Declaration of Helsinki.

Stimuli

Participants watched twelve short (6 s) animations in which three players were throwing each other a ball. These players were equally distanced and their relative position was constant during all the experiment: a blue and a red player were shown respectively on the left and on the right side of the screen, whereas a black player appeared in the central-lower side. The movies were organized in triplettes, whose order was constant during all the experiment: first, the red player threw the ball to the blue, afterwards the blue threw the ball to the black, and finally the black threw the ball to the red (see Fig. 1A). The point of view (i.e. the position of the camera) was constant within each triplette, but may vary across triplettes, depending on the experimental condition employed. Four different views were chosen: laterally drifted point of view (the black player was visible from the side — see Fig. 1B), from the back of the black player (the camera pointed directly over the shoulders of the black player — see Fig. 1C), and from the black players eye (see Fig. 1D), and from the ceiling (the three players were visible only form their upper half — see Fig. 1E).

Experimental setup

Participants laid supine with their head fixated by firm foam pads and their hand placed on a button-box for manual responses. Stimuli were displayed via an optic fiber goggle system (Avotec Inc., Jensen Beach, FL) that subtended 30°×23° of visual angle.

Each experimental session consisted of the following events: participants viewed a fixation cross for about 41 s, followed by a continuous sequence of 32 triplettes, 8 for each point of view, and then by a final pause of about 13 s. Each session lasted 10 minutes and 30 s. Within each session participants were engaged in one of two tasks: they were instructed to perform a key-press either when they saw the ball between the red player and the blue player (*Control Task* — see Fig. 1F, red dashed line), or after seeing the black player receiving the ball, but before the beginning of the next animation in which he threw the ball to the next player, as if the key-press triggered the black player's movement (*Agency Task* — see Fig. 1F, black continuous line). In addition, within each session, irrespective of the task employed, triplettes of the same point of view could be clustered together, yielding to four sequences of about 2 minutes and 30 s in which the point of view was fixed (*Fixed Views*). Alternatively, triplettes of different points of view could be intermingled, so that each triplette had a different point of view than the previous one (*Changeable Views*). Finally, within each session, irrespective to the point of view and of the task employed, 64 events of interests, each 9 s apart, were identified: half of them referred to the 32 onsets of the black player movement, whereas the other half referred the 32 midpoints between the onsets of the red and blue players movements (Fig. 1F).

This constitutes a 2×2×2 factorial design with TASK (Agency vs. Control) and VIEWS (Changeable vs. Fixed) and BALL's position (Black player vs. Red-Blue players) as factors. TASK and VIEWS factors yielded to four conditions, each of which was delivered in a separate session. The two levels of the BALL factor were instead modulated within each session, together with the low-level baseline events which corresponded to the beginning of each session in which the fixation cross was shown. Thus, our design resulted in 8 experimental conditions and 4 low-level baseline conditions (see Table 1). The overall experiment lasted about 42 minutes, corresponding to four sessions of 10 minutes and 30 s, the order of which was counterbalanced across subjects.

Image acquisition

The experiment was conducted on a Varian Unity Inova 4 Tesla whole-body MRI system (Varian NMR Instruments, Palo Alto, CA) equipped with a Magnex head gradient system (Magnex Scientific Ltd., Abingdon, UK). High-resolution 3D T1-weighted anatomical

