Neuropsychologia 49 (2011) 3136–3144

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Vestibular information is necessary for maintaining metric properties of representational space: Evidence from mental imagery

Patrick Péruch[a,*], Christophe Lopez[b], Christine Redon-Zouiteni[c], Guy Escoffier[c], Alain Zeitoun[d], Mélanie Sanjuan[e], Arnaud Devèze[e], Jacques Magnan[c,e], Liliane Borel[c]

[a] INSERM U751 Epilepsie & Cognition, Université de la Méditerranée, Marseille, France
[b] Department of Psychology, University of Bern, Bern, Switzerland
[c] UMR CNRS 6149 Neurobiologie Intégrative et Adaptative, Université de Provence, Marseille, France
[d] Cabinet de Kinésithérapie, Cannes, France
[e] Service d'Oto-Rhino-Laryngologie et Chirurgie Cervico-Faciale, Hôpital Nord, Marseille, France

ARTICLE INFO

Article history:
Received 11 December 2010
Received in revised form 19 July 2011
Accepted 21 July 2011
Available online 28 July 2011

Keywords:
Spatial ability
Mental imagery
Object-based mental transformations
Menière's disease
Vestibular compensation

ABSTRACT

The vestibular system contributes to a wide range of functions, from postural and oculomotor reflexes to spatial representation and cognition. Vestibular signals are important to maintain an internal, updated representation of the body position and movement in space. However, it is not clear to what extent they are also necessary to mentally simulate movement in situations that do not involve displacements of the body, as in mental imagery. The present study assessed how vestibular loss can affect object-based mental transformations (OMTs), i.e., imagined rotations or translations of objects relative to the environment. Participants performed one task of mental rotation of 3D-objects and two mental scanning tasks dealing with the ability to build and manipulate mental images that have metric properties. Menière's disease patients were tested before unilateral vestibular neurotomy and during the recovery period (1 week and 1 month). They were compared to healthy participants tested at similar time intervals and to bilateral vestibular-defective patients tested after the recovery period. Vestibular loss impaired all mental imagery tasks. Performance varied according to the extent of vestibular loss (bilateral patients were frequently the most impaired) and according to the time elapsed after unilateral vestibular neurotomy (deficits were stronger at the early stage after neurotomy and then gradually compensated). These findings indicate that vestibular signals are necessary to perform OMTs and provide the first demonstration of the critical role of vestibular signals in processing metric properties of mental representations. They suggest that vestibular loss disorganizes brain structures commonly involved in mental imagery, and more generally in mental representation.

1. Introduction

Vestibular signals that provide a sense of body rotation and translation in space are crucial for animal and human spatial navigation (e.g., Berthoz, Israël, Georges-François, Grasso, & Tzuzuku, 1995; Borel, Le Goff, Charade, & Berthoz, 1994; Mittelstaedt, 1999; Potegal, 1982; Seemungal, Rizzo, Gresty, Rothwell, & Bronstein, 2008; Smith, 1997; von Brevern, Faldon, Brookes, & Gresty, 1997; Zheng, Darlington, & Smith, 2006). To estimate body displacements, vestibular signals must be integrated with visual, proprioceptive, and auditory signals in brain structures devoted to spatial coding (Angelaki, Klier, & Snyder, 2009; Gu, DeAngelis, & Angelaki, 2007). Studies in rodents show that when vestibular signals are missing, the activity and structure of the brain regions involved in spatial coding are strongly affected (Stackman, Clark, & Taube, 2002; Stackman & Taube, 1997). Clinical observations corroborate these findings and show that patients with a vestibular loss may have difficulties in detecting and estimating body displacements in the dark. During goal-directed locomotion, these patients usually make errors in trajectory (e.g., Borel et al., 2004; Brandt, 2001; Cohen & Sangi-Haghpeykar, 2011). Spatial disorientation is even stronger during complex tasks such as reversing the trajectory along a triangular path or finding a shortcut (Glasauer, Amorim, Viaud-Delmon, & Berthoz, 2002; Guidetti, Monzani, Trebbi, & Rovatti, 2007; Péruch et al., 1999; Péruch, Borel, Magnan, & Lacour, 2005). All these studies were done on subjects who were exploring an environment, a situation in which vestibular receptors are naturally activated.

To date, animal research has only described how vestibular signals code self-motion during physical movements. It has

* Corresponding author at: INSERM U751 Epilepsie & Cognition, Faculté de Médecine de la Timone, Université de la Méditerranée, 27 Bd Jean Moulin, 13385 Marseille Cedex 05, France. Tel.: +33 491 299 817; fax: +33 491 789 914.
E-mail address: patrick.peruch@univmed.fr (P. Péruch).

0028-3932/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2011.07.026

not demonstrated that vestibular signals are involved in higher-order representations that do not require physical movements. In humans, because of the development of immersive virtual environments, subjects can navigate without physical and active body motion, and thus without vestibular feedback. Unilateral vestibular loss impairs navigation in virtual environments, even though only visual receptors are stimulated (Hüfner et al., 2007; Péruch et al., 1999, 2005). Recently, it was confirmed that bilateral vestibular loss impairs navigation in a virtual variant of the Morris watermaze (Brandt et al., 2005). All these studies underline the importance of vestibular signals in maintaining an internal, updated representation of the body position and movement in space for virtual displacements.

But how are vestibular signals involved in mental imagery, i.e., in the transformation of visuospatial mental images? (e.g., Mast, Bamer, & Newby, 2007). Mental imagery is considered important for action, navigation, and reasoning (Zacks & Michelon, 2005) and is a good means to evaluate spatial ability in humans. Spatial ability is defined as the ability to mentally generate, retain, retrieve, and transform well-structured visual images (Lohman, 1988). Studies that address the contribution of vestibular signals to mental imagery are based on visuospatial transformations of mental images. These transformations involve object-based mental transformations (OMTs), i.e., imagined rotations or translations of objects relative to the reference frame of the environment, and egocentric mental transformations (EMTs), i.e., imagined rotations or translations of one's point-of-view relative to that reference frame (Zacks, Mires, Tversky, & Hazeltine, 2000). Mental rotation of 2-D or 3-D objects and mental scanning are among the most studied OMTs, while mental rotation of one's own body or body part is considered an EMT. Performing mental rotation is attested by a linear increase in response times as a function of the amplitude of rotation (e.g., Shepard & Cooper, 1982; Shepard & Metzler, 1971). With mental scanning, participants mentally translate objects in an environment previously learned (Finke & Pinker, 1982; Kosslyn, Ball, & Reiser, 1978). When a person scans across the mental image of an environment, scanning times are linearly related to the physical distances scanned (Chabanne, Péruch, Denis, & Thinus-Blanc, 2004; Denis & Cocude, 1992; Kosslyn et al., 1978). Mental scanning has widely supported claims about the structural properties of visual images that spatial representations have precise metric properties.

At present, the contribution of vestibular signals to mental imagery is still a matter of debate. Core studies on mental rotation have been conducted with healthy participants tested in microgravity or during artificial vestibular stimulation. Studies performed in microgravity have provided divergent results depending on the nature of the task: EMTs, but not OMTs, are influenced by the absence of gravitational vestibular signals (Grabherr et al., 2007; Grabherr & Mast, 2010; Leone, Lipshits, Gurfinkel, & Berthoz, 1995). Mast, Merfeld, and Kosslyn (2006) reported that mental rotation of letters is impaired by caloric vestibular stimulation, and Lenggenhager, Lopez, and Blanke (2008) showed that galvanic vestibular stimulation affects mental rotation when an EMT strategy is involved. Recently, Grabherr, Cuffel, Guyot, and Mast (2011) showed that mental rotation performance of patients with bilateral vestibular loss declined with an EMT, and to a lesser extent with an OMT, whereas that of patients with compensated unilateral vestibular loss was not altered. We note that these authors tested patients several years after the vestibular lesion, so that it remains unclear whether the absence of mental rotation deficits was due to the fact that the vestibular deficits were compensated, or alternatively, to the fact that unilateral vestibular loss is not sufficient to impair mental transformation. A longitudinal study in patients with unilateral vestibular loss is thus needed to determine whether mental rotations can be impaired during the early stage after unilateral vestibular loss and then progressively improved, as are postural and oculomotor deficits (Borel, Lopez, Péruch, & Lacour, 2008; Halmagyi, Weber, & Curthoys, 2010). We finally note that no study has analyzed how vestibular signals can influence the structural properties of mental images, either during caloric and galvanic vestibular stimulation or after vestibular loss. For this, mental scanning is of particular interest because it gives access to the metric properties of the mental images (Denis & Cocude, 1992; Kosslyn et al., 1978).

