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RESEARCH ARTICLE

Mental transformation abilities in patients with unilateral and bilateral vestibular loss

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Abstract Vestibular information helps to establish a reliable gravitational frame of reference and contributes to the adequate perception of the location of one's own body in space. This information is likely to be required in spatial cognitive tasks. Indeed, previous studies suggest that the processing of vestibular information is involved in mental transformation tasks in healthy participants. In this study, we investigate whether patients with bilateral or unilateral vestibular loss show impaired ability to mentally transform images of bodies and body parts compared to a healthy, age-matched control group. An egocentric and an object-based mental transformation task were used. Moreover, spatial perception was assessed using a computerized version of the subjective visual vertical and the rod and frame test. Participants with bilateral vestibular loss showed impaired performance in mental transformation, especially in egocentric mental transformation, compared to participants with unilateral vestibular lesions and the control group. Performance of participants with unilateral vestibular lesions and the control group are comparable, and no differences were found between right- and left-sided labyrinthectomized patients. A control task showed no differences between the three groups. The findings from this study substantiate that central vestibular processes are involved in imagined spatial body transformations; but interestingly, only participants with bilateral vestibular loss are affected, whereas unilateral vestibular loss does not lead to a decline in spatial imagery.

Keywords Vestibular · Spatial cognition · Mental rotation · Subjective visual vertical · Rod and frame test

Introduction

Patients with vestibular loss show impaired performance in the control of posture and gait (e.g., Mamoto et al. 2002; Peterka 2002), oculomotor responses (e.g., Halmagyi et al. 1990), and perceptual tasks. The last point is illustrated by patients with unilateral vestibular loss that adjust the subjective visual vertical tilted toward their lesioned side (e.g., Bohmer and Mast 1999a). Moreover, in vestibular patients the perception of verticality strongly depends on visual cues (Guerraz et al. 2001; Lopez et al. 2006).

Much less is known about the effects vestibular loss can have on performance in cognitive tasks. Relatively few previous studies have investigated vestibular–cognitive interactions in patients with vestibular disorders, yet relevant literature is growing (for a review see Smith et al. 2005; Hanes and McCollum 2006; Borel et al. 2008). In this context, it is noteworthy that vestibular sensory information is processed in the central vestibular system including the vestibular nuclei, parts of the cerebellum and the thalamus (Chen-Huang and McCrea 1999; McCrea and Luan 2003; Dieterich and Brandt 2008), along with various cortical regions including the insula and parts of the

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temporal, parietal, and frontal lobes (Brandt and Dieterich 1999; de Waele et al. 2001; Emri et al. 2003), and the hippocampus (Vitte et al. 1996). Clinical studies revealed impaired performance of vestibular patients in spatial tasks such as spatial perception (Bohmer and Mast 1999a, b; Clement et al. 2009), spatial memory, and navigation (Schautzer et al. 2003; Brandt et al. 2005; Peruch et al. 2005). Moreover, research in healthy participants suggests that the processing of vestibular information is also involved in mental spatial transformations (Grabherr et al. 2007; Lenggenhager et al. 2008), but these cognitive tasks have not yet been tested in patients with vestibular loss. Thus, this study aims to investigate whether peripheral vestibular loss can cause deficits in mental transformation abilities. At least two types of mental transformations can be distinguished: object-based mental transformations (OMTs) and egocentric mental transformations (EMTs). OMTs concern a representation of an external object, which is mentally transformed (i.e., rotated or translated) in space. Behaviorally, performance typically decreases with increasing angle of mental rotation (Shepard and Metzler 1971). During an EMT, a mental representation of one's own body or body part is imagined to be moving relative to the environment (Parsons 1987a, b). Results from neuroimaging, behavioral, and clinical studies suggest that OMTs and EMTs rely in part on distinct brain areas (Ratcliff 1979; Zacks et al. 2002, 2003; Parsons 2003; Tomasino and Rumiati 2004; Blanke et al. 2005). A recent study investigated the influence of vestibular information on OMTs and EMTs using galvanic vestibular stimulation. Performance was impaired during right anodal stimulation but interestingly only when participants were engaged in an egocentric mental transformation strategy (Lenggenhager et al. 2008). Moreover, an OMT task using cubic stimuli has been tested in microgravity, but no detrimental or upgrading performance was found when compared to results from the ground (Leone et al. 1995). In contrast, another study (Grabherr et al. 2007) performed under microgravity conditions investigated EMTs using body and hand stimuli. It was hypothesized that an imagined body or body-part transformation is likely to use some reference information regarding the actual body position. Therefore, a missing update about the direction of gravity could interfere with EMTs. Response times and error rates were in fact increased during microgravity compared to normal gravity, thus suggesting that performance in EMTs is impaired when the gravitointertial force is no longer perceived by otolithic sensory information. Moreover, body-part stimuli were affected more strongly in microgravity than the body stimuli (Grabherr et al. 2007).

