

Allocentric visual cues influence mental transformation of bodies

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Identifying a human body stimulus involves mentally rotating an embodied spatial representation of one's body (motoric embodiment) and projecting it onto the stimulus (spatial embodiment). Interactions between these two processes (spatial and motoric embodiment) may thus reveal cues about the underlying reference frames. The allocentric visual reference frame, and hence the perceived orientation of the body relative to gravity, was modulated using the York Tumbling Room, a fully furnished cubic room with strong directional cues that can be rotated around a participant's roll axis. Sixteen participants were seated upright (relative to gravity) in the Tumbling Room and made judgments about body and hand stimuli that were presented in the frontal plane at orientations of 0°, 90°, 180° (upside down), or 270° relative to them. Body stimuli have an intrinsic visual polarity relative to the environment whereas hands do not. Simultaneously the room was oriented 0°, 90°, 180° (upside down), or 270° relative to gravity resulting in sixteen combinations of orientations. Body stimuli were more accurately identified when room and body stimuli were aligned. However, such congruency did not facilitate identifying hand stimuli. We conclude that static allocentric visual cues can affect embodiment and hence performance in an egocentric mental transformation task. Reaction times to identify either hands or bodies showed no dependence on room orientation.

Introduction

Embodiment holds that the nature of the human mind is largely determined by the form of the human body (Borghi & Cimatti, 2010; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). The relevant aspects of the body include the motor system (motoric embodiment) and the body's interaction with the environment (spatial embodiment). Using these embodied concepts can require conversion from a body reference frame (egocentric) to an external reference frame (allocentric). This paper examines this transformation using mental rotation of the body image to match an externally presented stimulus.

Mental rotation describes the ability to mentally rotate representations of two- or three-dimensional objects, a phenomenon first investigated in 1971 (Shepard & Metzler, 1971). Shepard and Metzler showed that the reaction time to solve a mental rotation task was linearly proportional to the angle of rotation from some canonical position. Mental rotation relies on a range of spatial transformation abilities. Previous work distinguished between mental rotation of objects (*object-based transformations*) and mental rotation of the self (*egocentric transformations*). Mental self-rotation has been reported to be less effortful (faster and more accurate) than object-based transformations (Keehner, Guerin, Miller, Turk, & Hegarty, 2006; Wraga, Creem, & Proffitt, 1999; Zacks & Michelon, 2005). Furthermore, processing time for self-

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rotations remains fairly constant at low angles, but there is a sudden increase for angles around 60°–90° (Graf, 1994; Keehner et al., 2006; Kozhevnikov & Hegarty, 2001; Michelon & Zacks, 2006). Object-based transformations show a constant increase also for small angular disparities (Graf, 1994; Keehner et al., 2006; Michelon & Zacks, 2006; Shepard & Metzler, 1971) but depend less on the plane of rotation (Zacks & Michelon, 2005). This difference could rely—at least in part—on the fact that the two processes involve different spatial frames of reference. Object-based transformations involve manipulation in an object-related frame of reference whereas egocentric transformations (e.g., mental rotation of body or body part stimuli) involve manipulation in an egocentric frame of reference (Grabherr, Cuffel, Guyot, & Mast, 2011; Kozhevnikov & Hegarty, 2001; Kozhevnikov, Motes, Rasch, & Blajenkova, 2006; Zacks, Mires, Tversky, & Hazeltine, 2000). Egocentric mental transformation involves a rotation of the self because participants mentally align a representation of their own body (or body part) with an externally presented stimulus in order to make judgments about it (see also Howard, 1982; Parsons, 1987). Therefore, egocentric mental transformations are grounded in the internal representation of one’s own body (i.e., the *body schema*) and the required transformations are *embodied*. According to Amorim, Isableu, and Jarraya (2006) egocentric mental transformations afford embodied processing at two distinct levels: spatial and motoric.

Spatial embodiment encodes the body or body part posture of a stimulus by mapping one’s own body axes onto the stimulus. Adding human body characteristics to stimuli (e.g., adding a human head to Shepard-and-Metzler figures) facilitates spatial embodiment (Amorim et al., 2006). Experiments using a rubber hand are another illustration of spatial embodiment; synchronous visual and tactile stimulation shifts the perception of hand position toward that of the seen rubber hand (Botvinick & Cohen, 1998). *Motoric embodiment* includes a representation of the motor actions required to covertly rotate the whole body (or a body part) in an egocentric mental transformation task. Body part stimuli rotated to impossible postures lose this advantage (Amorim et al., 2006). Reaction times to identify a body decrease when a participants’ body posture is congruent with the stimulus they are judging, suggesting a reduction in the amount of motoric transformation required (Kessler & Thomson, 2010; Tao, Yan, Wang, Zhou, & Sun, 2007).

