RESEARCH ARTICLE

Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations

Bigna Lenggenhager · Christophe Lopez · Olaf Blanke

Abstract The vestibular system analyses angular and linear accelerations of the head that are important information for perceiving the location of one's own body in space. Vestibular stimulation and in particular galvanic vestibular stimulation (GVS) that allow a systematic modification of vestibular signals has so far mainly been used to investigate vestibular influence on sensori-motor integration in eye movements and postural control. Comparatively, only a few behavioural and imaging studies have investigated how cognition of space and body may depend on vestibular processing. This study was designed to differentiate the influence of left versus right anodal GVS compared to sham stimulation on object-based versus egocentric mental transformations. While GVS was applied, subjects made left-right judgments about pictures of a plant or a human body presented at different orientations in the roll plane. All subjects reported illusory sensations of body self-motion and/or visual field motion during GVS. Response times in the mental transformation task were increased during right but not left anodal GVS for the more difficult stimuli and the larger angles of rotation. Post-hoc analyses suggested that the interfering effect of right anodal GVS was only present in subjects who reported having imagined turning themselves to solve the mental transformation task (egocentric transformation) as compared to those subjects having imagined turning the picture in space (object-based mental transformation). We suggest that this effect relies on shared functional and cortical mechanisms in the posterior parietal cortex associated with both right anodal GVS and mental imagery.

Keywords Spatial cognition · Mental rotation · Subjective visual vertical · Strategy · Human

Introduction

The vestibular system detects angular and linear accelerations of the head in space. Even though most previous studies on the human vestibular system focus on sensori-motor control of eye movements and posture, various studies in patients and healthy human subjects also suggest an important contribution of the vestibular system to cognitive aspects such as spatial and bodily cognition. Nevertheless, the underlying mechanisms are still largely unknown.

Clinical evidence suggests that peripheral vestibular loss leads to deficits in spatial cognition such as spatial navigation, learning or memory abilities (Brandt et al. 2005; Smith et al. 2005). Thus, patients with unilateral peripheral vestibular loss suffer from deficits in path integration during active goal-directed locomotion (Glasauer et al. 2002; Peruch et al. 2005) and navigation in virtual environments (Peruch et al. 1999, 2005) suggesting that vestibular processing contributes to spatial cognition. Vestibular mechanisms have also been shown to be important for own body processing. For example a functional and anatomical relationship between spatial neglect subsequent to right hemispheric brain damage—leading to deficits in spatial and bodily processing—and vestibular disturbances

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has previously been discussed (for an overview see Karnath and Dietrich 2006). This link is supported by the fact that caloric vestibular stimulation and galvanic vestibular stimulation (GVS) may temporarily decrease symptoms of spatial neglect such as rightwards bias in visuo-spatial tasks (Cappa et al. 1987; Rode et al. 1992; Bottini et al. 2005) as well as symptoms of disturbed bodily awareness (Vallar 1998; Fink et al. 2003). Vestibular dysfunctions have also been reported in neurological patients with disturbed own body perceptions due to damage in the temporo-parietal cortex (Devinsky et al. 1989; Blanke et al. 2004). Direct electrical stimulation of this region may also induce out-of-body experiences (Penfield and Erickson 1941; Blanke et al. 2002) as well as vestibular illusions (Blanke et al. 2002; Kahane et al. 2003) at similar stimulation sites. Collectively these findings suggest an important vestibular contribution to spatial and bodily processing (for review see Lenggenhager et al. 2006; Lopez and Blanke 2007).

Similarly, several studies have reported vestibular contributions to spatial and bodily processing in healthy subjects. Thus, it has been shown that visuo-spatial judgments such as line-bisection, visual vertical judgment and body orientation judgment (Fink et al. 2003; Mars et al. 2005), spatial memory (Bächtold et al. 2001), and mental transformation (Mast and Meissner 2004; Mast et al. 2006) can be influenced by vestibular stimulation. Mast et al. (2006) showed that caloric vestibular stimulation leads to impaired performance in mental transformation tasks, but not in a control task using mental imagery.

Here we will focus on mental transformation since it is a spatial cognitive ability that may also rely on bodily processing. At least two different kinds of mental transformation have initially been described, *object-based mental transformation* (Shepard and Metzler 1971) and *egocentric mental transformation* (Parsons 1987). Only a few studies have directly investigated the influence of vestibular processing on either type of mental transformation (Mast et al. 2006; Mast and Meissner 2004). Mast and colleagues (2006) showed that performance in mental transformation is generally decreased during caloric vestibular stimulation. More interestingly for the scope of the present study, they showed that in an egocentric mental transformation task performance can be modified in a direction-specific way by vestibular stimulation during physical body rotations (Mast and Meissner 2004). In this study, subjects were more accurate when the direction of physical rotation and egocentric mental transformation were congruent, suggesting that egocentric mental transformation shares mechanisms with physical body rotation. Thus, both actual and mental body transformation seem to rely on vestibular cues. This is further corroborated by the finding that egocentric mental transformations (imagined sensation of body motion) may induce a direction-specific vestibulo-ocular reflex (Rodio-nov et al. 2004) and that performance in mental transformation of pictures of human bodies and body parts decreases in microgravity (Grabherr et al. 2007). Collectively, these data suggest that egocentric mental transformation depends partly on vestibular processing.

The present study was designed to investigate the effects of GVS on mental transformations. First, we were interested whether there is an overall decrease in performance in mental transformation tasks during GVS as compared to sham stimulation. Mast et al. (2006) reported impaired performance in a mental transformation task, but not in a non-spatial control task during caloric vestibular stimulation. GVS may interact with mental transformation due to overlapping and interfering neural mechanisms between GVS and mental transformation. The comparison to sham stimulation was chosen to control for attentional effects due to skin/pain sensation. Second, we also investigated whether the direction of the illusory body motion induced by right and left GVS influences differently clockwise and counterclockwise mental transformations. Using binaural bipolar GVS it is possible to evoke illusory body motion to the right or the left by reversing electrode polarity (Fitzpatrick and Day 2004). Therefore, based on the results of Mast and Meissner (2004), we hypothesized that mental transformation performance might improve when the direction of the illusory body motion and mental transformation are congruent, but deteriorate when incongruent. Third, we investigated whether object-based and egocentric mental transformations are differently influenced by GVS. Previous literature suggests that subjects tend to use an object-based mental transformation (imagined rotation of the picture in space) when pictures of non-human objects are presented, but use an egocentric perspective-based mental transformation (imagined turning of oneself in space) for pictures of human bodies (Zacks and Tversky 2005). Based on these results and observations that egocentric perspective-based mental transformation seems to interact with vestibular processing (Rodinov et al. 2004; Mast and Meissner 2004), we hypothesized that the effect of GVS would be stronger for pictures representing a human body than a non-human object. Finally, we were interested whether left and right GVS would influence mental transformation differently. Fink et al. (2003) found different cerebral activation patterns for left versus right GVS. During right anodal stimulation they found bilateral activations in superior temporal, posterior insular and inferior parietal regions as well as right lateral occipito-parietal activations, whereas activations during left anodal GVS were confined to the right hemisphere only (superior temporal gyrus, posterior insular cortex, anterior inferior parietal cortex). Therefore, based on the above-mentioned assumption of common and interfering neural mechanisms we hypothesised that left and right GVS could differently influence cortical mental transformation processes.

