Journal of Vestibular Research 25 (2015) 73–89
DOI 10.3233/VES-150544
IOS Press

Vestibular involvement in cognition: Visuospatial ability, attention, executive function, and memory

Robin T. Bigelow* and Yuri Agrawal
Department of Otolaryngology, Head & Neck Surgery, Johns Hopkins University School of Medicine, Baltimore, MD, USA

Received 3 September 2014
Accepted 21 November 2014

Abstract. A growing body of literature suggests the inner ear vestibular system has a substantial impact on cognitive function. The strongest evidence exists in connecting vestibular function to the cognitive domain of visuospatial ability, which includes spatial memory, navigation, mental rotation, and mental representation of three-dimensional space. Substantial evidence also exists suggesting the vestibular system has an impact on attention and cognitive processing ability. The cognitive domains of memory and executive function are also implicated in a number of studies. We will review the current literature, discuss possible causal links between vestibular dysfunction and cognitive performance, and suggest areas of future research.

Keywords: Vestibular system, cognition, visuospatial ability

1. The vestibular system and cognitive functions

Classic teaching on the vestibular system emphasizes its role in maintaining gaze stability and balance via reflexive mechanisms. The typical symptoms associated with vestibular dysfunction include dizziness, unsteadiness, and vertigo, reflecting these cardinal roles of the vestibular system. However, a growing body of literature is providing insight into vestibular contributions to a variety of cognitive processes, including perceptual/visuospatial ability, memory, attention, and executive function. Clinicians have long reported anecdotally a connection between vestibular dysfunction and cognitive impairment, and complaints of memory loss and "brain fog" have also appeared on online message boards led by patients with vertigo and vestibular disease [19,61,119].

Cognitive function can be more precisely analyzed by breaking it down into a number of cognitive domains. While the classification into cognitive domains varies in the literature, most studies include the domains of visuospatial ability, memory, executive function, and attention [66,74,130]. Each of these domains will be further described in their respective sections of this review.

Within the vestibular literature, substantial animal research has shown impaired visuospatial abilities in animals with vestibular lesions [124]. This paper will review several lines of human research linking vestibular and cognitive function. The cognitive domains most often studied in human vestibular research are visuospatial ability and attention, with some studies also investigating memory and executive function. We will review the research linking vestibular dysfunction to impairments in visuospatial ability, attention, executive function, and memory, followed by research examining the cognitive effects of experimental vestibular stimulation and manipulation.

*Corresponding author: Robin T Bigelow, Department of Otolaryngology, Head & Neck Surgery, Johns Hopkins University School of Medicine, Baltimore, MD, USA. Tel.: +1 410 954 9825; Fax: +1 410 955 0035; E-mail: rbigelow@jhmi.edu.

ISSN 0957-4271/15/$35.00

2. Visuospatial ability

Visuospatial ability is a term used to describe how the mind organizes and understands two- and three-dimensional space. It includes a variety of skills including spatial memory, mental imagery, rotation, distance and depth perception, navigation, and visuospatial construction [109]. Spatial memory, navigation, and mental rotation have been studied in relation to vestibular dysfunction and will be reviewed here. A summary of the major studies can be found in Table 1.

2.1. *Spatial memory*

Spatial memory is a complex construct that encompasses information about several different components of one's environment: including geometry, relative position, distance, size, orientation, and coordinates [70]. A number of studies have examined spatial memory in patients with various types of vestibular deficits using the virtual Morris Water Maze Task (vWMT) [6,7,44,45,94,122]. First described in 1998 by Astur et al., the vWMT is a computerized version for humans of the Morris Water Maze that is used in studies of rats. Participants sit at a computer and have to locate a concealed platform in a virtual pool using visual cues [6]. A widely cited study by Brandt and Schautzer compared ten patients who underwent bilateral vestibular neurectomy to age-, sex-, and education-matched controls. The bilateral vestibular dysfunction (BVD) patients had significant decreases in hippocampal size (16.9%) and impaired performance on several aspects of the vWMT including longer path length and decreased time spent in the correct quadrant, but no difference in intelligence or non-spatial memory [25,123]. Interestingly, the BVD patients performed poorly on the vWMT even though the test does not involve any vestibular inputs (the head is stationary). However, descriptions of several BVD participants' performance suggest that the BVD patients had difficulties understanding the vWMT and did not participate in the task as well as the controls [25,123]. This raised questions about whether the BVD patients truly had spatial memory dysfunction vs. another cognitive deficit or lack of technological familiarity. Subsequent studies from the same research group examined unilateral vestibular dysfunction (UVD) patients and vestibular-trained individuals (dancers, slack liners (i.e. individuals who walk across loose ropes)). These studies found significantly worse performance on only one of several measures of the vWMT in right UVD patients, but found no other significant associations between vestibular function and visuospatial ability [67,69]. One way of interpreting these results would be that BVD leads to impaired visuospatial ability, while UVD and vestibular training lead only to mild or no changes in performance. Alternatively, the impairments with BVD but not with UVD or vestibular training could be due to methodological differences in the studies. The study on BVD patients included only 10 patients and compared them to age, sex, and education matched controls, while the latter two studies published in 2007 and 2011 on UVD and vestibular-trained individuals included more participants and matched them to controls more thoroughly, including on computer experience. Repeating the study on patients with BVD, including more participants and controls matched for computer experience would provide more insight into the association between BVD and performance on the vWMT and other visuospatial cognitive tests. Assessing vWMT performance in individuals with vestibular impairments other than BVD or UVD would be valuable as well.