It is known that the perceived orientation of one’s own body in space can be influenced by the surrounding visual scene (Bjasch, Bokisch, Straumann, & Tarnutzer, 2012; Haji Khamneh & Harris, 2010; see Howard, 1982 for a review). Given the strength of visual orientation cues on perceived spatial orientation,

we propose that allocentric visual cues alone can affect the construction of the body schema and in turn influence mental egocentric transformation abilities.

To investigate the influence of allocentric visual cues to orientation on egocentric mental transformations, we manipulated the orientation of the visual environment using the Tumbling Room at York University, Toronto. The Tumbling Room is a full-size furnished cubic room with strong directional cues. The entire room can be rotated around an earth-horizontal axis (see Figure 1A) thus separating vestibular and visual verticality information (see, for example, Chang, Harris, & Troje, 2010). Howard et al. (2000) showed that when the Tumbling Room was tilted 90° or 180° relative to gravity, most participants perceived themselves tilted by the same amount as the room with the room continuing to appear in a normally upright orientation. Howard and Hu (2001) defined the resulting visually induced misperception of the direction of gravity as a “static reorientation illusion” (see also Allison, Howard, & Zacher, 1999).

In order to investigate the influence of allocentric cues to orientation on mental egocentric transformation abilities we asked participants to identify body and body part stimuli (Figure 1) presented in different orientations relative to the participant while simultaneously manipulating allocentric cues to orientation. Solving these identifications required mental transformations, but only body stimuli have both a clear intrinsic (up and down distinction) and extrinsic (expected orientation relative to the environment) visual polarity in contrast to body parts such as the hand. Furthermore, mental transformation of the whole body relies on visual-spatial processing in an extrinsic (i.e., allocentric) coordinate system (Creem-Regehr, Neil, & Yeh, 2007), whereas body-part transformations require a dynamic representation of the intrinsic spatial relations of one part of the body relative to another (Buxbaum, Giovannetti, & Libon, 2000; Reed, 2002). Thus we expected that allocentric visual cues would modulate mental transformation of bodies but not hands.

Methods

Participants

Sixteen participants (20–58 years of age, eight male, three left-handed) were recruited from the Centre for Vision Research at York University, Toronto. All participants had normal or corrected-to-normal vision. The procedure was approved by the York University Ethics Review Board and carried out within the