Material and methods

Subjects

Eleven right-handed (Edinburgh handedness inventory; Oldfield 1971) volunteers (five females–six males, 23.3 ± 4 years) without a history of neurological, psychiatric or vestibular disorders (as verified by questioning) participated in this study. They all had normal or corrected-to-normal vision. Subjects had no prior experience with galvanic or caloric vestibular stimulation. Informed consent was obtained from all subjects prior to their inclusion in the study. The study protocol was approved by the local ethics research committee at the University of Lausanne and has been performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Galvanic vestibular stimulation

Galvanic vestibular stimulation (GVS) was applied using a bipolar, binaural configuration. A stimulator (Model Grass S48, Astor-Med Inc, West Warwick, RI, USA) was used to deliver a square wave pulse through an isolation unit (Model Grass SIU5) and a constant current stimulus unit (Model Grass CCU1) to the electrodes (diameter, 10 mm; Grass Gold Electrodes). This setting provides a safe and constant current output with the anode on one side and the cathode on the other side (Fig. 1a). For the GVS, the electrodes were placed on the left and right mastoid processes. We also introduced the principle of sham stimulation, as it is often used in transcranial magnetic stimulation (TMS)

studies (George et al. 1996; Pascual-Leone et al. 1996). The electrodes were placed on the left and right side of the neck ∼5 cm below the GVS electrodes. Right GVS refers to right anodal stimulation, and left GVS to left anodal stimulation. Using such a binaural bipolar configuration, GVS is known to increase the firing rate in vestibular afferents on the cathodal side and to decrease the firing rate on the anodal side (Goldberg et al. 1984). This change in the firing rate has been associated with illusory movements of both own body (Mars et al. 2005; Fitzpatrick et al. 2002) and visual field (Zink et al. 1998).

The individual threshold for stimulation was determined by progressively increasing the current amplitude (step size of 0.1 mA) separately for right and left GVS as well as for sham stimulations. For GVS, the current amplitude was first progressively increased until the subjects (who were naïve to the effects of GVS) reported vestibular sensations. Then, accounting for the fact that higher current amplitudes lead to stronger vestibular effects, the amplitude was further increased to the maximal current amplitude at which skin sensations were still judged as tolerable. The mean current amplitude was 1.0 ± 0.2 mA and did not differ between right and left GVS. For the sham stimulation no vestibular sensation was elicited and thresholds were fixed so that subjects reported approximately the same intensity of pain or heat sensation on the skin as during the GVS. The mean current was 0.6 ± 0.2 mA.

Visual stimuli

All stimuli were presented on a high-resolution computer screen (1,280 × 1,024 pixels) at 1 m distance from the subject

Fig. 1 Stimuli and experimental set-up. **a** For bipolar, binaural galvanic vestibular or sham stimulation an electrical stimulator was used to deliver a square wave pulse through an isolation unit and a constant current stimulus unit to the two output electrodes. **b** Object and body stimuli presented during the mental transformation task. **c** Each trial consisted of a 15 s galvanic stimulation. After an accommodation period of 3 s (with fixation point), eight pictures of either the plant or the body were shown
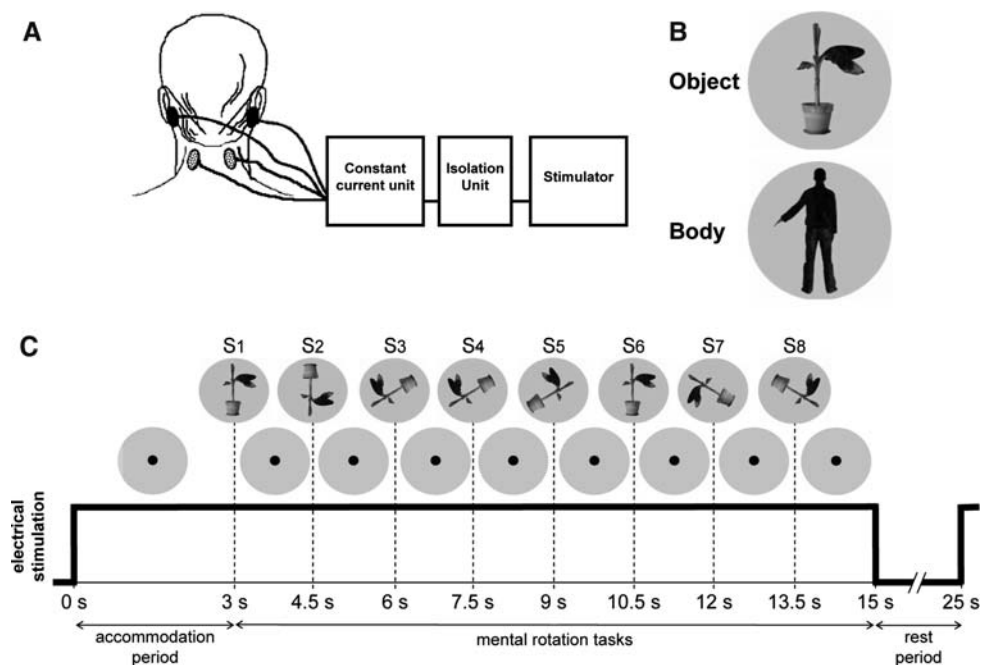
in a completely darkened and noise-isolated room. The frame of the computer screen was covered in order to narrow the visual field to the intended visual scene and to eliminate any horizontal and vertical reference cues.