In another study of vestibular dysfunction, spatial memory was assessed with the Corsi block test, a widely used and validated test of spatial memory [75]. Participants are asked to repeat a sequence tapped on a number of blocks, starting with short sequences and progressing to longer sequences until participants can no longer reproduce the pattern. Fifty compensated unilateral vestibular neuritis patients were compared to age- and sex-matched controls on the Corsi block test. Patients performed significantly worse than controls, and were also found to have higher co-morbid depression and anxiety [62]. It should be noted that while the patients and controls were matched for age and sex, the controls were recruited from healthcare staff. As such, differences between the groups could be due to differences in education, career choice, or familiarity with research.

2.2. *Spatial navigation*

Spatial navigation refers to the ability to move through one's environment. Related concepts include head direction, which is awareness of the direction that one's head is angled along the horizontal meridian, and path integration, which is the ability to monitor one's position along a planned trajectory. Spatial navigation is typically assessed by having subjects move along memorized trajectories or towards memorized targets. In rodents, the vestibular system has been shown to contribute to the formation of spatial representations of their environments both in light and dark, which is important for navigation [153]. Studies of spatial navigation in humans with vestibular loss have shown clear evidence of navigational impairment in patients compared to controls. Guidetti found that compared to controls, patients with compensated unilateral vestibular neuritis required more time to walk on a memorized square, circle, or triangular path with their eyes closed, but not eyes open. This finding suggests an impairment in spatial navigation when visual cues are removed [62]. Several studies of spatial navigation performed on patients before, immediately after, and month(s) after vestibular neurectomy provide well-matched controls and give insight into the effects of acute vs. chronic vestibular loss. Studies performed by Péruch in 1999 and 2005, Cohen in 2000, and Borel et al. in 2004 showed that surgical vestibular deafferentation led acutely to increased numbers of turn errors and increased time required to reach memorized targets when walking, particularly during eyes closed navigation when visual cues are absent. Many patients improved their navigational abilities over the months following surgery, but significant deficits often remained [21,36,104,105]. Similar studies performed months to years after surgical vestibular loss similarly revealed significant residual navigation deficits [55,56,127].

These studies indicate that patients with vestibular dysfunction have impaired navigational ability, especially when visual cues are removed in eyes-closed conditions. This suggests the importance of the vestibular system in an individual's awareness of their position in three-dimensional space. It is interesting to note that the majority of patients were able to improve their performance of navigation tasks over several weeks to months after vestibular lesion, suggesting that the temporary impairment may have been due to vestibular imbalance and was not a long-term change in cognitive visuospatial reasoning. Moreover, spatial navigation abilities may be improved by vestibular rehabilitation, suggesting that compensatory strategies for navigation can be developed. Cohen delivered gaze stabilization exercises to 53 patients with chronic vestibulopathy. She observed improvements in the subjects' path integration: they were less likely to veer off of a learned path when their vision was occluded. Patients with vestibular loss may improve their spatial navigation abilities through exercises that increase reliance on proprioception and visual cues [37].

2.3. Mental rotation

Another cognitive task that measures visuospatial ability is mental transformation or mental rotation. Subjects are shown two similar objects which are rotated in relation to each other. Subjects are asked to mentally rotate the images to determine whether they are identical or mirror images of one another [103]. Several authors have compared mental rotation ability in patients with a variety of vestibular disorders to controls and found vestibular patients had more errors and were slower on mental rotation tasks, particularly when the tasks involved human figures (egocentric) rather than objects or non-human figures [32,59]. Similarly, Wallwork found that self-reported dizzy individuals performed worse on mental rotation tasks than controls, although it was not established whether the dizzy patients had vestibular disease [136].