Whole-body movements stimulate the vestibular system, including its various central regions. We hypothesize that EMTs engage—at least partly—the same body representation, which is associated with the processing of real body movements. Previous research has shown that imagined whole-body movements can induce eye movements similar to those when the vestibular input is perceptually present (Rodionov et al. 2004). Taken together, we expect EMTs to be more affected by vestibular loss than OMTs.

The aim of this study is to provide further evidence for the involvement of central vestibular processes in spatial cognition. Knowing more about the cognitive consequences that vestibular loss can have will provide a more profound understanding of such patients and may help to establish rehabilitation procedures along those lines.

Methods

Participants

Eight patients with bilateral vestibular loss (bilateral vestibular patients, BVPs) and 15 patients with unilateral vestibular loss (unilateral vestibular patients, UVPs) were recruited for this study. Bilateral vestibular conditions were caused by congenital disorders (3 patients), ototoxicity (2 patients), Menière's disease (2 patients) and meningitis (1 patient). All BVPs showed absence of response to caloric stimulation measured with videonystagmography. All UVPs had undergone a labyrinthectomy: 10 UVPs on the right side and 5 UVPs on the left side. In 10 out of 15 UVPs, this surgery was performed because of severe forms of Menière's disease. Other reasons were intralabyrinthic neurinoma, delayed endolymphatic hydrops, fistula, and in two cases chronic otitis media. On average, patients were tested 8 (±5) years post-surgery. Medical exams show positive results on the Halmagyi test for the three canals on the side of the operated ear in all unilateral patients. No patients in the acute state were included. Moreover, 14 age-matched healthy control participants (CPs) took part in this study. Age-matched CPs were recruited to control for a potential age-related decline in performance because previous studies reported performance decreases in older participants when compared to younger participants (Inagaki et al. 2002; Saimpont et al. 2009). The CPs were screened with a vestibular diagnostic questionnaire to verify the absence of a vestibular medical condition. Table 1 provides group information about age, gender, and handedness. Participants were paid for their participation, and informed consent was obtained before commencing the tests. The study has been performed in accordance with the Declaration of Helsinki and was approved by the responsible ethics committee of the University Hospital of Geneva.

Table 1 Group characteristics

	BVPs	UVPs	CPs
Participants (*n*)	8	15	14
Age (mean ± standard deviation)	54 ± 16	53 ± 13	55 ± 5
Gender (women, men)	8 m	9 w, 6 m	8 w, 6 m
Handedness (right-handed, left-handed)	8 r	12 r, 3 l	12 r, 2 l

This table indicates number of participants, age, gender, and handedness per group

Tasks and stimuli

Mental transformation tasks and control task

One task was designed to elicit an egocentric mental transformation (EMT); the other task was designed to elicit an object-based mental transformation (OMT). Additionally, a control task requiring no mental transformation was administered. The same stimuli were used in all three tasks: line drawings of human bodies with one arm outstretched and line drawings of human hands. Bodies and hands were presented in separate blocks.

In the EMT task, participants were asked to make lateralization judgements (left or right). They had to indicate which arm is outstretched (if the stimulus is a body) or whether a left or a right hand is depicted (if the stimulus is a hand). Previous research suggests that participants use a mental representation of their own body or body part and rotate it mentally until it is aligned with the depicted stimuli (Parsons 1987a, b). The body stimuli were presented in 16 (4 × 2 × 2) different variations—in four different orientations in the picture plane: 0° (upright), 90° (clockwise), 180° (upside down), and 270° (90° counterclockwise), left or right arm outstretched, and in front (body figure facing the participant) or in back view (back of the body facing the participant). Moreover, two different body postures (outstretched arm extended straight away from the body's midline or the arm crossed over the chest) were used to render the task more difficult and to discourage participants from rote learning, which could have prevented them from relying on an EMT strategy. There was an equal amount of hand stimuli: four different orientations in the picture plane (0°, 90°, 180°, 270°), left or right hand, and front (palm facing the participant) or back view (back of the hand facing the participant). Also, two different hand postures were used. Examples of the stimuli are shown in Fig. 1.

In the OMT task, the stimuli appeared in pairs (either simultaneously two body or two hand stimuli). One stimulus appeared in the upright orientation (0°), while the second stimulus was presented in the same orientation or differed by a 90°, 180°, or 270° rotation in the picture plane. The participants had to indicate whether the two stimuli are identical or mirror reversed. Research on mental transformation suggests that participants mentally rotate one of the two stimuli in order to match it with the second stimulus (Shepard and Metzler 1971; Zacks et al. 2002).