To measure the subjective visual vertical, a white dotted line (15 cm in length subtending 8.6° of the visual field) was presented on the screen. The initial position in which the line was shown was either tilted counterclockwise (two trials) or clockwise (two trials) at a randomly chosen angle (in the range of ±4° with respect to the gravitational vertical).

In the mental transformation task, greyscale pictures of a plant and of a human body (seen from the back) were used (Fig. 1b). The plant had a big leaf extended to the right or to the left alternatively while the human body showed either an extended left or right arm. Both stimuli subtended 9° and 11.3° of visual field in the horizontal and vertical directions, respectively. Matlab (Mathworks Inc., Natick, MA, USA) with Psychophysics Toolbox v2.54 (Brainard 1997; Pelli 1997) was used for stimulus presentation. Stimuli were presented in six different orientations (0°, 60°, 120°, 180°, 240°, and 300°) in the picture plane. We chose transformation in the roll plane because GVS is known to predominantly evoke illusory motion of both body and visual field in the roll plane (Fitzpatrick and Day 2004). Picture rotations of 240° and 300° correspond to counterclockwise rotations of 120° and 60°, respectively.

Experimental procedures

One experimental session lasted about one hour and consisted of 4 blocks. Each block consisted of a different type of stimulation (GVS with anode left or right; sham stimulation with anode left or right). The sequence of blocks varied randomly across subjects. Within each block the following procedure was used:

First, the subjective visual vertical was measured. The line was presented four times while a rectangular current of 10 s was applied. During these 10 s, subjects were asked to move the line (in 0.2°-steps) clockwise or counterclockwise by pressing a corresponding right or left keyboard button until they judged the line to be vertically oriented. After the 10 s trial ended, subjects closed their eyes until the start of the next trial to avoid any kind of visual feedback of their previous visual vertical judgment that could have influenced the subsequent trial.

Next, we carried out the mental transformation task (six trials with body pictures; six trials with plant pictures). During each trial, GVS was applied for 15 s (during which the visual stimuli were presented) and followed by a 10 s rest period without galvanic stimulation (Fig. 1c). Each trial contained 8 pictures. The first stimulus was presented after an accommodation phase of 3 s in each trial (see Mars et al.

2005). Each stimulus was presented for 300 ms and a fixation point was shown between stimuli (interstimulus interval: 1.5 s). Blocks of body and plant pictures as well as the sequence of pictures within the trial were randomized. In total, this design led to eight stimuli repetitions for each angle of each object per stimulation (total of 96 stimulus presentations per block). Subjects had to indicate with their right hand as fast and as accurately as possible if the right or left hand/leaf was extended. Response time and accuracy were collected with a response box. Two practice sessions were done at the beginning of the experiment to minimize training effects during the different blocks of the experimental session.

Questionnaires

After the experimental sessions, participants filled out a questionnaire focused on determining the strategies they used in the mental transformation task (modified after Zacks and Tversky 2005). For body and for plant pictures, subjects were asked whether they had performed an object-based transformation (I imagined the picture turning), an egocentric transformation (I imagined myself turning), another strategy, or no strategy at all.

Subjects were also given a detailed questionnaire that inquired about the subjective experiences during GVS (modified and extended after Stephan et al. 2005; MacDougall et al. 2006, see electronic supplementary material). This questionnaire included questions about strength, direction and temporal characteristics of the illusory visual field and own body movements as well as the affected body part(s) in the latter. Additionally, we asked subjects about the strength of the experienced side effects during GVS as previously described in the literature (the questionnaire included a modified version of the Simulator Sickness Questionnaire of Lane and Kennedy 1988). In total, subjects answered 65 questions.

Data acquisition and processing

The mean subjective visual vertical (in degrees) was calculated by averaging the four consecutive values for each type of stimulation and each participant.

For the mental transformation task, two dependent variables were measured: the error rate and the response time (in ms). Since the mean error rate over all conditions was less than 2.5%, only response times were further analysed. Response times of correct trials were analysed using repeated-measures analyses of variance (ANOVAs) with the variables Type of Stimulation (GVS, sham stimulation), Side of Stimulation (right, left), Object (body, plant), Stimulus Orientation (clockwise, counterclockwise) and Angle of Rotation (0°, 60°, 120°, 180°) as within-subject factors.

Supplementary ANOVAs were performed with the mental transformation Strategy (object-based transformation, ego-centric transformation) used by the subjects as a between-subject factor and the above mentioned within-subject factors. Post-hoc paired *t* tests were used to further analyse the significant effects on the ANOVAs. Results were considered statistically significant for *P* < 0.05.

Results

Subjective experiences during GVS and side effects

All subjects reported vestibular effects during GVS. Most subjects reported a sensation of body tilt in the roll (72%) or yaw (18%) planes, mainly felt for the head. Motion of the visual field was experienced either as swaying (36%), translation to a fixed distance (36%), or rotation to a fixed angle (55%). With respect to the temporal characteristics of the perceived body motion, subjects reported GVS sensations as continuous (36%), progressive (27%), intermittent (18%), decreasing (18%), or other (55%).

Concerning side effects of GVS (Table 1), 91% of the subjects reported mild or moderate sensations of pain on the skin at the site of the anode. Frequent side effects were general discomfort (55%), mild vertigo (55%), eyestrain (55%), blurred vision (36%), headache (36%), head fullness (36%) and difficulty concentrating (36%).

Subjective visual vertical

Without stimulation, the subjective visual vertical was judged at 0.4° ± 0.9°. This was systematically changed by right (0.5° clockwise) and left GVS (0.4° counterclockwise, Fig. 2). Repeated-measures ANOVA on the visual vertical deviations showed a main effect of the Side of Stimulation [$F_{(1,10)} = 8.4$, $P < 0.05$] and an interaction effect of Type of Stimulation × Side of Stimulation [$F_{(1,10)} = 5.7$, $P < 0.05$] indicating that the different types of stimulation influenced the perceived visual vertical differently as function of the stimulated side. Detailed analyses showed that right GVS caused a significant tilt of the perceived visual vertical towards the anode (clockwise tilt) compared to the right sham stimulation ($t = 3.13$, $P < 0.05$) as well as to the condition without stimulation ($t = 3.07$, $P < 0.05$). Finally, right and left sham stimulations did not significantly influence the perception of the visual vertical.