The present study was designed to provide a detailed description of the role of vestibular signals in mental imagery by using two main OMT tasks: mental rotation of 3D-objects and mental scanning; the latter task deals with the ability to build reliable mental images (that is, having metric properties). We used two mental scanning tasks to distinguish the effects of vestibular loss on the metric properties of mental images for unfamiliar and familiar environments. If vestibular information is critical for elaborating mental images, their metric properties should be impaired for unfamiliar environments, while they should not be affected for familiar environments. The consequences of vestibular loss on mental imagery were measured in patients with bilateral vestibular loss and in patients tested before and after unilateral vestibular loss. Comparing the performance of these two groups should clarify whether the loss of one labyrinth is sufficient to disrupt mental imagery. Patients with unilateral loss were tested again during vestibular compensation (1 month after vestibular loss) to determine the recovery time-course of mental imagery deficits. Their performance was also compared to that of healthy control subjects. We hypothesized that the ability to perform mental imagery is affected after bilateral loss of vestibular inputs but also during the early stage of the unilateral loss, and that recovery appears gradually over time.

2. Materials and methods

2.1. Participants

Experiments were carried out in 15 unilateral vestibular-defective (UVD) patients suffering from Menière's disease (8 women, 7 men; mean age ± SD: 51.3 ± 11.4 years; mean education level: 13.9 ± 3.2 years; see Table 1). Patients had the classical triadic syndrome of hearing loss, tinnitus, and recurrent vertigo. Unilateral vestibular loss determined by bithermal caloric irrigation with cold (30 °C) and warm (44 °C) water averaged 31 ± 18.7%. Hearing loss averaged 50.1 ± 23.4 dB in the affected ear. The history of the disease averaged 7.3 ± 7 years. Because these patients became resistant to anti-vertigo drugs, they underwent a curative unilateral vestibular neurotomy (UVN). The surgical procedure was a retrosigmoid vestibular neurotomy (Magnan, 2000) performed on the right side for 11 patients and on the left side for 4 patients. UVD patients were compared with 12 healthy participants (6 women, 6 men; mean age: 48.9 ± 11.5 years; mean education level: 15.1 ± 4.2 years) without history of vestibular and oto-neurological disease. The groups were matched for age and education level.

Seven bilateral vestibular-defective (BVD) patients (5 women, 2 men; mean age: 64.7 ± 13.6 years; mean education level: 12.7 ± 2.7 years) were compared with UVD patients. These patients were tested on average 3.7 ± 4.3 years after their vestibular loss (see Table 1). At the beginning of the session, BVD patients completed the Mini Mental State test, on which they all scored more than 28/30, thus revealing no cognitive deficit (Folstein, Folstein, & McHugh, 1975).

All participants were right-handed and had normal or corrected-to-normal vision. Each participant gave informed consent to the study, which was approved by the local Ethics Committee.

2.2. Experimental sessions

UVD patients and controls were tested during three experimental sessions. UVD patients were tested 1 day before UVN (D − 1) when they were free of vertigo, 1 week after UVN (D + 7, early stage), and 1 month after UVN (D + 30, compensated stage). The intervals between the three sessions were the same for the healthy participants. BVD patients were tested during a single session.

2.3. Mental imagery tasks

During each experimental session, participants performed three mental imagery tasks involving OMTs: mental rotation of 3-D objects, mental scanning in a recently learned environment (here referred to as "unfamiliar"), and mental scanning in an environment whose memory was consolidated ("familiar"). The three tasks were carried out in balanced order across sessions. Each task comprised a learning phase,

Table 1
Patients' clinical status. Top: preoperative UVD patients. Bottom: BVD patients.

Patient	Gender	Age (years)	Side	History (years)	Vestibular loss (%)	Hearing loss (dB)	Education (years)	Aetiology
1	F	37	R	7	20	29	17	MD
2	F	64	R	9	22	Cophosis	8	MD
3	M	52	L	18	60	67	15	MD
4	M	27	R	4	24	60	14	MD
5	F	58	R	2	51	62	10	MD
6	F	61	R	7	29	63	12	MD
7	M	59	R	1	17	52	10	MD
8	M	59	L	10	32	41	15	MD
9	F	50	L	5	52	57	14	MD
10	M	64	L	2	47	78	14	MD
11	M	43	R	5	34	37	17	MD
12	F	45	R	6	35	14	18	MD
13	F	56	R	27	–	38	18	MD
14	M	59	R	5	–	93	10	MD
15	F	37	R	1	24	10	16	MD
1	F	63	R+L	3	BVA	–	16	Idiopathic
2	M	36	R+L	3	BVA	–	10	Autoimmune
3	M	77	R+L	1	BVA	–	12	Ototoxic antibiotic
4	M	69	R+L	1	BVA	–	12	Ototoxic antibiotic
5	M	75	R+L	1	BVA	–	12	Idiopathic
6	F	69	R+L	4	BVA	–	17	Bilateral MD
7	M	64	R+L	13	BVA	–	10	Bilateral MD

F, female; M, Male; R, right; L, left; MD, Menière's disease; BVA, bilateral vestibular areflexia.

immediately followed by a testing phase. Participants performed practice trials at the beginning of the session, which lasted for about 30 min. During each session, participants were sitting in front of a 17″ computer screen.

2.3.1. Mental rotation

Pairs of objects were those of the original studies by Shepard and collaborators (Cooper & Shepard, 1973; Shepard & Metzler, 1971). Each pair was composed of two identical objects ("same" pair) or two different objects ("different" pair) (see Fig. 1A). "Same" pairs were allocated to three categories depending on their level of difficulty, defined by the amount of rotation of the second object with respect to the first object (20°, 40°, and 80°). Three blocks of 21 pairs of objects were built. Each block was composed of 14 "same" pairs and of 7 "different" pairs. Pairs of objects were presented randomly in each block, and the presentation of the blocks was counterbalanced across the three experimental sessions. Stimulus presentation and response recording were performed using E-Prime v1.1 (Psychology Software Tools Inc., Pittsburgh, PA, USA). Pairs of objects were presented at the center of the screen as 10×10 cm black and white images (about $7^\circ \times 7^\circ$ of angular size). Each stimulus presentation was preceded by a fixation cross for 1 s (see Fig. 1A). Participants responded by pressing the keyboard "Y" key for a "same" pair and the "N" key for a "different" pair. Immediately after their response, the next pair of objects was presented. The maximum response delay was set at 20 s, during which the pair of objects was presented on the screen. If no response was given during this delay, the next pair was presented.

2.3.2. Mental scanning in an unfamiliar environment: circular garden

A map depicting a circular garden (14 cm in diameter) was constructed, with 5 objects at its periphery (see Fig. 1B). The objects were arranged in such a way that the distances between pairs of adjacent objects were all different. Distances ranged from 5.5 to 16.1 cm (mean garden distance: 11.9 ± 3.7 cm). Participants were shown the map on an A4 sheet of paper while an experimenter named the five objects. Then, they were required to study the map to create a vivid and accurate mental visual image of the garden and the objects. The learning phase was adapted from the procedure initiated by Kosslyn et al. (1978) and ensured that participants could remember the arrangement of objects. The time for this phase was not limited and it never exceeded a few minutes. To avoid learning the environment along the three experimental sessions, participants were shown three different maps of gardens in a counterbalanced order. Each map was composed of a new set of objects, located at different places, but with equivalent distances between pairs. The testing material was composed of 20 pairs of objects, including both combinations of each pair (e.g., "hat-rope" and "rope-hat"). The first object was the starting point of the mental scanning and the second object was the ending point. In addition, five "false" pairs of objects were presented, in which the first and second objects were identical (e.g., "hat-hat"). The presence of "false" pairs prevented participants from mentally scanning before the second object was presented. In total, 25 pairs of objects were presented in a pseudo-randomized order, with the constraints that the same object could not occur twice in two successive pairs and that two "false" pairs could not occur successively. Object presentation and data recording were performed using LabView v7.0 (National Instruments, Austin, TX, USA). Each object was presented at the center of the screen as an 8×8 cm colored image with constant mean luminance. The angular size of an object on the screen was about $6^\circ \times 6^\circ$.