Péruch performed a study of mental rotation ability comparing patients pre and post unilateral vestibular neurectomy to BVD patients and matched controls. Post-op and BVD patients were impaired in mental rotation of three-dimensional objects and in mental scanning of familiar and unfamiliar environments [106]. Mental rotation has also been studied in a number of experiments involving vestibular stimulation, which will be reviewed later in this paper.

2.4. Visuospatial conclusions

These studies suggest that altered or absent vestibular input may lead to a fundamental change in an individual's mental representation of three-dimensional space. The vWMT, Corsi block, and mental rotation tests are purely cognitive tests of spatial memory and mental rotation. These tests were performed seated, without stimulating the individual's peripheral vestibular system. Yet as described, patients with vestibular loss performed worse on these tests than controls. With respect to spatial navigation, patients with vestibular deficits had impairment in their spatial navigation abilities particularly in the absence of visual cues. In many patients these deficits persisted for months after the vestibular loss, long after vertigo symptoms subsided and compensatory mechanisms set in.

The vestibular system has been shown to activate a broad cortical network, including the insula, superior temporal gyrus, hippocampus, and the inferior parietal lobule, among other regions [43,134,151]. In addition to receiving vestibular input, these brain regions are part of a complex neural network for visuospatial processing and memory [7,77,95,131]. The neuroanatomic correlates of the psychophysical tests of visuospatial ability described above are beginning to be established. Brandt observed decreased hippocampal volumes in association with impaired spatial memory among BVD patients [25]. However, a similar study on UVD patients found no changes in hippocampal volumes or spatial memory, but did find smaller volumes of the superior temporal gyrus [68]. While sample sizes in these studies were small, these findings provide insight into the vestibulo-cortical connections that are disrupted with vestibular loss, and that manifest as impairment in visuospatial ability and mental representation of three-dimensional space. Further research examining the structural and functional neuroimaging characteristics of patients with vestibular disease would be valuable in providing insight into the mechanism of vestibular-related visuospatial impairment.

3. Attention

Another dimension of cognitive function that appears to be impacted by vestibular loss is attention. According to Kahneman's Capacity Model of Attention, an individual has a set amount of attention and cognitive resources available to allocate to mental tasks [74]. Individuals with vestibular dysfunction require additional cognitive resources to maintain balance. This leads to increased competition for limited cognitive resources, and decreased cognitive power available for other tasks. The validity of this theoretical model has been studied using the dual task testing paradigm, whereby participants are asked to undertake two tasks simultaneously. The participant's performance on both tasks is measured relative to their performance on each task undertaken separately. Performance of tasks that require processing by similar cognitive networks should decline in response to the increased cognitive demand of the concurrent task [1]. Studies of healthy individuals have used the dual task paradigm to examine postural control and the vestibulo-ocular reflex (VOR) and attention-demanding tasks such as asking the participant to press a button in response to auditory stimuli or counting backwards by three. These studies have consistently shown increases in response latency and/or decreases in accuracy on the attention-demanding cognitive tests in the setting of concurrent postural or vestibular challenges. These differences were accentuated in older individuals compared to younger individuals, and when participants' reliance on vestibular sensory information during the balance tasks was increased (e.g. eyes closed on foam) [13, 29,52,117,129,149]. Notably, performance on the balance and postural tasks, as measured by sway, did not worsen when attention-demanding tasks were added, suggesting that the brain prioritizes attentional resources to maintain balance at the expense of other cognitive tasks [13,29,52,117,129]. These studies performed on healthy individuals suggest that balance is indeed demanding of cognitive resources and is not simply reflexive.

Similar dual-task testing was done examining balance and posture and information processing in patients with vestibular dysfunction. A study by Andersson et al. [5] looked at 24 patients with vertigo and/or dizziness and 24 age- and sex-matched controls. Subjects completed a visuospatial mental task while undergoing concurrent posturography. Both patients and controls' performance on the visuospatial task worsened during eyes closed postural challenge, a test condition that increases reliance on vestibular (and proprioceptive) input. Controls and patients with good baseline balance had worse postural control (increased sway) when performing the mental task with eyes closed. On the other hand, patients with poor baseline balance actually had improvements in posture (decreased sway) during mental tasks. Andersson suggested that this could be due to an enhanced arousal in response to the mental task, although this is inconsistent with Kahneman's model whereby total cognitive resources are not variable [5,74]. Similar results, with postural control improving as task difficulty increases, have been observed in patients with phobic postural vertigo, although the cause of this phenomenon is poorly understood [115]. Future research that varies the postural conditions, mental tasks, and possibly levels of arousal and anxiety will be needed to provide insight into the mechanism behind the apparent dual task benefit.

