Behavioral/Systems/Cognitive

Mental Imagery of Self-Location during Spontaneous and Active Self–Other Interactions: An Electrical Neuroimaging Study

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Substantial data from the cognitive neurosciences point to the importance of bodily processing for the development of a comprehensive theory of the self. A key aspect of the bodily self is self-location, the experience that the self is localized at a specific position in space within one's bodily borders (embodied self-location). Although the neural mechanisms of self-location have been studied by manipulating the spatial location of one's visual perspective during mental imagery, such experiments were conducted in constrained, explicit, and unecological contexts such as explicit instructions in a prone/seated position, although most human interactions occur spontaneously while standing/walking. Using a motor paradigm, we investigated the behavioral and neural mechanisms of spontaneous self-location and mental body transformations during active human interaction. Using own-body imagery using spontaneous and explicit changes in self-location in standing participants, we report that spontaneous interactions with an avatar are neurally indistinguishable from explicit own-body transformation with disembodied self-location but differ from explicit own-body transformation with embodied self-location at 400–600 ms after stimulus onset. We discuss these findings with respect to the neural mechanisms of perspective-taking and self-location in spontaneous human interaction.

Introduction

Theoretical work converges on the importance of the bodily self for the development of a comprehensive theory of the self (Gallagher, 2000, 2005; Ruby and Decety, 2001; Metzinger, 2003, 2008). A key aspect of the bodily self is self-location, the experience that the self is localized at a specific position in space within one's bodily borders (embodied self-location) (Blanke and Metzinger, 2009). Self-location is difficult to study but, based on data from neurological patients with out-of-body experiences (OBEs) and related conditions (Irwin, 1985; Devinsky et al., 1989; Brugger et al., 1997; Kahane et al., 2003; Blanke et al., 2004) (disembodied self-location), neuroscientific approaches pointed to the importance of multisensory integration of body-related information in temporo-parietal cortex (Lobel et al., 1998; Blanke et al., 2002, 2004; Kahane et al., 2003).

Using neuroimaging, researchers investigated the neural mechanisms of self-location by manipulating the spatial location of one's visual perspective during mental imagery. This revealed activations within many brain areas: temporo-parietal, precuneus, prefrontal, premotor, superior temporal, and cingulate cortex (Ruby and Decety, 2001; David et al., 2006; Vogeley and Kupke, 2007). Recent electrical neuroimaging studies (Blanke et al., 2005; Arzy et al., 2006) showed that embodied and disembodied self-location differently activate the temporo-parietal junction (TPJ) and the lateral occipitotemporal cortex, including the extrastriate body area (Downing et al., 2001; Astafiev et al., 2004; David et al., 2007).

Most studies on self-location did not investigate self-location while an individual is interacting with another individual but used highly constant and constrained contexts rendering the experimental situations less ecologically valid. Typically, behavior and brain activity are tested in a prone/seated position, although many or even most interactions with humans occur in the standing or walking position (Parsons, 1987; Arzy et al., 2006; Reed and McGoldrick, 2007), and brain mechanisms may differ depending on the body position (Gaunet and Berthoz, 2000; Arzy et al., 2006; Lobmaier and Mast, 2007). Moreover, most neuroimaging studies [i.e., functional magnetic resonance imaging (fMRI) or positron emission tomography (PET)] are performed in the supine position. Finally, participants are generally instructed explicitly to perform own-body or perspective mental transformations (Zacks et al., 1999; Ruby and Decety, 2001, 2004; Vogeley et al., 2004; Blanke et al., 2005; Arzy et al., 2006). It is thus unclear whether and how the standing position as well as spontaneous versus explicit transformations affect mental imagery re-
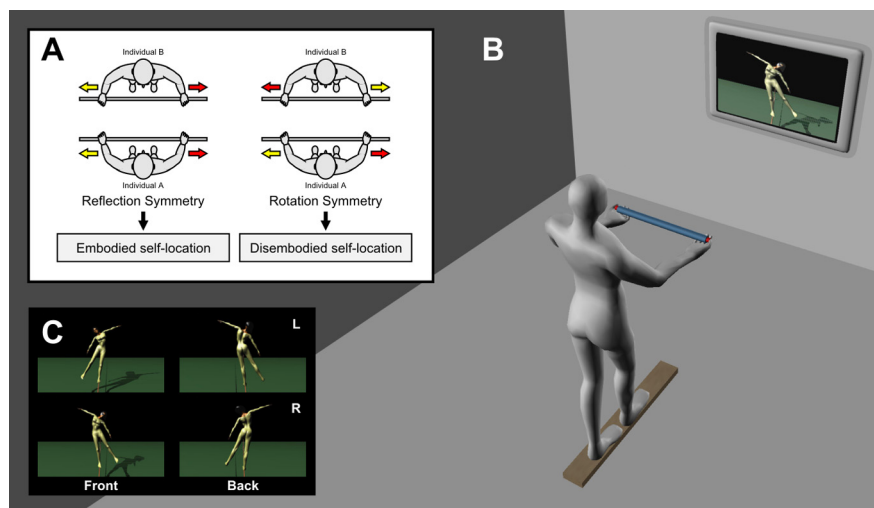
Figure 1. Theoretical setup and stimuli. ***A***, Reflection and rotation symmetry schema. Two individuals, *A* and *B*, are facing each other. In reflection symmetry (or embodied self-location), *A* is leaning to his left when *B* is leaning to his right (yellow arrows) and vice versa (red arrows) as if *A* were keeping his own visuospatial perspective while imagining his own body at its actual position (physical) and that *B*'s tilts were his own-body movements as reflected in a mirror. In rotation symmetry (or disembodied self-location), *A* is leaning to his left when *B* is leaning to his left (yellow arrows) and vice versa (red arrows), as if *A* were taking *B*'s visuospatial perspective by imagining his own-body at the *B*'s body position and performing a mental rotation of his body. ***B***, Experimental setup. Participants were facing a computer screen and standing in Romberg position on a wooden board that was fixed on the ground. They were holding a metal bar (with response buttons; indicated in red) horizontally in front of them. ***C***, Movie samples as used in the three tasks. *A* virtual female tightrope walker, performing whole-body tilts either to her left (L) or right (R), from different orientations (front or back facing), was shown on the computer screen (profile orientation not shown).

lated to self-location (Scheflen, 1964; Bavelas et al., 1987, 1988; Thirioux et al., 2009). Accordingly, the mechanisms of "spontaneous" mental body transformations in "naturalistic" and "ecologically more valid" conditions are still unknown.

Here, we adapted a spontaneous motor paradigm (Bavelas et al., 1988) and investigated, using electrical neuroimaging, the neural mechanisms of spontaneous and explicit changes in self-location. This was done in standing and moving participants interacting with an avatar that was standing and moving. We report behavioral and electrophysiological data revealing that spontaneous self–other interactions and explicit mental own-body transformations with disembodied self-location rely on indistinguishable behavioral and brain mechanisms.

Materials and Methods
Paradigm
To investigate whether and how individuals, under spontaneous conditions and without explicit instruction, interact with another individual with an embodied or disembodied self-location, we designed a motor paradigm that allows the participants to use spontaneously their own transformation strategy, comparable with strategies used in daily life. For this, we adapted the traditional psychological approach, an approach focusing on elementary mimicry (Bavelas et al., 1988) that is used to investigate, from the body posture, how individuals act together without explicit task instructions (Scheflen, 1964; O'Toole and Dubin, 1968; Stotland, 1969; Bavelas et al., 1986a,b, 1987, 1988; Chartrand and Bargh, 1999; Tessari et al., 2002). This rotation and reflection symmetry paradigm (Bavelas et al., 1988; Thirioux et al., 2009) was adapted and merged with a paradigm using embodied and disembodied self-location during mental own-body imagery.

According to the hypothesis by Bavelas et al. (1988), if individuals *A* and *B* are facing each other and *B* is leaning to his right, *A* can copy *B*'s tilt by leaning either to his left or right (Fig. 1*A*). In the first case, *A* reacts by mirroring *B*'s tilts. We hypothesized that such "reflection symmetry" (as labeled by Bavelas et al., 1987, 1988; or body tilts "in mirror reversal," as in the study by Brugger, 2002) indicates that *A*, imagining his own-body

at his actual body position [physical or "embodied" position (Arzy et al., 2006; Thirioux et al., 2009)], is further imagining that *B*'s tilts are his own-body movements as reflected in a mirror. In contrast, we hypothesized that the second case or "rotation symmetry" (Bavelas et al., 1987, 1988; or body tilts "with preservation of the lateral asymmetry," as in the study by Brugger, 2002) reflects that *A* is imagining himself at the *B*'s body position ("disembodied" position) (Arzy et al., 2006; Thirioux et al., 2009), by performing a mental transformation of his body (or mental rotation). Hence, the type of symmetry (either reflection or rotation symmetry) may provide an empirical criterion to infer which sort of mental body transformations is being performed within self–other interaction (i.e., either imagining the other's body as one's own body as reflected in the mirror or imagining one's own body at the other's body position). "Reflection" and "rotation" symmetry thus indicates that the "self" (the participant) is interacting with the "other" (an avatar, in the present case) with embodied and disembodied self-location, respectively, as shown in a recent behavioral study using virtual reality technology (Thirioux et al., 2009). Here, we will use "embodied self-location" (or mental body transformation with embodied self-location) and "disembodied self-location" (or mental body transformation with disembodied self-location) to refer to reflection symmetry and rotation symmetry, respectively.