Participants were informed that each trial would first consist in looking at an object presented on the screen. They were instructed to recall the visual image of the garden map and then to mentally focus on the location of the object presented. Second, they would see another object. If this object was different, they would have to scan across their mental image to reach the location of the second object. Participants were instructed to mentally scan between the two objects along a straight-line with constant velocity (for similar experimental procedures see Chabanne et al., 2004; Denis & Cocude, 1992). They indicated when they estimated they had mentally reached the second object by pressing the keyboard spacebar, which stopped a timer triggered by the presentation of the second object. When the second object was the same, participants were required to press the button as fast as possible. Each object was presented for 2 s after a fixation cross was presented for 1 s (see Fig. 1B). The maximum response delay was set at 20 s, during which the screen was blank. The next pair of objects was presented immediately after the response was given, or after a 20 s-delay if no response was given. At the end of each experimental session, participants drew the map of the garden with the objects in order to confirm that their mental image was accurate.

2.3.3. Mental scanning in a familiar environment: map of France

The map of France was printed on an A4 sheet of paper, with the names of six towns at the periphery (see Fig. 1C). The map of France has been used in previous mental imagery studies (e.g., Rode et al., 2010). The towns were chosen in such a way that the distances between pairs of towns were all different. Distances ranged from 3.3 to 20.8 cm (mean France distance: 13.3 ± 4.6 cm). Participants were shown the map and the six towns were named by an experimenter. Then they were required to study the map in order to create a vivid and accurate mental visual image. This learning phase lasted a few minutes. The testing material was composed of 15 pairs of towns and included all possible combinations of pairs in one direction (as revealed by pretests, using both directions for each pair of towns yielded too many trials for the patients). The first town was the starting point of the mental scanning and the second object was the ending point. In addition, three "false" pairs were presented, in which the first and second towns were identical. A total of 18 pairs of towns were presented in a pseudo-randomized order, with the constraints that the same town could not occur twice in two successive pairs and that two "false" pairs could not occur successively. As with the garden, participants were instructed to mentally scan with constant velocity between the two towns along a straight-line. Stimulus presentation and response recording were similar to those described above. At the end of each experimental session, participants located the six towns on a map of France printed on an A4 sheet to check that their mental image was correct.

2.4. Statistical analyses

For the mental rotation task, response times and error rates (including absence of response) were analyzed using a mixed-design analysis of variance (ANOVA) with Group (UVD patients, controls) as between-participant factor, and Session ($n = 3$) and Item ($n = 21$) as within-participant factors. Performance for each session of the UVD patients was compared to that of the single session of the BVD patients, using mixed

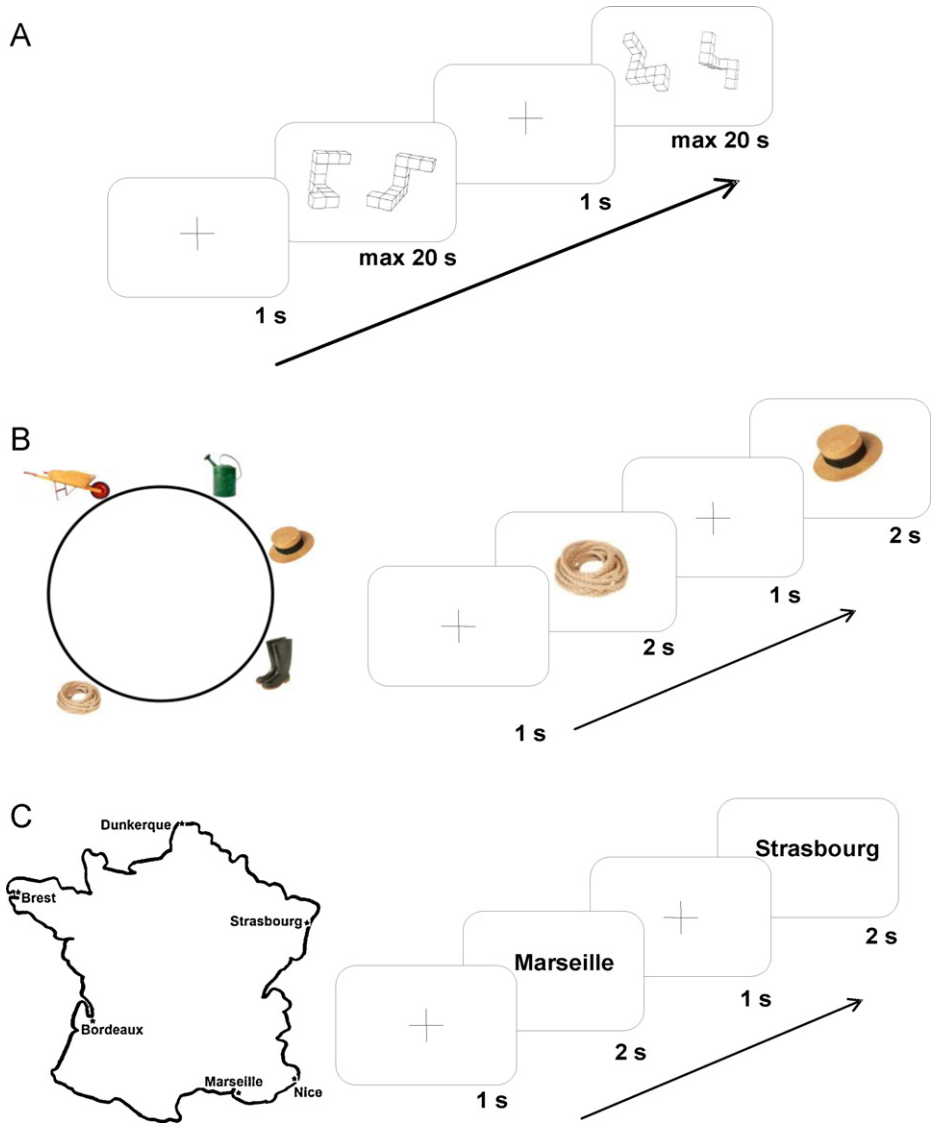

Fig. 1. Experimental procedures for three mental imagery tasks. (A) Mental rotation. Two examples of 3-D objects are shown successively: a "same" pair (the object to the right is rotated 40° clockwise) and a "different" pair. (B) Mental scanning in an unfamiliar environment. Left: example of a circular garden with five objects (wheelbarrow, watering can, boots, hat, rope) shown during the learning phase. The objects have been enlarged for clarity. The minimum distance (watering can to hat) is 5.5 cm, the maximum distance (watering can to rope) is 16.1 cm. Right: example of stimuli shown during the testing phase. (C) Mental scanning in a familiar environment. Left: map of France with six towns (Dunkerque, Strasbourg, Nice, Marseille, Bordeaux, Brest) shown during the learning phase. The minimum distance (Marseille to Nice) is 3.3 cm and the maximum distance (Brest to Nice) is 20.8 cm. Right: example of stimuli shown during the testing phase.

ANOVAs with Group as between-participant factor and Item as within-participant factor.