Yardley studied performance on both spatial and non-spatial cognitive tasks in 48 patients with a variety of vestibular disorders and 24 healthy controls. Participants completed the cognitive tasks while standing still or on a moving platform, and their postural sway was assessed. With increasing postural challenge (platform movement), cognitive performance in terms of timing and accuracy was impaired in both patients and controls, but postural sway remained stable. In this study, the patient group consistently performed worse than the control group on cognitive tasks across postu-

Table 1
Summary of studies on visuospatial – vestibular interactions

Year authors	Participants controls	Outcome measures	Visuospatial ability	Comments
2003 Schautzer 2005 Brandt (Reporting on same data)	10 BVD patients 5–10 years status post vestibular neurectomy 10 age, sex, education matched controls	virtual Morris Water Maze Task (vWMT) MRI Volumetry	Patients performed significantly worse on several aspects of vWMT Five of nine patients at or below 25% on Corsi block testing (visuospatial memory)	Significant 16.9% decrease in hippocampal volume in cases compared to controls, although data was not collected and/or not calculated for 3 of the 10 patients and 1 of the 10 controls. Impaired memory in only 1 patient
2007 Hüfner et al.	16 UVD patients 5–13 years status post acoustic neuroma resection Age, sex, education, and computer experience matched controls	vWMT MRI Volumetry	Performance on vWMT only slightly worse in R UVD patients, no different in L UVD patients	No differences in hippocampal volume seen on MRI. Few differences between groups, better matched controls than Schautzer and Brandt studies. Suggests little or no effect of UVD on vWMT (spatial memory)
2011 Hüfner et al.	21 professional dancers and slack liners (vestibular experts) Age, sex, education, computer experience, athletic experience (non-vestibular) matched controls	vWMT MRI Volumetry	No significant difference in vWMT performance between vestibular experts and controls	Vestibular experts had smaller anterior hippocampal volume and larger posterior hippocampal volume compared to controls. Authors speculate this is due to destabilizing vestibular inputs being deemphasized (smaller anterior hippocampus) in favor of using visual cues (larger posterior hippocampus)
2008 Guidetti et al.	50 compensated UVD patients 50 age and sex matched controls recruited from healthcare staff	Corsi block test Walking navigation (eyes open, closed in triangle, circle, square)	Patients performed worse than controls on Corsi block test of visual memory. Patients also performed worse on walking navigation tasks	Worse visual memory and navigation, but controls not education matched and recruited exclusively from healthcare providers
1999 Péruch et al.	8 Ménière's disease patients (MD) before and after UVD surgery 6 age and education matched controls	Walking navigation (blindfolded, reproducing paths, reversing paths, making shortcuts)	Patients performed worse on navigation tasks one week, but not one month after surgery	Patients were able to compensate for vestibular loss within one month of surgery
2000 Cohen	31 Acoustic neuroma (AN) patients pre and post op 55 chronic peripheral vestibular impaired patients (CV) 24 controls	Walking navigation (eyes open, eyes closed walking a straight course)	Walking navigation impaired in CV patients and immediately post-op patients, improvement in surgical patients by three weeks post-op	Patients compensate for navigational effects of vestibular loss within the first month. AN/CV patients performed much worse with eyes closed, indicating vestibular input is used for mental path integration
2004 Borel et al.	9 Ménière's disease patients before and after vestibular neurectomy 10 healthy controls	Walking navigation (eyes open, eyes closed walking a straight course)	Walking navigation impaired after surgery, improvement in eyes open but not eyes closed navigation by three months	Partial compensation within one month, with residual deficits when vestibular input is required for path integration (eyes closed)
2011 Grabherr et al.	8 BVD patients 15 UVD patients 14 age matched controls	Mental rotation of objects and humans	BVD patients worse at mental rotation than UVD and controls	BVD is sufficient to cause difficulties in mental rotation, while UVD is not
2013 Candidi et al.	14 BPPV patients 9 vestibular neuritis patients (VN) 16 healthy volunteers	Mental rotation of self and human figure	BPPV and VN patients performed worse than controls on rotation tasks	Patients average age was 58, compared to 43 of controls
2013 Wallwork et al.	118 self reported 'dizzy' individuals from a large internet based survey Age, gender, and pain matched controls	Mental rotation	Dizzy participants significantly slower than controls at mental rotation tasks	Patients were recruited from the internet and self-reported dizziness, which may or may not be due to vestibular pathology
2011 Péruch et al.	15 Ménière's disease patients pre and post vestibular nerve destruction surgery 7 BVD patients on average 3.7 years after vestibular loss 12 healthy education, age, sex matched controls	Mental rotation, scanning of environment	BVD and post-op patients were impaired in mental rotation and scanning of environments	BVD and acute UVD cause impairments in visuospatial ability, surgical UVD patients can compensate with time

ral conditions. Performance was similarly affected on spatial and non-spatial cognitive tasks, suggesting the impaired cognitive performance is not due to competition for spatial processing resources, but is instead due to general capacity limitations, and is proportional to the attentional demands of both tasks [151]. Other studies have also observed greater impairments in information processing and other cognitive tasks (such as counting backwards by three), during concurrent balance tasks in patients with vestibular disorders (such as surgical UVD, vestibular neuritis) relative to controls [96,118,120,152].