As in the EMT task, only one stimulus was presented in the control task (Blanke et al. 2005). The stimuli were shown either upright (0°) or upside down (180°). The participants made lateralization judgements about whether the outstretched arm (when the stimulus is a body) or the thumb (when the stimulus is a hand) is on the left or on the right side of the computer screen. No mental transformation is required to solve this task. The control task aims to separate processes associated with visual perception, decision making (lateralization judgment), and the motor response from mental transformation processes.

Subjective visual vertical and rod and frame test

In addition to the spatial transformation tasks, spatial perception was assessed using the subjective visual vertical

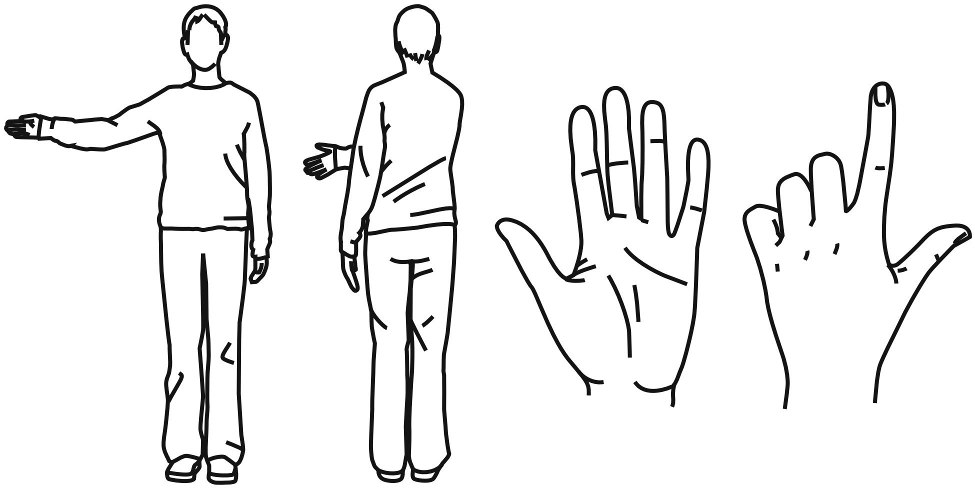


Fig. 1 Examples of stimuli. Examples of the body and hand stimuli used in the mental transformation and control tasks

(SVV) and the rod and frame test (RFT). The test was performed in order to investigate whether a bias in visual orientation perception can also be found in mental transformation tasks. For example, a patient with a right-sided unilateral vestibular lesion is expected to tilt the rod toward the right side (the lesioned side), and his or her performance in mental rotation for stimuli tilted to the right (90° clockwise) compared to stimuli tilted to the left (90° counterclockwise) could be subject to a similar directional bias. The computerized test consisted of four different conditions: the rod (subtending a visual angle of 3.1°) presented without a frame on the screen for the adjustment of the SVV, the rod presented within an upright frame (subtending a visual angle of 6.1°), and the frame either tilted 20° to left (counterclockwise) or 20° to the right (clockwise) with respect to the gravitational vertical. Nine trials were completed per condition. The participants could adjust the orientation of the rod in clockwise and counterclockwise direction by operating two keys on the keyboard. After each trial, a visual mask appeared for 800 ms. The SVV and the RFT test were carried out in the dark and a black cardboard with a circular aperture was mounted over the computer screen to cover its edges. The rod was slightly low-pass filtered to prevent aliasing effects.

Questionnaires

A French version (author's translation) of the Vividness of Movement Imagery Questionnaire (VMIQ) was used (Isaac et al. 1986). The VMIQ measures one's ability to imagine different actions like how vividly, on a scale from one to five, can you imagine yourself walking, climbing a wall, or riding a bike. Only the second part of the questionnaire was administered in which participants were instructed to imagine performing the movement themselves.

Participants were also asked to report about the strategies they used to solve the four mental transformation tasks (EMT bodies, EMT hands, OMT bodies, OMT hands). For each task, they had to report on a scale from one to five (1 = never, 5 = always) whether they used an egocentric mental transformation strategy (I used my own body as reference/I imagined myself rotating), an object-based mental transformation strategy (I rotated one of the stimuli) or whether they used a different strategy.

Experimental procedures

Participants were tested in a single test session that lasted about 1.5 h. Half of the participants started with the EMT task (one block of body stimuli and one block of hand stimuli, counterbalanced in order across participants), while the other half started with the OMT tasks. Practice trials including feedback (correct or incorrect) preceded each task. Participants were instructed to respond as fast and as accurately as possible. They responded with their left index finger when the answer was "left" (or "same" for OMT), and they responded with their right index finger when the answer was "right" (or "mirror-reversed" for the OMT). The stimuli were presented until the participants responded by pressing a button. This response triggered a fixation cross (1,000 ms) before presenting the next stimulus. All tasks were computerized (Flash animation) and response times and errors were recorded. In each block, the same stimulus was presented four times, and thus 128 stimuli per block were presented (4 orientations × 2 possible answers × 2 views × 2 postures × 4 repetitions). The SVV and the RFT were conducted in-between the OMT and EMT tasks. The control task was administered last and consisted of 64 stimuli. Throughout the test session, the participants were comfortably seated on a chair.