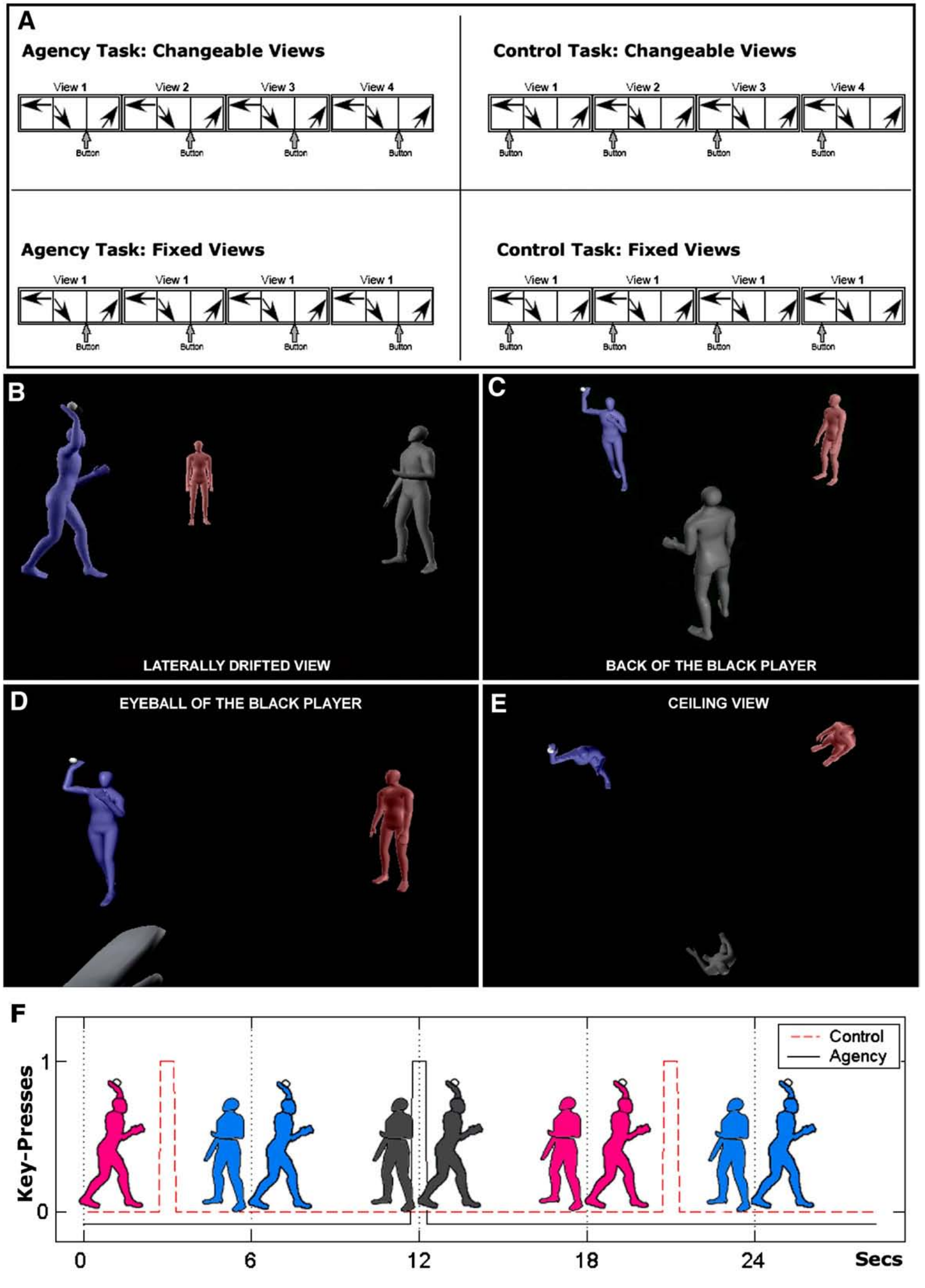

Table 1

Summary of eight experimental conditions in the 2×2×2 factorial design and four baseline conditions, each of which corresponds to the initial stage of each session in which participants viewed a fixation cross

Experimental and Baseline conditions		
Experimental conditions		
1	*AFB*	Agency task with Fixed views, during the onset of the Black player's action.
2	*AFR*	Agency task with Fixed views, between the onsets of the Red and Blue players.
3	*ACB*	Agency task with Changeable views, during the onset of the Black player's action.
4	*ACR*	Agency task with Changeable views, between the onsets of the Red and Blue players.
5	*CFB*	Control task with Fixed views, during the onset of the Black player's action.
6	*CFR*	Control task with Fixed views, between the onsets of the Red and Blue players.
7	*CCB*	Control task with Changeable views, during the onset of the Black player's action.
8	*CCR*	Control task with Changeable views, between the onsets of the Red and Blue players.
Baseline conditions		
1	*AF_Bas*	Agency task with Fixed views, when the fixation cross was shown.
2	*AC_Bas*	Agency task with Changeable views, when the fixation cross was shown.
3	*CF_Bas*	Control task with Fixed views, when the fixation cross was shown.
4	*CC_Bas*	Control task with Changeable views, when the fixation cross was shown.

MR images were acquired with a quadrature bird-cage radio-frequency (RF) coil (The John P. Robarts Research Institute, London, Ontario, Canada). The following parameters were used for acquiring anatomical images: repetition time (TR) = 110 ms, echo time (TE) = 6.2 ms, flip angle (FA) = 11°, matrix size = 256 × 256 × 180, and voxel size = 1 × 1 × 1 mm. A quadrature bird-cage RF coil (Subjects 1–12: The John P. Robarts Research Institute, London, Ontario, Canada — subjects 13–17: Nova Medical Inc., Minneapolis, MN, USA) was also used (for both transmit and receive) to acquire functional (T2*-weighted) and coregistered anatomical (T1-weighted) images. Functional images were scanned using an echo-planar imaging (EPI) pulse sequence with a TR of 2570 ms, a TE of 25 ms and an FA = 40. Each volume comprised 25 axial slices with an in-plane resolution of $3.75 \times 3.75\ \text{mm}^2$ (field of view [FOV] = $24 \times 24\ \text{cm}^2$), a slice thickness of 5 mm, and no gap between slices. For each subject, 980 volumes were acquired in four experimental sessions (245 per session). During all four experimental sessions, heartbeat was monitored with a pulse oximeter, and respiration with a pressure sensor. Both signals were recorded along with the timing of RF pulses for later corrections of physiological fluctuations.

Image processing and data analyses

After EPI image reconstruction, cardiac and respiratory fluctuations were further removed using a retrospective estimation and correction method (Hu et al., 1995). For each subject, the first 6 volumes of each session were discarded. Furthermore, to correct for subject motion, all functional images were realigned to the first functional image, which were then normalized to a template based on 152 brains from the Montreal Neurological Institute (MNI), and smoothed by convolution with a Gaussian kernel of 8 mm (full-width at half-maximum). Finally, a high-pass filter (with a cut-off of 128 s) was applied to the dataset.