Participants
Thirteen healthy volunteers took part in this experiment. We excluded the data from four participants because of EEG artifacts attributable to standing position and leaning movements. For the final analysis, we included the data from the remaining nine participants (four women, five men; aged 23–32 years; mean ± SD age, 27 ± 2.5 years). All participants were right-handed according to the Edinburgh handedness inventory (Oldfield, 1971) and had normal or corrected-to-normal vision. None reported neurological or psychiatric disorders. All were naive to the purpose of the experiment and gave written informed consent. The study protocol was approved by the local ethics research committee at the University of Lausanne [University Hospital (Centre Hospitalier Universitaire Vaudois), Lausanne, Switzerland] and has been performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Experimental setup and procedures
Stimulus and apparatus
Participants stood in front of a computer screen (size, 18.6 × 24.8° of visual angle) at a viewing distance of 80 cm. The computer screen was mounted at eye level and adjusted for each participant (Fig. 1*B*). We presented movies of a computer-generated female tightrope walker (images per movie, 37; refresh rate, 100 Hz; movie duration, 1480 ms) (Fig. 1*C*). The tightrope walker was designed using the AnyFlo System (Bret, 1988), which generates virtual avatars with a neural network model taking into account the rules of natural movements and biomechanical constraints of the body (Viviani and Terzuolo, 1982; Viviani and Flash, 1995; Berthoz, 1997). Movies were presented using E-Prime software (Psychology Software). A trial contained one movie and was initiated after a variable interstimulus interval (randomly chosen between 500 and 2000 ms; mean, 1500 ms) during which a white fixation cross was embedded onto a black screen. The movies presented the tightrope walker standing on a rope with the arms horizontally outstretched (Fig. 1*C*). The tightrope walker was shown either in front-, profile-, or back-facing orientation. For each orientation, the tightrope walker executed tilts to either her left or her right. Hence, we presented six different movies (see

supplemental data, available at www.jneurosci.org as supplemental material). In each movie, the onset of the tilt of the tightrope walker was delayed with respect to the stimulus onset by 50 ms (i.e., the tightrope walker stood motionless on the rope for 50 ms).

To reinforce interaction giving participants the impression to act in the same spatial environment as the tightrope walker, participants stood on a wooden board (3 × 10 × 75 cm, height × width × length) approximating the unbalanced position as the tightrope walker. We asked participants to stand in the so-called "Romberg position" (Romberg, 1846) with one foot in front of the other and to choose the most comfortable position (i.e., either with the right or left foot in front of the other). Five participants (two women, three men) chose standing with their right foot in front of the left. Participants held a metal bar (length, 65 cm) horizontally in front of them and placed their thumbs on two buttons positioned at the left and right end of the bar (Fig. 1B). These buttons were used to record the tilt direction (left or right) and reaction times (RTs).

Tasks
Spontaneous task. Participants were instructed to observe the tilts of the tightrope walker and to lean when she was leaning. We consider this condition as spontaneous insofar as no instruction with respect to type of transformation strategy or direction of leaning was given. This allowed us to investigate whether participants would lean spontaneously according to an embodied or disembodied self-location (see also below). The exact instruction was as follows: "You are going to see a female tightrope walker leaning on a rope. Please lean when she is leaning." All participants started with this spontaneous task (SPO task) and then continued with the two explicit tasks.

Explicit tasks. To investigate whether the spontaneous transformation strategies are relying on the same or distinct brain mechanisms as explicit mental own-body transformations with embodied or disembodied self-location (Arzy et al., 2006), participants, in the second and third experimental tasks, were instructed explicitly to perform two mental body transformation tasks while leaning [own-body-transformation task (OBT task); mirroring task (MIR task)]. The order of both explicit tasks was counterbalanced (in five participants, the OBT task was delivered before the MIR task; reversed order in the remaining participants).

In the OBT task, participants were asked to lean when the tightrope walker was leaning, while imagining their body in the position of the tightrope walker's body (i.e., using disembodied self-location) (Arzy et al., 2006). For the front- and profile-facing orientations, we expected the direction of participants' body tilts toward their left when the tightrope walker leaned to her left and vice versa. For the back-facing orientation, we expected an ipsilateral leaning pattern (left tilt of participants when the tightrope walker leans to her left and vice versa).

In the MIR task (Arzy et al., 2006), participants were instructed to lean while imagining their body at their actual body position (or embodied self-location) and that the tightrope walker's tilts were their own-body movements as reflected in a mirror. Accordingly, we expected for the front- and profile-facing orientations that the participants lean to their right when the tightrope walker leaned to her left and vice versa. For the back-facing orientation, we expected right tilts when the tightrope walker leans to her right and vice versa.

In all tasks, participants were instructed to initiate their tilt with the same speed as the avatar's tilt and to press with their thumb the left or right button of the bar corresponding to the direction of their tilt (i.e., the left and right button in case of tilt to the left and right, respectively) when they judged that their tilt had arrived at its maximal amplitude. In a training session, before the experiment, participants were instructed to lean to the left or right and to press the corresponding button at the same time. Before task performance and after the spontaneous task, OBT and MIR tasks were trained in 90 trials (on average, participants performed correctly in 85% of trials). In OBT and MIR tasks, participants were instructed to perform the requested mental imagery before giving the response.

Each condition contained three blocks. Within a block, in a random order, each of the six movies appeared 15 times, giving rise to 90 trials per block and 270 trials per condition. Our major aim was to investigate the behavioral and neural patterns of spontaneous mental body transformations and compare them with those of explicit mental body transforma-

tions. Because our previous EEG work on explicit mental body transformations with embodied and disembodied self-location only considered front- and back-facing orientations (Blanke et al., 2005; Arzy et al., 2006; Mohr et al., 2006) and to facilitate statistical analysis and comparability with this previous work, we here focus for behavioral and EEG analysis also on the front- and back-facing orientations in all three tasks.

Acquisition and analysis of behavioral data
For each trial, E-Prime recorded the tilt direction (left or right as indicated by button presses) and the reaction time. For each combination of task (SPO, OBT, and MIR tasks) and orientation (front and back), we computed the percentage of tilts according to embodied or disembodied self-location (see above, Experimental setup and procedures). For the MIR and OBT tasks, we computed mean reaction times for responses with embodied and disembodied self-location, respectively. For the SPO task, we calculated the mean reaction times for tilts in OBT or MIR manner.

For statistical analysis, we first computed a 3 × 2 repeated-measures ANOVA on the percentage of tilts in OBT manner with the factors task (SPO, OBT, and MIR tasks) and orientation (front and back). The direction of tilts allowed analyzing whether tilts in SPO were similar to those of the OBT or MIR task. For response speed, we computed a 3 × 2 ANOVA on the RTs with task and orientation as factors.

Electroencephalography acquisition and preprocessing
Continuous EEG was acquired from 192 scalp electrodes (Biosemi Active Two System; 2048 Hz sampling rate) in a darkened electrically shielded booth. To calculate the event-related potentials (EPs), epochs of EEG (from 100 ms before movie onset to 1300 ms after movie offset), from trials that provided the prevailing symmetry in the SPO task and the correct responses in the explicit tasks (i.e., tilts related to embodied and disembodied self-location for MIR and OBT tasks, respectively), were averaged for each of the three tasks and for each participant. We rejected sweeps in which any channel exceeded the amplitude of ±100 μV. To reject epochs with blinks, eye movements, or other sources of transient noise, the data were additionally visually inspected. Artifacted channels were excluded and interpolated (Perrin et al., 1987). After this procedure and before group averaging, EPs were bandpass filtered (1–40 Hz) and recalculated against the average reference (Lehmann, 1987). Furthermore, for each task, the EPs of each participant were aligned such that the global field power (GFP) (Lehmann and Skrandies, 1980) peak of the P1 component was at 100 ms poststimulus onset (PSO). This was done to minimize intersubject variability of the evoked brain responses as reported in previous work (Morand et al., 2000; Picton et al., 2000; Goffaux et al., 2003; Murray et al., 2004).