In a study by Talkowski, 16 surgical UVD patients with no residual dizziness or imbalance were compared to healthy age- and sex-matched controls. Subjects completed an auditory reaction time (RT) task requiring information processing (respond with right or left hand depending on stimulus) during vestibular (rotational chair), visual (fixation on moving laser), or combined vestibular-visual stimulation. Both patients and controls had increases in RT during vestibular stimulation and during ocular pursuit. Patients showed greater increases in RT during rotation than did controls. The prolongation of reaction times in response to vestibular stimulation suggests that the VOR, a reflexive behavior, can interact with and disrupt higher level cognitive processing [128].

A summary of the major studies can be found in Table 2. The majority of studies showed that posture and balance were similar between patients and controls, but performance on cognitive tasks were not. This seems to be an adaptive response, with priority given to diverting attention to prevent falls and maintain safety, at the expense of other cognitive tasks. An 'orientation-first' principal, that orientation and posture are prioritized and may draw attentional resources, has been proposed previously [60].

4. Associations between vestibular, executive, and memory function

Relationships between vestibular function, executive function and memory have also been reported in a number of studies dating back to the 1970s, but most of these early studies suffered from methodologic limitations.

In 1989 Grimm et al. reported on 102 patients with perilymph fistula syndrome (a vestibular disease caused by minor head trauma), of whom a surprising 85% reported memory loss and 80% reported confusion. A subset of these patients underwent cognitive testing, which revealed deficits in memory (digit symbol, auditory recall, paired associate learning tests), visuospatial ability (block design, picture arrangement, paired associate learning, trail making tests), and executive function (digit symbol, picture arrangement, trail making tests) [61]. However, this study was limited by potential sampling bias in the cognitive tests and confounding head injury. A study by Risey and Briner in 1990 found that subjects with vertigo skipped and displaced whole sequences of numbers when counting backwards by two, suggesting impairment of executive function. These subjects with vertigo also had lower scores on the arithmetic (executive function) and digit span (memory, attention) portions of the Wechsler Adult Intelligence Scale [119]. In another study that reviewed 33 cases of gentamicin vestibulotoxicity, 22 patients (66%) reported cognitive dysfunction, which included short-term memory loss, concentration problems, difficulty with word retrieval, reading problems, and inability to prioritize tasks [19]. While these studies are suggestive of executive function and memory impairments, the field of vestibular cognition would benefit from more rigorous research with well-defined groups, matched controls, and standardized memory and executive function tests.

Many authors have suggested that a functional vestibular system is important for normal cognitive development and learning. A study performed by Franco and Panhoca in 2008 found that children with poor school performance were far more likely to have concurrent vestibular dysfunction compared to their peers [51]. Similar data were found in studies performed in the 1970s and 1980s reported in the learning disability literature. Many studies found vestibulocerebellar function was decreased in children with learning disabilities, particularly dyslexia, compared to normal controls [8,31,82,97–100,140]. However, these deficits in vestibular function were not consistent across all studies [28,110,111]. These observed associations between poor school performance and vestibular dysfunction could be due to problems with oculomotor function, leading to impaired reading ability, increased attentional demands of maintaining balance, as reviewed earlier, a concurrent emotional disturbance (which could be related to vestibular symptoms), or another insult that led to both cognitive and vestibular dysfunction [27,144].

5. Effects of vestibular manipulation on cognition

We have described some of the research that has been done linking vestibular disease to cognitive dysfunction, but what happens to cognitive function when the vestibular system is experimentally altered? Here we will review the effects of microgravity and vestibular stimulation on cognitive function.

5.1. Microgravity and cognitive function

The otoconia dependent portions of the vestibular system, the utricle and saccule, both require linear ac-