Statistical analysis was then carried out using the general linear model framewor (Friston et al., 1995) implemented in the SPM2 software package (Wellcome Department of Imaging Neuroscience, London). On the first level, for each individual subject, we fitted a linear regression model (general linear model) to the data, by modelling the event sequence of each of the experimental and baseline conditions (see Table 1) as a hemodynamic response function. We also included six differential realignment parameters assessed for each session as regressors to control for movement-related variance. Additionally, for each session a vector distinguishing between participants keeping their eyes opened and those keeping their eyes closed was entered as a regressor of no interest. Specific effects were tested by applying appropriate contrasts to the parameters estimated for each condition. On the second level, one-sample t-tests were performed on the above contrast images of all subjects to generate random-effects statistical parametric maps (SPMs). Areas of activation were identified as significant if they passed a threshold of $p < 0.05$, corrected for multiple comparisons at the cluster-level, with an underlying voxel-level height threshold of $t = 3.69$ (corresponding to an uncorrected $p < 0.001$).

Localization of activated areas with respect to cytoarchitectonic areas was analyzed based on probabilistic cytoarchitectonic maps derived from the analysis of cortical areas in a sample of 10 human post-mortem brains, which were subsequently normalized to the MNI reference space. Significant results of the random effects analysis were compared to the cytoarchitectonic maps using the SPM Anatomy toolbox (Eickhoff et al., 2005).

Results

Clusters of activated voxels, which survived a threshold of $p < 0.05$, corrected for multiple comparisons, are reported in Table 2.

Main effects

No differential activation for the Agency task, in comparison to the Control task [$\text{Agency} - \text{Control} = (AFB + AFR + ACB + ACR - 2 * (AF\_Bas + AC\_Bas)) - (CFB + CFR + CCB + CCR - 2 * (CF\_Bas + CC\_Bas))$] was observed (when applying a threshold of $p < 0.05$,

Fig. 1. Experimental design and Stimuli. (A) diagram describing the factors TASK (Agency vs. Control) and VIEWS (Fixed vs. Changeable). Participants saw movies which were organized in triplettes: first, the red player threw the ball to the blue (←), afterwards the blue threw the ball to the black (↘), and finally the black threw the ball to the red (↗). During the Agency Task, for each triplette participants key-pressed (⇑) at the onset of the third movie, that is, when the ball was in the black player's hands. During the Control Task, for each triplette, participants key-pressed during the first movie, that is, when the ball was between the red and the blue player. The viewpoints were fixed within each triplette, but varied across triplette. Under Fixed Views, triplettes of the same view were clustered together, whereas under Changeable Views triplettes with different views were intermingled. (B–D) Movie snapshots depicting each of the four points of view used. (F) Irrespective of the task employed and of the viewpoints, two events of interest were used in the analysis: one was the onset of the third movie of each triplette, which corresponded to participants' key-presses during the Agency task (straight line); the second was the middle point of the first movie of each triplette, which corresponded to participants' key-presses during the Control task (red dashed line).

Table 2
Clusters of voxels showing significant activation in: (1) the TASK main effect, (2) the BALL main effect, (3) the TASK * VIEWS interaction, and (4) the TASK * BALL interaction. All clusters survived a threshold of $p<0.05$, corrected for multiple comparisons at the cluster level for the whole brain or for the region of interest (ROI), respectively. Coordinates (in standard MNI space) refer to maximally activated foci as indicated by the highest t value within an area of activation: x = distance (mm) to the right (+) or the left (−) of the midsagittal line; y = distance anterior (+) or posterior (−) to the vertical plane through the anterior commissure (AC); z = distance above (+) or below (−) the inter-commissural (AC–PC) line. L and R refer to the left hemisphere and right hemisphere, respectively, whereas K_e refers to the number of consecutive voxels subtending each cluster.

REGION	Cytoarchitectonic probabilistic maps	SIDE	Coordinates			K_e
			x	y	z	
1. TASK main effect: *Agency Task > Control Task*						
Insula		L	−44	−12	−4	48§
2. BALL main effect:						
(a) Red_Blue players > Black player						
Superior occipital gyrus	Area 17 [100–100%]	L	6	−92	2	390†
	Area 18 [10–60%]		6	−94	20	
(b) Black player > Red_Blue players						
Superior occipital gyrus	Area 18 [0–10%]	R	−12	−94	14	264‡
	Area 17 [10–20%]		−28	−76	10	
3. TASK * VIEWS interaction:						
(*Agency_Chang. > Agency_Fixed*) > (*Control_Chang. > Control_Fixed*)						
Middle temporal gyrus		R	40	−70	22	363‡
Middle occipital gyrus			32	−82	−24	
4. TASK * BALL interaction:						
(a) (Agency_Black > Control_Black)>(Agency_RedBlue > Control_RedBlue)						
Middle cingulate cortex	Area 4a [40–60%]	L	−6	−28	50	664*
Central sulcus	Area 3a [20–40%]		−20	−36	50	
Precentral gyrus	Area 6 [30–50%]		−28	−20	50	
(b) (Agency_RedBlue > Control_RedBlue)>(Agency_Black > Control_Black)						
Superior occipital gyrus	Area 18 [40–80%]	R	12	−74	−2	491†
	Area 17 [80–90%]	L	−4	−82	4	