The total number of included trials for each EP across tasks and orientations did not differ with respect to the number of tilts in the right or left direction (3 × 2 × 2 ANOVA with factors task, orientation, and tilt direction): tilt direction ($F_{(1,8)} = 2.187$; $p = 0.177$); task × tilt direction ($F_{(2,16)} = 0.152$; $p = 0.861$); tilt direction × orientation ($F_{(1,8)} = 0.229$; $p = 0.645$); task × tilt direction × orientation ($F_{(2,16)} = 0.144$; $p = 0.867$). The total number of trials in the front-facing OBT task was 56 ± 5 (mean ± SEM), with the same number of tilts to the left (28 ± 3) and right (28 ± 2). The same was found for back orientation (56 ± 7; left, 28 ± 3; right, 28 ± 4). In the MIR task [total front, 46 ± 5 (left, 23.1 ± 2.9; right, 22.8 ± 2.8); total back, 33 ± 7 (left, 18 ± 4; right, 16 ± 4)] and the SPO task [total front, 61 ± 6 (left, 31 ± 3; right, 30 ± 3); total back, 58 (left, 30 ± 3; right, 29 ± 2)], the same number of right–left tilts were observed as well. Hence, the number of trials for our EPs analysis included, on average, between 46 and 58 artifact-free epochs per condition (except back MIR task condition; for additional discussion, see behavioral results). We note that EPs based on ~50 epochs may be noisy and characterized by large variability. This may have rendered it difficult to reliably detect modulations of small-amplitude components in the present study. However, our experiment was already quite long, and participants were standing and performed full-body movements during the EEG recording. For these reasons, we decided to not prolong the experiment and record more epochs per condition.

EP topographical mapping

EP analysis was based on the examination of spatial variations of the scalp voltage distribution over time and between tasks. Known as EP topographical mapping (Michel et al., 2001, 2004; Blanke et al., 2005; Murray et al., 2005, 2008a; Arzy et al., 2006; Mercier et al., 2009), this approach searches for time periods of stable map topography within and across experimental conditions. Periods of stable map topography (or EP map) were defined by using a clustering algorithm [hierarchical clustering: atomize and agglomerate hierarchical clustering (AAHC) (adapted from Tibshirani et al., 2005)]. This AAHC is dependent on the quantification of the global explained variance (GEV):

$$GEV = \frac{\sum_{t=1}^{t_{max}} (GFP^2 \times ev)}{\sum_{t=1}^{t_{max}} GFP^2},$$

which corresponds to the goodness of fit of a template map during a certain time period (Murray et al., 2008a) and the instantaneous GFP (Lehmann and Skrandies, 1980):

$$GFP_u = \sqrt{\frac{\sum_{i=1}^{n} u_i^2}{n}}.$$

The AAHC identifies the dominant map topographies on the scalp in the group-averaged EPs across the experimental tasks over time. This temporal topographical analysis labeled each time frame of the EEG data to the corresponding dominant EP map. This is graphically rendered with a color and number per template EP map (see Fig. 3B). The optimal number of the template EP maps is determined by both a modified cross-validation (CV) criterion (Pascual-Marqui et al., 1995; Murray et al., 2008a; Mercier et al., 2009) and the Krzanowski–Lai (KL) criterion (Tibshirani et al., 2005; Murray et al., 2008a). The absolute minimum of the CV, in which the degrees of freedom and the GEV are optimized for a given set of template maps, gives the optimal number of segments, and the highest value of the KL indicates the optimal clustering (for a detailed description, see Murray et al., 2008a).

A major aim of our study was to investigate whether spontaneous mental own-body transformation strategies elicit the same or distinct brain mechanisms as explicit mental own-body transformations with embodied (MIR task) or disembodied self-location (OBT task). Our analysis of the behavioral data (see below) showed that, despite generally prolonged RTs for the SPO task, the behavior with respect to orientation in the SPO task was similar to the OBT task but differed from the MIR task. To investigate the presence of such similarities/differences in the EPs, we computed a segmentation of the group-averaged data with the grand average EP for SPO, OBT, and MIR tasks in the front and back orientations (3 × 2 factorial design).

For statistical analysis, the presence of a given EP map as identified in the group-averaged data was verified in the EPs of the individual subjects, by means of a fitting procedure based on the spatial correlation between template maps obtained from the group-averaged EPs data and the individual subjects data (Brandeis and Lehmann, 1986; Pegna et al., 1997; Blanke et al., 2005; Arzy et al., 2006). Thus, the dominant EP maps as identified by the segmentation procedure in the group-averaged data were fitted to the EPs of each individual subject (Blanke et al., 2005; Murray et al., 2008a; Mercier et al., 2009). This fitting procedure is based on the spatial correlation between template EP maps obtained from the group-averaged EPs data and the individual subject data (Brandeis and Lehmann, 1986; Pegna et al., 1997; Blanke et al., 2005; Arzy et al., 2006; Murray et al., 2008a; Mercier et al., 2009). This allowed us to determine the duration (map presence) and the amount of GEV. Map presence was determined to analyze the presence of a given EP map versus another EP map in the EP data during the time period as detected by segmentation analysis. GEV was determined to analyze the goodness of fit of the EP
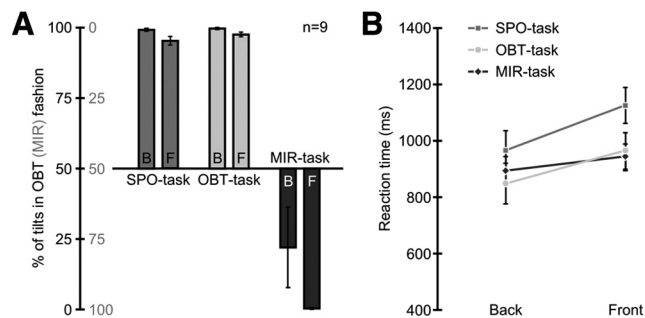

Figure 2. Behavioral results: leaning performance and reaction times. **A**, Tilt performance. Results show that, in the SPO task, participants behaved as in the OBT task: they performed tilts in a OBT manner independently of the stimulus orientation. In the SPO and OBT tasks, tilt performance decreased when the rotation angle between the participants' body and the avatar's body increased (from back to front). The MIR task was characterized by the inverse tilt pattern. B, Back; F, front. **B**, Reaction times. Consistent with tilt performance, RTs increased from back to front orientation in the SPO and OBT tasks. There was no significant difference between the back and front orientation in the MIR task.

data with a given EP during the time period as detected by segmentation analysis. Values for map presence and GEV for a given EP map were then subjected to statistical analysis (repeated-measures ANOVA).

Distributed source localization

The neural generators were estimated by using a distributed linear inverse solution based on a local auto-regressive average (LAURA) model (Grave de Peralta Menendez et al., 2004) and biophysical constraints, producing adequate source localizations with high temporal resolution (Blanke et al., 2005; Arzy et al., 2006; Mercier et al., 2009; Plomp et al., 2009). Within the gray matter of the Montreal Neurological Institute (MNI) 152 template brain, we defined a solution space of 4022 evenly spread source points (or solution points). We transformed the MNI volume to a best-fitting sphere [Spherical Model with Anatomical Constraints (Spinelli et al., 2000)] and used a three-shell spherical head model to calculate the lead field for the 192 electrodes and the LAURA inverse solution. Thus, we estimated current densities throughout the source space for each participant at each time point for each condition and spatial orientation.

The source reconstruction was performed at two levels (Michel et al., 2001, 2004; Murray et al., 2004; Mercier et al., 2009). First, we applied LAURA to those EP maps that differed between conditions as identified by the segmentation and statistical EP analysis. This was done for the time period when these EP maps were found to differ between conditions by the topographical analysis (i.e., between 517 and 628 ms in the front orientation). This allowed us to visualize the underlying neural generators. Second, we performed statistical analysis at the level of the source reconstruction. For this, we calculated the mean difference between source estimations for each condition across subjects in the time period identified by the segmentation analysis (at 517–628 ms). To identify solution points in the solution space for statistical comparisons, we applied a threshold of one-third of the amplitude of the unsubtracted source estimations to this difference. This identified eight clusters of solution points. Then, we determined for each participant and each condition (between 517 and 628 ms; see below) the scalar values from the solution points of each cluster and submitted them to repeated-measures ANOVAs (one for each cluster) with two factors (task and solution points within cluster) (Murray et al., 2008b). We used a Bonferroni's corrected α level of 0.00625.

Results

Behavioral data

Participants performed correctly for OBT and MIR tasks leaning correctly with disembodied self-location in the OBT task (98.6 ± 0.7%, mean ± SEM) (Fig. 2A; Tables 1, 2) and with embodied self-location in the MIR task (88.6 ± 11%) (Fig. 2A; Tables 1, 2).

