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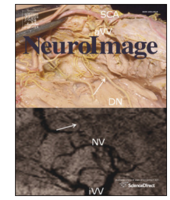

Q4 # Disentangling neural processes of egocentric and allocentric mental spatial transformations using whole-body photos of self and other ☆

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A B S T R A C T

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.

Q7 ## 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., 2005a; Q8 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., 2005a; Zacks et al., 1999, 2002). Q9 No study to date has directly contrasted 1PP to 3PP MST of viewers' own bodies. The experimental setups of previous studies allow for the 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., 2005a; Q10 Zacks et al., 1999, 2002), but these drawings were not very realistic and

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Box 1

Drawback 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.

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.

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).

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

- Arzy et al., 2006 and Blanke et al., 2005a,b, 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.

were instead rather object-like. Moreover, sometimes these cartoon drawings of human bodies were presented in unrealistic angles, ranging from inverted to upright positions, thereby emphasizing their object-like character (Zacks et al., 1999). 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 (Blanke et al., 2005b; 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 towards 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

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