$^{*}p<0.001$ $^{\dagger}p<0.01$ $^{\ddagger}p<0.05$ $^{\S}p<0.05$ corrected for the ROI.
All clusters survived a threshold of $p<0.05$, corrected for multiple comparisons at the cluster level for the whole brain or for the region of interest (ROI), respectively. Coordinates (in standard MNI space) refer to maximally activated foci as indicated by the highest t value within an area of activation: x = distance (mm) to the right (+) or the left (−) of the midsagittal line; y = distance anterior (+) or posterior (−) to the vertical plane through the anterior commissure (AC); z = distance above (+) or below (−) the inter-commissural (AC–PC) line. L and R refer to the left hemisphere and right hemisphere, respectively, whereas K_e refers to the number of consecutive voxels subtending each cluster.

corrected form multiple comparisons for the whole brain). Following the studies by Ruby and Decety (2001) and Farrer and Frith (Farrer and Frith, 2002; Farrer et al., 2003), we hypothesized that the insula, which they found to be involved when participants experienced their self as the cause of an action (relative to experiencing another person as being the cause of that action), should also be activated in our experiment. We therefore restricted our analysis to the insula bilaterally, using the SPM WFU Pick Atlas toolbox (Maldjian et al., 2003), and found a significant increase of the BOLD (Blood Oxygenation-Level Dependent) signal in the left posterior insula ($x=-44$, $y=-12$, $z=-4$, extending posteriorly to $y=-26$; $K_e=48$, $p<0.05$ corrected for the Region Of Interest (ROI) - see Fig. 2). In contrast, the Control task, relative to the Agency task [Control − Agency $=(CFB+CFR+CCB+CCR-2*(CF\_Bas+CC\_Bas))-(AFB+AFR+ACB+ACR-2*(AF\_Bas+AC\_Bas))$] led to no suprathreshold differential activity.

With regard to the main effects of VIEWS and BALL, differential activation was found neither during fixed, relative to changeable, points of view [Fixed − Changeable $=(AFB+AFR+CFB+CFR-2*(AF\_Bas+CF\_Bas))-(ACB+ACR+CCB+CCR-2*(AC\_Bas+CC\_Bas))$], nor in the opposite contrast, i.e. during changeable, relative to fixed, points of view [Changeable − Fixed $=(ACB+ACR+CCB+CCR-2*(AC\_Bas+CC\_Bas))-(AFB+AFR+CFB+CFR-2*(AF\_Bas+CF\_Bas))$]. Finally, irrespective of the task employed and the perspective, the events corresponding to the onset of the black player's action, relative to those between the onsets of the red and blue players' actions [Black − Red $=(AFB+ACB+CFB+CCB)-(AFR+ACR+CFR+CCR)$], led to differential activation in the left superior occipital gyrus, corresponding to Brodmann Area (BA) 17. In contrast, the events between the onset of the red and the blue players' actions, relative to those events corresponding to the onset of the black player's action [Red − Black $=(AFR+ACR+CFR+CCR)-(AFB+ACB+CFB+CCB)$], led to a differential activation in the right superior occipital gyrus (BA 17) that extended to BA 18.

Interactions

*TASK * VIEWS interaction*

In order to compare task differences with either fixed or changeable points of view, the TASK × VIEWS interaction was examined. The Agency (rather than the Control) task during changeable points of view, controlled for the Agency (rather than the Control) task during fixed points of view [(Agency_changeable − Control_changeable) − (Agency_Fixed − Control_Fixed) $=((ACB+ACR-2*AC\_Bas)-(CCB+CCR-2*CC\_Bas))-((AFB+AFR-2*AF\_Bas)-(CFB+CFR-2*CF\_Bas))$], led to a significant increase in the BOLD response in the posterior part of the right middle temporal gyrus, extending to the middle occipital gyrus (local maxima: $x=40$, $y=-70$, $z=22$). This cluster extends mediolaterally from $x=22$ to $x=50$, horizontally from $y=-90$ to $y=-50$ and vertically from $z=16$ to $z=36$. A percentage signal change analysis showed that this interaction was resulted from an increased neural activity during the Agency task (relative to the Control task) under changeable points of view. When the view was fixed, no significant

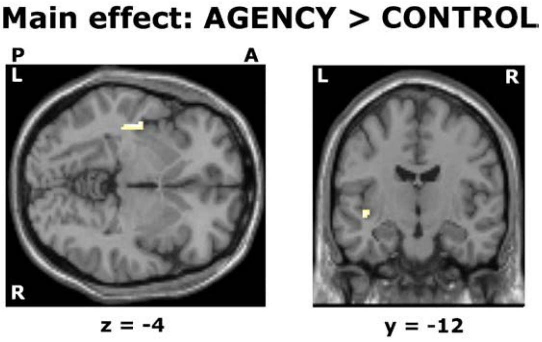

Fig. 2. Functional contrast testing the main effect of TASK: horizontal ($z=-4$) and coronal ($y=-12$) section.