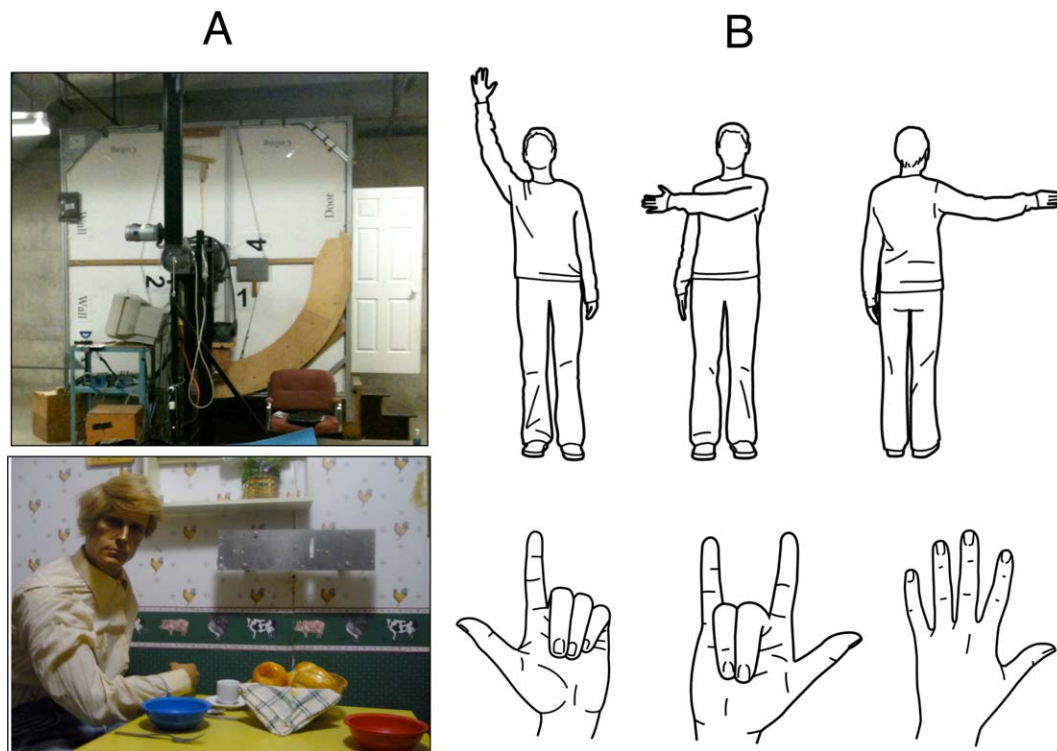


Figure 1. (A) The York Tumbling Room: The floor, door, wall and ceiling constitute the visual frame. Manikin “Hans” and the objects and furniture inside the room provided extrinsic and intrinsic polarity cues. The lower photograph provides an inside view of the Tumbling Room and it was taken from the perspective of the participant, shifted a little bit to the left in order to show the manikin “Hans.” (B) Examples of the human body and body part (hand) stimuli used in the experiment. Participants had to identify which arm was extended or which hand was presented. The full stimulus set is provided in the Supplementary Material.

guidelines of Helsinki. Participants received Swiss chocolate for participation.

Apparatus

The orientation of the visual environment with respect to the participant was manipulated using the York Tumbling Room. The Tumbling Room is a fully furnished, cubic room ($2.4\text{ m} \times 2.4\text{ m} \times 2.4\text{ m}$), which can be rotated around the participant’s roll axis (Figure 1A). The room contains many visual cues to provide a clear sense of orientation. There is a table with bowls and cutlery, a chair on which sits a full-sized human manikin (Hans) in a natural pose looking to one side, a book case with books and other objects, a window through which can be seen (a photograph of) a rural scene and even the animal wallpaper contains clear orientation cues. A chair is mounted on an axis protruding through the center of one wall at the level of the chest of a seated participant. In the present experiment participants remained in an upright position relative to gravity, strapped into this chair. Stimuli were presented using SuperLab 4.0 (Cedrus Corporation, San Pedro, CA) on a 15-inch laptop (model Latitude E5510; Dell Inc., Round Rock, TX) screen

subtending 10.9° mounted 147 cm on the wall facing the participant. The screen therefore rotated relative to the participant along with the room of which it was a part. The axis of rotation went through the center of the screen. A movie clip illustrating the experimental setup is available in the Supplementary Material.

Convention

The orientation of the stimuli are described 0° when aligned with the observer’s body and 90° corresponding to tilted clockwise relative to the observer. The room orientation is described as 0° when aligned with gravity and 90° when tilted clockwise relative to the observer.

Task and stimuli

Subjects were asked to make judgments about either body or hand stimuli. For the *body stimulus rotation task*, participants were presented with line drawings of human body figures with one arm outstretched (Figure 1B) and asked, “Which arm is outstretched?” The body stimuli were presented in 48 different variations: orientation (relative to the viewer: 0° , 90° , 180° , 270°)

where 0° corresponds to the upright relative to the observer), left or right arm outstretched, front or back view, position of the outstretched arm (up, side, crossed) ($4 \times 2 \times 2 \times 3$). Front and back views and the three different positions of the outstretched arm were used to increase task difficulty and to minimize learning effects.

For the *hand rotation task*, participants were presented with line drawings of human hands and asked, “Is it a left or right hand?” The hand stimuli consisted of 48 different variations: four orientations (relative to the viewer: 0°, 90°, 180°, 270°, where 0° corresponds to fingers pointing “up” relative to the observer), left or right hand, front or back view, and three different compositions (two, three or five extended digits) ($4 \times 2 \times 2 \times 3$) (Figure 1B). Again, different variations (front or back view, number of extended fingers) were used to increase task difficulty and minimize learning effects. An illustration of all the stimuli used in this experiment is provided in the Supplementary Material.

