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Disentangling neural processes of egocentric and allocentric mental spatial transformations using whole-body photos of self and other☆

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ABSTRACT

Mental imagery of one's body moving through space is important for imagining changing visuospatial perspectives, as well as for determining how we might appear to other people. Previous neuroimaging research has implicated the temporoparietal junction (TPJ) in this process. It is unclear, however, how neural activity in the TPJ relates to the rotation perspectives from which mental spatial transformation (MST) of one's own body can take place, i.e. from an egocentric or an allocentric perspective. It is also unclear whether TPJ involvement in MST is self-specific or whether the TPJ may also be involved in MST of other human bodies. The aim of the current study was to disentangle neural processes involved in egocentric versus allocentric MSTs of human bodies representing self and other. We measured functional brain activity of healthy participants while they performed egocentric and allocentric MSTs in relation to whole-body photographs of themselves and a same-sex stranger. Findings indicated higher blood oxygen level-dependent (BOLD) response in bilateral TPJ during egocentric versus allocentric MST. Moreover, BOLD response in the TPJ during egocentric MST correlated positively with self-report scores indicating how awkward participants felt while viewing whole-body photos of themselves. These findings considerably advance our understanding of TPJ involvement in MST and its interplay with self-awareness.

Introduction

Mental imagery of one's own body moving through space is important for imagining changing visuospatial perspectives, as well as for autobiographical memory retrieval and self-projection to the future (Arzy et al., 2008; Buckner and Carroll, 2007). It is also important for knowing whether a reflection in a window or mirror is one's own body (Knoblich, 2002), and to imagine how we might appear to other people (Christoff et al., 2011). Mental imagery of one's own body can take place along two perspectives: from a third-person perspective (3PP), e.g. imagining what your body would look like to the audience if you were standing on a theater stage; and from a first-person perspective (1PP), e.g. imagining yourself looking at the audience from that theater stage.

Previous neuroimaging research on mental imagery of one's own body rotating through space has implicated in this process a region on the border of the temporal and parietal human cortices, the temporoparietal junction (Arzy et al., 2006; Blanke et al., 2005; Wraga et al., 2005; Zacks et al., 1999, 2000, 2002, 2003). It is unclear, however, if and how TPJ activity is related to the rotation perspectives by which mental spatial transformation (MST) of one's own body can take place, i.e. 1PP or 3PP (Box 1).

Earlier neuroimaging studies on MST of one's own body did not explicitly distinguish between 1PP and 3PP MST of one's own body. Rather, they contrasted 1PP MST of one's own body to 3PP MST of objects in space (Wraga et al., 2005; Zacks et al., 2000, 2003), or to 3PP MST of object-like cartoon drawings of human bodies (Arzy et al., 2006; Blanke et al., 2005; Zacks et al., 1999, 2002). No study to date has directly contrasted 1PP to 3PP MST of viewers' own bodies. The experimental setups of previous studies allow for a first alternative explanation that the reported higher TPJ activity is related to general MST of one's own body versus MST of objects, irrespective of the 1PP or 3PP from which this MST of one's own body takes place.

In addition, it is also unclear whether the TPJ activity previously associated with 1PP MST of one's own body is specific to one's own body, or whether the TPJ may also be involved in MST of human bodies other than self. As mentioned above, some of the earlier neuroimaging studies contrasted 1PP MST of one's own body to a 3PP MST of cartoon drawings of other human bodies (Arzy et al., 2006; Blanke et al., 2005; Zacks et al., 1999, 2002), but these drawings were not very realistic

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Box 1

Drawbacks of paradigms in previous MST* studies.

Paradigms from classic mental rotation studies (Parsons, 1987; Zacks et al., 1999, 2002) were later adapted and applied in neuroimaging studies of out-of-body experiences (Arzy et al., 2006; Blanke et al., 2010) and vestibular processes (Lenggenhager et al., 2008; Ionta et al., 2011). Several drawbacks in the adopted paradigms, however, allow for alternative interpretations of previous findings regarding the role of the TPJ** in egocentric MST (see Box 2). These drawbacks, listed below, are tackled by the paradigm applied in the current study.

1. Drawn human figures in previous MST studies are more object-like than human-like

- Use of schematic (drawn) figures of human bodies instead of photos of real human bodies
- Unrealistic angles of the schematic human figure, e.g. varying from upright to upside down in increments of 30° in the picture plane, making the human figure more object-like than human-like.

2. Use of indirect tasks to induce egocentric MST was no guarantee egocentric MST really happened

- Classis mental rotation studies (e.g. Zacks et al., 1999, 2002) used an indirect task (left/right judgment) to induce egocentric MST.
- But left/right tasks are no guarantee that participants adopt an egocentric MST. Participants can also apply heuristics instead of MST to answer left/right questions.
- A recent report indicates only 45% of the participants adopted an egocentric MST when asked to make left/right decisions without explicit instruction to perform an egocentric MST. Participants also spontaneously switched strategies when the picture was presented upside down (Lenggenhager et al., 2008).

3. Direct instructions in some previous studies did not contrast egocentric to allocentric MST

- Arzy et al., 2006 and Blanke et al., 2005, for example, used direct, explicit instructions to perform egocentric MST in order to solve left/right questions. However, they contrasted egocentric MST against a no-rotation condition and not against an allocentric MST condition.

In summary, no previous study has directly contrasted egocentric to allocentric MST using photos of real (instead of drawn) human bodies in its design. Also, no previous MST study has contrasted self to other, e.g. egocentric MST towards photos of participants themselves versus egocentric MST towards photos of another person. Box 2 describes the alternative explanations of previous findings that arise due to this empirical hiatus.
*MST = mental spatial transformation. **TPJ = temporoparietal junction.

and were instead rather object-like. Moreover, sometimes these cartoon drawings of human bodies were presented in unrealistic angles, ranging from inverted to upright positions (Zacks et al., 1999), thereby emphasizing their object-like character. No neuroimaging study so far has directly contrasted MST of the actual self-body to MST of an actual, more realistic, body of another person. A second alternative explanation of previous TPJ findings, therefore, is that the TPJ is generally involved in MST of actual human bodies versus MST of objects or object-like drawings of human bodies, irrespective of the identity of the actual human body, e.g. self or other.