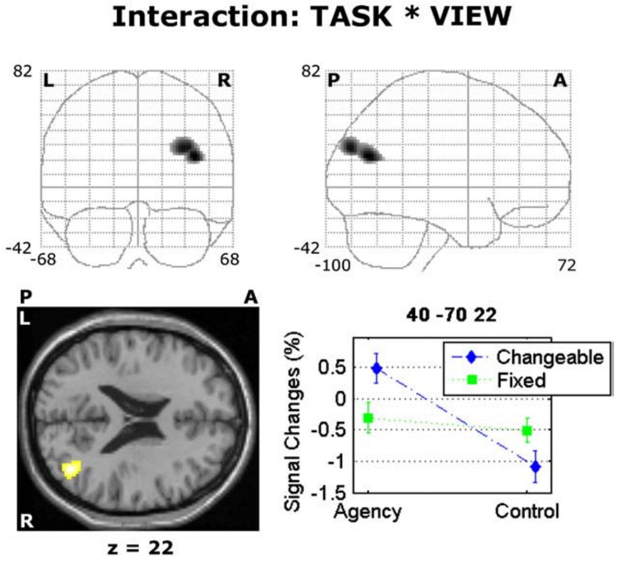

Fig. 3. Glass-brain images and horizontal section at $z=22$ of the functional contrast testing the TASK * VIEWS interaction. The percentage signal changes associated with the local maximum ($x=40$, $y=-70$, $z=22$) of the activated area in the right middle temporal gyrus are also displayed together with standard error (σ_M) bars.

difference between the two tasks was found (see Fig. 3). With regard to the opposite contrast [(Agency_Fixed − Control_Fixed) − (Agency_changeable − Control_changeable) = $((AFB+AFR-2*AF\_Bas)-(CFB+CFR-2*CF\_Bas))-((ACB+ACR-2*AC\_Bas)-(CCB+CCR-2*CC\_Bas))$], no differential activation was observed.

*TASK * BALL interaction*

In order to compare task differences across different events within each session, we tested the interaction TASK * BALL [(Agency_Black − Control_Black) − (Agency_Red − Control_Red) = $((AFB+ACB)-(CFB+CCB))-((AFR+ACR)-(CFR+CCR))$]. Such contrast allows to assess significant increase of neural activity associated with the Agency (relative to the Control) task during the black player's movement onset, as well as with the Control (relative to the Agency) task in the events corresponding to the midpoint between the red and the blue players' movement onsets. To rule out the effects due to increased neural activity associated with the Control task in the events when the ball was between the red and blue player, we used a mask to exclude the voxels exhibiting a main effect in the Control_Red - Agency_Red (i.e., $(CFR+CCR-(CF\_Bas+CC\_Bas))-(AFR+ACR-(AF\_Bas+AC\_Bas))$ comparison ($t>1.75$, corresponding to an uncorrected voxel-level threshold of $p<0.05$) from the analysis. We found a significant increase of the BOLD signal in the left middle cingulate cortex and the precentral gyrus (corresponding to BA 6 and 4a) that extended to the left postcentral gyrus (BA 3a). A percentage signal change analysis showed that this interaction was resulted from an increased neural activity during the Agency task (relative to the Control task) in the events corresponding to the black player's movement onset. On the other hand, in the events when the ball was between the red and blue players, no significant difference between the two tasks was observed (see Fig. 4A). Moreover, it should be mentioned that, using a less conservative threshold (e.g., 150 consecutive voxels), we found activation on the left middle frontal gyrus (local maxima: −18, 22, 50 — $K_e=178$ voxels) extending to the superior medial gyrus (−8, 34, 48). This cluster is located over and around the agency-related left middle frontal activation reported David et al (2006) who