The visual environment was varied using four different room orientations: room upright (0°), upside down (180°), or horizontal (90° and 270°). For each stimulus type, this resulted in 16 stimulus-room combinations: room orientation (0°, 90°, 180°, 270°) \times stimulus orientation (0°, 90°, 180°, 270°). The participants were instructed to respond as quickly and accurately as possible by pressing one of two response buttons. The participants pressed the left button with their left hand to indicate a left arm (or hand) and the right button with their right hand to indicate a right arm (or hand). Error rates and response times were measured.

Procedure

The experiment consisted of two main blocks in which the two different types of stimuli (bodies and hands) were presented separately. The order of the blocks was counterbalanced across participants and the orientation of the room varied within the blocks. This resulted in a total of eight short sessions (four sessions per block), where the participants performed the body and hand rotation task in four different room orientations: upright (0°), upside down (180°), and tilted (90° and 270°). Each session consisted of random 48 trials in which either body or hand stimuli were presented depending on the block. Hence, each stimulus variation was presented once, resulting in a total of 12 trials for each stimulus orientation (0°, 90°, 180°, 270°) for each room orientation. Stimuli were presented until a button press was received indicating the decision (a left or right arm or hand). After participants had finished one session, the orientation of

the room was changed and the next trial started. The sequence of room orientations was counterbalanced across participants. Prior to the actual experiment participants completed a short practice session. After the main experiment, participants were asked whether they perceived themselves or the room as upside down during the 180° room orientation trials.

Data analysis

For both the error rates and reaction time data, we aggregated the data across arm position for the body task and across number of extended fingers for the hand task. In order to be sure that none of the aggregated factors had a modulating effect on task performance, we performed separate repeated-measure ANOVAs. Neither arm position nor number of extended fingers interacted with room orientation or body/hand (respectively) stimulus orientation ($p > 0.05$).

Data sets of two participants for the body task and one for the hand task were excluded from analysis due to an overall performance at chance level.

Results

Error rates

Body task

The mean error rate for the mental body rotation task was 14.9% ($SD = 14.7$). A repeated-measures $4 \times 2 \times 4$ ANOVA on error rates with factors room orientation (0°, 90°, 180°, 270°), view (front, back) and stimulus orientation (0°, 90°, 180°, 270°) revealed a main effect of body stimulus orientation, $F(3, 39) = 6.5$, $p < 0.001$, $\eta_p^2 = 0.33$. There was no main effect for room orientation, $F(3, 39) = 1.1$, $p = 0.36$, $\eta_p^2 = 0.08$ and no main effect for view, $F(1, 13) = 1.23$, $p = 0.29$, $\eta_p^2 = 0.09$. There was an interaction between room and body stimulus orientation, $F(9, 117) = 13.83$, $p < 0.001$, $\eta_p^2 = 0.52$, and there was a three-way interaction between room orientation, body stimulus orientation and view $F(9, 117) = 9.05$, $p < 0.001$, $\eta_p^2 = 0.41$. Interestingly, separate analysis for front and back view revealed that the modulating effect of room orientation on mental body transformation was stronger for back view configurations, $F(9, 117) = 51.64$, $p < 0.001$, $\eta_p^2 = 0.8$, than for front view configurations, $F(9, 117) = 1.8$, $p = 0.07$, $\eta_p^2 = 0.12$. A table summarizing all means and standard deviations for the 32 conditions is provided in Supplementary Material. None of the remaining main effects or interactions was significant ($p > 0.14$).