Table 1. Tilt performance and reaction times (group data)

	MIR task		OBT task		SPO task	
	% MIR	RT (ms)	% OBT	RT (ms)	% OBT	RT (ms)
Back	77.7 ± 14.4	895 ± 51	99.6 ± 0.3	848 ± 46	99.0 ± 0.5	963 ± 72
Front	99.5 ± 0.3	942 ± 47	97.6 ± 0.8	965 ± 38	95.4 ± 1.5	1126 ± 65
All	88.6 ± 11	918 ± 48.5	98.6 ± 0.7	906 ± 45.5	97.1 ± 1.3	1045 ± 72.2

Percentages of tilts (in MIR manner for the MIR task, in OBT manner for the OBT and SPO tasks), and corresponding reaction times are shown for each spatial orientation (back and front). Final row shows the mean tilts and RTs averaged across the two orientations.

Table 2. Tilt performance and reaction times (individual data)

	MIR task				OBT task				SPO task			
	Back		Front		Back		Front		Back		Front	
	% MIR	RT (ms)	% MIR	RT (ms)	% OBT	RT (ms)	% OBT	RT (ms)	% OBT	RT (ms)	% OBT	RT (ms)
P1	100.0	843	100.0	856	100.0	718	100.0	778	100.0	722	100.0	903
P2	98.6	1014	100.0	972	100.0	939	100.0	995	100.0	921	100.0	939
P3	2.2	688	98.8	844	100.0	807	93.0	1015	100.0	763	95.0	1028
P4	1.2	790	100.0	791	97.7	663	95.5	862	100.0	731	97.8	881
P5	98.8	1053	100.0	1203	98.9	900	97.7	986	100.0	1100	94.4	1259
P6	100.0	991	100.0	1015	100.0	962	98.9	996	100.0	1009	95.8	1184
P7	98.3	998	97.5	1017	100.0	886	97.5	1007	95.3	1271	84.7	1345
P8	100.0	651	100.0	760	100.0	690	95.5	875	97.8	877	95.6	1200
P9	100.0	1018	98.8	1021	100.0	1069	100.0	1172	98.9	1279	93.3	1396

Tilts and RTs are indicated as in Table 1 but are shown here for each participant (P) and each spatial orientation separately (back and front).

Visual inspection revealed that the tilt performance in the SPO task followed closely the tilt performance in the OBT task but differed from the tilt performance in the MIR task (Tables 1, 2): although we gave no explicit instructions (concerning the direction of leaning or transformation strategies) in the SPO task (that was always performed first), all nine participants leaned in OBT manner in almost all trials (97.1 ± 1.3%) (Fig. 2A; Tables 1, 2). This was confirmed by a 3 × 2 repeated-measures ANOVA on the leaning performance (number of OBT tilts in all conditions; see Materials and Methods) for the three tasks showing a significant effect of task ($F_{(2,16)}$ = 140.992; $p < 0.001$) that was attributable to a significant difference between the MIR and OBT tasks [$p < 0.001$, pairwise comparison, least significant difference (LSD)] and the MIR and SPO tasks ($p < 0.001$). By contrast, the SPO and OBT tasks did not significantly differ ($p = 0.216$). The 3 × 2 ANOVA also showed a trend for the factor orientation ($F_{(2,16)}$ = 3.526; $p = 0.097$). There was no task × orientation interaction ($F_{(2,16)}$ = 1.639; $p = 0.189$).

As expected, in the OBT task, correct performance was higher in the back (99.6 ± 0.3%) than in the front (97.6 ± 0.8%) orientation (Fig. 2A; Tables 1, 2), in accordance with previous data (Arzy et al., 2006). In the MIR task, our results showed the inverse behavioral pattern as in the OBT task. Correct performance was higher in the front (99.5 ± 0.3%) than in the back (77.7 ± 14.4%) orientation (Fig. 2A; Tables 1, 2), also concordant with previous data (Arzy et al., 2006). In the SPO task, OBT tilt performance was higher in the back (99 ± 0.5%) than in the front (95.4 ± 1.5%) orientation (Tables 1, 2; Fig. 2A). The absence of a significant orientation × interaction effect was probably attributable to large variability in tilt performance in the back-facing condition of the MIR task: analysis of each participant's individual data showed that, for the back orientation, two outliers (one male and one female; both are included in group analysis) performed most tilts with disembodied self-location [participant 3: tilts in OBT manner, 96.8%; tilts in MIR manner, 3.2%; participant 4: tilts in OBT manner, 98.8%; tilts in MIR manner, 1.2% (Table 2)]. In contrast, inspection of the OBT task and SPO task data indicates that participants performed more tilts with disembodied self-

location for the back than the front orientation (Fig. 2A; Tables 1, 2). To check whether the gender of the participant might have influenced performance in our task, we performed an unpaired 3 × 2 × 2 repeated-measures ANOVA (with task, spatial orientation, and gender as factors). We found no effect of gender ($F_{(1,7)}$ = 1.262; $p = 0.298$), no task × gender interaction ($F_{(2,14)}$ = 0.096; $p = 0.909$), no orientation × gender interaction ($F_{(2,14)}$ = 0.124; $p = 0.735$), and no task × orientation × gender interaction ($F_{(2,14)}$ = 0.055; $p = 0.947$).

For RTs, statistical analysis (3 × 2 repeated-measures ANOVA with the factors task and orientation) showed a significant effect of task ($F_{(2,16)}$ = 5.966; $p = 0.012$), a significant effect of orientation ($F_{(1,8)}$ = 25.292; $p = 0.001$), and a significant task × orientation interaction ($F_{(2,16)}$ = 11.524; $p = 0.001$). RTs were longer during the SPO task (1045 ± 72.2 ms; mean RT) than the OBT task (906 ± 45.5 ms; $p = 0.016$, pairwise comparisons) and MIR task (918 ± 48.5 ms; $p = 0.039$) (Fig. 2B; Tables 1, 2). In the OBT task, the spatial orientation affected the RTs, similarly to the tilt performance: RTs were faster for the back (848 ± 46.0 ms) compared with the front (965 ± 37.8 ms; $p = 0.001$, pairwise comparison) orientation (Fig. 2B; Tables 1, 2). In the MIR task, as already mentioned for tilt performance, RTs were not higher in the back-facing condition, as we predicted based on previous data (Arzy et al., 2006): participants were somewhat faster for the back orientation (895 ± 51.4 ms) than for the front orientation (942 ± 47.0 ms) (Fig. 2B; Tables 1, 2). This was not found to be significant ($p = 0.078$). In the SPO task, participants were significantly faster for the back (963 ± 72.3 ms) than for the front (1126 ± 64.7 ms; $p = 0.001$, pairwise comparison) orientation (Fig. 2B; Tables 1, 2), again similar to the effects observed during the OBT task.

Collectively, these behavioral data show that, although participants performed generally slower in the SPO task, the responses were compatible with those in the explicit OBT task: participants leaned with disembodied self-location and showed similar dependencies of tilt performance and response speed on the spatial orientation. Thus, performance in the SPO task shows an orientation effect as in the OBT task, and, in both tasks, OBT tilts decrease and RTs increase when the rotation angle between the

participant's body and the body of the tightrope walker increases, replicating and extending previous behavioral findings (Parsons, 1987; Zacks et al., 1999; Blanke et al., 2005; Arzy et al., 2006; Mohr et al., 2006). The tasks only differed in that participants were slower in the SPO task than in the OBT task, suggesting that the explicit instruction in the OBT task, probably involving motor preparation, may have contributed to reducing the time that participants needed to react. At a motor representational level, this spontaneous leaning performance pattern in an OBT-like manner may be compatible with the "active intermodal matching model" (Meltzoff and Moore, 1997, 2002) assuming that observed movements are reproduced by the corresponding anatomical body parts (for instance, raising one's own right arm while a facing individual is raising his right arm) via "the representation of both actions within a single representational framework of organs relations" (Chiavarino et al., 2007). In contrast, the distinct leaning performance in the MIR task is rather compatible with the perceptual-motor mapping model (Butterworth, 1990; Gray et al., 1991; Wohlschläger et al., 2003) according to which perceiving an action activates automatically the observer's corresponding motor program by the activation of a common representational coding so that one's own movements visually match the model's movements [for instance, raising one's own left arm while a facing individual is raising his right arm (Wohlschläger et al., 2003)].

EP mapping and source localization
Our behavioral data showed that the behavior with respect to orientation in the SPO task was similar to the OBT task but differed significantly from the MIR task. To investigate the potential presence of comparable differences (between the SPO and OBT tasks with respect to the MIR task), at the neural level, we computed a segmentation of the group-averaged data with the grand average EP for SPO, OBT, and MIR tasks in the front and back orientations.