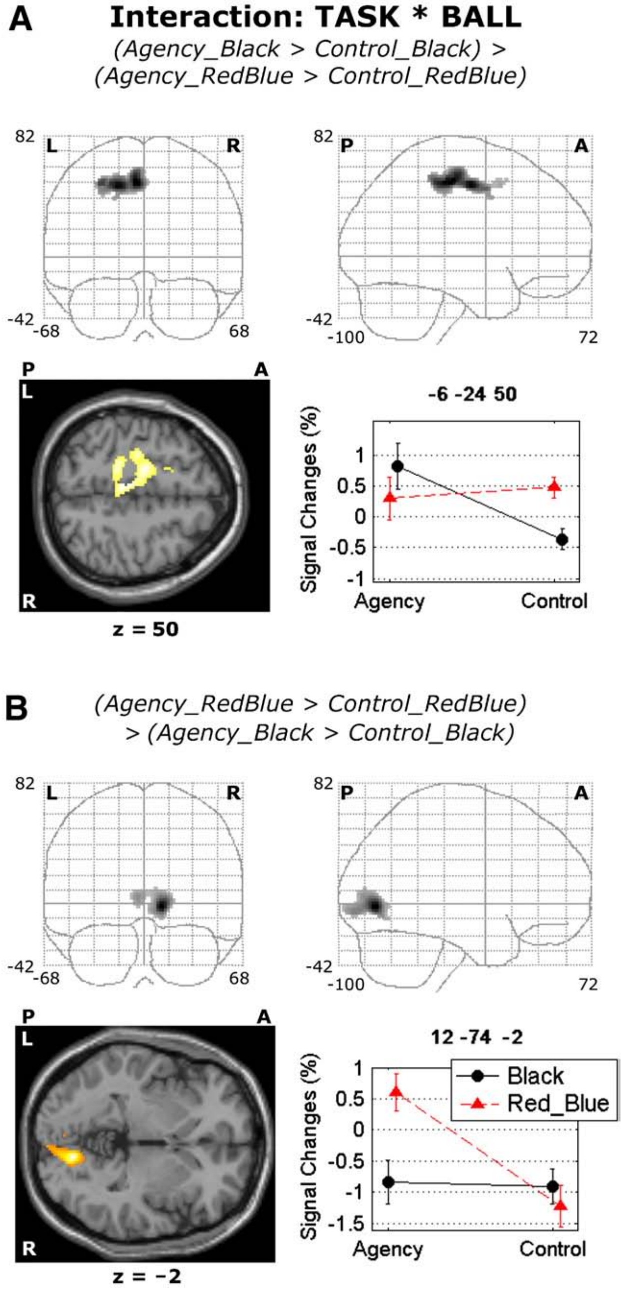

Fig. 4. Functional contrasts testing either the TASK * BALL interaction. (A) Glass-brain images and horizontal section ($z=50$) of the functional contrast (Agency_Black − Control_Black) − (Agency_Red − Control_Red). The percentage signal changes associated with the local maximum ($x=-6$, $y=-24$, $z=50$) of the activated area in the left middle cingulate cortex and precentral gyrus are also displayed together with standard error (σ_M) bars: black circles refer to the onset of the black player's movement, whereas red triangles over dashed lines refer to those events in which the ball was between the red and the blue players. (B) Glass-brain images and horizontal section ($z=-2$) of the functional contrast (Agency_Red − Control_Red) − (Agency_Black − Control_Black). The percentage signal changes associated with the local maximum ($x=12$, $y=-74$, $z=-2$) of the activated area in the right superior occipital gyrus are also displayed.

employed an experimental paradigm similar to our own. The opposite interaction [(Agency_Red − Control_Red) − (Agency_Black − Control_Black) = $((AFR+ACR)-(CFR+CCR))-((AFB+ACB)-(CFB+CCB))$], revealed a significant increase of BOLD activity in the right superior occipital gyrus, corresponding to BA 18 that extended to the left BA 17. A percentage signal changes analysis revealed that such an interaction was resulted from an increased neural activity for the Agency task (relative to the Control task) in the events when the ball was between the red and blue players. When the ball was instead in the black player's hands, no significant difference between the two tasks was observed (see Fig. 4B).

Neither the VIEWS * BALL interaction, nor the TASK * VIEWS * BALL interaction, were associated to any significant BOLD increase.

Discussion

The sense of Agency towards the fictional player's movement

The present experiment had participants carrying out an Agency task (as opposed to a Control task) in which they were asked, whilst watching movies in which three fictional players were throwing each other a ball, to key-press as if they were triggering the movement of one of the players. This task tests an effect of explicit (or *reflexive*) agency, in which participants are aware of the relation between a seen movement and their own (as opposed to implicit, or *prereflexive*, agency, in which participants start feeling their selves to be the cause of a seen action, in that this is compatible with their outgoing motor commands — see David et al., 2007; Synofzik et al., in press). We found increased activity of the left posterior insula associated with the main effect of TASK; this region was more active during the employment of the Agency, as opposed to the Control, task. Moreover, we found increased activity in the left middle cingulate cortex, extending to the postcentral and precentral gyri, and to the middle frontal gyrus, extending to the superior medial gyrus, associated with the TASK * BALL interaction; this region was more active during those events in which the ball reached the hands of one of the players to whom the participants were instructed to relate. Activity in all these regions has been found in numerous studies involving self-attribution of one's movements. For instance, in hemiplegic patients, a damage of the right insula is often correlated with anosognosia, the unawareness of one's motor impairment (e.g., Berti et al., 2005; Karnath et al., 2005). Studies using neuroimaging techniques have documented an insular activation in the left (Leube et al., 2003), right (Farrer et al., 2003) or both hemispheres (Farrer and Frith, 2002) during tasks in which participants viewed stimuli on a video-display that behaved consistently with their self-produced movements. Furthermore, Ruby and Decety (2001) found increased activities in regions within both the left posterior insula and the superior portion of the precentral and postcentral gyri when subjects imagined themselves (but not others) using a tool presented to them either visually or auditorily. The same portion of the postcentral gyrus was also activated when participants were asked to predict their own (but not others') reactions when faced with everyday situations (Ruby and Decety, 2003, 2004). Together, the literature reviewed above converge with the claim that during the Agency task employed in our study the center of the experiences of participants is projected toward the position in space occupied by the fictional character, thus processing those sensorimotor events which are associated to the player as their own.