Table 2
Summary of studies on attention – vestibular interactions

Year authors	Participants controls	Outcome measures	Attention	Comments
1997 Barin et al.	48 individuals aged 20–60	Dual task balance and attention demanding cognitive task	Reaction time increased as sensory input decreased	As sensory inputs decrease and reliance on vestibular input for balance increases
1993 Teasdale et al.	8 young and 9 old participants	Dual task postural and reaction time test	Elderly performed worse as reliance on vestibular system for balance increased	Postural task became increasingly difficult in elderly as sensory inputs were removed
1999 Brown et al.	25 healthy individuals	Dual task of backward digit recall during postural challenge	Worse performance during postural challenge	Worse performance on digit recall during postural challenge
2002 Redfern et al.	19 younger adults (mean 23 years old) 19 older adults (mean 79 years old)	Dual task reaction time and postural challenge	Worse performance on digit recall during postural challenge, worse with age	Postural challenge causes a brief and temporary increased reaction time, indicating that maintaining balance and posture is cognitively demanding
2003 Furman et al.	20 young subjects (mean 23 years). 20 older subjects (mean 69 years)	Dual task information processing during combinations of vestibular and visual stimuli	Vestibular stimulation caused increased reaction times in the dark, reaction time worse with age	During off vertical axis rotation (stimulating otolith organs) increased reaction time in younger, but not older subjects, possibly due to declining otolith function with age
1998 Andersson et al.	24 patients with vertigo and/or dizziness 24 age and sex matched controls	Dual task visuospatial mental task and posturography	Patients and controls performed worse on cognitive tasks during postural challenge	Patients with poor baseline balance actually improved their balance during increased cognitive load. Possibly due to enhanced arousal during the stress of difficult dual tasks or due to abandonment of maladaptive balance strategies during distraction by mental tasks
2001 Yardley	48 patients with mild chronic partially compensated vestibular disorders 24 healthy controls	Dual task spatial and non-spatial mental tasks with postural challenge	Vestibular patients had lower accuracy and longer reaction times compared to controls, both groups' performance worsened similarly during postural challenge	Worse performance overall but similar declines with postural challenge suggests a global decrease in baseline mental task function in vestibular patients
2002 Yardley	20 patients with vertigo due to vestibular imbalance, 36 healthy controls	Dual task reaction time and orientation, arithmetic and orientation	There was only weak evidence for interference between performance and orientation in healthy individuals. Disoriented individuals had worse performance on arithmetic	Authors conclude that disoriented individuals need to devote substantial cognitive resources toward orientation, leading to worse performance on arithmetic and other cognitive tasks
2004 Redfern et al.	15 compensated UVD patients status post nerve resection. Age and gender matched controls	Dual task information processing auditory reaction times during postural challenge	UVD patients had slower reaction times across all conditions, both groups increased reaction time similarly with postural challenge	Compensated UVD patients have an increased baseline cognitive requirement to maintain balance and posture
2005 Talkowski et al.	16 compensated UVD patients Healthy age and sex matched controls	Dual task study of reaction time and combinations of vestibular and visual stimuli	UVD patients had greater increases in reaction time during vestibular stimulation compared to controls	Interference between vestibular-ocular processing and reaction time suggests greater cognitive demands for orientation in compensated UVD patients compared to controls
2010 Nascimbeni et al.	14 vestibular neuritis patients 17 healthy controls	Dual task gait and counting backward by 3	Vestibular patients performed significantly worse than controls on cognitive task while walking and balancing	Attentional demands of gait task led to worse performance on cognitive math/attentional task in vestibular patients
2011 Roberts et al.	15 BPPV patients 15 patients with other vestibular disease 15 controls recruited from lab staff	Dual task combinations of locomotion, naming task, motor task	Patients were more impaired than controls in their ability to walk in a straight line as cognitive tasks were added	Vestibular patients require more attentional resources for locomotion than controls, particularly when visual cues are absent

celeration to function. Gravity, the major source of linear acceleration on earth, is largely absent in a microgravity environment such as in space. Semicircular canal function, on the other hand, does not rely on gravitational forces and remains functional even in a microgravity environment. Space exploration has provided a unique testing environment of the effect of temporary reduction of otolith stimulation on a variety of tasks.

Astronauts have anecdotally reported decreases in cognitive and motor function while in space, collectively described as 'mental viscosity' or 'the space stupids' [35]. Studies of cognitive function in microgravity have inconsistently found impairments in executive function (judgement, arithmetic), memory, and language (i.e. grammatical reasoning), but more consistently found deficits in visuospatial ability (tracking, spatial mental representation) and attention (i.e. dual-task performance) [20,38,57,86–88,139], for reviews see [34,50,58,89]. These studies of microgravity corroborate the studies of vestibular disorders reviewed above which suggest that balance and orientation require additional attention when vestibular information is altered. Astronauts' impairments were particularly notable during transition periods including the first three weeks in space and the first two weeks back on earth [50,89]. This temporal pattern of acute cognitive deficit followed by subsequent improvement parallels the cognitive problems and improvements seen in patients soon after vestibular lesioning. These findings are based on small studies but they warranted concern significant enough for NASA to fund an ongoing larger, longitudinal, comprehensive study of neurocognitive performance before, during, and after space flight [76].