The aim of the current study is to adjudicate on these two possible alternative explanations by disentangling neural process involved in 1PP MST from neural processes involved in 3PP MST involving actual human bodies of the self and other. Before continuing with our approach to achieve this aim, we here add a note on terminology. Previous perspective-taking studies have sometimes assigned meanings other than rotation perspective to the terms 1PP and 3PP, for example to distinguish between self and other (Mohr, Rowe, and Blanke, 2010; Ruby and Decety, 2001). We here use the terms *egocentric* respectively *allocentric* to refer to two different rotation perspectives, with the difference between the two being the point of departure of the MST: egocentric MST refers to MST with the agent's body (the one who is performing the MST) as point of departure, and allocentric MST refers to MST with a human body in the space outside of the agent's body as the point of departure. Both egocentric and allocentric MSTs can involve bodies of the agent who performs the MST (self) and bodies of strangers (others), e.g. egocentric MST towards a photo image of the agent's body or egocentric MST towards a photo image of a stranger (see also Fig. 1A).

In order to achieve this aim, we will test three hypotheses: the perspective hypothesis, the self hypothesis, and, combining the two, the perspective-self hypothesis. See Boxes 2 and 3 for an overview of the alternative explanations discussed above and the hypotheses tested in the current study to address these alternative explanations. Based on previous literature (Zacks et al., 2003), the perspective hypothesis predicts that neural activity in the TPJ will be higher in egocentric MST compared to allocentric MST of human bodies. Confirmation of this hypothesis will support the findings from earlier studies. Testing the alternative explanations (see above), the self hypothesis predicts higher neural activity in the TPJ during MST of one's own body than during MSTs involving someone else's body, irrespective of rotation perspective (egocentric, allocentric).

Finally, combining the two hypotheses above, the perspective-self hypothesis predicts that the effect of rotation perspective (egocentric > allocentric MST) on TPJ involvement will be stronger for MST of one's own body than for MST of someone else's body. In other words, when participants engage in egocentric MST towards an image of themselves, we predict higher neural activity in the TPJ than when participants engage in egocentric MST towards an image of someone else. The theoretical context for the perspective self-hypothesis is that the neural regions involved in the purely “cognitive” process of MST can be interfered by emotional processes (Koechel et al., 2011; Mueller, 2011), such as heightened self-consciousness and associated feelings of embarrassment or awkwardness at seeing one's own image (Rochat, 2003, 2009).

To test these hypotheses, we employed a novel paradigm using functional magnetic resonance imaging (fMRI). We measured functional brain activity, as indicated by blood oxygen level-dependent (BOLD) response (Ogawa et al., 1990), in twenty-three healthy participants, while they performed a series of egocentric MSTs and allocentric MSTs in relation to whole-body photographs of themselves and a same-sex stranger (Fig. 1A). To improve ecological validity, that is, to make the design comparable to “real world” situations (Schilbach, 2010; Schilbach et al., 2013), we varied the angles of the whole-body photographs in 3D, so that photos either faced participants directly (0° condition), or the photos faced away from the participants, either looking towards the left (−45° condition) or the right (45° condition) visual field of participants (Fig. 1B). In egocentric MST, participants imagined rotating themselves towards the body on the photo (Fig. 1C). In allocentric MST, participants imagined rotating the body on the photo towards their own body (Fig. 1C).

We explicitly instructed participants to perform either an egocentric or an allocentric mental spatial transformation relative to the human body on the photo (self or other). After stimulus presentation, subjects indicated in which direction they had performed the mental spatial transformation, that is, either clockwise or counterclockwise. We also explicitly informed participants beforehand that the whole-body

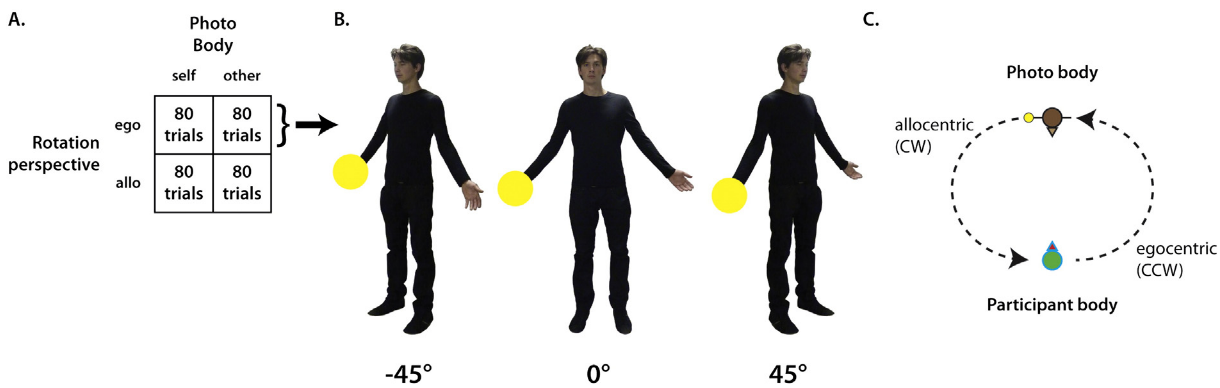

Fig. 1. Experimental design. (A) Schematic of the 2 × 2 experimental design with the factors rotation perspective (egocentric vs. allocentric mental spatial transformation) and photo body (self vs. other). (B) Each of the four cells contains 80 trials, consisting of whole-body photographs in three different angles (−45°, 0° and 45°). A yellow dot appeared on one of the hands (left or right). (C) Schematic example of a counterclockwise (CCW) egocentric and a clockwise (CW) allocentric mental spatial transformation involving a whole-body photo with the yellow dot on the right hand (dorsal view). In the imagined end situation, the noses of both participant body and photo body point in the same direction.

photos could be of self or of a same-sex stranger, but we intentionally did not instruct the participants to treat the photos differently.

As an extra check to determine whether participants processed photos of self differently from photos of other, we presented participants with a post-scanning evaluation form, where they indicated how awkward they had found it to view the photos. Previous psychological research has indicated that seeing one's own mirror image or a photograph of self raises feelings of embarrassment and awkwardness, as it makes us realize how (imperfect) we appear to other people (Rochat, 2003, 2009, 2010). According to Rochat, the expression of embarrassment and awkwardness in front of mirrors by two-year olds serves as the 'acid test of self-concept' (Rochat, 2009, p. 90). It signals the start of self-awareness and an evaluative stance towards the public appearance of our own body image during development, that we maintain throughout our adult lives. In line with this, we predicted that participants would report higher awkwardness scores for photos of self than of other, due to heightened self-awareness after recognizing their own photo.