Performances in the mental transformation tasks

To test our hypotheses we first employed a five-way ANOVA with the within-subject factors Type of Stimulation (GVS, sham stimulation), Side of Stimulation (left,

Table 1 Side effects of galvanic vestibular stimulation

Symptom	Absent	Mild	Moderate	Severe
Pain under the electrodes	0	4	6	1
Heat sensation under the electrodes	7	4	0	0
Metallic taste in the mouth	11	0	0	0
Increased salivation	10	1	0	0
Decreased salivation	9	1	1	0
General discomfort	5	4	2	0
Flushing	11	0	0	0
Pallor	10	1	0	0
Cold sweat	10	0	1	0
Sweating	9	2	0	0
Sickness	9	1	1	0
Nausea	10	1	0	0
Retching	10	1	0	0
Vomiting	10	0	1	0
Vertigo	5	6	0	0
Faintness	9	2	0	0
Eyestrain	5	6	0	0
Blurred vision	7	3	1	0
Headache	7	4	0	0
Head tension	8	2	1	0
Difficulty concentrate	7	4	0	0
Somnolence	6	5	0	0
Fatigue	7	4	0	0
Tachycardia	10	1	0	0
Burping	10	1	0	0

The table shows the side effects of galvanic stimulation assessed by questionnaire. The values refer to the absolute number of subjects reporting a side effect

right), Object (human, plant), Stimulus Orientation (clockwise, counterclockwise) and Angle of Rotation (60°, 120°).[1]

Influence of the angle of stimuli rotation

We found a significant effect of Angle of rotation [$F_{(1,10)} = 83.82$, $P < 0.001$] showing longer response times for 120° compared to 60° rotations. No main effect of Stimulus Orientation was observed suggesting symmetrical response times for clockwise and counterclockwise rotations [$F_{(1,10)} = 3.00$, $P = 0.12$]. The main effect of the Angle of Rotation remained highly significant when all six angles were taken

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[1] The upright (0°) and the upside-down conditions (180°) were not included in this first ANOVA since they cannot be assigned to either a clockwise or counterclockwise Stimulus Orientation and subjects reported having used other strategies than mental rotation for the 180°angle (see below).
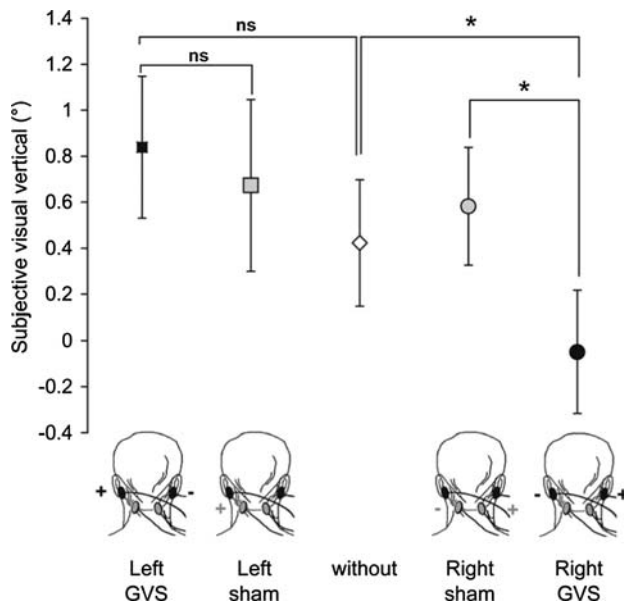
Fig. 2 Influence of GVS on the subjective visual vertical. Mean subjective visual vertical (±standard error to the mean, vertical bars) are shown for each type and side of stimulation. Positive values are corresponding to a counterclockwise deviation (in degree), negative values to a clockwise deviation. * Significant statistical difference ($P < 0.05$)

into account [$F_{(1,10)} = 81.18$, $P < 0.001$] (Fig. 3). The mental rotation rates were 653°/s for bodies and 680°/s for objects which are similar to previously reported rates for mental transformation tasks (Cooper 1975).

Influence of the object presented

Our data indicate that mental transformation of the plant (mean response time: 553 ± 50 ms) was more difficult than mental transformation of the body [538 ± 49 ms; $F_{(1,10)} = 31.21$, $P < 0.001$]. This is also in agreement with results of our questionnaire, showing that 55% of the subjects considered mental transformation of the plant more difficult than that of the body while only 18% reported the opposite.

Influence of the type and side of stimulation

Figure 4 represents the effects of right and left GVS as compared to sham stimulations on response times in the conditions requiring larger mental transformations. Data show that response times significantly increased only during right GVS and for angles of 120°. No comparable effect was found for left GVS or right GVS at 60°. This was reflected in a significant four-way interaction of Type of stimulation × Side of stimulation × Object × Angle of rotation [$F_{(1,10)} = 8.92$, $P < 0.05$]. For the plant, post-hoc tests showed that response times were significantly increased during right GVS (as compared to right sham
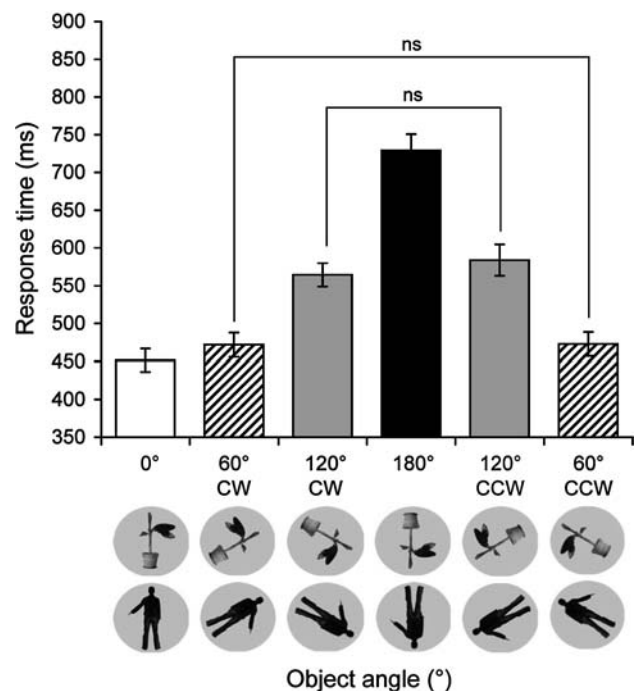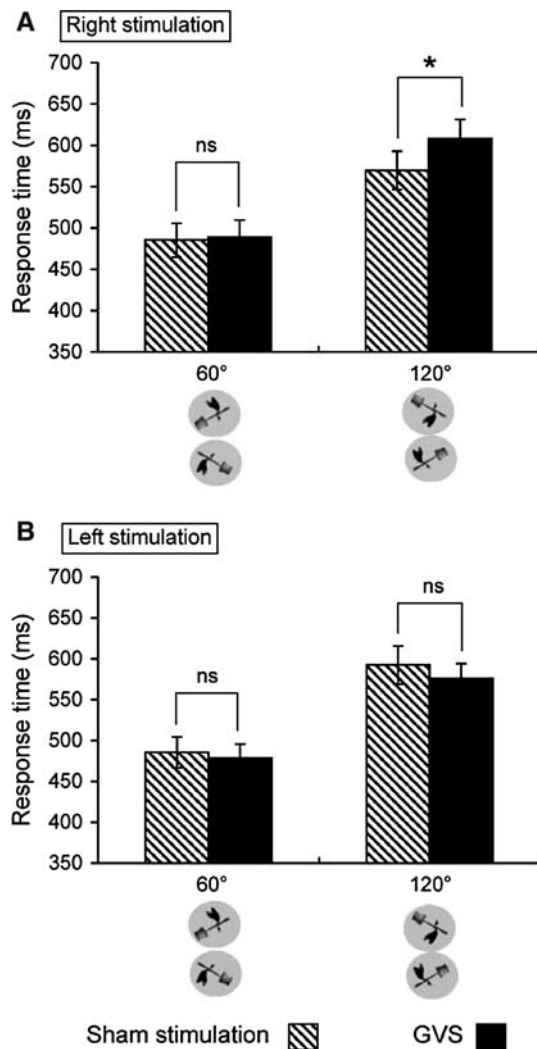

