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.

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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, & Tuzuku, 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 (Glaser, Anwani, Vlaim-Delmon, & Berthoz, 2002; Guidetti, Monzani, Trebbi, & Rovati, 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...
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 water maze (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 & Coudce, 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 & Coudce, 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 3-D 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 triad 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 ± 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,
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