For the mental scanning tasks, we rejected "false" trials and scanning times exceeding twice the times for similar distances (less than 1% of the trials). To compare mental scanning in both environments, we computed the ratio France distance/Garden distance (=1.12), and the scanning times for the map of France were divided by this ratio. In the first step, scanning times of each environment were submitted to mixed-design ANOVAs with Group (UVD patients, controls) as between-participant factor, and with Session ($n = 3$) and Distance ($n = 20$ in the unfamiliar environment, $n = 15$ in the familiar environment) as within-participant factors. UVD patients' performance in each session was compared to that of the single session of the BVD patients, using mixed ANOVAs with Group as between-participant factor and Distance as within-participant factor. In the second step, mean individual correlation values (Pearson r) between scanning times and distances were analyzed using a mixed ANOVA with Group (UVD patients, controls) as between-participant factor and Session as within-participant factor. Mean individual correlation values for each test session of the UVD patients were compared to those of the BVD patients, using ANOVAs with Group as between-participant factor. Finally, ANOVAs with Environment (Garden, France) as within-participant factor were computed to compare the mental scanning in the two environments.

Effect sizes were calculated using η_p^2. Following Cohen (1988), an η_p^2 above .01 reflects a small effect, above .06 a medium effect, and above .14 a large effect.

3. Results

3.1. Mental rotation

Since average response times for correct trials did not differ from those of all trials, ANOVAs were performed on all trials. Response times averaged 8628 ± 304 ms (±95% confidence intervals for the mean) in UVD patients, 7444 ± 309 ms in controls, and 10,514 ± 969 ms in BVD patients. ANOVA on response times revealed no effect of Group (see Fig. 2A). There was a main effect of Session [$F(2,50) = 8.18$, $p < .008$, $\eta_p^2 = .03$], with response times decreasing along sessions, thus suggesting a training effect. The Item effect was also significant [$F(20,500) = 10.22$, $p < .001$, $\eta_p^2 = .04$], with response times increasing with item difficulty (amount of rotation). There was no significant interaction.

ANOVAs comparing response times in BVD and UVD patients showed no significant difference between groups for each session (see Fig. 2A). For each analysis, there was a significant effect

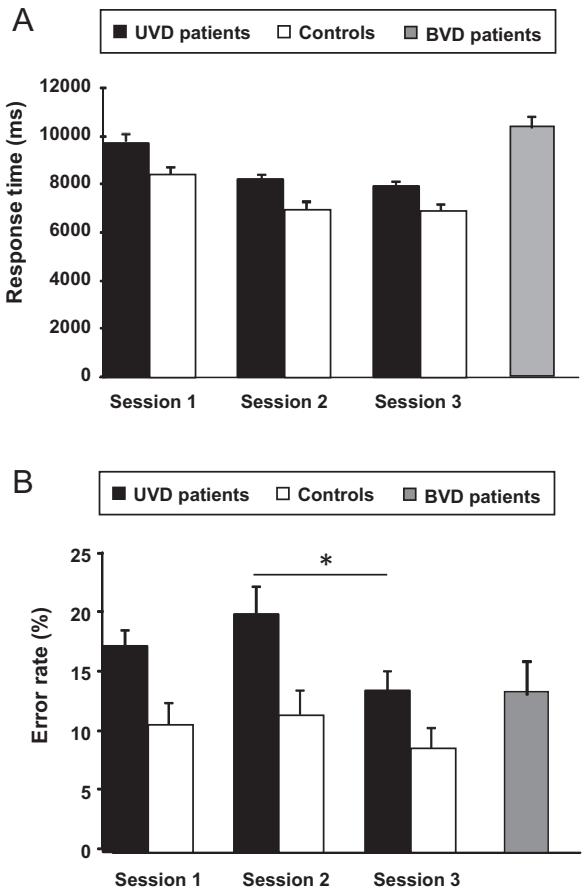

Fig. 2. Mental rotation. The histograms represent the (A) mean response times and (B) mean error scores for each group of participants. In UVD patients, Sessions 1, 2, and 3 correspond respectively to 1 day before UVN (D − 1), 1 week after UVN (D + 7), and 1 month after UVN (D + 30). Vertical bars represent the 95% confidence intervals for the mean. Significant differences between groups and/or experimental conditions are indicated by asterisks. $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .005$.

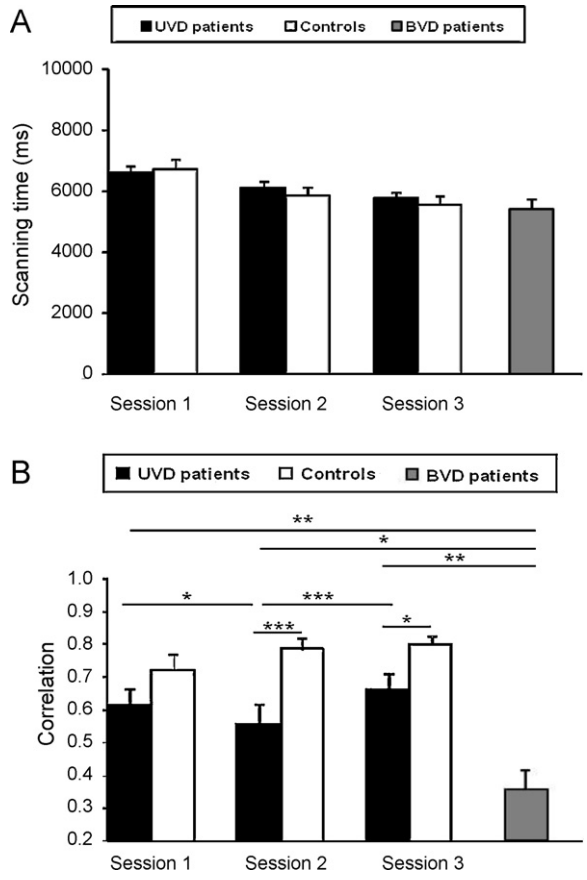

Fig. 3. Mental scanning in an unfamiliar environment (circular garden). The histograms represent the (A) mean scanning times and (B) mean coefficients of correlation for each group of participants. Same conventions as in Fig. 2.

of Item, with response times increasing with item difficulty. The Group × Item interaction was not significant.

Error rates averaged 17.03 ± 2.4% in UVD patients, 10.31 ± 2.17% in controls, and 13.61 ± 5.61% in BVD patients. ANOVA revealed a significant main effect of Group [$F(1,25) = 4.55$, $p < .042$, $\eta_p^2 = .15$], with higher error rates in UVD patients than in controls (see Fig. 2B). There was a main effect of Session [$F(2,50) = 4.14$, $p < .021$, $\eta_p^2 = .14$], but no interaction between Group and Session. In UVD patients, planned comparisons revealed that error rates were higher on Session 2 than on Session 3 [$F(1,25) = 9.22$, $p < .005$, $\eta_p^2 = .26$]. Moreover, a main effect of Item [$F(20,500) = 8.78$, $p < .001$, $\eta_p^2 = .25$], and a non-significant interaction Group × Item, indicated that error rates increased with the amount of rotation in both groups.

ANOVAs comparing BVD and UVD patients for each session revealed similar error rates. Finally, there was a significant effect of Item for each session, with error rates increasing with item difficulty, but no significant Group × Item interaction.

3.2. Mental scanning in an unfamiliar environment

Scanning times averaged 6156 ± 213 ms in UVD patients, 6063 ± 249 ms in controls, and 5443 ± 316 ms in BVD patients. ANOVA revealed no effect of Group or Session (see Fig. 3A). There was a significant effect of Distance [$F(19,475) = 59.26$, $p < .000$, $\eta_p^2 = .70$], with scanning times increasing with distances. The Group × Distance interaction was significant [$F(19,475) = 3.027$, $p < .000$, $\eta_p^2 = .11$]: scanning times measured in UVD patients were overestimated for shorter distances and underestimated for longer distances.

ANOVAs comparing scanning times in BVD and UVD patients showed no significant difference between groups for each session (see Fig. 3A). For each analysis, there was a significant effect of Distance, with scanning times increasing with distances.