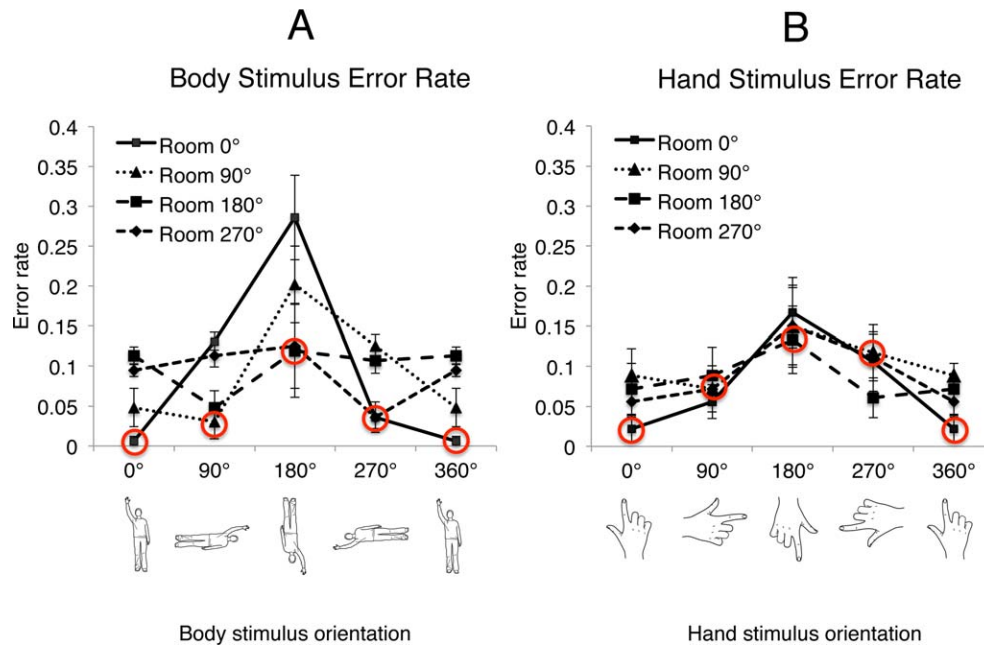


Figure 2. Variation of error rate with stimulus and room orientation (1 refers to 100%). (A) For the body stimulus task, error rate was dependent on both stimulus orientation and room orientation. Circles indicate the “congruent conditions” when the room and stimulus orientations were aligned. (B) Performance with the hand stimulus task depended solely on the orientation of the hand stimulus. There was no interaction between stimulus and room orientation. Error bars show standard errors. The 0° data have also been plotted at 360° for clarity.

In order to further examine the influence of room orientation on task performance we compared congruent versus incongruent room/body stimulus conditions. Congruent means that room and stimulus orientation were aligned; incongruent means all other conditions (body stimuli opposed or orthogonal to room orientation). Analysis revealed a significant difference between congruent and incongruent room/stimulus orientations, $t(13) = -6.26$, $p < 0.001$. Participants’ performance was better when stimulus and room orientations were congruent (mean = 0.05, $SEM = 0.02$) than when they were incongruent (mean = 0.12, $SEM = 0.02$) (Figure 2A). Furthermore, in order to elucidate the significant interaction between room and body stimulus orientation, we calculated post-hoc analyses within the factors room orientation. Pairwise comparisons of body stimuli in upright and upside down orientation relative to room orientation are reported in Table 1. The results show that error rates were smaller for congruent room/body stimulus configurations when compared to configurations where the body stimulus was upside down relative to the environment ($p < 0.001$). This was true for all room orientations except for 180°. When the room was upside down, there was no difference between body stimuli in 0° and 180° orientation ($p = 0.92$). We also performed post-hoc analyses within the factor body stimulus orientation. Pairwise comparisons of room upright and upside-down relative to the body stimulus

are reported in Table 2. The results show that error rates were lower for congruent room-body configurations when compared to configurations where the body stimulus was upside down relative to the environment ($p \leq 0.002$).

Hand task

Mean error rate for the mental hand rotation task was 11.6% ($SD = 12.4$). A repeated-measures $4 \times 2 \times 4$ ANOVA of error rates with factors room orientation (0°, 90°, 180°, 270°), view (front, back) and hand orientation (0°, 90°, 180°, 270°) revealed a significant main effect for hand orientation $F(3, 45) = 6.07$, $p = 0.001$, $\eta_p^2 = 0.29$ but no effect for room orientation, $F(3, 45) = 0.25$, $p = 0.86$, $\eta_p^2 = 0.02$, and no main effect for view $F(1, 15) = 3.12$, $p = 0.1$, $\eta_p^2 = 0.17$. The difference between hand stimuli in front and back view was not significant, there was only a tendency for fewer errors for hand stimuli in back view (back mean = 0.08, $SEM = 0.03$; front mean = 0.15, $SEM = 0.04$). None of the remaining main effects or interactions was significant ($p > 0.27$).