Box 2

Alternative explanations to TPJ* findings in previous MST studies.**

Previous findings implicate TPJ involvement in MST of one's own body moving through space, as imagined from a so-called egocentric, or first-person perspective. Due to the experimental conditions that were compared in previous MST studies, however, findings from these studies do not rule out two possible alternative explanations:

Alternative explanation 1

Higher neural TPJ activity found in previous MST studies reflects MST of one's own body when compared to mental rotation of objects, irrespective of the MST perspective, that is, egocentric or allocentric.

Alternative explanation 2

Higher neural TPJ activity found in previous MST studies reflects MST of any human body when compared to mental rotation of objects, irrespective of the identity of the human body, that is, self or other.

*TPJ = temporoparietal junction.
**MST = mental spatial transformation.

Furthermore, an important aspect of MST of one's own body moving through space is that one remains aware of one's actual body and its location, so as not to confuse the mental image of one's body moving through space with one's actual body. In other words, during mental projection of one's own body through space, we need to maintain a sense of spatial unity between self and body (Blanke and Metzinger, 2009). Interestingly, the TPJ has also been implicated in neurological conditions where this sense of spatial unity between self and body is compromised (Blanke et al., 2002). In these conditions, also termed out-of-body experiences (OBEs), patients feel as if they are projected out of their physical body, and from this extracorporeal position can look back at their physical body (Blanke et al., 2005; Lopez and Blanke, 2007). Egocentric MST, like OBEs (Blanke et al., 2005; Braithwaite and Dent, 2011), may also involve projecting the self out into extracorporeal space (Fig. 1C). Moreover, many paradigms in neuroscientific research of OBEs are based on those used in earlier mental rotation studies by Zacks and colleagues (Arzy et al., 2006; Lenggenhager et al., 2008), underscoring the phenomenal similarities between MST in healthy people and OBEs and the potential role of self-projection in both phenomena. Unlike self-projection in egocentric MST in healthy people, however, self-projection in OBEs is characterized by a disruption in the sense of spatial unity between self and body, which may lead to feelings of confusion and discomfort (Blanke and Mohr, 2005). We expected that in some of our participants, self-projection during egocentric MST might evoke OBE-like experiences of a disrupted spatial unity between self and body, whereas in other participants the sense of spatial unity between self and body during self-projection in egocentric MST may remain preserved.

To explore the prevalence of self-projection and the OBE-like experience of a disruption of the spatial unity between self and body during egocentric MST, we also asked participants in the post-scanning evaluation form about their self-projection strategies and OBE-like experiences during the experiment (see Methods). Based on the literature, we expected to find more self-projection and higher OBE-ratings in

Box 3
Hypotheses tested in the current study.

Hypothesis	Greater TPJ activity predicted in
1. Perspective hypothesis*	Egocentric MST human bodies > allocentric MST human bodies
2. Self hypothesis	MST self body > MST other body
3. Perspective-self hypothesis**	Egocentric MST > allocentric MST, self body > other body

*Confirmed.
**Confirmed in post-hoc analysis.

egocentric than allocentric MST for photos of self, relative to photos of other. We do note that the exact link between the neural processes underlying egocentric MST, self-projection and OBEs is still unclear, as is the relation between self-projection and a disruption of the sense of spatial unity between self and body (see for example Braithwaite and Dent, 2011). Since our main focus was not on OBEs but on normal processes of egocentric MST in healthy people and associated self-projection, we used the post-scanning OBE ratings to control for a potential effect of OBE-like experiences on the neural data.

Methods

Materials and methods

Participants

Twenty-three right-handed healthy participants (mean age 23 years, standard deviation 4 years; 11 males) with graduate or undergraduate education levels, normal or corrected-to-normal visual acuity and without self-reported neurological or psychiatric disorders participated in the experiment.

All subjects gave written informed consent for this study according to the institutional guidelines set forth by the local ethics committee on human research (Dutch: *Commissie Mensgebonden Onderzoek*) of the region Arnhem–Nijmegen, prior to the experiment. Subjects either received study credits or 20 euros for their participation. One participant was excluded from the data analysis because she reported minor feelings of disorientation during the fMRI task, leaving the total number of analyzed participants at twenty-two.

Procedure

Mental spatial transformation task (MST)

Prior to scanning, participants filled out an informed consent form in the lab and read a written instruction sheet describing the mental spatial transformation task. The experimenter subsequently read the procedures out loud again and checked per step whether the participant understood what to do. We instructed participants to perform the task so that both the egocentric and the allocentric MST tasks would yield an imagined end situation, where the noses of both participant and person on the photo were aligned (e.g. end situations in Fig. 1C). While lying in the scanner, participants completed a fixed set of twelve practice trials to become familiar with the task. The ensuing single fMRI scanning session lasted approximately 50 min ($M = 49.84$ min, $SD = 1.39$), during which participants performed either an egocentric MST, that is, mentally rotating their self-body towards the person on the photo, or an allocentric MST, that is, mentally rotating the person in the photo towards themselves, depending on the instruction on the screen.

Trials appeared in twenty "super blocks", each consisting of four blocks, with four trials per block, adding up to a total of 320 trials. The order of the super blocks, blocks and trials was randomized according to a multilevel application of four 4×4 balanced Latin Squares, to approximate that each condition followed immediately after every other condition an equal number of times (Edwards, 1962). Each block was dedicated to one of the following MST conditions (Fig. 1A): egocentric — photo of self; allocentric — photo of self; egocentric — photo of other; and allocentric — photo of other. Furthermore, the design of trial order within a block did not allow for a repetition of two trials in a row of the same type, that is, a trial with the same angle and with the same hand covered by the yellow dot.

A trial consisted of a low contrast gray fixation cross of 2–4 s (mean 3 s), followed by a white fixation cross of 300 ms, a photo stimulus of 3 s (Supplementary Text T1), and a response screen with a fixed duration of 2 s. A prompt screen of 3 s preceded each new block, with an instruction text as well as a color-and-place cue indicating the required MST (Fig. 2).

After each stimulus presentation, a question about the rotation direction of the performed MST appeared on the screen for 2 s (Q1). Within those 2 s, participants indicated with a button box whether they had performed the required mental spatial rotation by rotating in clockwise (CW) or counterclockwise (CCW) direction. The order of CW and CCW options on the screen was counterbalanced across participants, so that half of the participants had to press their right index finger to indicate CW and their right middle finger to indicate CCW, whereas the other half of the participants had to press their right index finger for CCW and their right middle finger for CW. Responses to Q1 trials allowed us to test whether our manipulation worked. As a basic manipulation check, we predicted that participants would consistently choose the shortest imagined rotation path in the 45° and −45° conditions.