Fig. 3 Influence of the angle of rotation. The histogram shows the mean response time in milliseconds (±standard error to the mean, *vertical bars*) averaged over body and plant stimuli for each angle of rotation (*CW* clockwise, *CCW* counterclockwise). The main effect of angle revealed a typical mental rotation function

stimulation), especially for large angles of rotation [$F_{(1,10)} = 8.05$, $P < 0.05$, Fig. 4a]. Left GVS did not induce such an effect [$F_{(1,10)} = 0.46$, $P = 0.51$, Fig. 4b]. Together, these data suggest that only the right GVS interferes with mental transformation and that this effect is observed only for the most difficult object (plant) and angle of rotation (120°).

Influence of the mental transformation strategy

As vestibular processing has been linked to egocentric-perspective changes and our subjects showed individual differences with respect to the strategy that was employed for mental transformation, we also tested whether interference of GVS with mental transformation differed in subjects employing an egocentric mental transformation than in subjects employing an object-based mental transformation.

In the questionnaire on mental transformation strategies 55% of the subjects ($n = 6$) described that they performed an object-based mental transformation (imagined turning of the image) for pictures of body and plant. The remaining subjects ($n = 5$) reported an egocentric mental transformation (imagined turning of themselves). All subjects reported having used the same strategy for the pictures of the body and the plant. In addition, 45% of the subjects ($n = 5$) reported spontaneous use of a different strategy for pictures

Fig. 4 Influence of the side of stimulation. The histograms show the mean response time in milliseconds (±standard error to the mean, vertical bars) for the plant presented at 60° and 120° (averaged over clockwise and counterclockwise stimuli) during (**a**) *right* and (**b**) *left* anodal galvanic vestibular stimulation compared to right and left sham stimulation

presented upside-down (180°) than for the other angles by just mirroring the body/plant in respect to the median vertical axis of the picture and pressing on the left button if the arm/leaf was on the right, and vice-versa.

We thus analyzed the performance of both subpopulations of subjects by including Strategy as a between-subject factor in the above-described ANOVAs. For right GVS, we found a significant interaction Strategy × Type of stimulation [$F_{(1,9)} = 7.10$, $P < 0.05$] for pictures of plant (Fig. 5), and a trend for pictures of body [$F_{(1,9)} = 4.10$, $P = 0.074$]. Post-hoc analyses suggest that the described interfering effect of right GVS on the mental transformation exists mainly in subjects employing an egocentric mental transformation strategy because only this subpopulation showed

a significant difference between GVS and sham stimulation ($t = 2.9$, $P < 0.05$, compared to $t = 0.6$, $P = 0.55$).

Discussion

This study investigated the influence of vestibular processing and illusory own body motion on mental transformation. Performance in mental transformation tasks during GVS were compared to performance during sham stimulation (a control condition for attentional influence). We tested whether there is an effect of right versus left GVS on mental transformation, whether a different influence of GVS exists for egocentric versus object-based mental transformation, and whether specific directional effects exist when the direction of illusory self-motion and mental transformation are congruent.

General influence of galvanic vestibular stimulation versus sham stimulation

Our data show increased response times for objects presented at larger angles of rotation when applying right anodal GVS. We could not observe the directional effects of GVS on mental transformation as reported by Mast and Meissner (2004). This speaks for a more general effect of GVS on mental transformation due to overlapping and interfering cortical networks. A similar decrease in performance due to vestibular-spatial interaction effects has been found in other studies that used vestibular stimulation in combination with specific cognitive tasks (Fink et al. 2003; Mars et al. 2005). Brain imaging studies suggest that areas in the posterior parietal cortex involved in mental transformation (Kosslyn et al. 1998; Zacks et al. 1999) are also activated during GVS-induced illusory body motion (Lobel et al. 1998; Stephan et al. 2005). Therefore, GVS activation of these areas presumably interferes and impairs mental transformation, corroborating findings of Mast et al. (2006) who showed that caloric vestibular stimulation had a disruptive effect on mental transformation but not on a cognitive control task not involving spatial imagery.