As expected, our data revealed a positive correlation between scanning times and distances (df = 18, $p < .05$) for each participant and each session. Correlation values averaged .612 ± .051 in UVD patients, .770 ± .034 in controls, and .356 ± .063 in BVD patients. ANOVA on correlation values showed a significant effect of Group [$F(1,25) = 6.88$, $p < .014$, $\eta_p^2 = .17$], with lower correlation values in UVD patients than in controls (see Fig. 3B). ANOVA also revealed a main effect of Session [$F(2,50) = 4.52$, $p < .015$, $\eta_p^2 = .15$]. The Group × Session interaction was significant [$F(2,50) = 3.61$, $p < .034$, $\eta_p^2 = .12$], indicating that mental scanning performance varied differently with sessions in UVD patients and in controls. In UVD patients, planned comparisons showed that correlations decreased from Session 1 to Session 2 [$F(1,25) = 4.38$, $p < .046$, $\eta_p^2 = .14$] and increased from Session 2 to Session 3 [$F(1,25) = 10.72$, $p < .003$, $\eta_p^2 = .30$], revealing the impact of vestibular loss over time. In contrast, correlation values increased along sessions in control participants, suggesting a training effect. Moreover, correlation values were similar in both groups at D − 1, while they were lower in patients than in controls at D + 7 [$F(1,25) = 10.41$, $p < .003$, $\eta_p^2 = .29$] and D + 30 [$F(1,25) = 6.23$, $p < .019$, $\eta_p^2 = .19$].

Finally, BVD patients were by far the most impaired population in the mental scanning task since ANOVAs revealed significantly lower correlation values than in UVD patients tested before neurotomy [Session 1: $F(1,20) = 8.82$, $p < .007$, $\eta_p^2 = .31$] as well

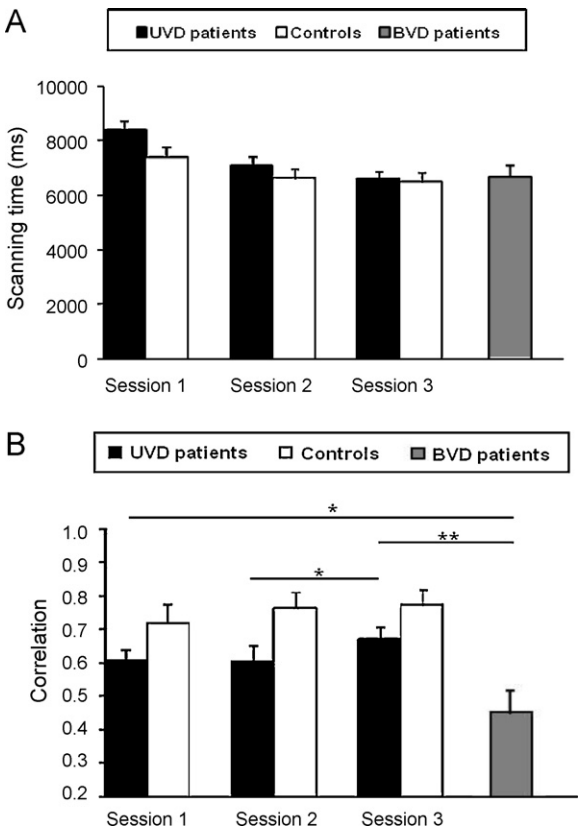

Fig. 4. Mental scanning in a familiar environment (map of France). The histograms represent the (A) mean scanning times and (B) mean coefficients of correlation for each group of participants. Same conventions as in Fig. 2.

as after [Session 2: $F(1,20) = 4.41$, $p < .048$, $\eta_p^2 = .18$; Session 3: $F(1,20) = 15.11$, $p < .009$, $\eta_p^2 = .43$].

3.3. Mental scanning in a familiar environment

Scanning times averaged 7376 ± 307 ms in UVD patients, 6853 ± 342 ms in controls, and 3721 ± 395 ms in BVD patients. ANOVA revealed no effect of Group. There was a significant effect of Session [$F(2,50) = 3.56$, $p < .035$, $\eta_p^2 = .12$], with scanning times decreasing along sessions (see Fig. 4A), and a main effect of Distance [$F(14,350) = 28.29$, $p < .000$, $\eta_p^2 = .53$], with scanning times increasing with distances. No interaction was significant.

ANOVAs comparing scanning times in BVD and UVD patients showed no significant difference between groups for each session (see Fig. 4A). For each analysis, there was a significant effect of Distance, with scanning times increasing with distances.

Scanning times and distances were correlated ($df = 13$, $p < 0.05$) for each participant and each session. Correlations averaged $.626 \pm .040$ in UVD patients, $.753 \pm .049$ in controls, and $.451 \pm .070$ in BVD patients. ANOVA on the correlation values showed a significant effect of Group [$F(1,25) = 4.66$, $p < .041$, $\eta_p^2 = .15$], with lower correlations in UVD patients than in controls (see Fig. 4B). There was a main effect of Session [$F(2,50) = 3.29$, $p < .045$, $\eta_p^2 = .12$], but no interaction between Group and Session. In UVD patients, correlation values increased from Session 2 to Session 3 [planned comparisons, $F(1,25) = 11.84$, $p < .002$, $\eta_p^2 = .32$].

BVD patients' performance did not significantly differ from that of UVD patients tested during the early stage after the neurotomy. By contrast, BVD patients had lower performance than UVD patients at D − 1 [$F(1,20) = 5.39$, $p < .031$, $\eta_p^2 = .21$] and at D + 30 [$F(1,20) = 9.11$, $p < .006$, $\eta_p^2 = .31$].

Finally, ANOVAs on scanning times and on correlation values revealed no effect of the factor 'Environment', indicating similar difficulty in mental scanning for the familiar and unfamiliar environments.

4. Discussion

This study investigated how vestibular signals contribute to mental imagery involving object-based mental transformations (OMTs). Unilateral and bilateral vestibular loss impaired mental rotation of 3D objects, mental scanning in an unfamiliar environment, and mental scanning in an environment whose memory is consolidated. Mental imagery performance varied according to the extent of vestibular loss (bilateral versus unilateral) and to the time elapsed after the total unilateral vestibular loss.

4.1. Mental rotation

The present data show for the first time that the loss of only one labyrinth can impair OMTs, as indicated by higher error rates in UVD patients than in controls. Our study also revealed interesting performance variations in UVD patients: error rates were maximal at the early stage after the neurotomy (1 week) and decreased during the first postoperative month. A previous study showed that performance in mental rotation involving OMT tasks was similar for healthy subjects and for patients tested several years after UVN (Grabherr, Cuffel, Guyot, & Mast, 2011). In the literature, there is a global consensus about the contribution of vestibular signals to mental imagery (Grabherr et al., 2007; Lenggenhager et al., 2008; Mast et al., 2006), despite somewhat divergent results (see Grabherr & Mast, 2010; Leone et al., 1995).

In addition, similar performance was observed in UVD and BVD patients, suggesting that the extent of vestibular loss is not decisive for mental rotation. This may be due to the large variability of response times and error rates in BVD patients. An alternative explanation may be the nature of the task, since previous studies suggested the contribution of vestibular signals differs according to the type of mental imagery. The absence of gravity seems to impair EMTs specifically (Grabherr et al., 2007; Grabherr & Mast, 2010; Leone et al., 1995). Lenggenhager et al. (2008) showed that galvanic vestibular stimulation affects mental rotation only when an EMT strategy is involved. Similar conclusions have been drawn from studies performed after bilateral vestibular loss. For these patients, mental rotation was less impaired with OMTs than with EMTs (Grabherr et al., 2011). According to those authors, OMTs may be achieved by using a purely visuospatial strategy, rendering this type of mental imagery less dependent on vestibular signals than EMTs. But our results support the hypothesis that OMTs are dependent on vestibular signals because they show that mental rotation is significantly impaired in UVD patients.

Neuroimaging studies of mental rotation of 3D cubes have revealed activations of the inferior and superior parietal cortices and visual cortex (area 19) (Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Zacks & Michelon, 2005). Interestingly, these parietal regions overlap with the parietal vestibular cortex (review in Lopez & Blanke, 2011). Of importance for the present study, Bense et al. (2004) reported that early vestibular loss decreased the metabolism in these parietal regions and in occipital regions (area 19). Therefore it is possible that, by affecting brain activity in these areas, vestibular loss may disorganize the neural network commonly involved in mental rotation and vestibular processing.