Twenty percent of the trials involved a "catch trial" condition, where participants had to solve a left–right question (Q2). The Q2 questions had a fixed duration of 3.5 s and were counterbalanced for left and right hands of the photo stimulus, so that in half of the Q2 trials, a question probed if the yellow dot was on the right hand, while the other half of the Q2 trials probed if the yellow dot was on the left hand, to which participants responded yes or no with a button press. The order of the

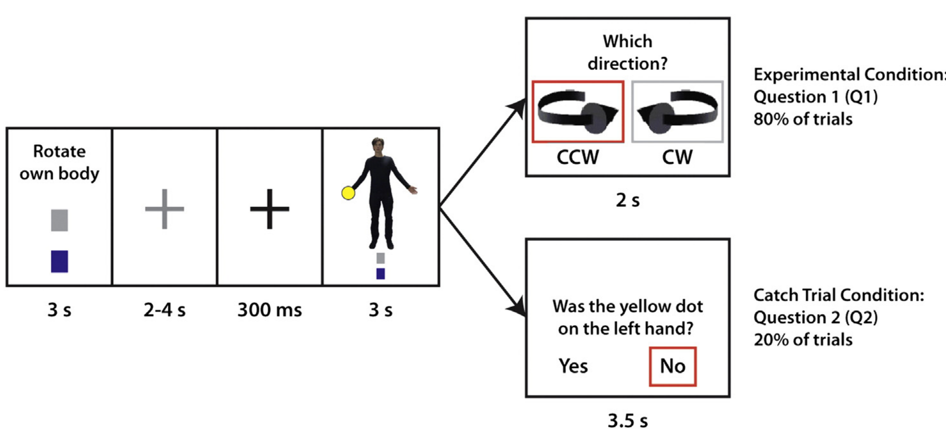

Fig. 2. Schematic of a trial. A prompt screen indicated the beginning of a new block and consisted of the rotation instruction, i.e. "rotate own body", for egocentric and "rotate photo body" for allocentric mental spatial transformations. The prompt screen also contained a color-place cue, where the bottom box symbolized the participant in the scanner and the top box the body on the photo. In the allocentric condition, the bottom box was gray and the top box orange. A low contrast fixation cross with a duration between 2 and 4 s (average 3 s) preceded a white fixation cross of 300 ms. The photo stimulus ensued with a fixed duration of 3 s, followed by a question about the rotation direction that participants had chosen (Q1, 80% of trials), to which participant responded with clockwise (CW) or counterclockwise (CCW). In 20% of the trials, a catch question (Q2) appeared instead of Q1. In half of the catch trials the question was whether the yellow dot was on the right hand (yes/no). The other half of the catch trials concerned the left hand. Q2 questions had a fixed duration of 3.5 s. Color-place cues and order of response buttons were counterbalanced across participants.

yes and no response options on the screen was counterbalanced across participants. Accuracy of the responses to Q2 trials served as an additional manipulation control (see Supplementary Text T2 and Fig. S1E) to ensure that participants formed a clear representation of the required end situation after each mental spatial transformation, namely that the noses of both participant and the body on the photograph were aligned, e.g. the end situations in Fig. 1C.

Post-scanning self-reports

Immediately after scanning, participants completed a pen-and-paper exit questionnaire, where we asked about their experience of the experiment as well as how they had performed the egocentric and allocentric MST tasks. A set of Likert-scaled questions probed experienced difficulty, e.g. "how difficult did you find it to perform the egocentric mental spatial transformation towards self?" (0 = not difficult at all; 100 = very difficult)[1]; experienced awkwardness, as an indicator for self-recognition and self-awareness (Rochat, 2009; Schilbach, 2010), e.g. "how awkward did you find it to see your own photo?" (0 = not awkward at all; 100 = very awkward); and extent of OBE-like experience (Table 1), e.g. "while I was mentally rotating my own body that was lying in the scanner, I had the feeling that I was getting out of my body." (0 = does not apply at all; 100 = applies very much). Additionally, we included three open-ended questions to probe adopted self-projection strategies for the egocentric and allocentric conditions: 1) "when you mentally rotated your body in the scanner, did you stay on the same spot or did you mentally move yourself towards the person in the photo (mentally put yourself in their shoes)?", for egocentric MST across photo-self and photo-other conditions; 2) "when you mentally rotated your body in the photo, did it stay on the same spot or did you mentally move your photo-body towards yourself in the scanner (mentally put your photo-body in your own shoes as you were lying in the scanner)?", for allocentric MST in the photo-self condition; and 3) "when you mentally rotated the other person's body in the photo, did the body stay on the same spot or did you mentally move the other person's photo body towards yourself in the scanner (mentally put the other person's photo body in your own shoes as you were lying in the scanner)?", for allocentric MST in the photo-other condition. We used open-ended questions to assess self-projection so that participants could elaborate on the strategies they adopted during the tasks. After text analysis, we recoded responses to the self-projection question during egocentric MST into three response categories: 1) no self-projection, when participants indicated that their body had remained on the same spot; 2) self-projection, when participants reported that their body as lying in the scanner had mentally shifted towards the body in the photo; or 3) a combination of these two.

Apparatus

All neuroimaging took place at the Donders Centre for Cognitive Neuroimaging (DCCN, Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands) using a Siemens Trio 3 T whole body MR scanner (Erlangen, Germany) with a thirty-two channel head coil. An LCD projector presented the stimuli onto a rear-projection screen mounted at the head end of the scanner bore; screen size = 38.6 × 29.1 cm; default resolution = 1024 × 768; refresh rate = 60 Hz; and distance from screen to pupils = 80 cm. Participants viewed the stimuli through a custom made mirror positioned on the head coil. All stimuli were delivered using Presentation software version 14.9 (Neurobehavioral Systems, Davis, CA, USA) run on a Dell Workstation (Austin, TX, USA).

[1] We used the scale of 0–100 to allow for as much detail as possible, following a similar approach in Newman-Norlund et al. (2009).

Table 1
Post-scanning questions about OBE-like experience during MST tasks with example scores of one individual.
Please answer the following question by giving it a score between 0 and 100, that applies best to you.
0 = does not apply at all.
100 = applies very much.