The value of these experiments, summarized in Table 3, is that they provide a healthy population in which the effects of temporary reduction of otolith input and the resulting impairment in vertical orientation can be studied. While the type of experiments and the outcome measures differ from those used in studies of vestibular patients, both the astronauts in space with reduced otolith input and the vestibularly impaired patients appear to have deficits in visuospatial ability and attention. These convergent data suggest that the cognitive deficits seen in vestibular patients are likely due to the lack of vestibular input, not other potential confounding factors like concurrent illness or adverse effects of surgery/anesthesia. However, the results seen in astronauts may not be externally valid. Microgravity does impair otolith function, which may be a factor in the cognitive impairments seen. But, the cognitive impairments may also be partly due to other complex and unique circumstances of space travel, such as stress or emotional disturbance, which has been described in a number of astronauts.

These impairments in attention and other domains of cognitive function seen when vestibular input is altered (both in space and among the vestibularly-impaired) may be related to Sopite syndrome, a condition similar to motion sickness. During long periods of movement some individuals experience substantial fatigue and activity limitation. These symptoms of Sopite syndrome can occur in relation to or independent from other symptoms of motion sickness. The pathophysiology of Sopite syndrome is unknown, although it has been attributed to visual-vestibular mismatch. One study found changes in cortisol and melatonin in response to conflicting streams of sensory information regarding orientation, suggesting that hormonal and/or neurotransmitter changes are responsible for the symptoms of Sopite syndrome [53,78].

5.2. Vestibular stimulation

Several studies have experimentally stimulated the vestibular system with physical motion and tested the effect of this vestibular stimulation on cognitive function. Van Elk found reaction times on mental rotation tasks improved when the image was mentally rotated in the same direction as physical rotation [133]. Similarly, Wang et al. found the latency of characteristic EEG patterns in an auditory attention task decreased in response to angular rotation, but increased in response to linear acceleration [137]. The cause for this difference in cognitive speed between rotation and linear acceleration is unclear, but it may indicate that linear acceleration is more disorienting than rotation, and therefore diverts more attention away from other cognitive tasks. These provide further evidence that cognitive function in specific tasks related to attention and visuospatial ability may actually improve with horizontal semi-circular canal stimulation, but that vertical disorientation due to linear acceleration is more profound and leads to cognitive slowing.

The vestibular system can also be stimulated experimentally using several different techniques, providing yet another way of testing the effects of abnormal vestibular function on cognition. In caloric vestibular stimulation (CVS) cold and/or warm water is infused into the external auditory canal; the change in temperature leads to a change in density and subsequent motion of the endolymphatic fluid of the horizontal semicircular canal, leading to perceived head motion in the plane of the canal and nystagmus [14]. Galvanic vestibular stimulation (GVS) is a technique in which electrodes placed on the mastoid bones are used to stimulate the vestibular afferent nerve [132]. This stimulation simulates excitation (or inhibition) of all three semicircular canals and two otoliths simultaneously, and typically results in an eye movement response that has horizontal and torsional components [38,71,138]. Since these stimuli affect different components of the vestibular system and may be inconsistently applied, it is difficult to draw conclusions from this literature.

Several studies of caloric stimulation have shown mixed changes in cognitive function. Two studies

Table 3
Summary of studies on cognitive function in microgravity

Year authors	Participants	Outcome measures	Perceptual/ visuospatial ability	Attention	Comments
1993 Manzey et al.	1 astronaut	Cognitive tests before, during, and after spaceflight	Impaired tracking during space flight		Psychomotor processes/spatial tracking ability may be impaired in microgravity – a unique environment in which otolith, but not semicircular canal function is impaired
1995 Manzey et al.	1 astronaut	Cognitive tests before, during, and after spaceflight	Impaired tracking during space flight	Impairments in dual task performance of cognitive tasks during space flight	Psychomotor processes/spatial tracking ability may be impaired in microgravity
1998 Manzey	1 astronaut	Cognitive tests before, during, and after spaceflight	Impaired tracking during first week of space flight	Impairments in dual task performance during first month, but not subsequent months, of space flight	No impairments in grammatical reasoning during space flight
1997 Watt	5 astronauts	Pointing to targets with eyes open and closed before and after spaceflight	Greater errors in ability to point to targets in space than on the ground		Authors concluded that errors in microgravity due to lack of knowledge of target, not limb position, indicating impaired internal representation of three dimensional space in microgravity
2010 Bock et al.	3 astronauts	Cognitive tests before, during, and after spaceflight	Impaired tracking during space flight, mental rotation impaired during dual task paradigm	Dual task on rhythm production and visuospatial orientation worse than regular choice reaction time test	
2007 Grabherr et al.	8 healthy volunteers	Mental rotation during microgravity simulating parabolic flight	Responses on egocentric rotation delayed and less accurate during microgravity		Rotations of body parts more delayed than responses to whole-body rotations
2013 Dalecki et al.	6 healthy volunteers	Mental rotation during microgravity simulating parabolic flight	No impairments in rotation seen during microgravity		No impairments seen on letter, hand, or scene rotations during simulated microgravity – subjects were provided visual and tactile vertical reference frames