Including “number of extended fingers” (two, three, five) instead of view as a third factor revealed similar results. There was a main effect for hand orientation $F(3, 45) = 6.07$, $p = 0.001$, $\eta_p^2 = 0.29$ but no effect for finger configuration $F(2, 30) = 1.36$, $p = 0.27$, $\eta_p^2 = 0.08$ and no effect for room orientation $F(3, 45) = 0.25$, $p =$

Room orientation	Body stimulus orientations	Mean \pm SD	Post-hoc comparison
0°	0°	0.01 \pm 0.02	$t(13) = -5.15, p < 0.001$
	180°	0.29 \pm 0.2	
90°	90°	0.03 \pm 0.08	$t(13) = 4.95, p < 0.001$
	270°	0.13 \pm 0.05	
180°	0°	0.11 \pm 0.04	$t(13) = -0.1, p = 0.92$
	180°	0.12 \pm 0.22	
270°	90°	0.11 \pm 0.05	$t(13) = -5.64, p < 0.001$
	270°	0.04 \pm 0.05	

Table 1. Post-hoc analyses within the factor room orientation: Pairwise comparisons of body stimulus orientations upright and upside-down relative to the room orientation.

0.86, $\eta_p^2 = 0.02$. Hence, there was no difference between the three finger configurations. None of the remaining main effects or interactions was significant ($p > 0.25$).

Response times

Body task

A repeated-measures $4 \times 2 \times 4$ ANOVA of reaction times with factors room orientation (0°, 90°, 180°, 270°), view (front, back) and body stimulus orientation (0°, 90°, 180°, 270°) revealed a significant main effect for body stimulus orientation, $F(3, 36) = 24.95, p < 0.001, \eta_p^2 = 0.68$, no main effect for room orientation, $F(3, 36) = 0.31, p = 0.82, \eta_p^2 = 0.03$ and a main effect for view, $F(1, 12) = 9.56, p = 0.01, \eta_p^2 = 0.44$. Response times were faster for body stimuli in back view (back mean = 781.24 ms, $SEM = 85.54$; front mean = 1057.6 ms, $SEM = 164.59$). Furthermore, there was also an interaction between body stimulus orientation and view $F(3, 36) = 9.27, p < 0.001, \eta_p^2 = 0.44$. The interaction was due to the fact that responses to back view stimuli were always faster than to front view stimuli ($p < 0.01$), but not when the body stimulus was upside down ($p = 0.55$). There was no interaction between room and body stimulus orientation, $F(9, 108) = 1.25, p = 0.28, \eta_p^2 = 0.09$. None of the remaining main effects or interactions was significant ($p > 0.22$).

Body stimulus orientation	Room orientation	Mean \pm SD	Post-hoc comparison
0°	0°	0.01 \pm 0.02	$t(13) = -7.87, p < 0.001$
	180°	0.11 \pm 0.04	
90°	90°	0.03 \pm 0.08	$t(13) = 6.75, p < 0.001$
	270°	0.11 \pm 0.05	
180°	0°	0.29 \pm 0.2	$t(13) = 3.89, p = 0.002$
	180°	0.12 \pm 0.22	
270°	90°	0.13 \pm 0.05	$t(13) = -8.45, p < 0.001$
	270°	0.04 \pm 0.05	

Table 2. Post-hoc analyses within the factor body stimulus orientation: Pairwise comparisons of room orientations upright or upside-down relative to the body stimulus.

Hand task

A repeated-measures $4 \times 2 \times 4$ ANOVA of reaction times with factors room orientation (0°, 90°, 180°, 270°), view (front, back) and body stimulus orientation (0°, 90°, 180°, 270°) revealed a main effect for hand orientation $F(3, 39) = 19.61, p = 0.001, \eta_p^2 = 0.6$ and a tendency for view $F(1, 13) = 4.3, p = 0.06, \eta_p^2 = 0.25$, but no main effect for room orientation, $F(3, 39) = 1.16, p = 0.34, \eta_p^2 = 0.08$. Response times were faster for back view hand stimuli than for front view stimuli (back mean = 991.74 ms, $SEM = 102.57$; front mean = 1167.85 ms, $SEM = 120.31$). None of the remaining main effects or interactions was significant ($p > 0.07$).

Including “number of outstretched fingers” (two, three, five) as a third factor instead of view revealed similar results. There was a main effect for hand orientation $F(3, 39) = 16.31, p < 0.001, \eta_p^2 = 0.56$ but no effect for finger configuration $F(2, 26) = 1.34, p = 0.28, \eta_p^2 = 0.09$. Hence, there was no difference between the three finger configurations. None of the remaining main effects or interactions was significant ($p > 0.08$).

Judgment of own body orientation

Fourteen out of 16 participants (87.5%) reported feeling “upside down” when the room was in the 180° orientation.