Nr	Question	Score
A	When observing photos of yourself	
1	While mentally rotating my own body that was lying in the scanner, I had the feeling that I was getting out of my body.	50
2	While mentally rotating my own body in the photo, I had the feeling that I was getting out of my body.	5
B	When observing photos of the other person	
3	While mentally rotating my own body that was lying in the scanner, I had the feeling that I was getting out of my body.	50
4	While mentally rotating the other person's body in the photo, I had the feeling that I was getting out of my body.	5

The OBE score during egocentric MST was calculated as the mean between scores on A1 and B3.
OBE = out-of-body experience.
MST = mental spatial transformation.

fMRI data acquisition

We collected all functional images in a single scanning session using an echo-planar imaging (EPI) sequence sensitive to BOLD contrast (T2*) (TR = 2200 ms, TE = 30 ms, flip angle = 90°, voxel size = 3.5 × 3.5 × 3.0 mm). The 1210 volumes (34 transversal slices, slice gap = 0.5 mm, FOV = 224 mm, slice matrix size = 64 × 64) were acquired in ascending order and allowed for complete brain coverage, except parts of the cerebellum. Following functional imaging, we acquired anatomical images using a T1-weighted 3D MP-RAGE 32 Grappa2 sequence (192 sagittal slices, TR = 2300 ms, TE = 3.03 ms, flip angle = 8°, voxel size = 1 × 1 × 1 mm).

fMRI data analysis

We preprocessed and analyzed functional imaging data in SPM5 (Wellcome Institute of Cognitive Neurology, London, UK; http://www.fil.ion.ucl.ac.uk/spm), using a general linear model (GLM). Preprocessing steps involved spike removal, spatial realignment, slice timing correction, extended co-registration, normalization to the Montreal Neurological Institute (MNI) template with a resolution of 2 × 2 × 2 mm, and spatial smoothing by an isotropic 8-mm full-width-half-maximum (FWHM) Gaussian kernel. For each participant we computed linear contrasts of parameter estimates (β) for each comparison at each voxel. These contrast images were subsequently entered into random effects analyses. In these random-effects analyses, resulting SPMs of the *t*-statistic were corrected for multiple comparisons at the cluster-level, using a voxel-wise threshold of $p < .001$. We focused the second-level analysis on the contrasts egocentric > allocentric MST to test the perspective hypothesis concerning TPJ activity. For the self hypothesis we defined the model self > other (across rotation perspectives), and for the perspective-self hypothesis we defined the model egocentric > allocentric MST, self > other. Since we were only interested in the direct comparisons between egocentric and allocentric MSTs, we did not include a separate (low-level) baseline condition in the experiment.

Results

Behavioral results

Analysis of the behavioral data supports the success of our experimental manipulation by showing, among others, that participants consistently chose the shortest path to perform the MST tasks (Supplementary Text T2 and Fig. S1). Participants, furthermore, retrospectively

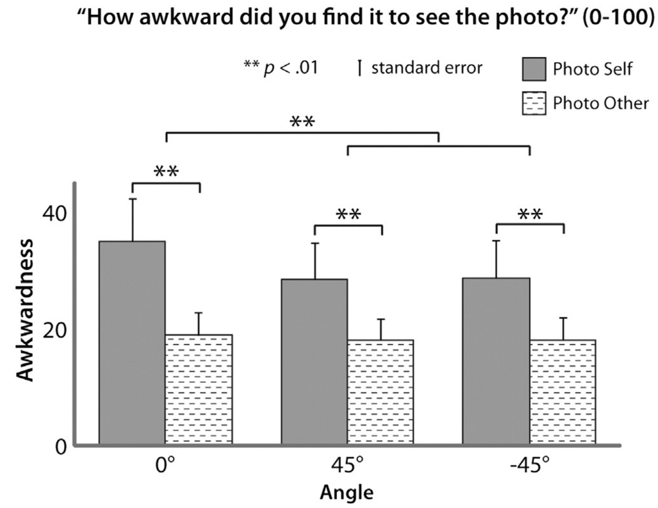

Fig. 3. Higher awkwardness ratings for seeing photo of self than of other ($n = 22$). Post-scanning debriefing reports revealed that participants experienced significantly higher feelings of awkwardness at seeing photos of self than photos of the same-sex stranger, $p = .009$. Results also indicated higher awkwardness ratings for photos in the 0° than in the 45° and −45° conditions, $p = .007$, and a mild trend towards and interaction effect of photo body × angle, suggesting that participants experienced relatively higher awkwardness when self-photos faced them directly, $p = .07$. See the main text for statistical details. See also Supplementary Text T5, Table ST1 and Fig. S5 for an additional post-hoc exploration of the potential role of gender in awkwardness scores (not further treated in the main text).

judged egocentric MST as more difficult than allocentric MST, Wilk's Lambda $F_{1,\ 22} = 63$, $p = .043$ (Fig. S1C).

Text analysis of the post-scanning evaluation assessing self-projection strategies adopted in the egocentric and allocentric conditions revealed that, during egocentric MST, 57.14% of the participants imagined projecting their self into space, towards the body on the photo (self-projection); 23.81% imagined their body stayed on the spot; and 19.05% experienced a combination of these two. In the allocentric condition, 35% of the participants imagined grasping the body on the photo with their hand to perform the allocentric MST. The remainder of participants just imagined the body on the photo turning to the desired position. Analysis of post-scanning reports furthermore revealed a weak trend towards greater OBE-like experiences during egocentric MST, Wilk's Lambda $F_{1,\ 22} = 3.09$, $p = .093$ (Fig. S1F). See also Supplementary Text T3 and Fig. S2.

Notably, post-scanning self-reports confirmed our self-recognition prediction (Rochat, 2003, 2009, 2010) that participants would evaluate seeing photos of themselves as more awkward than photos of a same-sex stranger (Fig. 3). A 2 × 3 ANOVA, composed of the within-subjects factors photo body (self, other) and angle (0°, 45°, −45°), revealed a main effect of photo body on awkwardness scores, Wilk's Lambda $F_{1,\ 21} = 8.26$, $p = .009$. Furthermore, participants evaluated seeing photos facing them directly (0° condition) as more awkward than photos not facing them directly (45° and −45° conditions), as reflected by a main effect of angle, Wilk's Lambda $F_{2,\ 20} = 6.47$, $p = .007$. Results also showed a mild trend towards an interaction-effect of photo body × angle, suggesting that photos of self directly facing participants were evaluated as the most awkward, Wilk's Lambda $F_{2,\ 20} = 3.05$, $p = .07$ (Fig. 3). These results indicate that, at least on an affective level, participants processed photos of self differently from photos of the other. These results are further considered in relation to our neuroimaging data in a post-hoc analysis described below. See Supplementary Text T3 and Fig. S2 for a post-hoc exploration of the relation between self-projection, OBE-like experience and awkwardness scores in our sample. Due to the lack of sufficient participants per response category of self-projection (body stayed on spot, self-projection, and a combination of these two), however, we were not able to perform further statistical analyses on the relation between these variables.