Reflecting the behavioral data, brain activations differed according to orientation and whether the SPO/OBT task or the MIR task was performed. This was reflected by the presence of three different EP maps (Fig. 3B). One EP map (labeled by the segmentation analysis as "Map_6") (Fig. 3B, black segment) was present in the SPO/OBT task and another EP map ("Map_{14}") (Fig. 3B, gray segment; see also A) in the MIR task (Fig. 3B) but only in the front-facing conditions. An additional EP map ("Map_{11}") (Fig. 3B, light gray segment) was found in all six conditions but was more strongly associated with the back-facing conditions. Map_6 appeared between 517 and 628 ms PSO, and the MIR task was characterized, during the same time period, by Map_{14}. In the back conditions, we did not find Map_6 and Map_{14} in the time period between 517 and 628 ms and not in earlier as well as later time periods (Fig. 3B). To test the dependence of Map_6 and Map_{14} on the factors task and orientation, we fitted both template EP maps to the individual participants' data in all six conditions in the time period from 517 to 628 ms ($3 \times 2 \times 2$ repeated-measures ANOVA with the factors task, orientation, and map). Concerning map presence, this analysis revealed a significant task $\times$ map $\times$ orientation interaction ($F_{(2,16)} = 3.988$; $p = 0.039$) and a significant orientation $\times$ map interaction ($F_{(1,8)} = 9.782$; $p = 0.014$). *Post hoc* tests (pairwise comparison, LSD) revealed that the presence of Map_6 and Map_{14} in the front orientation dominated differently according to whether the SPO/OBT tasks or the MIR task were performed. Map_6 was significantly more present in the OBT task than in the MIR task ($p = 0.010$) and in the SPO task than in the MIR task ($p = 0.004$). There was

no significant difference between the SPO and OBT tasks ($p = 0.509$). We found the inverse pattern for Map_{14} that was significantly more present in the MIR task than in the OBT task ($p = 0.010$) and in the MIR task than in the SPO task ($p = 0.004$). Again, there was no significant difference between the SPO task and the OBT task ($p = 0.509$) (Fig. 3C). *Post hoc* analysis of Map_6 and Map_{14} in the back conditions revealed no significant effect (all $p > 0.6$).

The same statistical analysis for the GEV of Map_6 and Map_{14} ($3 \times 2 \times 2$ ANOVA with the factors task, orientation, and map) showed a significant task $\times$ map interaction ($F_{(2,16)} = 4.8$; $p = 0.023$), a significant orientation $\times$ map interaction ($F_{(1,8)} = 11.604$; $p = 0.009$), and a trend for task $\times$ orientation $\times$ map interaction ($F_{(2,16)} = 3.229$; $p = 0.066$). *Post hoc* tests revealed that the GEV of Map_6 and Map_{14} in the front orientation dominated differently according to whether the SPO/OBT tasks or the MIR task were performed, compatible with the data on map presence. The GEV of Map_6 was significantly higher in the OBT task than in the MIR task ($p = 0.023$) and in the SPO task than in the MIR task ($p = 0.007$). There was no significant difference between the OBT and SPO tasks ($p = 0.822$). Similar to the GEV of Map_6, the GEV of Map_{14} was significantly higher in the SPO task than in the MIR task ($p = 0.029$), and there was no significant difference between the SPO and OBT tasks ($p = 0.111$). In contrast, we found no significant difference between the OBT and MIR tasks ($p = 0.826$) (Fig. 3D). These data on GEV of Map_6 and Map_{14} have to be regarded with caution because statistical analysis was not corrected for multiple comparisons. *Post hoc* analysis of Map_6 and Map_{14} in the back conditions revealed no significant effect (all $p > 0.7$), also compatible with data on map presence. These findings were also reflected at single-scalp electrodes as reported in previous work (Blanke et al., 2005; Arzy et al., 2006; Mercier et al., 2009).

LAURA localized the main brain activation for Map_6 to the TPJ of both hemispheres [maximum; x, y, z Talairach coordinates; right, $(52, -49, 21)$; left, $(-53, -49, 21)$] with a right predominant activation and to the posterior parietal cortex of both hemispheres [right, $(15, -70, 47)$; left, $(-21, -70, 47)$], close to the intraparietal sulcus, with a left predominant activation (Fig. 4A). The main brain activations for Map_{14} were localized in the dorsolateral prefrontal and/or premotor cortex of both hemispheres [right, $(27, -25, 54)$; left, $(-26, -13, 53)$] with a right predominant activation, to the right $(54, -7, -13)$ and left $(-54, -7, -13)$ mid-to-anterior temporal cortex with a right predominant activation and to the right postcentral gyrus $(39, -33, 51)$ (Fig. 4B). Weaker activations were also found in the right TPJ $(52, -54, 16)$ (Fig. 4B).

The segmentation of the group-averaged data also revealed another EP map (Map_{11}) that was present in the three tasks (Fig. 3B). Map_{11} appeared between 370 and 555 ms PSO (i.e., 147 ms earlier than Map_6 and Map_{14}) and was more present in the back than in the front conditions, regardless of the tasks (Fig. 3B). Statistical analysis (3×2 ANOVA with the factors task and orientation) only showed a significant orientation effect ($F_{(1,8)} = 25.963$; $p = 0.001$). *Post hoc* tests (pairwise comparisons, LSD) showed that Map_{11} was more present in the back than in the front orientation ($p = 0.001$). There was no effect of task ($F_{(2,16)} = 0.077$; $p = 0.927$) and no task $\times$ orientation interaction ($F_{(2,16)} = 1.684$; $p = 0.217$) (Fig. 3E). This was also reflected by the GEV, and statistical analysis showed a significant effect of orientation ($F_{(1,8)} = 11.781$; $p = 0.009$), with the GEV of Map_{11} being higher in the back than in the front conditions ($p = 0.009$). There was no effect of task
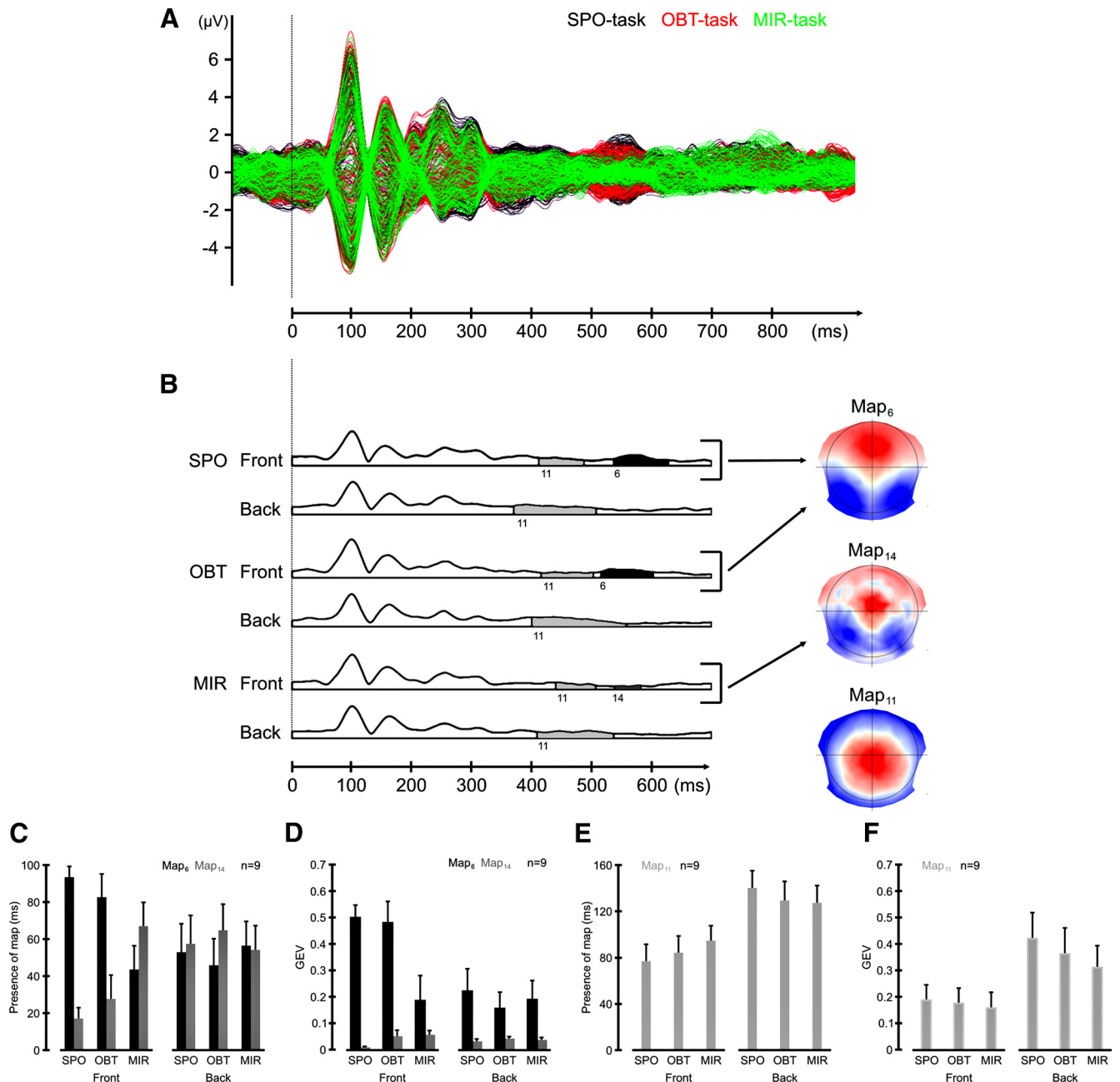
Figure 3. EEG results. **A**, Visual comparison of the superimposed group-averaged EPs waveforms across 192 electrodes in the front orientation showed a phase of differential responses between the SPO, OBT, and MIR tasks at ∼517–628 ms PSO (the stimulus onset was at 0, as indicated by the light gray line). **B**, Segments of stable voltage topography during the three tasks are shown in the time period from 0 to 700 ms. In the front conditions, one EP segment (shown in black; Map_6) was present in the SPO and OBT tasks between 517 and 628 ms PSO but not in the MIR task. The MIR task was characterized, during the same time period, by a different segment (shown in gray; Map_{14}). A third EP segment (shown in light gray; Map_{11}) was present in all three tasks in front- and back-facing orientations, between 370 and 550 ms PSO. Note that Map_{11} was more present in the back than in the front conditions. **C**, Additional analysis showed that Map_6 and Map_{14} dominated differently according to the tasks but only in the front conditions. Map_6 was more present in the OBT task than in the MIR task and in the SPO task than in the MIR task. There was no significant difference between the SPO and OBT tasks. The inverse pattern was found for the presence of Map_{14}. **D**, GEV analysis showed that the GEV of Map_6 in the front conditions also reflected these similarity/differences according to the performed task. This was also the case for Map_{14}, except for the comparison between the OBT and MIR tasks that was not found to be significant. **E**, Statistical analyses on the presence of Map_{11} showed that Map_{11} was significantly more present in the back than in the front conditions. There was no difference between the tasks. **F**, Reflecting the data on map presence, the GEV analysis showed that the GEV of Map_{11} was higher in the back than in the front conditions and did not differ between the tasks.