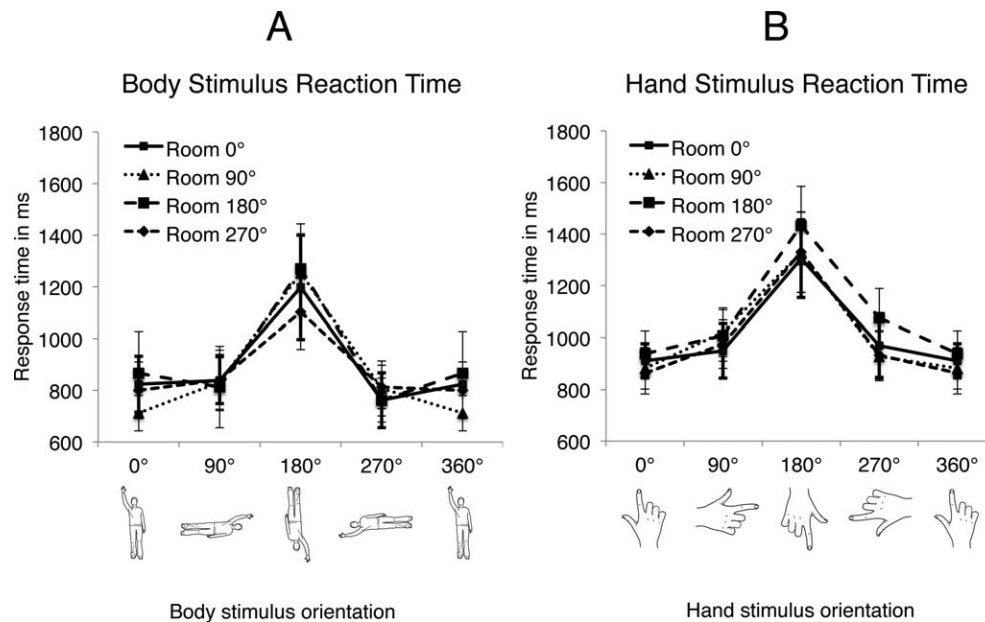


Figure 3. Response time (RT) depended only on stimulus orientation. Response time increases for both body (A) and hand (B) stimuli when the stimuli were in the 180° orientation relative to the observer. Error bars show standard errors. The 0° data have also been plotted at 360° for clarity.

Discussion

The goal of the present study was to examine the influence of the visual allocentric reference frame on two egocentric mental transformation tasks to explore the nature of embodiment. The hand and body task involve bodily representations but differ in their respective recruitment of the *body schema*. Mental transformation of body stimuli requires a mental rotation of the whole body (i.e., with respect to an allocentric reference frame), whereas mental transformation of hand stimuli requires a mental rotation of the hand relative to other body parts (i.e., with respect to an egocentric reference frame). We demonstrated that the orientation of the visual surround modulated performance of a mental body transformation task: Performance improved when the visual polarity of the stimulus matched the orientation of the visual environment. However, there was no effect of the visual frame on the mental hand transformation task.

Previous studies have consistently reported that mental rotation of body stimuli depends on the angle of rotation and is the most difficult for stimuli in a 180° orientation (Parsons, 1987). The general increase in response time for larger angles of rotation we report here is consistent with previous findings (Graf, 1994; Keehner et al., 2006; Kessler, 2000; Kessler & Thomson, 2010; Michelon & Zacks, 2006). These findings have been attributed to the motor system covertly imitating the displayed body posture (Amorim et al., 2006; Hartmann, Falconer, & Mast, 2011; Tao et

al., 2007). Neuroimaging studies indeed suggest that the neural substrate of *egocentric transformations* involves parietal regions and the temporo-parietal-junction, areas that have been associated with the *body schema* (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke et al., 2005; Keehner et al., 2006; Zacks & Michelon, 2005). This suggests that participants mentally rotate the representation of their own body (which is constructed from the *body schema*) to solve an egocentric mental transformation. As an example, let us compare performance for inverted body stimuli (180°) with the room upright and upside down (Figure 2A). As expected, when the room was in an upright (0°) orientation, performance was worst for body stimuli in the 180° orientation. When the room was inverted to match the 180° stimulus orientation, performance improved (error rates decreased from 29% to 12%), despite the fact the stimulus in both examples had the same retinal orientation (see Table 2). Mental rotation of the body is cognitively demanding and thus error-prone. However, tilting the room 180° induces a powerful reorientation illusion and a feeling of being “upside down,”¹ overriding the conflicting information from the vestibular organ. The representation of the subject’s own body is rotated by 180° as a result of the surrounding room. Our results indicate that this visually-induced reorientation illusion led to a better performance for body stimuli that were congruent with the illusory body orientation compared to incongruent arrangements. The congruent room orientation facilitates the cognitively demanding egocentric mental transformation by bringing the representation of the

subject's body into a kind of stimulus-congruent orientation in which both have been "inverted" albeit in separate reference frames.