Neuroimaging results

A whole brain analysis of egocentric > allocentric MST confirmed the perspective hypothesis by revealing relatively higher neural activity, as indicated by BOLD response, in bilateral TPJ for egocentric MST, $t_{21} > 5.77$, $p < .001$ (Figs. 4A–B). These effects remained after controlling for self-reported difficulty of performing the mental spatial transformation (Fig. S1C) and OBE-like experiences (Fig. S1F), $t_{19} > 6.23$, $p < .001$. Results furthermore revealed significant peak activations in the left precuneus in Brodmann area (BA) 5 (Fig. 4C), extending into the primary somatosensory cortex. These results suggest that participants were engaging in self-related visuospatial motor imagery, for a review see Cavanna and Trimble (2006). Egocentric versus allocentric MST furthermore recruited higher neural activity in regions linked with motor imagery and body processing (Wraga et al., 2005, 2010), more specifically the left supplementary motor area (BA 6) and the bilateral fusiform gyri (BA 37), $t_{21} > 5.04$, $p < .007$. See Supplementary Text 4a for an analysis of the inverse contrast allocentric vs. egocentric MST (Fig. S3). See Table 2 for a full overview of significant neural activations, exact coordinates, cluster sizes and statistics.

A whole brain analyses of photo self MST > photo other MST across egocentric and allocentric rotation perspectives did not reveal any surprathreshold voxels, thereby failing to confirm the self hypothesis testing the alternative explanation that higher neural activity in the TPJ is caused by MST of one's own body versus MST of someone else's body, irrespective of rotation perspective. Surprisingly, a whole brain analysis of egocentric > allocentric MST, photo self > photo other, did not reveal any significant results either ($p > .79$), thereby failing to confirm the perspective-self hypothesis. However, as described above, post-scanning self-reports did reveal higher awkwardness scores for photo-self than for photo-other conditions, indicating that, on an affective level, participants did process photos of self differently from photos of other (Fig. 3). We used these data from the post-scanning questionnaire to perform post-hoc analyses of the neural data.

Post-hoc analysis: awkwardness scores correlate with TPJ activity during mental spatial transformations

A post-hoc whole brain analysis of egocentric > allocentric, photo self > photo other, with awkwardness scores in the photo-self condition (Fig. 3) as a covariate, revealed a significant 3-way interaction effect, rotation perspective × photo body × awkwardness scores. Considering the multiplicity of possible ways to interpret 3-way interaction effects, as well as our a-priori hypotheses, we here choose to focus the interpretation of this 3-way interaction effect only on individuals with high awkwardness scores in the photo-self condition, which allows us to describe the 2-way interaction effect of rotation perspective × photo body for this group. Described from the perspective of high awkwardness individuals, bilateral BOLD response in the TPJ during egocentric versus allocentric MST was higher for photo-self than for photo-other conditions, $t_{20} > 5.12$, $p < .001$ (Fig. 5).[2] These post-hoc findings support the perspective-self hypothesis in a nuanced way by demonstrating that, when awkwardness scores of seeing photos of self are taken into account, egocentric MST involving photos of self, indeed, recruits relatively higher neural activity in the TPJ compared to egocentric MST involving photos of a same-sex stranger. See Table ST2 for an overview of significant activations, exact coordinates, cluster sizes and statistics.

[2] In the Supplementary Text T4b we additionally describe a significant interaction involving awkwardness scores in the inverse contrast, allocentric vs. egocentric MST (Fig. S4).