$(F_{(2,16)} = 23.205; p = 0.143)$ and no task × orientation interaction $(F_{(2,16)} = 0.678; p = 0.078)$ (Fig. 3F).

LAURA localized the generator of Map_{11} to the TPJ of both hemispheres [left, $(-53, -55, 16)$]; right, $(55, -32, 15)$] with a predominant activation in the left hemisphere (extending also more anteriorly) (Fig. 4C). We found the same brain activation in all tasks, suggesting that body transformations in back orienta-

tion may not differ according to the tasks, at least under the present experimental conditions. However, behavioral analysis suggests that this may rather be attributable (at least partly) to task performance in some participants. Although succeeding in front orientation, the same participants were unable to perform the requested MIR transformations in back orientation and responded in the way that they responded in SPO and OBT tasks.
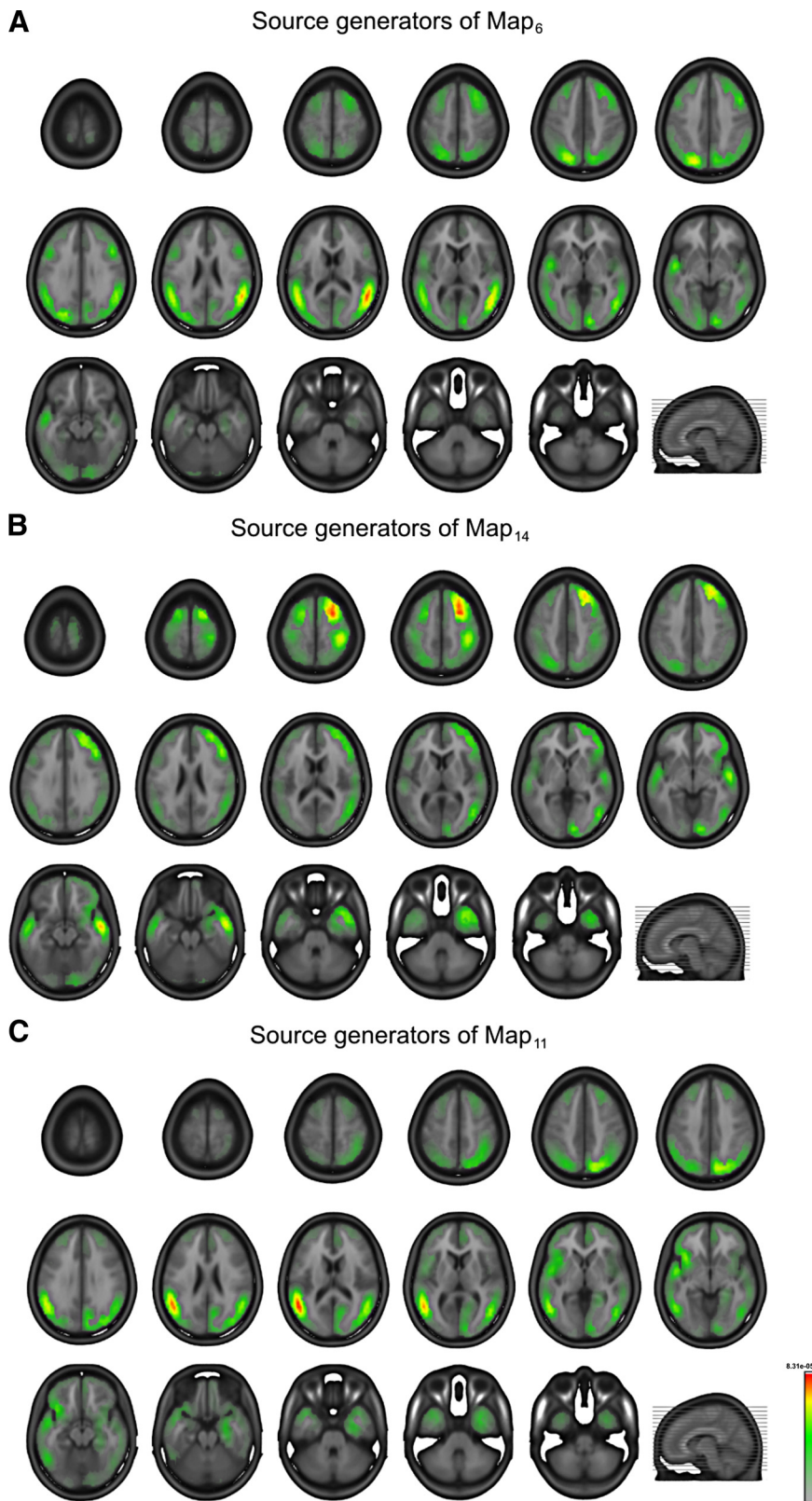
Figure 4. Source localization of Map$_6$, Map$_{14}$, and Map$_{11}$. **A**, An inverse solution localized the generators of Map$_6$ mainly to the TPJ of both hemispheres with a right predominant activation and to the posterior parietal cortex of both hemispheres, close to the intraparietal sulcus, with a left predominant activation. **B**, The generators of Map$_{14}$ were localized in the dorsolateral prefrontal and/or premotor cortex of both hemispheres with a right predominant activation, to the right and left mid-to-anterior temporal cortex with a right predominant activation, and to the right postcentral gyrus. **C**, The generators of Map$_{11}$ were localized to the TPJ of both hemispheres, with a predominant activation in the left hemisphere extending also more anteriorly.

This may underline that mental body transformation in back orientation is the most difficult of all tested body transformations, in accordance with previous work (Arzy et al., 2006; Mohr et al., 2006; Easton et al., 2009). We therefore suggest that we were not able to distinguish SPO/OBT from MIR task related to brain activations in the back orientation because, in the MIR task, the performance was more variable and several participants actually performed OBT transformations.