Influence of the mental transformation strategy

Our data suggest that the disturbing effects of GVS are only present in subjects who performed egocentric mental transformation and not object-based mental transformation. This suggests that mental transformation simulates the properties of physical egocentric transformation, since real body movements involve vestibular processes whereas physical object transformation does not. The results are in line with previous observations showing that egocentric mental transformation is influenced by actual vestibular stimula-
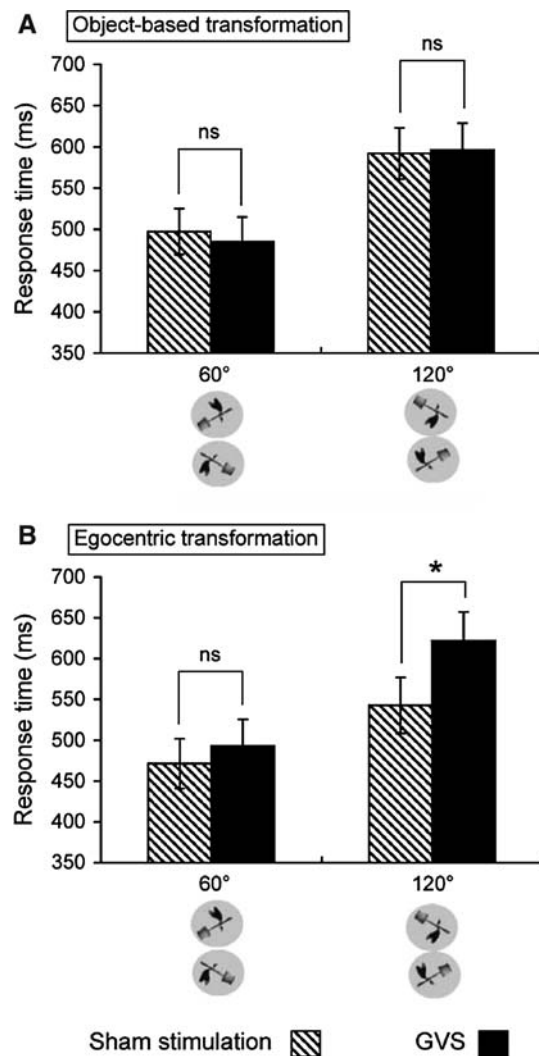
Fig. 5 Influence of the mental transformation strategy. The histograms show the mean response time in milliseconds (±standard error to the mean, *vertical bars*) for the plant presented at 60° and 120° (averaged over clockwise and counterclockwise stimuli) for subjects using (**a**) an object-based versus (**b**) an egocentric mental transformation strategy

tion during physical body rotations (Mast and Meissner 2004) and that egocentric mental transformation influences vestibulo-ocular functions (Rodinov et al. 2004). Differing from earlier findings (Parsons 1987; Zacks and Tversky 2005), the strategy our subjects used did not depend on the visually presented stimuli (plant or human body). Our subjects indicated the use of either an object-based mental transformation (55%) or an egocentric perspective-based mental transformation (45%) for both types of pictures. This suggests that mental transformation depends more on idiosyncratic selection of a strategy involving either egocentric or allocentric references, thereby corroborating evidence from studies on spatial navigation (Wraga et al. 2005) and theories of vicarious processing in spatial cognition (Ohlmann and Marendaz 1991).

What are the anatomical substrates of specific interactions between GVS and egocentric mental transformation? Several neuroimaging studies in healthy subjects have shown that cerebral activations associated with egocentric and object-based strategies can be differentiated during spatial navigation (Jordan et al. 2002; Hartley et al. 2003) and mental transformation (Zacks and Tversky 2005). The exact anatomical location of these mental transformation processes is still controversial and seems to depend on additional variables such as sex, handedness, task difficulty and the control task (Kosslyn et al. 1998; Jordan et al. 2002). Nevertheless, as described in a meta-analysis by Zacks and Michelon (2005), object-based transformation would rely predominantly on unilateral right fronto-parietal cortex, while egocentric transformation would involve a more bilateral network (temporo-parieto-occipital junction; superior parietal lobule) with either right or left hemispheric predominance (Vallar et al. 1999; Zacks et al. 1999; Creem et al. 2001; Vogeley and Fink 2003; Blanke et al. 2005). Thus, the more bilateral cortical network activated by right GVS (see below) may interfere more strongly with mental transformation employing egocentric transformation.

Differences between right and left galvanic vestibular stimulations

The results of this study indicate that only the right GVS interfered with mental transformation. This finding was further confirmed by the effects on the subjective visual vertical (only right GVS led to a significant deviation, see below). This selective effect was not due to different current amplitudes applied during right versus left GVS. We therefore suggest that either a functional asymmetry of the peripheral vestibular apparatus exists or, more likely, a set of common neural mechanisms between right GVS and mental transformation exists that may be responsible for this effect.

Concerning the functional asymmetry of the peripheral vestibular system, several studies have suggested asymmetrical effects of left and right GVS even on basic parameters such as eye movements and postural control (Quark et al. 1998; Bent et al. 2000). However, the data on such peripheral asymmetries are contradictory, with some authors reporting a dominance of the left (Lacour et al. 1974), some the right (Quark et al. 1998) vestibular apparatus, or even a symmetrical sensitivity for both ears (Zink et al. 1998).

With respect to the hypothesis of a set of common neural mechanisms between right GVS and mental transformation, our result may be due to more extensive overlap and interference of brain regions activated by right GVS (as opposed to left) with brain regions involved in mental transformation. In an fMRI study, Fink et al. (2003) compared the cortical activation associated with right versus left GVS using a similar stimulation protocol as in the present study.

These authors found that right anodal GVS involved a bilateral hemispheric activation of the superior temporal gyrus, posterior insula, anterior inferior parietal cortex, as well as right lateral occipito-parietal activation, whereas activations during left anodal GVS were confined to the right hemisphere only (superior temporal gyrus, posterior insula, anterior inferior parietal cortex). As mental transformation has been shown to rely on bilateral parietal and temporo-occipital activations (bodies: Zacks et al. 1999; Creem et al. 2001; Blanke et al. 2005, objects: Kosslyn et al. 1998; Vingerhoets et al. 2001), we speculate that bilateral activations due to right GVS interfere more strongly with bilateral activations during mental transformation in superior temporal gyrus, posterior insula, and inferior parietal cortex. Interference of right GVS at these sites might thus lead to the observed decrease in task performance.

The differential effects between left and right GVS on mental transformations in the present study were confirmed by the results of the visual vertical judgments. Only right anodal GVS influenced the perception of the vertical significantly, evidenced by a clockwise deviation of the subjective visual vertical. Given that the amplitude of the visual vertical deviation depends on current intensity (Mars et al. 2005), and that we used small current amplitudes compared to previous studies, our values appear to be consistent with that of previous findings (Zink et al. 1998; Mars et al. 2005). A significantly stronger influence of right GVS on the subjective visual vertical has also been reported in patients with right parietal damage (Saj et al. 2006). Moreover, the brain regions involved in the visual vertical judgment [a bilateral fronto-parieto-occipital network including inferior frontal cortex, anterior insula and posterior parietal cortex (Lopez et al. 2005)] would be more affected by right than left GVS.