Interestingly, room orientation had a stronger effect on task performance when body stimuli were seen in back-view leading to a better-matched spatial congruence of body stimulus and participant who imagined themselves projected forwards. This is supported by other studies showing that body posture strongly affects the efficiency of body transformations (Ionta & Blanke, 2009; Kessler & Thomson, 2010). Future studies should specifically investigate the interaction between body posture and visual allocentric cues on mental transformation abilities in order to disentangle and quantify the relative influence of these two factors.

Egocentric mental transformation requires embodiment, which involves a projection of body coordinates onto the stimulus (spatial embodiment) and a mental rotation of the body representation (Amorim et al., 2006). The results from this study suggest that the orientation of the visual surround affected embodiment because the congruity of room orientation and body stimulus reduced the level of spatial ambiguity. When the Tumbling Room was upside down and a congruent body stimulus was presented subjects' ability showed a decreased error rate suggesting that their capacity to embody the stimulus was facilitated. In contrast, the spatial ambiguity presented by incongruent room-body configurations resulted in an increased error rate. For example, when the room was upside down, performance for upright body stimuli was significantly worse compared to an upright (0°) room orientation (from 0.6% to 11%) (see Table 2).

The orientation of surrounding visual orientation cues had no modulating influence on response time. Participants still needed the same amount of time to mentally rotate the stimuli independent of any spatial congruency between the stimulus and the surrounding room. Falconer and Mast (2012) used a body transformation task during caloric vestibular stimulation and they found a decrease in reaction times when the direction of illusory body motion was congruent with the direction of mental rotation. Their results may suggest that illusory body motion (*dynamic allocentric cues*) affects the motoric component of embodiment. For the present results, however, one possible explanation—although speculative at this point in time—is that *static allocentric cues* affect spatial embodiment.

Interestingly, the orientation of the visual surround had no influence on performance in the intrinsic hand stimulus rotation task. Error rates and reaction times were independent of room orientation. Although mental transformation of body parts involves spatial and motoric embodiment as a representation of the own hand is projected onto the hand stimulus and is rotated mentally to align with the stimulus, the hand's

orientation is not bound to the orientation of the visual environment: That is, the representation of a body part is not coded in allocentric coordinates. In contrast to body stimuli, body part stimuli like hands have no clear intrinsic or extrinsic correct or natural orientation relative to the environment. Mental transformation of a body part thus involves only egocentric proprioceptive information about the position of the body part relative to the rest of the body (Buxbaum et al., 2000; Reed, 2002). Consequently, visual orientation cues about the orientation of the body or body part relative to the environment do not affect the representation of the hand; embodiment was not affected by the orientation of the visual surround during mental rotation of hand stimuli.

In the present study we showed that visual allocentric cues modulate mental transformation abilities for whole body stimuli. Allocentric visual cues modulate perceived body orientation in space and therefore affect task performance in mental body orientation that is sensitive to allocentric orientation cues. One limitation is that although body stimuli have a clear intrinsic "up and down" natural orientation we cannot exclude that task performance involving other objects with a clear up-down axis may not also be influenced by room orientation—in other words we cannot be sure that this effect is exclusive to a representation of the body. Future studies should also investigate the effect of visual allocentric cues on object transformation abilities.

Conclusion

The present findings contribute to our understanding of mental spatial transformations and to our understanding of the nature of embodiment. We have shown that mental transformations of body stimuli not only depend on an egocentric reference frame but also on the orientation of the visual surround and hence an allocentric reference frame. This shows that a visual reorientation illusion not only affects how we perceive and orient in space but also influences how we solve cognitive tasks that rely on a spatially embodied representation of our own body.

Keywords: mental rotation, egocentric mental transformation, environmental frame of reference, reorientation illusion, York Tumbling Room, spatial cognition

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Footnote

¹87.5% of the participants (14/16) reported feeling “upside down” when the room was in the 180° orientation.

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