To further analyze the differences between brain activations reflecting the SPO/OBT tasks versus the MIR task in the front orientation, we performed additional statistical analysis at the level of the reconstructed sources. Statistical analysis was performed by calculating the mean difference between source estimations of the SPO/OBT tasks and the MIR task in the front orientation (comparing the average of the SPO/OBT tasks with the MIR task between 517 and 628 ms PSO). This analysis identified eight clusters of solution points with robust responses (that we labeled from "cluster 1" to "cluster 8") (Table 3). The smallest and largest clusters contained 5 and 105 contiguous solution points, respectively (Table 3). Activations that were stronger in the SPO/OBT tasks were found in the left TPJ [(−60, −42, −2); cluster 1], left precuneus [(−34, −72, 35); cluster 2], and right occipital cortex [(15, −78, 34); cluster 3] (Fig. 5, indicated in green; Table 3). Activations that were stronger in the MIR task were found in the right inferior occipital cortex [(21, −93, −5; cluster 4], right postcentral gyrus [(33, −31, 54); cluster 5], right premotor cortex [(31, −2, 52); cluster 6], right dorsolateral prefrontal cortex [(27, 48, 30); cluster 7], and right anterior temporal cortex [(57, −15, −9; cluster 8] (Fig. 5, indicated in blue; Table 3). Accordingly, eight ANOVAs were calculated (Bonferroni's corrected $\alpha = 0.00625$; see Materials and Methods). The right inferior occipital cortex (cluster 4; task × solution point interaction), right postcentral gyrus (cluster 5; effect of task), right premotor cortex (cluster 6; task × solution point interaction), right anterior temporal cortex (cluster 8; task × solution point interaction), and left TPJ (cluster 1; task × solution point interaction) revealed significant differences. Most clusters were more strongly activated during the MIR task, except the left TPJ. Note that all the clusters showed a significant effect of solution point (data not reported) (Table 3).

To summarize, our EP data show that explicit mental body transformations

Table 3. Results of the statistical analyses (repeated-measures ANOVAs) for the eight identified clusters of solution points

Cluster #	Hemisphere	Number of SPs	Task effect	Task × SP interaction	SPs with $p < 0.05$	Smallest p value	Talairach coordinates	Localization
1	Left	22	NS	$F_{(21,168)} = 3.81$ $p < 0.0001**$	0	$p = 0.0507$	$-60.73, -42.2, -2.79$	Temporo-parietal junction
2	Left	14	NS	NS				
3	Right	5	NS	NS				
4	Right	18	NS	$F_{(17,136)} = 2.33$ $p = 0.0037**$	10	$p = 0.0403$	$21.27, -93.68, -5.56$	Inferior occipital cortex
5	Right	12	$F_{(1,8)} = 18.36$ $p = 0.0027**$	$F_{(11,88)} = 2.03$ $p = 0.0348*$	12	$p = 0.0008$	$33.76, -31.29, 54.55$	Postcentral gyrus
6	Right	27	$F_{(1,8)} = 11.26$ $p = 0.0100*$	$F_{(26,208)} = 4.51$ $p < 0.0001**$	27	$p = 0.0072$	$31.68, -2.17, 52.65$	Premotor cortex
7	Right	14	$F_{(1,8)} = 10.44$ $p = 0.0120*$	NS	12	$p = 0.0068$	$27.67, 48.27, 30.02$	Dorsolateral prefrontal cortex
8	Right	105	$F_{(1,8)} = 10.81$ $p = 0.0111*$	$F_{(104,832)} = 1.90$ $p < 0.0001**$	105	$p = 0.0111$	$57.57, -15.95, -9.93$	Anterior temporal cortex

Clusters 1, 4, 6, and 8 showed a significant task × solution point interaction, and cluster 5 showed a significant effect of task. Concerning cluster 1, *post hoc* tests only reported a trend (*$\alpha = 0.05$; **$\alpha = 0.00625$, Bonferroni's corrected).
SP, Solution point.

with embodied self-location (MIR task) activated more strongly the inferior occipital cortex, postcentral gyrus, anterior temporal cortex, and premotor cortex of the right hemisphere. Spontaneous (SPO task) and explicit mental body transformations with disembodied self-location (OBT task) tend to differ from the MIR task, in generating greater activation in the left TPJ. This was found to occur for the front orientation in the time period between 517 and 628 ms PSO. Concerning timing, studies on disembodied self-location (Blanke et al., 2005; Arzy et al., 2006) found the mean onset of TPJ activation at ∼370 ms, ∼140 ms earlier than in the present front conditions and at the same time as in the present back conditions. First, differences in visual stimuli may have induced this timing difference: the human body was static (previous work) or dynamic (present study). Second, the information relative to the left/right response was provided simultaneously with the visual stimulus onset (previous work) or delayed (present study; the onset of avatar tilt was delayed from stimulus onset by 50 ms). Moreover, because the tilt of the avatar is extended in time, the leaning direction only becomes available over time. Third, body positions were different and participants were in seated/prone position (previous work) or standing position (present study). Fourth, participants indicated their right/left judgments via finger responses (previous work) or leaned while pressing the button on the bar (present study).

Our EP data further show that brain activations for spontaneous as well as explicit OBT transformations start earlier for the back orientation (370–555 ms) than the front orientation (517–628 ms), reflecting the overt behavior of our participants. These dissociations were confirmed by analyzing the moment of occurrence of the respective transformation map (time frame of best correlation) in the SPO and OBT tasks. We again found that it occurred earlier in the back orientation than in the front orientation, reflecting RTs in the same conditions. The same pattern, reflecting RTs, was found for the MIR task. This dependence of map onset on stimulus orientation, that is the transformation
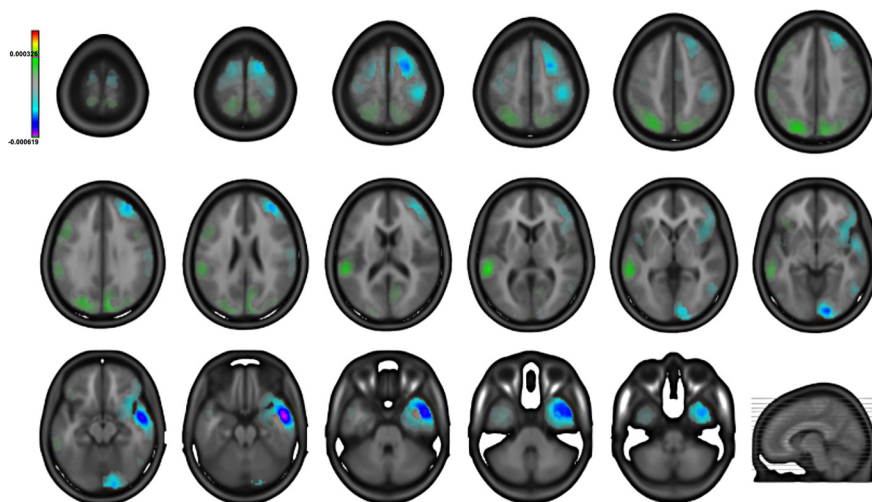

Figure 5. Differential source localizations between SPO/OBT tasks versus MIR task activations at 517–628 ms PSO. The SPO/OBT tasks generated stronger activations in the left TPJ ($-60, -42, -2$), the left precuneus ($-34, -72, 35$), and the right occipital cortex (15, -78, 34). The MIR task more activated the right inferior occipital cortex (21, -93, -5), the right postcentral gyrus (33, -31, 54), the right premotor cortex (31, -2, 52), the right dorsolateral prefrontal cortex (27, 48, 30), and the right anterior temporal cortex.

maps in the front orientation occurring after their onset in the back orientation, is compatible with our behavioral observation that mental body transformations with disembodied and embodied self-location in the front orientation were more difficult (longer RTs and higher error rates) than in the back orientation. These EP data have to be regarded with caution because our total number of artifact-free trials per condition was low (because of the standing position and the prolonged procedure).

Furthermore, we hypothesize that leaning performance, RTs, as well as associated brain activation in the SPO task concord in suggesting that participants imagined their body spontaneously to be localized at the position of the tightrope walker's body. Leaning performance was most variable in the back orientation in the MIR task, and RTs did not allow us to distinguish whether participants in this condition used mental own-body transformation with an embodied or disembodied self-location. This was also reflected in the EP data because MIR, OBT, and SPO tasks were associated with the same brain activation. The back orientation is the condition with highest difficulty (Arzy et al., 2006; Mohr et al., 2006; Easton et al., 2009), and may also be character-

ized by higher intersubject variability concerning embodied and disembodied rotation strategies.