Limitations

While this study revealed disruptive effects of GVS on mental transformation, the effects were rather small and specific. We believe that this is mainly due to the low intensity and heterogeneous effects of GVS and/or due to a too low task difficulty (error rate smaller than 2.5%). The large number of stimulus repetitions required the use of a relatively weak mean current of about 1 mA, probably resulting in a reduced strength of overall illusory body motion. The two previous studies that showed vestibular influence on mental transformation used actual body rotation (Mast and Meissner 2004) or caloric vestibular stimulation (Mast et al. 2006), both of which yielded stronger vestibular sensations. Additionally, important inter-individual differences in the direction, amplitude and temporal characteristics of the illusory movements due to GVS were reported. MacDougall et al. (2002) suggested that these differences result from the unnatural stimulation of all semicircular and otolith organs

simultaneously and from individual differences in the interpretation of these uncommon vestibular stimuli. The fact that not all subjects reported illusory movement could also account for the lack of direction-specific effects in this study. This is further confounded by the fact that subjects used different mental rotation strategies, and that the direction of the mental transformation differed across subjects. For example, for a stimulus angle of 60° clockwise, subjects using an egocentric strategy would imagine turning their body rightwards while subjects using an object-based transformation would imagine turning the picture leftwards.

Conclusion

Although the interaction between GVS and mental transformation was not as strong as assumed based on previous literature, this study reveals novel results concerning the contribution of the vestibular system to high level spatial and bodily processing. The results suggest that GVS may impair demanding mental transformation tasks. This is mainly true for right GVS and for egocentric mental transformation, suggesting a shared neural processing in the posterior parietal cortex.

Based on these results several implications for further studies can be derived: Studies on the effects of GVS and bodily and spatial processing should consider sham stimulation as it is routinely used in transcranial magnetic stimulation studies. Task complexity should generally be high enough in order to observe potential GVS effects, and these effects should further be investigated by systematically manipulating task difficulty. Since we found differences between left and right GVS, future studies should also investigate GVS over both mastoids separately. Moreover, for mental transformation tasks it would be interesting to assess and manipulate mental transformation strategies, since they seem to rely on different neural processes. Finally, to test our hypothesis of a shared brain mechanism between right GVS and mental transformation it would be important to combine neuroimaging with GVS as done previously to demonstrate this common neural substrate between GVS and line bisection (Fink et al. 2003).

References

Bächtold D, Baumann T, Sandor PS, Kritos M, Regard M, Brugger P (2001) Spatial- and verbal-memory improvement by cold-water caloric stimulation in healthy subjects. Exp Brain Res 136:128–132

Bent LR, McFadyen BJ, Merkley VF, Kennedy PM, Inglis JT (2000) Magnitude effects of galvanic vestibular stimulation on the trajectory of human gait. Neurosci Lett 279:157–160

Blanke O, Landis T, Spinelli L, Seeck M (2004) Out-of-body experience and autoscopy of neurological origin. Brain 127:243–258

Blanke O, Mohr C, Michel CM, Pascual-Leone A, Brugger P, Seeck M, Landis T, Thut G (2005) Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. J Neurosci 25:550–557

Blanke O, Ortigue S, Landis T, Seeck M (2002) Stimulating illusory own-body perceptions. Nature 419:269–270

Bottini G, Paulesu E, Gandola M, Loffredo S, Scarpa P, Sterzi R, Santilli I, Defanti CA, Scialfa G, Fazio F, Vallar G (2005) Left caloric vestibular stimulation ameliorates right hemianesthesia. Neurology 65:1278–1283

Brainard DH (1997) The psychophysics toolbox. Spatial Vision 10:443–446

Brandt T, Schautzer F, Hamilton DA, Bruning R, Markowitsch HJ, Kalla R, Darlington C, Smith P, Strupp M (2005) Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans. Brain 128:2732–2741

Cappa S, Sterzi R, Vallar G, Bisiach E (1987) Remission of hemineglect and anosognosia during vestibular stimulation. Neuropsychologia 25:775–782

Cooper L (1975) Mental rotation of random two-dimensional shapes. Cogn Psychol 7:20–43

Creem SH, Downs TH, Wraga M, Harrington GS, Proffitt DR, Downs JH 3rd (2001) An fMRI study of imagined self-rotation. Cogn Affect Behav Neurosci 1:239–249

Devinsky O, Feldmann E, Burrowes K, Bromfield E (1989) Autoscopic phenomena with seizures. Arch Neurol 46:1080–1088

Fink GR, Marshall JC, Weiss PH, Stephan T, Grefkes C, Shah NJ, Zilles K, Dieterich M (2003) Performing allocentric visuospatial judgments with induced distortion of the egocentric reference frame: an fMRI study with clinical implications. Neuroimage 20:1505–1517

Fitzpatrick RC, Day BL (2004) Probing the human vestibular system with galvanic stimulation. J Appl Physiol 96:2301–2316

Fitzpatrick RC, Marsden J, Lord SR, Day BL (2002) Galvanic vestibular stimulation evokes sensations of body rotation. Neuroreport 13:2379–83

George MS, Wassermann EM, Post RM (1996) Transcranial magnetic stimulation: a neuropsychiatric tool for the 21st century. J Neuropsychiatry Clin Neurosci 8:373–382

Glasauer S, Amorim MA, Viaud-Delmon I, Berthoz A (2002) Differential effects of labyrinthine dysfunction on distance and direction during blindfolded walking of a triangular path. Exp Brain Res 145:489–497

Grabherr L, Bach S, Indermaur K, Metzler S, Mast F (2007) Mental transformations of bodies and body-parts in microgravity. J Vest Res (in press)

Hartley T, Maguire EA, Spiers HJ, Burgess N (2003) The well-worn route and the path less traveled: distinct neural bases of route following and wayfinding in humans. Neuron 37:877–888

Jordan K, Wustenberg T, Heinze HJ, Peters M, Jancke L (2002) Women and men exhibit different cortical activation patterns during mental rotation tasks. Neuropsychologia 40:2397–2408

Kahane P, Hoffmann D, Minotti L, Berthoz A (2003) Reappraisal of the human vestibular cortex by cortical electrical stimulation study. Ann Neurol 54:615–624

Karnath HO, Dieterich M (2006) Spatial neglect-a vestibular disorder? Brain 129:293–305