Data analysis

Mean response times (RTs) and error rates (ERs) were computed for each task (EMT, OMT, control), type of stimuli (bodies, hands), and orientation (0°, 90°, 180°, 270°). For the analysis of RTs, only correct answers were taken into account. RTs longer than 8 s were excluded, and RTs 2.5 times the standard deviation above or under the mean were discarded as outliers and excluded from further analysis. For each of the four conditions tested in the SVV and the RFT, mean deviation from the gravitational vertical was determined by averaging the last eight trials (first trial not counted). RTs, ERs, and mean deviations were analyzed with analyses of variance (ANOVAs) using SPSS 17.0. Huynh–Feldt correction was used when sphericity was not assumed. Significant effects were further analyzed using post hoc tests (Bonferroni).

Results

Subjective visual vertical and rod and frame test

The SVV was analyzed using a univariate ANOVA with the between-subjects factor *group* (right-sided UVPs, left-sided UVPs, BVPs, CPs), revealing a significant difference between *groups* [F (3,33) = 5.70, $P < .01$, $\eta_p^2 = .34$]. Post hoc tests show a significant difference between UVPs with right-sided lesions compared to UVPs with left-sided lesions ($P < .01$). UVPs adjusted the SVV so that the rod was tilted toward the lesioned side. That is, right-sided UVPs tilted the rod toward their right ear, while the left-sided UVPs set the rod toward their left ear. No significant differences were found between the BVPs and the CPs. Both groups were able to adjust the rod with little deviation

Table 2 SVV and RFT

	SVV (no frame)	Frame upright	Frame tilted left	Frame tilted right
UVPs right	+1.5 ± 0.6	+0.6 ± 0.3	−0.1 ± 1.2	+4.1 ± 0.9
UVPs left	−1.0 ± 0.2	−0.3 ± 0.2	−4.3 ± 3.7	−5.5 ± 4.7
BVPs	0.0 ± 0.3	0.0 ± 0.1	−3.4 ± 2.2	+3.5 ± 2.2
CPs	−0.1 ± 0.3	−0.2 ± 0.1	−0.9 ± 0.5	+1.4 ± 0.6

Mean deviations (in degrees) from the true vertical and standard errors of the mean (±) are shown for each group and each condition. Deviations are indicated for clockwise (+) or counterclockwise (−) direction

from the gravitational vertical. The results of the SVV are summarized in Table 2.

The RFT was analyzed using a repeated measures ANOVA with the between-subjects factor *group* (right-sided UVPs, left-sided UVPs, BVPs, CPs) and the within-subjects factor *condition* (frame tilted to the left, frame tilted to the right). Absolute values were used and results were bias corrected, meaning that frame tilted to the left and frame tilted to the right conditions were each corrected for a possible bias in the frame upright condition. The analysis of the RFT revealed no significant main effects, nor a significant interaction. The results of the RFT are summarized in Table 2. Two groups, the UVPs left and the BVPs, show relatively high standard errors. Three participants (one UVP left and two BVPs) had deviations greater than 10° from the upright and thus mainly contributed to this effect (please refer to Table 4 in the electronic supplementary material for individual data in the SVV and the RFT).

Mental transformation and control tasks: error rates

In contrast to the SVV, statistical analysis using repeated measures ANOVAs revealed no significant differences between UVPs with vestibular lesions on the right side and UVPs with vestibular lesions on the left side in any of the three tasks. Thus, for further analysis, the data from all UVPs were pooled. A repeated measures ANOVA with the between-subjects factor *group* (UVPs, BVPs, CPs) and the within-subjects factors *stimulus* (bodies, hands) and *orientation* was performed for each task separately. The factor *orientation* was computed with four levels (0°, 90°, 180°, 270°) in the EMT and the OMT task; the control task was computed with two levels (0°, 180°).