The right parieto-temporal-occipital junction is implicated in diverse forms of Disembodiment

As already mentioned in the introduction section, Hihara et al. (2006) implicated a region in the vicinity of MSTda and TPOc of the macaque brain in the tool-use behavior. It has been suggested that this region is involved in the ability of assessing the equivalence between the monkey body representation (which is believed to be stored within the IPS) and the tool, thus allowing the monkey to establish *self-objectification* (Iriki, 2006). In our study, a region in the right middle temporal gyrus, extending to the middle occipital gyrus and bordering the right parietal cortex, exhibited functional properties similar to those found in the macaque temporo-parietal junction (Hihara et al., 2006; Iriki, 2006). This region was revealed by the analysis of the interaction AGENCY * VIEW and was found to be more activated during the Agency (but not the Control) task, and only in those conditions in which the views changed continuously. No differential activity between the Agency and Control task was observed when the views were fixed, thus confirming that this region is not sensitive to mere processing of the self in a location of the outside space, but rather to the reassignment of the self in new disembodied positions. In contrast to the monkey brain, in which the temporo-parietal junction in both hemispheres was implicated, only the right hemisphere in our study was associated with the interaction of AGENCY * VIEW.

Regions over and around the parieto-temporal-occipital (PTO) *junction complex* were already implicated in studies in which participant imagined to "drift" away from their egocentric position towards a new location in space. Wraga and colleagues, for instance, asked participants to imagine to move towards a new position in space and to predict how a stimulus there would look like (Creem et al., 2001; Wraga et al., 2005). They found that the self manipulation in the outside space was associated with a network involving the supplementary motor area, as well as the left middle occipital gyrus and right middle temporal gyrus. Aichhorn et al. (2006), asked participants to predict how the spatial relations between two objects would appear from the viewpoint of a fictional character (but not from their own position) and found an activation in the left temporo-parietal junction. Zacks et al. (1999), instead, showed subjects the picture of a frontal human body on which a mark could appear either on the right or the left hand. They asked participants to assess the laterality of the marked hand, thus forcing them to commensurate their own egocentric coordinates with those of the picture, and found a significant increase of neural activity in the left PTO *complex*. Zacks et al. (1999)'s task has been recently used by Blanke and colleagues who, additionally, instructed participants to imagine their self being rolled-out from their own body and occupying the position of the human picture that was presented as stimulus (Arzy et al., 2006; Blanke et al., 2005). They found that such a task induced a differential activity in the bilateral PTO which was significantly higher than the one induced by mental rotation of alphabetic stimuli (Blanke et al., 2005), or by the similar task in which participants refrained from imagining their selves being drifted away (Arzy et al., 2006).

It has been suggested (Povinelli, 2001) that, in order to recognize an external agent as a *disembodied* self (e.g., looking at one's own photograph), one needs to establish an equivalence relationship between a representation of the self and the agent. It is on the basis of recognizing that what is true of the self is also true of the agent, therefore the two must be equivalent, and therefore the agent eventually is an *objectified* self. This model is a good candidate for describing how *disembodiment* may occur and potentially contribute to further higher mental processes. In our task participants were explicitly asked to key-press at the onset of the external agent's movement; in this way they treated the information about the agent as equivalent to the information about themselves. This process resulted in the recruitment of the PTO junction which, in turn, makes the agent coded as *disembodied* self, that is, included in what we consider to be "ours". This last process may represent the circuitry emerged in the brain of the macaques after they learned, following extensive training, to be skilled tool-users (Hihara et al., 2006). Moreover, the literature reviewed above suggests that *disembodiment,* the consequent processing of an *objectified* self*,* may not be only triggered by the sensory information about an agent which is processed as equivalent to ourselves, but also through a process of mental simulation in which someone represents which his own bodily states would be, if moved in a position that is different from his own. This process may explain the implication of neurons within the PTO junction in experimental paradigms, such as the visual-perspective tasks (e.g. Wraga et al., 2005; Aichhorn et al., 2006), where no external agent is present. Finally, *disembodiment* may be also triggered by an electrical stimulation of the PTO junction, which has been documented resulting in the hallucinatory experience of seeing one's own body as if this was in position different from the one of the observer's (e.g. Devinsky et al., 1989; Blanke et al., 2002).