Kosslyn SM, DiGirolamo GJ, Thompson WL, Alpert NM (1998) Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. Psychophysiology 35:151–161

Lacour M, Bonnet M, Roll JP (1974) [Spinal effects of electric vestibular stimulation in man. Demonstrated evidence of vestibular prevalence and role in motion laterality]. Acta Otolaryngol 78:399–409

Lane NE, Kennedy, RS (1988) A new method for quantifying simulator sickness: development and application of the simulator sickness questionnaire (SSQ). Technical Report No. EOTR 88-7, Essex Corporation, Orlando

Lenggenhager B, Smith S, Blanke O (2006) Functional and neural mechanisms of embodiment: Importance of the vestibular system and the temporal parietal junction. Rev Neurosci 17:643–657

Lobel E, Kleine JF, Bihan DL, Leroy-Willig A, Berthoz A (1998) Functional MRI of galvanic vestibular stimulation. J Neurophysiol 80:2699–2709

Lopez C, Blanke O (2007) Neuropsychology and neurophysiology of self-consciousness. Multisensory and vestibular mechanisms. In: Holderegger A, Sitter-Liver B, Hess CW (eds) Hirnforschung und Menschenbild. Beiträge zur interdisziplinären Verständigung. Schwabe, Basel

Lopez C, Lacour M, Ballester M, Dumitrescu M, Anton J-L, Nazarian B, Roth M, Borel L (2005) Brain activations during subjective visual vertical judgment: a functional magnetic resonance imaging study. Gait and Posture 21(Suppl 1):13

MacDougall HG, Brizuela AE, Burgess AM, Curthoys IS (2002) Between-subject variability and within-subject reliability of the human eye-movement response to bilateral galvanic (DC) vestibular stimulation. Exp Brain Res 144:69–78

MacDougall HG, Moore ST, Curthoys IS, Black FO (2006) Modeling postural instability with Galvanic vestibular stimulation. Exp Brain Res 172:208–220

Mars F, Vercher JL, Popov K (2005) Dissociation between subjective vertical and subjective body orientation elicited by galvanic vestibular stimulation. Brain Res Bull 65:77–86

Mast FW, Meissner F (2004) Mental transformations of perspective during whole-body roll-rotation. J Vestib Res 14:113

Mast FW, Merfeld DM, Kosslyn SM (2006) Visual mental imagery during caloric vestibular stimulation. Neuropsychologia 44:101–109

Ohlmann T, Marendaz C (1991) Vicarious processes involved in spatial perception. In: Wapner S (ed) Bio-psycho-social factors in cognitive style. Lawrence Erlbaum, Hillsdale, pp 106–129

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Parsons LM (1987) Imagined spatial transformation of one's body. J Exp Psychol Gen 116:172–191

Pascual-Leone A, Rubio B, Pallardo F, Catala MD (1996) Rapid-rate transcranial magnetic stimulation of left dorsolateral prefrontal cortex in drug-resistant depression. Lancet 348:233–237

Pelli DG (1997) The VideoToolbox sotware for visual psychophysics: transforming numbers into movies. Spat Vis 10:437–442

Penfield W, Erickson T (1941) Epilepsy and Cerebral Localization, Charles C. Thomas, Springfield

Peruch P, Borel L, Gaunet F, Thinus-Blanc G, Magnan J, Lacour M (1999) Spatial performance of unilateral vestibular defective patients in nonvisual versus visual navigation. J Vestib Res 9:37–47

Peruch P, Borel L, Magnan J, Lacour M (2005) Direction and distance deficits in path integration after unilateral vestibular loss depend on task complexity. Brain Res Cogn Brain Res 25:862–872

Quarck G, Etard O, Normand H, Pottier M, Denise P (1998) Low intensity galvanic vestibulo-ocular reflex in normal subjects. Neurophysiol Clin 28:413–422

Rode G, Charles N, Perenin MT, Vighetto A, Trillet M, Aimard G (1992) Partial remission of hemiplegia and somatoparaphrenia through vestibular stimulation in a case of unilateral neglect. Cortex 28:203–208

Rodionov V, Zislin J, Elidan J (2004) Imagination of body rotation can induce eye movements. Acta Otolaryngol 124:684–689

Saj A, Honore J, Rousseaux M (2006) Perception of the vertical in patients with right hemispheric lesion: Effect of galvanic vestibular stimulation. Neuropsychologia 44:1509–1512

Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. Science 171:701–703

Smith PF, Zheng Y, Horii A, Darlington CL (2005) Does vestibular damage cause cognitive dysfunction in humans? J Vestib Res 15:1–9

Stephan T, Deutschlander A, Nolte A, Schneider E, Wiesmann M, Brandt T, Dieterich M (2005) Functional MRI of galvanic vestibular stimulation with alternating currents at different frequencies. Neuroimage 26:721–732

Vallar G (1998) Spatial Hemineglect in Human. Trends Cogn Sci 2:87–97

Vallar G, Lobel E, Galati G, Berthoz A, Pizzamiglio L, Le Bihan D (1999) A fronto-parietal system for computing the egocentric spatial frame of reference in humans. Exp Brain Res 124:281–286

Vingerhoets G, Santens P, Van Laere K, Lahorte P, Dierckx RA, De Reuck J (2001) Regional brain activity during different paradigms of mental rotation in healthy volunteers: a positron emission tomography study. Neuroimage 13:381–391

Vogeley K, Fink GR (2003) Neural correlates of the first-person-perspective. Trends Cogn Sci 7:38–42

Wraga M, Shephard JM, Church JA, Inati S, Kosslyn SM (2005) Imagined rotations of self versus objects: an fMRI study. Neuropsychologia 43:1351–1361

Zacks JM, Michelon P (2005) Transformations of visuospatial images. Behav Cogn Neurosci Rev 4:96–118

Zacks JM, Tversky B (2005) Multiple systems for spatial imagery: transformations of objects and bodies. Spatial Cognit Comput 5:271–306

Zacks J, Rypma B, Gabrieli JD, Tversky B, Glover GH (1999) Imagined transformations of bodies: an fMRI investigation. Neuropsychologia 37:1029–1040

Zink R, Bucher SF, Weiss A, Brandt T, Dieterich M (1998) Effects of galvanic vestibular stimulation on otolithic and semicircular canal eye movements and perceived vertical. Electroencephalogr Clin Neurophysiol 107:200–205