The analysis of the EMT task revealed as hypothesized a significant effect of *group* [F (2,34) = 3.29, $P < .05$, $\eta_p^2 = .16$]. Post hoc tests show that BVPs had significantly higher ERs when compared to the CPs ($P < .05$). There was no significant difference between BVPs and UVPs ($P = .485$) and between UVPs and CPs ($P = .552$). As expected in a mental transformation task, the effect of *orientation* was significant [F (3,55) = 29.31, $P < .001$, $\eta_p^2 = .46$]. Post hoc tests show that error rates (ERs) were higher when the stimuli were inverted (180°, mean ER 21.5% ± 2.5 SD) compared to when they were upright (0°, mean ER 10.2% ± 1.7 SD, $P < .001$). There was no difference between stimuli tilted 90° (mean ER 10.6% ± 1.7 SD) and 270° (mean ER 9.2% ± 1.6 SD). These intermediate orientations did not differ from upright stimuli but were significantly different from inverted stimuli ($P < .001$). Moreover, *orientation* interacted with the factor *stimulus* [F (3,53) = 5.03, $P < .05$, $\eta_p^2 = .13$]. The increase in ERs for inverted stimuli was more pronounced when the stimulus depicted a body compared to a hand.

The analysis of the OMT task revealed no significant effect of *group* [F (2,34) = 1.57, $P = .223$, $\eta_p^2 = .09$]. Therefore, the OMT did not discriminate between patients and CPs. The factor *orientation* was significant [F (3,53) = 31.15, $P < .001$, $\eta_p^2 = .478$]. Post hoc tests show that ERs increase with increasing angle from the upright. Participants made significantly fewer errors to upright stimuli (0°, mean ER 4.5% ± 1.2 SD) compared to 90° (mean ER 7.6% ± 1.2 SD, $P < .01$) and 270° (mean ER 8.3 ± 1.3 SD, $P < .001$) and performed better at these intermediate orientations than for inverted stimuli (180°, mean ER 19.1 ± 2.7 SD, $P < .001$). There was no difference between stimuli tilted 90° and 270°. No other effect was significant. The results are illustrated in Fig. 2.

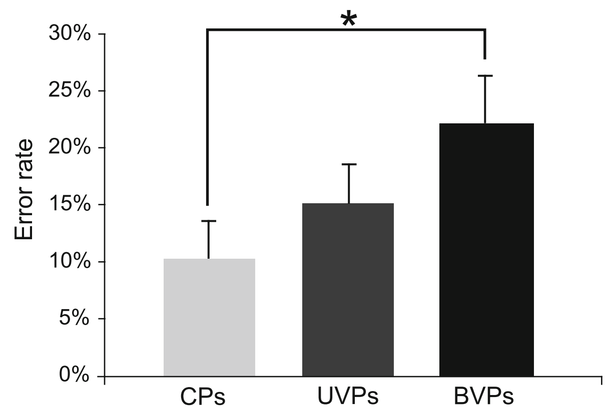
The analysis of the control task revealed no significant effects. The participants' performance did not depend on the *orientation* of the stimuli, and thus it is unlikely that they applied a mental transformation strategy in the control task. Also, no differences between *groups* or *stimuli* were found. Mean ERs of the control task are shown in Table 3.

Mental transformation and control tasks: response times

As for ERs, there were no differences between UVPs with vestibular loss on the right side and UVPs with vestibular loss on the left side in any of the three tasks. Thus, the data from all UVPs were pooled for further analysis. As for ERs, repeated measures ANOVAs with the between-subjects factor *group* and the within-subjects factors *stimulus* and *orientation* were computed for each task separately.

The analysis of the EMT task revealed as hypothesized a significant effect of *group* [F (2,34) = 5.43, $P < .01$, $\eta_p^2 = .24$]. Post hoc tests show impaired performance in BVPs when compared to UVPs ($P < .01$) and CPs ($P < .05$). No difference was found between UVPs and CPs. We also observed a significant effect of *orientation* [F (2,74) = 117.60, $P < .001$, $\eta_p^2 = .78$]. Post hoc tests indicate that response times (RTs) increase with increasing angle from the upright. Participants responded significantly

(A) Egocentric mental transformation task



(B) Object based mental transformation task

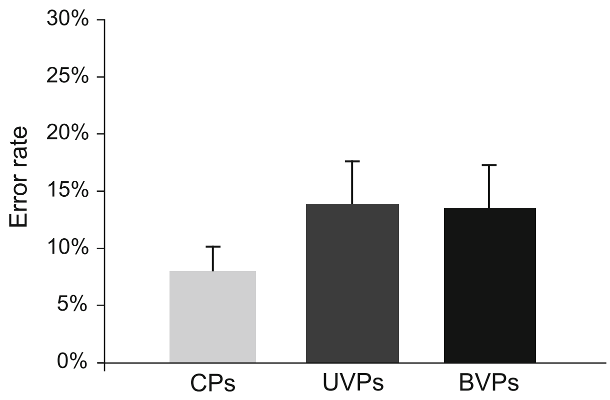


Fig. 2 Error rates in the mental transformation tasks. The histogram indicates mean error rates in percent and the standard error of the mean averaged over both types of stimuli and all four orientations. Significant group differences are indicated (*). **a** In the EMT task, participants with bilateral vestibular loss had significantly higher error rates compared to the control group but no difference between the control group and the participants with unilateral vestibular lesions were observed. Also, no difference between the two patient groups was found. **b** In the OMT task, no group differences were observed