Disembodiment, imagined translation and social cognition

It is possible that the *disembodiment* process described by the activation of the PTO junction reflect a visuo-vestibular integration due to the imagined translation in space. This is an intriguing possibility, which is strengthened by the fact that neurons in the temporo-parietal junction are known to be sensitive to caloric stimulation of the ears (Dieterich et al., 2003), whereas temporo-parietal regions have also been suggested as a focus for vestibular epilepsy, characterized by rotational or linear vertigo accompanied by body or head and eye rotation (Altay et al., 2005; Smith, 1960). Moreover, the medial and inferior parietal cortex as well as the middle temporal complex of the human brain were associated with computing visual information of the real deambulation (Maguire et al., 1998; Maguire et al., 1999; Morrone et al., 2000). Recently, Indovina et al. (2005) reported an activation of both the right and (to a lesser degree) left temporo-parietal junction during both vestibular caloric stimulation and the perception of visual motion which appears to be coherent with natural gravity (see also Andersen et al., 1999, who related dorsal medial superior temporal region (MSTd) in the monkey brain to computing vestibular information about self-navigation).

However, this interpretation can hardly account for the results of studies showing the involvement of the PTO junction in mentalizing (e.g., Frith and Frith, 2006; Saxe, 2006, for a review). In these kinds of studies participants are usually presented with a set of short stories and then have to predict the main characters (true or false) mental states. Regions in the temporo-parietal junction, especially in the right hemisphere, were typically documented to be implicated in such tasks (e.g. Saxe and Kanwisher, 2003; Saxe and Wexler, 2005), whereas damage to left temporo-parietal regions was found to cause selective deficits in judging the contents of others beliefs (Samson et al., 2004). These data, together with our present results, suggest that the *disembodiment* process in which the PTO junction is involved may go beyond a mere sensory integration due to imagined self-navigation in the outside space. Indeed, *disembodiment* might also be described as a process which allows us to *objectify* one's own mental states, that is, project them a context which is different from one's own.

This interpretation, however, holds only for those instances in which the mental states to be inferred are one's own, or of someone who is considered fairly similar to us. Indeed, a putative *disembodiment* of one's own states cannot be productively used whilst mentalizing about people who are known to be dramatically different from ourselves (see, Saxe, 2005; Mitchell et al., 2006; Frith and Frith, 2006, for a similar argument). Moreover, since *disembodiment* (and therefore the PTO junction) does not occur when we have experience of ourselves from an egocentric perspective, *disembodiment* of one's own mental states should not occur in the instances in which we infer the mental states of an agent in a context that is too similar to our own.

This prediction is in agreement with what was described by Vogeley et al. (2001), who show activation of the right temporo-parietal junction when participants have to predict which mental states they (but not others) would have if inserted in a give context described by short stories. Moreover, Aichhorn et al. (2006) suggested that both the temporo-parietal junction and the posterior portion of the superior temporal sulcus were involved in a mentalizing task only when the task required dealing with perspective differences, that is, to realize that the states we would experience from another perspective are different from the states we are currently experiencing. A third argument in favor of our prediction can be found in Saxe and Wexler (2005) who asked participants to infer the internal states of an agent whose intentions were either similar or opposite to their own (e.g., a participant was asked to predict the internal states of an agent who "is really looking forward to living alone", which was consistent with participant's wishes, or who "is happy living with her parents", which diverged from participant's wishes). Moreover, it was also described that the agents were inserted in a social context which could be either similar to or dissimilar from participants' (e.g., the agent lived "in New York City", which was a background familiar to participants, or in a rural community in which "it is uncommon and even suspicious for a woman to live alone", which was a background foreign to participants). The analysis of the right temporo-parietal junction in their study revealed a significant interaction of which our results are reminiscent: this region was more activated by a foreign, with respect to a familiar, context but only when the agent whose mental states were to be inferred had intentions which were similar to participants'. However, the right temporo-parietal junction in their study was not modulated by the social background when the agent was described to have intentions diverged from participants'.

To conclude, *disembodiment* of one's own mental states cannot account for all the instances involving mentalizing, but it can account for the instances in which one predicts what his internal states would be in a context that is different from his own. Mentalizing tasks under these constraints were associated with the activation in temporo-parietal regions (Vogeley et al., 2001; Saxe and Wexler, 2005; Aichhorn et al., 2006), just like in the present study where the PTO junction was found to be implicated in seeing one's own action performed from a different points of view. This strengthens the hypothesis that the *disembodiment* process, as described in the present study, is also recruited during mentalizing tasks.

Summary

In a fortunate gag in the movie *Seven Years of Bad Luck* (Linder, 1921), a valet, who inadvertently broke the master's mirror, places a servant on the other side of the mirror frame and asks him to pretend to be the master's reflection. When the master gets into the room, he sees his own movements mimicked by the servant and, therefore, he believes the servant to be himself. Even though we might laugh at the master's behavior, this actually reflects a major component of the human cognitive system: the ability to recognize an entity, which is physically separated from us, as the self. This ability is made possible by a *disembodiment* process, which allows us to project properties of the self away from the boundaries of one's own body to an agent in the outside space. Consistent with previous accounts, the right PTO junction was found to be associated with the *disembodiment* of the self. Our results specify, both anatomically and functionally, a brain region involved in a process which is considered as one of the most important evolutive achievements of the human cognitive system, in that it allows us to recognize our own face in a photograph, to plan actions by accounting external tools, to move remotely a video-game character, and, unfortunately, to be tricked by clever servants.

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