4.2. Mental scanning

Substantial effects of vestibular loss were found for mental scanning in an unfamiliar environment (garden). This was attested by

the significantly lower correlation coefficients in UVD patients than in controls. The difference in performance between UVD patients and healthy subjects was maximal 1 week after UVN. Moreover, the performance of UVD patients decreased between the first (before UVN) and the second session (1 week after UVN), whereas healthy subjects improved their performance during the same time interval. Note that 1 month after UVN, UVD patients remained impaired. In addition, mental scanning in an unfamiliar environment led to the greatest impairment in BVD patients, who always performed worse than UVD patients, even when the latter were tested during the early stage of UVN. With regard to mental scanning in a familiar environment (map of France), correlation coefficients were lower in UVD patients than in controls, showing again that vestibular loss impairs mental scanning. Major differences between UVD and BVD patients were found 1 month post-lesion, suggesting that, contrary to what is observed after a bilateral vestibular loss, there is no long-lasting effect of unilateral vestibular loss on mental scanning in an environment whose memory is consolidated. The present data show that vestibular loss impairs mental scanning, that is, imagery dealing with the metric properties of mental images.

We note that there was no global effect of the familiarity of the environment on mental scanning. This suggests that vestibular signals are generally involved in mental imagery, but not specifically in the elaboration of new mental images (as required to mentally simulate a movement in the circular garden). Nevertheless, a detailed analysis of the performance in the unfamiliar environment revealed a clear deficit in UVD patients during the early stage after surgery, as compared to the preoperative data. Such a local decrease in performance was not found in the familiar environment. For mental scanning in an unfamiliar environment, patients had to elaborate a new mental image during each session, whereas for mental scanning in the familiar environment, patients – who have been familiar with the map of France for years – needed only the first session to consolidate their mental image. In the two subsequent sessions, they could merely refresh this image during the learning phase. Generating, maintaining, and transforming mental images involve different cognitive processes and brain structures (Dror & Kosslyn, 1994), thus increasing cognitive demand. Any economy in demand during a processing stage could benefit the others. This could partly explain the stable performance in mental scanning in an environment whose memory is consolidated. In addition, it has been shown that repeated testing, even in the absence of repeated learning, reactivates knowledge and favors memory consolidation (e.g., Latini-Corazzini, Thinus-Blanc, Nesa, Geminiani, & Péruch, 2008). Thus, the transient deficit observed in the unfamiliar environment may be due to an impaired ability to elaborate a mental image 1 week after surgery.

The present results are original because, contrary to the previous studies, they demonstrate a strong influence of vestibular signals on OMT tasks. The mental scanning task differs from the mental rotation task because it deals with the metric properties of the mental image. This may explain why the effect of vestibular loss on OMTs is stronger than that described in previous studies. More generally, the deficit in mental scanning could result from the inability of UVD and BVD patients to correctly estimate movements in the imagined environment, as is the case for these patients in the physical environment. There is evidence that directions and distances are not correctly coded in vestibular-defective patients (Brandt, 2001; Cohen & Sangi-Haghpeykar, 2011; Péruch et al., 2005). Similarly, the perception of body rotations is impaired in such patients (von Brevern et al., 1997). Because mental scanning involves homology between the physical space and the represented space, the inability to code distances and angles in physical space could thus hamper mental scanning. Finally, because mental scanning refers to the relation between distance and time and because perceptual space and time are closely related for the estimation of distance traveled (Glasauer, Schneider, Grasso, & Ivanenko, 2007), we cannot exclude that deficits in time perception are also present in vestibular patients. It has been proposed that time perception is related to vestibular signals in healthy participants (e.g., Capelli, Deborne, & Israël, 2007; Israël et al., 2004). The deficits in mental scanning could be related to changes in brain regions commonly involved in vestibular processing and mental scanning. Mental scanning activates fronto-parietal regions and the hippocampus, as well as vestibular regions, including the inferior parietal lobule, insula, and precuneus (e.g., Ghaem et al., 1997; Mellet et al., 2002). Interestingly, structural and metabolic changes have been observed in multimodal parieto-temporal brain regions after vestibular loss. In UVD patients, the white matter is atrophied in the supramarginal gyrus, postcentral gyrus, superior temporal gyrus, and area MT (Hüfner et al., 2009), and hippocampal atrophy has been reported in BVD patients (Brandt et al., 2005). However, no atrophy has been found in the hippocampus of UVD patients (Hüfner et al., 2007, 2009). Finally, unilateral vestibular loss has been related to hypermetabolism in the hippocampus and parieto-insular cortex and to hypometabolism in the inferior parietal lobule, superior temporal gyrus, and precuneus (Bense et al., 2004). Because these regions overlap with the neural networks involved in spatial cognition, mental imagery (Berthoz, 1997; Ghaem et al., 1997; Mellet et al., 2002), and whole-body motor imagery (Blanke et al., 2005; Creem et al., 2001), we speculate that abnormal brain activity due to vestibular loss has disorganized spatial representation and the ability to simulate movement in an environment mentally represented. This hypothesis is supported by electrophysiological evidence in animals showing that vestibular lesions can disorganize hippocampal activity, rendering it more difficult for the animal to locate itself in the physical environment (e.g., Liu, Zheng, King, Darlington, & Smith, 2003a, 2003b; Stackman et al., 2002; Zheng, Kerr, Darlington, & Smith, 2003). Such difficulty to localize the body during navigation in the physical environment, as in virtual environments, may be extrapolated to simulated movements in an imagined space (the two mental scanning tasks in the present case).

4.3. Indirect influences of the vestibular loss on mental imagery

Finally, one cannot exclude that part of the deficits observed in these various mental imagery tasks are related to indirect influences of vestibular loss on cognitive functions (for extensive reviews, see Hanes & McCollum, 2006; Smith, Zheng, Horii, & Darlington, 2005). For instance, the spontaneous nystagmus, deficient gaze stabilization, and unbalance often reported after vestibular loss would decrease the attentional resources allocated to the cognitive task, resulting in poorer performance. Thus, the necessity to control balance and stabilize gaze through various cognitive and behavioral strategies (e.g., Berthoz, 1988) would somehow act as a 'dual task' and would be detrimental to the cognitive task. Several authors reported that maintaining equilibrium in challenging postures decreases the performance in cognitive tasks in vestibular-defective patients (Redfern, Talkowski, Jennings, & Furman, 2004; Yardley et al., 2001). Similar conclusions were drawn from analysis of the interactions between vestibulo-ocular processing and cognitive tasks (Talkowski, Redfern, Jennings, & Furman, 2005). In the present study, it is possible that similar mechanisms may have interfered with the mental imagery tasks. However, note that in the studies cited above, patients were placed in challenging postures, with a strong influence on the cognitive task. By contrast, in our study, patients were seated on a chair, which may have reduced the potential dual-task effect related to postural control. To form a more faithful picture of the direct influence of vestibular loss on cognitive tasks, further investigation should involve a control task requiring no mental imagery. In addition to attentional deficits, spontaneous nystagmus, deficient

gaze stabilization, or blurred vision – resulting from a deficient vestibulo-ocular reflex and diplopia – have often been reported during the early stage after unilateral lesion. Oscillopsia is also a common symptom in patients with bilateral vestibular loss. However, in the present study, patients did not have to move their heads to perform the different mental tasks, thus reducing the influence of deficient gaze stabilization. During the clinical examination, no patient complained of blurred vision, either in the early stage or 1 month after vestibular loss. Finally, abnormal spatial and bodily perception could also have interfered with mental imagery since unilateral patients tested in the early stage after vestibular loss and patients with a bilateral vestibular failure may also report abnormal perception of the external world and of their own body (Gomez-Alvarez & Jauregui-Renaud, 2011; Jauregui-Renaud et al., 2008). Although several of these indirect influences could have interfered with mental imagery, they are difficult to separate from direct vestibular influences since they all are components of the vestibular syndrome.