Discussion

In ecologically more valid conditions, we investigated the neural mechanisms of spontaneous self-location and mental own-body transformations when standing and moving participants interacted with an avatar. The present behavioral and electrophysiological approach highlights the advantage and importance of EEG-based functional imaging in such interactions. Other neuroimaging techniques such as fMRI, PET, and magnetoencephalography are performed in the supine or sitting position and require head fixation and absence of body/head movements during the recording of brain activity. The present study demonstrates the feasibility of EP mapping and electrical neuroimaging under experimental conditions that approach naturalistic situations of spontaneous interactions in standing and moving humans. We here show that spontaneous mental body transformations (SPO task) in response to the avatar's body tilts trigger indistinguishable behavioral and neural patterns as explicit mental body transformations with disembodied self-location (OBT task), i.e., when participants leaned while imagining themselves in the avatar's body position via a translocation of the egocentric viewpoint (Berthoz, 1991; Vogeley and Fink, 2003). This differed from explicit mental body transformations with embodied self-location (MIR task), when participants imagined their body at its actual body position (egocentric viewpoint) and the avatar's movements as their own movements as reflected in a mirror, eliciting the opposite behavioral pattern and recruiting partially distinct neural mechanisms. In the SPO/OBT tasks, tilt performance (with preservation of the lateral asymmetry) decreased and RTs increased with the increase of the rotation angle between the participants' body and the avatar's body. In the MIR task, tilt performance (in mirror reversal) increased from the back to the front orientation.

In the front conditions, these indistinguishable behavioral patterns in the SPO/OBT tasks, differing from the MIR task, were further reflected in the EPs. The segmentation and fitting procedure showed that a single template EP map (Map_6) characterized the SPO and OBT tasks at 517–628 ms, whereas the MIR task was characterized at the same time period by another template EP map (Map_{14}). Statistical analysis confirmed that Map_6 significantly differed between the SPO/OBT tasks and the MIR task. Map_{14} showed the opposite pattern during the same time period. Thus, the topography was the same between the SPO and OBT tasks but differently modulated between the SPO/OBT tasks and the MIR task. This shows that different stable brain microstates underlie the SPO/OBT tasks and the MIR task, suggesting the recruitment of different neural generators. At 517–628 ms, the SPO/OBT tasks tended to more activate some solution points of the cluster localized to the left TPJ compared with the MIR task. Despite a significant task × solution points interaction, we consider these results with caution because the *post hoc* tests revealed a trend, probably attributable to the relative low number of our EP data. Although preliminary, this finding seems to corroborate previous studies revealing that the TPJ is involved in multisensory coding of the human body and self (Lobel et al., 1998; Blanke et al., 2002, 2004; Kahane et al., 2003), visual processing of human bodies (Beauchamp et al., 2002; Grossman and Blake, 2002), and mental own-body imagery for full human bodies (Zacks et al., 1999; Blanke et al., 2005; Arzy et al., 2006). Concordant with studies reporting TJP activation in explicit own-body transformation tasks with disembodied self-location (Blanke et al., 2005; Arzy et

al., 2006), our results suggest the involvement of the left TPJ for spontaneous disembodied self-location in the standing position. We found no differential activation between the tasks at the right TPJ (although this region was found to be activated when localizing Map_6). This somewhat differs with previous work on disembodied self-location with healthy subjects (Blanke et al., 2005; Arzy et al., 2006) and data from neurological patients with lesion at the right TPJ and OBEs (Blanke et al., 2002, 2004). However, the left TPJ recruitment may be coherent with the lesion location in patients with a related visual own-body illusion called heautoscopy, i.e., pathological embodiment and self-location in which patients experience to see, in front of them, a reduplication of their own body (Menninger-Lerchenthal, 1935; Hécaen and Ajuriaguerra, 1952; Brugger et al., 1994; Brugger, 2002). Interestingly, heautoscopy mostly occurs in the standing position, whereas OBEs occur in the seated/prone position (same as by Blanke et al., 2005; Arzy et al., 2006). We suggest that this trend for left TPJ activation in our data may be attributable to the participant's standing position. This concords with Brugger's proposition (2002) that heautoscopy, in addition to deficient multisensory own-body processing, relies on deviant perspective-taking mechanisms, occurring under normal conditions spontaneously within self–other interactions in the standing position. The left TPJ activation in our SPO/OBT tasks relying on imagined changes in self-location may be, thus, compatible with the role of the TPJ in third-person perspective (3PP), conceptual (Ruby and Decety, 2003; Schulte-Rüther et al., 2007), visuospatial (Maguire et al., 1998; Vallar et al., 1999), and perceptual (Ruby and Decety, 2001; Vogeley and Fink, 2003; Decety and Lamm, 2007; Blanke and Metzinger, 2009) perspective-taking. According to a neuroimaging meta-analysis (Decety and Lamm, 2007), the TPJ implication in multisensory body-related information processing, self-body processing, and social–cognitive abilities suggests its implication in inferring other's bodily, mental and emotional states, actions, intentions, and in experiencing the other's perspective. We here hypothesize that the similar properties in leaning, RTs, and left TPJ activation in the SPO and OBT tasks suggest that participants automatically embodied the avatar's perspective (3PP), i.e., located themselves spontaneously in the avatar's body.

Although probably recruiting also the TPJ, embodied imagery in the front orientation was significantly associated with stronger activations at the premotor, postcentral gyrus, inferior occipital cortex, and anterior temporal cortex of the right hemisphere. The frontal activation pattern differs from that found in previous work using similar tasks, revealing activations in temporo-parietal and temporo-occipital cortex (Arzy et al., 2006), probably as a result of task/stimulus differences. The standing position and leaning movements (seated/prone position and finger response in the study by Arzy et al., 2006) may have enhanced motor/executive components and a higher frontal recruitment. However, these activations cannot be explained as the mere effect of standing position and leaning movement (or the observation of the avatar) because they were absent in SPO/OBT tasks. These frontal activations are also not related to motor loads or response differences, suggesting that MIR task-specific transformations induced the frontal activations. We cannot exclude that participants performed the MIR task into a mirror imitation task, known to activate the premotor/prefrontal cortex (Iacoboni et al., 1999). We rather hypothesize that these frontal activations were caused by self-attribution processes: participants may have attributed the avatar's movements to themselves, by imagining her movements as their own-body movements as reflected in a mirror. This could be further concordant with neuroimaging

data showing that self-attribution of another's actions or emotions activates the premotor and prefrontal cortex (Carr et al., 2003; Iacoboni et al., 2005; Schulte-Rüther et al., 2007). Moreover, the activation of the right or bilateral premotor and/or prefrontal cortex may corroborate the proposed dominance of the right prefrontal cortex in self-referential processing, first-person perspective (1PP) (Devinsky, 2000; Fossati et al., 2003; Northoff and Bermpohl, 2004), and self-recognition in front-facing images of one's face (Keenan et al., 2000; Uddin et al., 2005). The activations of the right inferior occipital cortex, associated with self-face recognition (Uddin et al., 2005), and the right anterior temporal cortex, associated with representation of social concepts (Zahn et al., 2007) but also self-face (Platek et al., 2006), further confirm the recruitment of self-referential processes. This suggests that imagining/simulating the avatar's body as one's own body as reflected in a mirror is sufficient to activate brain areas related to self-recognition. Moreover, the selective activation of the right postcentral gyrus in the MIR task supports previous work on perspective-taking, showing that first-person conceptual perspective and 1PP in emotional contexts more activates the postcentral gyrus compared with 3PP (Ruby and Decety, 2003, 2004). Accordingly, we hypothesize that these different behavioral–neural patterns in embodied and disembodied self-location may relate to first-person (MIR task) and third-person (SPO/OBT task) perspective-taking, respectively, linking the neural mechanisms of perspective-taking to those of mental body transformations (Keehner et al., 2006).

Although not tested specifically in the present experiment, we speculate that interacting with the avatar, especially in the MIR task, may have relied more strongly on some core components of the human mirror neuron system (hMNS) in premotor cortex (Binkofski and Buccino, 2006), whereas this was less the case in the SPO/OBT tasks. This is of interest to previous studies on hMNS, suggesting that 1PP and self-attribution are linked to the hMNS (di Pellegrino et al., 1992; Rizzolatti et al., 2001; Carr et al., 2003; Gallese, 2007; Shmuelof and Zohary, 2008). Thus, observing and imitating the others' actions, observing complementary and imitative actions (Newman-Norlund et al., 2007), or imagining own actions (Buccino et al., 2001, 2004; Filimon et al., 2007) enhance premotor, parietal, temporo-parietal, and inferior frontal activity, comparable with activity changes when observers execute these actions (Grèzes et al., 2003; Schulte-Rüther et al., 2007). Our results may reinforce this hypothesis showing that this is only the case during embodied mental imagery at 517–628 ms after stimulus onset. This also suggests that the hMNS activation in the frontal cortex depends on whether participants interact with other individuals from 1PP or 3PP and that the activation of the hMNS in the frontal cortex may be less prominent during disembodied self-location.

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