Table 3 Error rates and response times in the control task

	ERs (%)	SEM	RTs (ms)	SEM
BVPs	.7	.5	880	125
UVPs	1.0	.6	709	76
CPs	.2	.1	641	37

The table indicates mean error rates in percent and mean response times in milliseconds as well as the corresponding standard error of the mean (SEM) averaged over both types of stimuli and both orientations (0° and 180°)

faster to upright stimuli (0°, mean RT 1,857 ms ± 126 SD) compared to 90° (mean RT 2,132 ms ± 151 SD, $P < .001$) and 270° (mean RT 2,117 ms ± 150 SD, $P < .001$) and were faster at these intermediate orientations than for inverted stimuli (180°, mean RT 2,957 ms ± 177 SD, $P < .001$). There is no difference between stimuli tilted 90° and 270°. There was also a significant effect of *stimulus*. RTs were higher for hand stimuli than for body stimuli [F (1,34) = 10.07, $P < .01$, $\eta_p^2 = .23$]. No significant interaction effects were observed.

The analysis of the OMT task also revealed a significant effect of *group* [F (2,34) = 3.87, $P < .05$, $\eta_p^2 = .19$]. Post hoc tests show that BVPs have significantly increased RTs compared to CPs ($P < .05$), and a trend toward significance between BVPs and UVPs was observed ($P = .055$). UVPs and CPs did not differ in their performance. A significant main effect of *orientation* was obtained [F (2,71) = 165.08, $P < .001$, $\eta_p^2 = .83$]. Post hoc tests show that RTs increase with increasing angle from the upright. Participants responded significantly faster to upright stimuli (0°, mean RT 2,071 ms ± 159 SD) compared to 90° (mean RT 2,636 ms ± 158 SD, $P < .001$) and 270° (mean RT 2,573 ms ± 162 SD, $P < .001$) and were faster at these intermediate orientations than for inverted stimuli (180°, mean RT 3,641 ms ± 193 SD, $P < .001$). There is no difference between stimuli tilted 90° and 270°. No other effect revealed to be significant. Results are illustrated in Fig. 3.

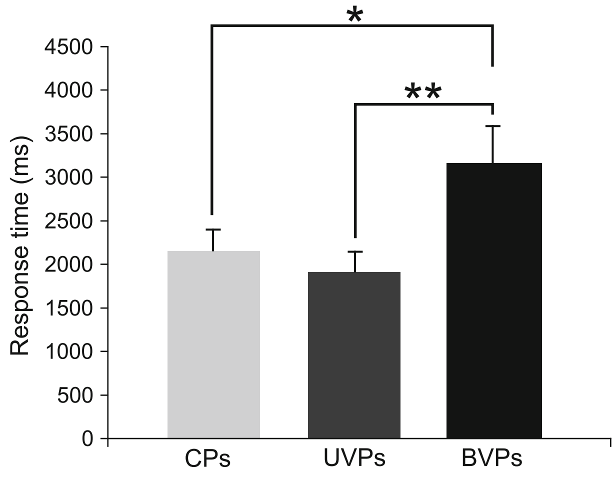
The analysis of the control task did not show any significant effects. No effect of *orientation* was observed, suggesting that a mental transformation strategy was not required to solve the task. Moreover, neither *group* differences between BVPs, UVPs, and CPs nor between the different types of *stimuli* were found. Mean RTs of the control task are indicated in Table 3.

Questionnaires

The scores from the VMIQ (self-scale) revealed a trend toward significance between *groups* [F (3,33) = 2.78, $P = .056$, $\eta_p^2 = .20$], suggesting that healthy participants tend to obtain higher scores when compared to the vestibular patients. The mean scores were as follows: for bilateral patients, 72 (±6 SEM); for unilateral patients with loss on the right side, 66 (±12 SEM); for unilateral patients with loss on the left side, 74 (±19 SEM); and for the control participants, 99 (±7 SEM). Vestibular patients tended to give a low score to those movements that are difficult for them to perform (e.g., "balancing on one leg" or "jumping off a high wall"). Interestingly, however, the two items about falls ("falling forwards" and "slipping over backwards") obtained relatively high scores among vestibular patients. A frequent comment was that falls are easy to imagine because they can happen in everyday life. Please see Table 5 in the electronic supplementary material for more details on the results per item in the VMIQ.