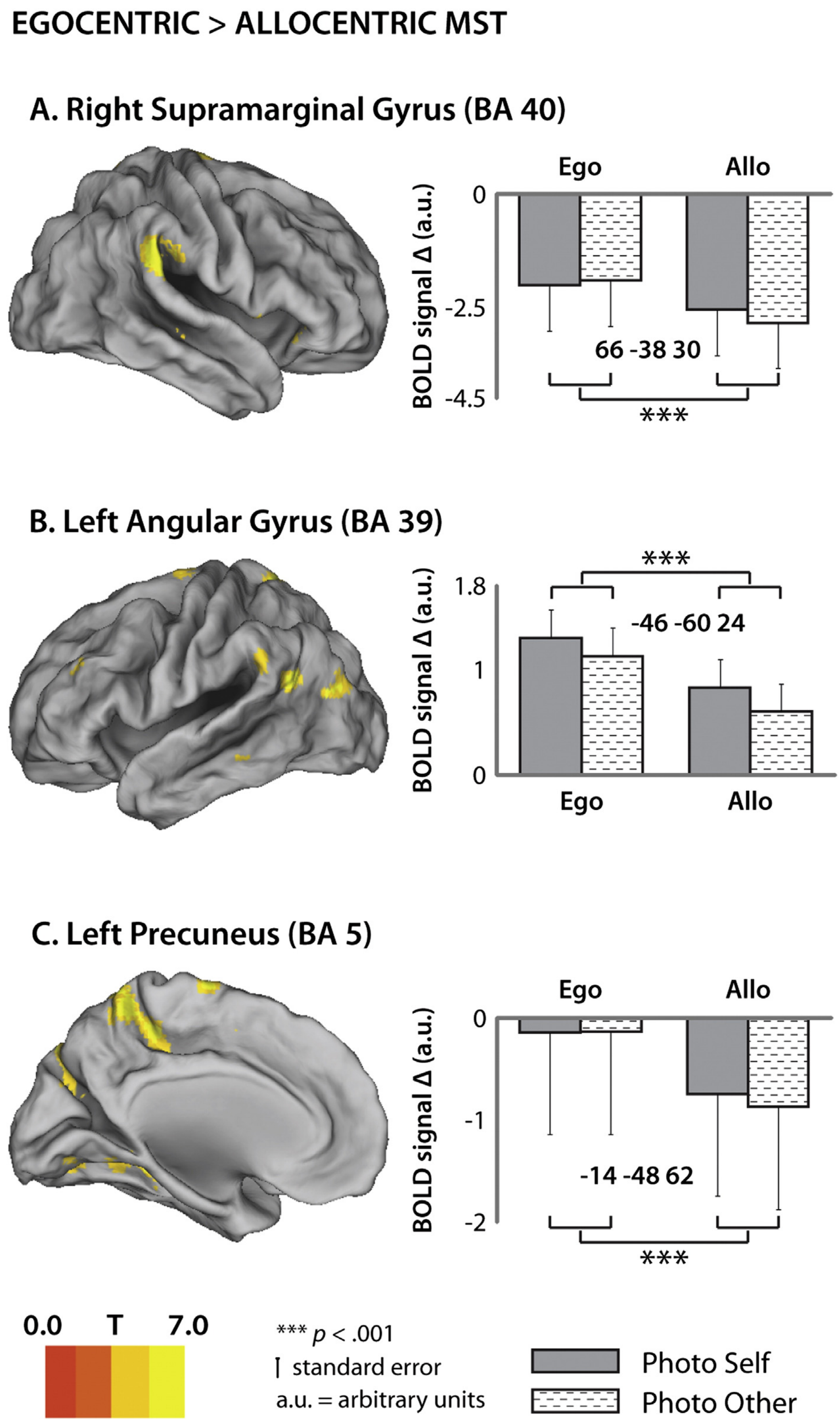

Fig. 4. Neuroimaging results of the contrast egocentric > allocentric MST. Whole brain analysis confirmed the perspective hypothesis by revealing larger neural activity during egocentric versus allocentric MST in the (A) right supramarginal gyrus, and (B) left angular gyrus, as well as other regions implicated in visuospatial body imagery, e.g. (C) the left precuneus. Images show the relevant SPM *t*-contrast, $p < .001$ cluster-corrected, random effect analysis. Images are depicted and rendered on the Population-Average, Landmark- and Surface-based (PALS) human atlas in MNI space with Caret 5.6 software. See Table 2 for statistical details.

Discussion

The aim of the current study was to disentangle neural processes involved in egocentric versus allocentric MSTs of photographed bodies of self and other (Boxes 1–2). Results from a whole brain analysis of egocentric versus allocentric MST confirmed the perspective hypothesis that TPJ involvement is related to egocentric MST (Figs. 4A–B). These results are in line with the interpretations of neural activity in the TPJ reported in earlier MST studies (Zacks et al., 2003). A second aim was to rule out the alternative explanation that higher TPJ activity in

Table 2
Whole brain analysis of egocentric vs. allocentric mental spatial transformations.

Brain region	BA	x	y	z	k_E	t	p
Egocentric > allocentric mental spatial transformation							
L. Precuneus	5	−14	−48	62	1074	6.96	.000
R. Supramarginal gyrus	40	66	−38	30	508	6.01	.000
L. Angular gyrus	39	−46	−60	24	466	5.77	.000
R. Fusiform gyrus	37	32	−32	−20	190	5.62	.006
L. Supplementary motor area	6	−4	−10	74	399	5.36	.000
L. Fusiform gyrus/hippocampus	37	−32	−40	−12	185	5.04	.007
L. Superior occipital gyrus	19	−12	−80	42	156	4.94	.016
L. Middle frontal gyrus	46	−32	32	28	167	4.83	.011

Coordinates in Montreal Neurological Institute (MNI) space. Labeling according to SPM Anatomy Toolbox. *p*-Values in whole brain analyses are cluster-corrected, with 21 degrees of freedom and a voxelwise height threshold of $p < .001$ uncorrected.

egocentric MST versus object-related MST, reported in earlier studies, could be due to general MST of one's own body, irrespective of the egocentric or allocentric rotation perspective (Boxes 2–3). According to this self-hypothesis, TPJ activity would be specifically related to MST of one's own body (across egocentric and allocentric MSTs), relative to MST of another person's body. A whole brain analysis contrasting MST involving photos of self to MST involving photos of other, across egocentric and allocentric rotation perspectives, did not confirm the self hypothesis and ruled out this alternative explanation. Surprisingly, however, a whole brain analysis of the interaction between rotation perspectives (egocentric, allocentric) and person in photo (self, other) did not yield any significant results either, thereby failing to confirm the perspective-self hypothesis (Boxes 2–3).

Nevertheless, using a post-hoc analysis including post-scanning awkwardness scores for seeing photos of self, we did confirm the perspective-self hypothesis in a nuanced way. Results indicated that awkwardness scores significantly covaried with relative BOLD response in the bilateral TPJ during egocentric MST. Described from the perspective of individuals with high awkwardness scores for seeing photos of themselves, results indicate that bilateral TPJ activity during egocentric versus allocentric MST was higher for photographs of self than for photographs of other (Fig. 5). These findings are in line with theories from comparative developmental psychology (Rochat, 2003, 2009, 2010), that higher awkwardness scores for seeing one's own body image in a photo or mirror, relative to someone else's photo, indicate self-awareness, or self-recognition.

Being aware that the body on the photo is self may also have confused the sense of spatial unity between self and body that we normally have, thereby possibly recruiting more bilateral TPJ activity in an effort to correct for the illusory suggestion of a disruption of this spatial unity. This interpretation is supported by evidence from studies showing impaired TPJ functioning in patients suffering from a disrupted sense of spatial unity between self and body, a typical symptom of full-body illusions such as OBE, where patients feel as if they are hovering outside of their own body (Blanke et al., 2004; Blanke and Metzinger, 2009; Lopez et al., 2008) and the related neurological condition of heautoscopy, where patients experience seeing their double in front of them (Blanke and Metzinger, 2009). A typical symptom in heautoscopy, mainly associated with impairments in the left TPJ, is that patients alternate between experiencing being in their actual body and being in the imagined double in front of them. TPJ functioning has also been strongly connected to processes of self-consciousness and self-awareness (Blanke and Metzinger, 2009; Ionta et al., 2011; Lopez et al., 2008; Ruby and Decety, 2001). Moreover, a recent study in healthy