5. Conclusion

The present results indicate that vestibular signals are necessary to perform OMTs and provide the first demonstration of the critical role of vestibular signals in mental scanning, i.e., in the processing of the metric properties of mental representations. As with spatial cognition and navigation in real and virtual environments, mental imagery requires the integrity of the sensory systems. This is in line with studies showing that mental imagery ability is generally correlated with spatial cognition and navigation performance (Hegarty & Waller, 2004; Palermo, Iaria, & Guariglia, 2008). As for posture, locomotion, and spatial perception (Borel et al., 2008; Halmagyi et al., 2010; Lacour, Dutheil, Tighilet, Lopez, & Borel, 2009; Lopez, Lacour, Leonard, Magnan, & Borel, 2008), impairments are stronger in the early stage after vestibular asymmetry and are gradually compensated. These results further support the cognitive and neuropsychological influences of vestibular pathology (Hanes & McCollum, 2006; Lopez, Halje, & Blanke, 2008; Yardley et al., 2001). Finally, they open new perspectives for the study of spatial representation by suggesting that vestibular dysfunction may disorganize the neural networks commonly involved in vestibular processing and mental imagery.

Acknowledgements

This study was supported by grants from Ministère de l'Enseignement Supérieur et de la Recherche (INSERM U751 & CNRS UMR 6149) and from Institut Fédératif de Recherche 131 "Sciences du Cerveau et de la Cognition". We are grateful to all patients and healthy subjects for their participation.

References

Angelaki, D. E., Klier, E. M., & Snyder, L. H. (2009). A vestibular sensation: Probabilistic approaches to spatial perception. *Neuron*, *64*, 448–461.
Bense, S., Bartenstein, P., Lochmann, M., Schlindwein, P., Brandt, T., & Dieterich, M. (2004). Metabolic changes in vestibular and visual cortices in acute vestibular neuritis. *Annals of Neurology*, *56*, 624–630.
Berthoz, A. (1988). The role of gaze in compensation of vestibular disfunction: The gaze substitution hypothesis. *Progress in Brain Research*, *76*, 411–420.
Berthoz, A. (1997). Parietal and hippocampal contribution to topokinetic and topographic memory. *Philosophical Transactions of the Royal Society of London, Biological Sciences*, *352*, 1437–1448.
Berthoz, A., Israël, I., Georges-François, P., Grasso, R., & Tzuzuku, T. (1995). Spatial memory of body linear displacement: What is being stored? *Science*, *269*, 95–98.
Blanke, O., Mohr, C., Michel, C. M., Pascual-Leone, A., Brugger, P., Seeck, M., et al. (2005). Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. *Journal of Neuroscience*, *25*, 550–557.
Borel, B., Harlay, F., Lopez, C., Magnan, J., Chays, A., & Lacour, M. (2004). Walking performance of vestibular-defective patients before and after unilateral vestibular neurotomy. *Behavioral and Brain Research*, *150*, 191–200.
Borel, L., Le Goff, B., Charade, O., & Berthoz, A. (1994). Gaze strategies during linear motion in head free humans. *Journal of Neurophysiology*, *72*, 2451–2466.
Borel, L., Lopez, C., Péruch, P., & Lacour, M. (2008). Vestibular syndrome: A change in internal spatial representation. *Clinical Neurophysiology*, *38*, 375–389.
Brandt, T. (2001). Vestibulopathic gait. Walking and running. In E. Ruzicka, M. Hallett, & J. Jankovic (Eds.), *Gait disorders. Advances in neurology* (pp. 165–172). Philadelphia: Lippincott, Williams and Wilkins.
Brandt, T., Schautzer, F., Hamilton, D. A., Brüning, R., Markowitsch, H. J., Kalla, R., et al. (2005). Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans. *Brain*, *128*, 2732–2741.
Capelli, A., Deborne, R., & Israël, I. (2007). Temporal intervals production during passive self-motion in darkness. *Current Psychology Letters*, *22*, 1–15.
Chabanne, V., Péruch, P., Denis, M., & Thinus-Blanc, C. (2004). Mental scanning of images constructed from visual experience or verbal descriptions: The impact of survey versus route perspective. *Imagination, Cognition and Personality*, *23*, 163–171.
Cohen, H. S., & Sangi-Haghpeykar, H. (2011). Walking speed and vestibular disorders in a path integration task. *Gait & Posture*, *33*, 211–213.
Cohen, J. (1988). *Statistical power analysis for the behavioral sciences*. San Diego, CA: Academic Press.
Cooper, L. A., & Shepard, R. N. (1973). *Chronometric studies of the rotation of mental images*. New York: Academic Press.
Creem, S. H., Downs, T. H., Wraga, M., Harrington, G. S., Proffitt, D. R., & Downs, J. H., 3rd. (2001). An fMRI study of imagined self-rotation. *Cognitive, Affective, & Behavioral Neuroscience*, *1*, 239–249.
Denis, M., & Cocude, M. (1992). Structural properties of visual images constructed from poorly or well-structured verbal descriptions. *Memory & Cognition*, *20*, 497–506.
Dror, I. E., & Kosslyn, S. M. (1994). Mental imagery and aging. *Psychology and Aging*, *9*, 90–102.
Finke, R. A, & Pinker, S. (1982). Spontaneous imagery scanning in mental extrapolation. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *8*, 142–147.
Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-Mental-State". A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatry Research*, *12*, 189–198.
Ghaem, O., Mellet, E., Crivello, F., Tzourio, N., Mazoyer, B., Berthoz, A., et al. (1997). Mental navigation along memorized routes activates the hippocampus, precuneus, and insula. *Neuroreport*, *8*, 739–744.
Glasauer, S., Amorim, M. A., Viaud-Delmon, I., & Berthoz, A. (2002). Differential effects of labyrinthine dysfunction on distance and direction during blindfolded walking of a triangular path. *Experimental Brain Research*, *145*, 489–497.
Glasauer, S., Schneider, E., Grasso, R., & Ivanenko, Y. (2007). Space–time relativity in self-motion reproduction. *Journal of Neurophysiology*, *97*, 451–461.
Gomez-Alvarez, F. B., & Jauregui-Renaud, K. (2011). Psychological symptoms and spatial orientation during the first 3 months after acute unilateral vestibular lesion. *Archives of Medical Research*, *42*, 97–103.
Grabherr, L., Cuffel, C., Guyot, J.-P., & Mast, F. W. (2011). Mental transformation abilities in patients with unilateral and bilateral vestibular loss. *Experimental Brain Research*, *209*, 205–214.
Grabherr, L., Karmali, F., Bach, S., Indermaur, K., Metzler, S., & Mast, F. W. (2007). Mental own-body and body-part transformations in microgravity. *Journal of Vestibular Research*, *17*, 279–287.
Grabherr, L., & Mast, F. W. (2010). Effects of microgravity on cognition: The case of mental imagery. *Journal of Vestibular Research*, *20*, 53–60.
Gu, Y., DeAngelis, G. C., & Angelaki, D. E. (2007). A functional link between area MSTd and heading perception based on vestibular signals. *Nature Neuroscience*, *10*, 1038–1047.
Guidetti, G., Monzani, D., Trebbi, M., & Rovatti, V. (2007). Peripheral vestibular damage causes impaired navigation tasks on memorized routes in humans. *Annales d'Otolaryngologie et Chirurgie Cervico-Faciale*, *124*, 197–201.
Halmagyi, G., Weber, M. K., & Curthoys, P. I. S. (2010). Vestibular function after acute vestibular neuritis. *Restorative Neurology and Neuroscience*, *28*, 37–46.
Hanes, D., & McCollum, A. G. (2006). Cognitive–vestibular interactions: A review of patient difficulties and possible mechanisms. *Journal of Vestibular Research*, *16*, 75–91.
Hegarty, M., & Waller, D. (2004). A dissociation between mental rotation and perspective-taking spatial abilities. *Intelligence*, *32*, 175–191.
Hüfner, K., Hamilton, D. A., Kalla, R., Stephan, T., Glasauer, S., Ma, J., et al. (2007). Spatial memory and hippocampal volume in humans with unilateral vestibular deafferentation. *Hippocampus*, *17*, 471–485.
Hüfner, K., Stephan, T., Hamilton, D. A., Kalla, R., Glasauer, S., Strupp, M., et al. (2009). Gray-matter atrophy after chronic complete unilateral vestibular deafferentation. *Annals of the New York Academy of Sciences*, *1164*, 383–385.
Israël, I., Capelli, A., Sable, D., Laurent, C., Lecoq, C., & Bredin, J. (2004). Multifactorial interactions involved in linear self-transport distance estimate: A place for time. *International Journal of Psychophysiology*, *53*, 21–28.
Jauregui-Renaud, K., Sang, F. Y., Gresty, M. A., Green, D. A., & Bronstein, A. M. (2008). Depersonalisation/derealisation symptoms and updating orientation in patients with vestibular disease. *Journal of Neurology, Neurosurgery & Psychiatry*, *79*, 276–283.
Kosslyn, S. M., Ball, T. M., & Reiser, B. J. (1978). Visual images preserve metric spatial information: Evidence from studies of image scanning. *Journal of Experimental Psychology: Human Perception and Performance*, *4*, 47–60.