The responses obtained in the strategy questionnaire showed that in the EMT tasks, 28 participants out of the 37 participants reported to use an egocentric strategy, 2

(A) Egocentric mental transformation task



(B) Object-based mental transformation task

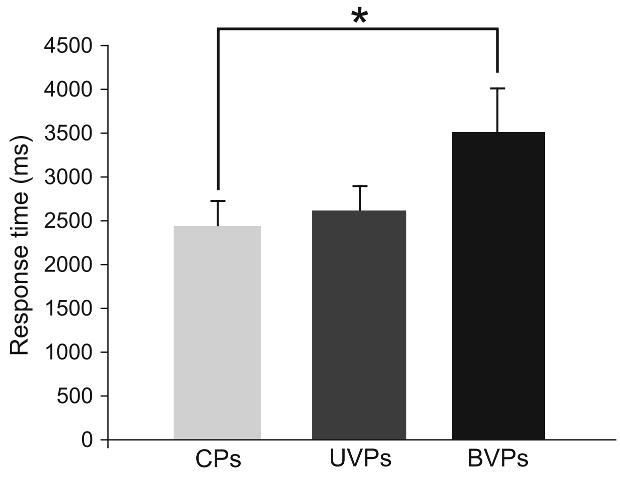


Fig. 3 Response times in the mental transformation tasks. The histogram indicates mean response times in milliseconds and the standard error of the mean averaged over both types of stimuli and all four orientations. Significant group differences are indicated (*). **a** In the EMT task, participants with bilateral vestibular loss needed significantly more time to respond compared to participants with unilateral vestibular lesions as well as the control group. **b** In the OMT task, participants with bilateral vestibular loss needed significantly longer time to respond compared to the control group. Performance of participants with unilateral vestibular lesions and the control group were comparable in both tasks

reported to use an object-based strategy, 6 reported to use another strategy or a mix of strategies and one person did not know which strategy she applied. In the OMT tasks, 22 participants reported to use an object-based strategy, 5 reported to use an egocentric strategy, 3 reported to use another strategy or a mix of strategies and seven participants did not know which strategy they applied to solve the task. Thus, almost one out five participants expressed difficulties when having to report explicitly the strategy they used to solve the task. However, the use of different types of strategies did not lead to differences in performance and was not group specific.

Discussion

Results from the SVV showed that UVPs adjust the rod toward their lesioned side in order to perceive it vertically. This confirms findings from earlier studies and shows that the SVV can still be an indicator of the lesioned side in otherwise well-compensated patients (Bohmer and Mast 1999a, b; Vibert and Hausler 2000; Lopez et al. 2006; Lopez et al. 2007). BVPs and CPs adjusted the SVV with little deviation from the upright. The RFT showed no group differences, although mean deviations were slightly higher in vestibular patients compared to healthy controls. It has to be noted that the mean deviations we report in this study were rather small, which can be explained by the use of a computerized rod and frame test when compared to a mechanical rod and frame test (Isableu et al. 2008).

Results from the mental transformation tasks demonstrate the consequences vestibular loss can have on spatial imagery. ERs and RTs increased with increasing angle of rotation in the three groups. This suggests that all groups of participants indeed used a mental transformation strategy to solve the tasks. Moreover, ERs and RTs are relatively high in all groups compared to the results from other studies that used similar mental rotation tasks (e.g., Zacks et al. 2000; Lenggenhager et al. 2008). These differences can be attributed to the more advanced age of our participants. Previous studies have reported an age-related decline in performance (Inagaki et al. 2002; Saimpont et al. 2009). Interestingly, the performance among the groups varied. Contrary to the observed difference in the SVV task, performance of the UVPs was comparable to the performance of CPs in the other tasks (EMT, OMT, control). Their performance differed neither in terms of response times nor in terms of error rates. It has to be noted that none of the patients was in the acute stage, and it would be interesting to compare performance between acute and chronic UVPs. BVPs, however, responded significantly more slowly in the EMT when compared to the CPs as well as the UVPs. Their response times were also significantly slower in the OMT task when compared to the CPs. Moreover, BVPs made more errors in the EMT task compared to the CPs, but there were no differences in error rate between groups in the OMT task. Thus, the BVPs' impairment seems to be more pronounced in the EMT task. Their impairment was evident in the mental transformation of whole-body figures and body-part stimuli. A control task requiring no mental transformation revealed no difference between BVPs, UVPs and age-matched healthy CPs.

Results from the VMIQ show that UVPs and BVPs have the tendency to rate their ability to imagine different movements lower compared to healthy CPs. This seems especially true for movements that can be difficult for them to perform. Please note that although UVPs seem to obtain lower scores in the VMIQ, they do not show impaired performance in the mental transformation tasks.