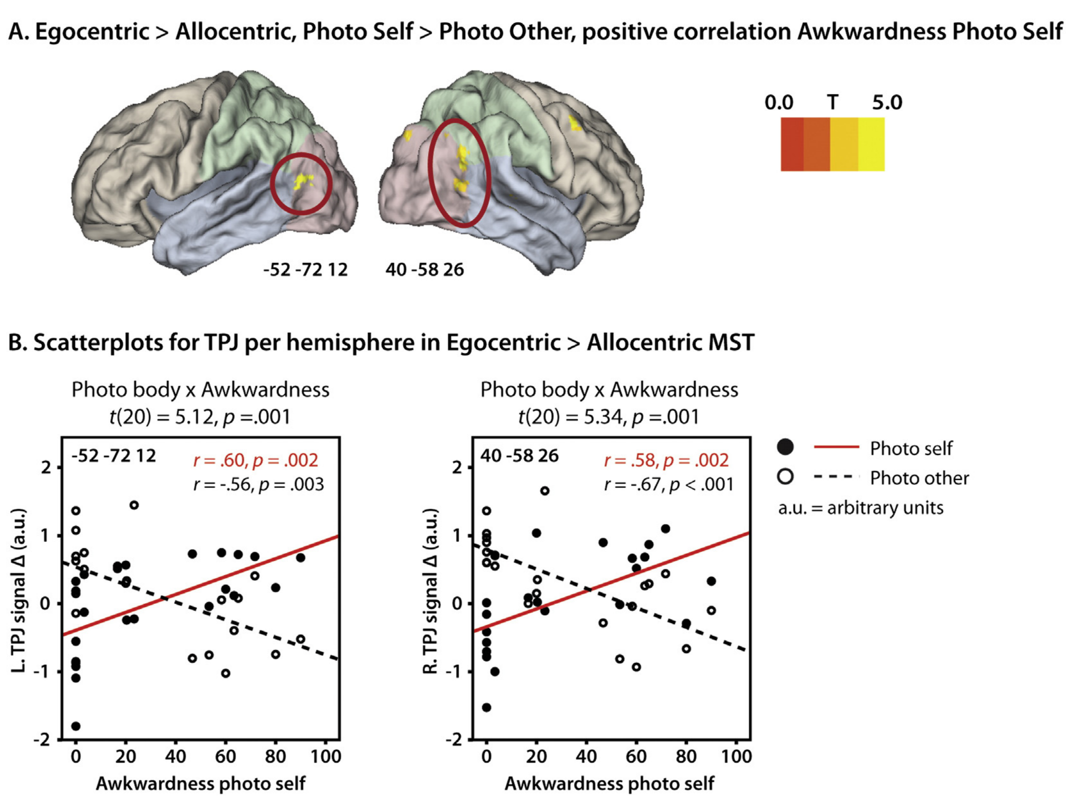

Fig. 5. Post-hoc whole brain analyses with individual awkwardness scores as covariate. (A) Feeling awkward by seeing one's own whole-body in extracorporeal space modulates neural activity during egocentric and allocentric mental spatial transformations. Described from the perspective of high awkwardness individuals, bilateral TPJ activity during egocentric versus allocentric mental spatial transformations was stronger in photo-self than in photo-other conditions. Images show the relevant SPM *t*-contrast, $p < .001$ cluster-corrected, random effect analysis, depicted and rendered on the Population-Average, Landmark- and Surface-based (PALS) human atlas in MNI space with Caret 5.6 software. Cortex colors distinguish between frontal, temporal, parietal, and occipital lobes. (B) Scatter plots showing relative signal change of TPJ areas marked in (A). See Table ST2 for statistical details.

individuals has also implied higher TPJ activity in processes of updating self-location (Ionta et al., 2011), and the authors argued that increased TPJ activity reflects visuo-vestibular effects on altered self-location from an egocentric perspective. This fits nicely with the debriefing reports in our study, revealing that to perform the egocentric MST, the majority of our participants imagined projecting themselves into space, towards the body on the photo (self-projection). As we already considered in the Introduction, for some participants self-projection during egocentric MST may have evoked OBE-like experiences, such as a disrupted sense of spatial unity between the self and the body.

Our findings that the bilateral TPJ is both involved in egocentric versus allocentric MST (Figs. 4A–B), and that bilateral TPJ activity correlates with feelings of awkwardness when seeing the extracorporeal presented self-body (Fig. 5), contribute to the current discussion of whether neural processes of egocentric MST are the same as those implicated in full-body illusions, such as OBE (Arzy et al., 2006; Braithwaite and Dent, 2011; Mohr et al., 2006) and heautoscopy.

We contend that during egocentric versus allocentric MST in healthy individuals, the self is indeed mentally projected out of the body, as evidenced by the debriefing reports of our participants, but at the same time, a sense of spatial unity of self and body needs to be preserved. We propose that the TPJ may be involved in processes of self-projection as well as in processes of maintaining a sense of spatial unity, and a challenging focus for future research is to disentangle both processes within a single study. The small number of participants per cell in our post-scanning questionnaire data of self-projection strategies (Fig. S2) did not allow for a statistical analysis of the relation between self-projection, OBE-like experiences and awkwardness scores. A suggestion for future research is to pre-select a sufficient number of participants in the three self-projection categories (no self-projection, self-projection and the combination) and then follow the same experimental procedures as described in the present research.

By disentangling neural processes of egocentric versus allocentric MST involving photographs of one's own body and someone else's body, the current study substantially advances our understanding of the role of the TPJ in egocentric MST. The findings ruled out possible alternative explanations (Box 2) that TPJ activity found in earlier studies may reflect MST of one's own body irrespective of rotation perspectives, or that higher TPJ activity may reflect MST of human bodies in general, including both self and other, relative to MST of objects. The modulatory effect of self-recognition, indicated by awkwardness scores of seeing photos of self (Rochat, 2003, 2009, 2010), on TPJ activity during egocentric MST, furthermore, underscores the potential role of the TPJ in self-awareness, as speculated by previous researchers (Blanke and Metzinger, 2009; Ionta et al., 2011; Lopez et al., 2008; Ruby and Decety, 2001). By using photographs of real humans instead of schematic drawings of human bodies and by directly contrasting egocentric to allocentric MST, the novel paradigm introduced in this study has opened new and exciting roads to investigate the specific contributions of the TPJ in processes of MST of human bodies versus objects, self-projection, and maintaining a sense of spatial unity between self and body. We encourage future research initiatives to further explore the neurocognitive processes underlying MST, as the ability to project our self in space and time may underlie and contribute to diverse human abilities and behaviors, such as theory of mind, emotional distancing and autobiographical memory.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.05.003.

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