Kosslyn, S. M., DiGirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. *Psychophysiology*, *35*, 151–161.

Lacour, M., Dutheil, S., Tighilet, B., Lopez, C., & Borel, L. (2009). Tell me your vestibular deficit, and I'll tell you how you'll compensate. *Annals of the New York Academy of Sciences*, *1164*, 268–278.

Latini-Corazzini, L., Thinus-Blanc, C., Nesa, M. P., Geminiani, G. C., & Péruch, P. (2008). Differentiated forgetting rates of spatial knowledge in humans in the absence of repeated testing. *Memory*, *16*, 678–688.

Lenggenhager, B., Lopez, C., & Blanke, O. (2008). Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations. *Experimental Brain Research*, *184*, 211–221.

Leone, G., Lipshits, M., Gurfinkel, V., & Berthoz, A. (1995). Is there an effect of weightlessness on mental rotation of three-dimensional objects? *Brain Research Cognitive Brain Research*, *2*, 255–267.

Liu, P., Zheng, Y., King, J., Darlington, C. L., & Smith, P. F. (2003a). Long-term changes in hippocampal n-methyl-D-aspartate receptor subunits following unilateral vestibular damage in rat. *Neuroscience*, *117*, 965–970.

Liu, P., Zheng, Y., King, J., Darlington, C. L., & Smith, P. F. (2003b). Nitric oxide synthase and arginase expression in the vestibular nucleus and hippocampus following unilateral vestibular deafferentation in the rat. *Brain Research*, *966*, 19–25.

Lohman, D. F. (1988). Spatial abilities as traits, processes, and knowledge. In R. J. Sternberg (Ed.), *Advances in the psychology of human intelligence* (pp. 181–248). Hillsdale, NJ: Lawrence Erlbaum.

Lopez, C., & Blanke, O. (2011). The thalamocortical vestibular system in animals and humans. *Brain Research Reviews*, *67*, 119–146.

Lopez, C., Halje, P., & Blanke, O. (2008). Body ownership and embodiment. Vestibular and multisensory mechanisms. *Clinical Neurophysiology*, *38*, 149–161.

Lopez, C., Lacour, M., Leonard, J., Magnan, J., & Borel, L. (2008). How body position changes visual vertical perception after unilateral vestibular loss. *Neuropsychologia*, *46*, 2435–2440.

Magnan, J. (2000). Vestibular neurotomy by the retrosigmoid approach. In O. Sterkers, E. Ferrary, R. Dauman, J. P. Sauvage, & P. Tran Ba Huy (Eds.), *Ménière's disease. Update* (pp. 793–797). The Hague: Kugler.

Mast, F. W., Bamert, L., & Newby, N. (2007). Mind over matter? Imagined body movements and their neuronal correlates. In F. W. Mast, & L. Jäncke (Eds.), *Spatial processing in navigation, imagery and perception* (pp. 353–368). New York: Springer Science + Business Media.

Mast, F. W., Merfeld, D. M., & Kosslyn, S. M. (2006). Visual mental imagery during caloric vestibular stimulation. *Neuropsychologia*, *44*, 101–109.

Mellet, E., Bricogne, S., Crivello, F., Mazoyer, B., Denis, M., & Tzourio-Mazoyer, N. (2002). Neural basis of mental scanning of a topographic representation built from a text. *Cerebral Cortex*, *12*, 1322–1330.

Mittelstaedt, H. (1999). The role of the otoliths in perception of the vertical and in path integration. *Annals of the New York Academy of Sciences*, *871*, 334–344.

Palermo, L., Iaria, G., & Guariglia, C. (2008). Mental imagery skills and topographical orientation in humans: A correlation study. *Behavioural Brain Research*, *192*, 248–253.

Péruch, P., Borel, L., Gaunet, F., Thinus-Blanc, C., Magnan, J., & Lacour, M. (1999). Spatial performance of unilateral vestibular defective patients in nonvisual versus visual navigation. *Journal of Vestibular Research*, *9*, 37–47.

Péruch, P., Borel, L., Magnan, J., & Lacour, M. (2005). Direction and distance deficits in path integration after unilateral vestibular loss depend on task complexity. *Cognitive Brain Research*, *25*, 862–872.

Potegal, M. (1982). Vestibular and neostriatal contributions to spatial orientation. In M. Potegal (Ed.), *Spatial abilities. Development and physiological foundations* (pp. 361–387). London: Academic Press.

Redfern, M. S., Talkowski, M. E., Jennings, J. R., & Furman, J. M. (2004). Cognitive influences in postural control of patients with unilateral vestibular loss. *Gait & Posture*, *19*, 105–114.

Rode, G., Cotton, F., Revol, P., Jacquin-Courtois, S., Rossetti, Y., & Bartolomeo, P. (2010). Representation and disconnection in imaginal neglect. *Neuropsychologia*, *48*, 2903–2911.

Seemungal, B. M., Rizzo, V., Gresty, M. A., Rothwell, J. C., & Bronstein, A. M. (2008). Cortical processing in vestibular navigation. *Progress in Brain Research*, *171*, 339–346.

Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge, MA: MIT Press.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*, 701–703.

Smith, P. F. (1997). Vestibular–hippocampal interactions. *Hippocampus*, *7*, 465–471.

Smith, P. F., Zheng, Y., Horii, A., & Darlington, C. L. (2005). Does vestibular damage cause cognitive dysfunction in humans? *Journal of Vestibular Research*, *15*, 1–9.

Stackman, R. W., Clark, A. S., & Taube, J. S. (2002). Hippocampal spatial representations require vestibular input. *Hippocampus*, *12*, 291–303.

Stackman, R. W., & Taube, J. S. (1997). Firing properties of head direction cells in the rat anterior thalamic nucleus: Dependence on vestibular input. *Journal of Neuroscience*, *17*, 4349–4358.

Talkowski, M. E., Redfern, M. S., Jennings, J. R., & Furman, J. M. (2005). Cognitive requirements for vestibular and ocular motor processing in healthy adults and patients with unilateral vestibular lesions. *Journal of Cognitive Neuroscience*, *17*, 1432–1441.

von Brevern, M., Faldon, M. E., Brookes, G. B., & Gresty, M. A. (1997). Evaluating 3D semicircular canal function by perception of rotation. *American Journal of Otology*, *18*, 484–493.

Yardley, L., Gardner, M., Bronstein, A., Davies, R., Buckwell, D., & Luxon, L. (2001). Interference between postural control and mental task performance in patients with vestibular disorder and healthy controls. *Journal of Neurology, Neurosurgery & Psychiatry*, *71*, 48–52.

Zacks, J. M., & Michelon, P. (2005). Transformations of visuospatial images. *Behavioral and Cognitive Neuroscience Reviews*, *4*, 96–118.

Zacks, J. M., Mires, J., Tversky, B., & Hazeltine, E. (2000). Mental transformations of objects and perspective. *Spatial Cognition and Computation*, *2*, 315–332.

Zheng, Y., Kerr, D. S., Darlington, C. L., & Smith, P. F. (2003). Unilateral inner ear damage results in lasting changes in hippocampal CA1 field potentials in vitro. *Hippocampus*, *13*, 873–878.

Zheng, Y., Darlington, C. L., & Smith, P. F. (2006). Impairment and recovery on a food foraging task following unilateral vestibular deafferentation in rats. *Hippocampus*, *16*, 368–378.