The impairment due to bilateral vestibular loss in the OMT task was unexpected insofar as previous studies have shown in healthy participants that performance in this task remains unchanged when tested in the absence of gravity-related vestibular input in microgravity (Leone et al. 1995) or a supine body position (Mast et al. 2003). These findings suggest that the OMT task can be solved by means of purely visuospatial processes, and thus changes in central vestibular processing due to vestibular loss do not interfere with task performance. In contrast, there is empirical evidence for the involvement of vestibular information in the EMT task (Grabherr et al. 2007; Grabherr and Mast 2010). Clearly, however, comparing performance of BVPs with healthy participants in microgravity (no otolithic input besides the resting discharge level) or under body tilt (complete vestibular input but the direction of the gravitational force is not aligned with the body axis) has its limits. How can we explain the finding that RTs were increased in BVPs in the EMT and the OMT task? We used identical stimuli in the mental transformation tasks (apart from presenting pairs of stimuli in the OMT task and one stimulus only in the EMT task) in order to rule out any influence of factors unrelated to mental transformation such as object recognition or stimulus complexity. This is important to control for since—at least in animal studies—deficits in object recognition were found after peripheral vestibular lesions (Zheng et al. 2004). However, the fact that whole-body and body-part stimuli were used for the object-based mental transformation strategy could have given the participants the possibility to project a mental representation of their own body onto the depicted stimuli. Amorim et al. (2006) reconfigured the classical Shepard and Metzler cubes (abstract 3D objects) with human features. Making the stimuli more human like improved the performance. The authors argued that participants were able to map their own bodily coordinates onto one of the stimuli, which led to a more holistic instead of a "piecemeal like" transformation process. Therefore, we cannot completely rule out the possibility that our participants also used such a process in order to improve their performance. However, this would suggest that there is no clear-cut distinction between the OMT and EMT task we applied and that the OMT task is no longer a purely visual–spatial task. Studies that did not reveal influences of vestibular cues in OMT tasks used objects like the Shepard and Metzler cubes, letters and plants as stimuli (Leone et al. 1995; Mast et al. 2003; Lenggenhager et al. 2008). Despite the disadvantage of using different types of stimuli, future studies may want to include such object stimuli. Last but not least, there is also the possibility that BVPs showed increased RTs in both mental transformation tasks due to a general decrease in attention as other studies have found decreased attention in vestibular patients (for a discussion see Smith et al. 2005; Hanes and McCollum 2006). However, if more general effects were the cause, one would also expect—at least in part—impairment in unilateral patients. But this was not the case; UVPs and CPs showed similar performances. In addition to this, there were no group differences in the control task. It is therefore unlikely that the decrease in performance observed in BVPs can be explained by a general lack of attention.

BVPs showed impaired performance to mentally transform own-body and body-part representations. The role of vestibular information in constituting a body representation has been shown previously. For example, Bisiach et al. (1991) described a patient with somatoparaphrenia, whose abnormal ownership for the left arm was normalized by means of caloric vestibular stimulation. This type of vestibular stimulation also led to body schema changes in amputees (Andre et al. 2001) and paraplegic participants (Le Chapelain et al. 2001). More research needs to be done to better explore how cortical vestibular processing is nested and intertwined with the brain areas associated with EMTs. In BVPs, the absence of vestibular input is complete and chronic. Interestingly, decreased spatial memory and navigation abilities were found in bilateral vestibular patients (Brandt et al. 2005) but not in unilateral vestibular patients (Hufner et al. 2007). Along with these behavioral findings, neuroanatomical findings revealed hippocampal atrophy in bilateral vestibular patients (Brandt et al. 2005) but not in unilateral vestibular patients (Hufner et al. 2007). However, the effect complete vestibular loss can have on other brain areas is less understood, and the involvement of yet other brain areas is likely for the types of tasks we used. For example, neuroimaging and clinical studies have shown that different areas such as the temporo-parietal junction and the inferior and the superior parietal cortex are involved in EMT tasks (Zacks et al. 1999; Blanke et al. 2005; Creem-Regehr et al. 2007). Interestingly, these areas are also found to receive vestibular input (e.g., Lobel et al. 1999; Bense et al. 2001; de Waele et al. 2001; Dieterich et al. 2003). The results from this study provide further evidence for impaired spatial cognitive abilities in bilateral but not unilateral vestibular patients.

Conclusion

Tasks involving mental transformations of bodies and body parts were more challenging for patients with bilateral vestibular loss when compared to healthy controls.

We conclude that central vestibular processes are involved in imagined spatial body and body-part transformations. Participants with unilateral vestibular loss, however, showed no impairment in mental transformation performance, suggesting that they can fully compensate for a potential decline in cognitive performance. This study adds to the growing body of evidence that persons with vestibular disorders can experience cognitive deficits. In the future, a more profound understanding of the cognitive effects as a consequence of vestibular disorders may help to design more specific rehabilitation procedures.

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