found improvements in visuospatial ability (mental rotation, spatial memory) in response to unilateral CVS [9,47], while another found no effect on a quantitative visual-imagery recognition task [4]. But a study by Mast et al. in 2006 with fewer participants found CVS did not change performance on low-imagery cognitive tasks (deciding if a statement was true or false) and, contrary to the previous studies, CVS worsened performance on high imagery tasks (mental rotation, memory of an image). These authors suggested the changes (both improvement and impairments) in cognitive performance could be explained by changes in cerebral blood flow that has been seen in functional imaging during CVS, but the changes seen in functional brain imaging are not entirely consistent across studies and could be used to justify either conclusion [9,15,22,90,126,143]. The studies' timing of stimulation relative to cognitive tests, cognitive tests used as outcomes, and exact method of caloric stimulation differed, which could explain the seemingly contradictory results.

Sub-threshold GVS involves low-power current that is insufficient to induce nystagmus or motion perception. Small studies and case reports using sub-threshold GVS suggest an improvement in visuospatial ability (visual memory, perceptual deficits) with sub-threshold GVS. However, the largest and most rigorous study published by Dilda et al. in 2012 found

Table 4
Summary of studies on cognitive function and vestibular stimulation

Year authors	Participants controls	Outcome measures	Perceptual/ visuospatial ability	Memory	Comments
2005 Wilkinson et al.	1 patient with brain injury leading to inability to recognize or remember faces	Facial recognition during sub-threshold GVS	Facial recognition improved with GVS when current alternated between testing blocks		Small sample size of 1, uncertain physiologic effect of sub-threshold GVS
2008 Wilkinson et al.	12 participants, 12 controls	Facial recognition with sub-threshold GVS and sham	Sub-threshold GVS improved participants' reaction times with no changes in accuracy		Uncertain physiologic effect of sub-threshold GVS
2010 Wilkinson et al.	1 patient with brain injury leading to inability to accurately copy figures	Rey-Osterrieth complex figure copy task with sub-threshold GVS and sham	During sub-threshold GVS the accuracy of copied figures was improved		Small sample size of 1, uncertain physiologic effect of sub-threshold GVS, possibility of learning effects
2012 Dilda et al.	120 healthy volunteers	Cognitive tests before, during, and after randomization to sham, sub-threshold, or supra-threshold GVS	Supra-threshold GVS worsened performance on mental rotation and short term spatial memory	Supra-threshold GVS worsened performance on short term spatial memory	No effects seen in sub-threshold GVS. Impaired performance during supra-threshold GVS on mental rotation and spatial memory may be due to disorientation during stimulation
2014 Ghaheri et al.	60 healthy women	Performance on Corsi block testing during sub-threshold GVS	Improvement in Corsi block performance during sub-threshold GVS	Improvement in Corsi block performance during sub-threshold GVS	Authors suggest that effect may be due to inherent learning during the course of the study
2008 Lenggenhager et al.	11 healthy right handed volunteers	Mental rotations during left, right, or sham GVS	Mental rotation slower during right sided GVS compared to sham or left sided		Effect of GVS on mental rotation was more pronounced during egocentric rather than object based rotations
2001 Bächtold et al.	108 healthy right handed male university students	Object and verbal memory tasks with right, left, or sham caloric stimulation during learning phase	Object location memory improved with left, but not right or sham caloric stimulation	Verbal and spatial memory improved with caloric stimulation	Effects on verbal (left brained) and spatial (right brained) abilities were specific for the hemisphere of the brain activated during calorics (primarily contralateral to the ear stimulated).
2012 Falconer and Mast	14 healthy right handed adults	Mental rotation of objects and humans with caloric stimulation	Mental rotations of humans, but not objects, was improved with caloric vestibular stimulation		
1994 Alway et al.	11 healthy subjects	Visual-imagery task with unilateral caloric stimulation	No change observed on imagery task with caloric stimulation		
2006 Mast et al.	8 healthy volunteers	Performance on visual imagery, mental rotation, and low imagery task with caloric stimulation and sham	Visual imagery and mental rotation was impaired during calorics compared to sham stimulation		Caloric stimulation influenced visuospatial tasks (imagery and mental rotation) but did not alter performance on low imagery task (true-false statements)
2004 Wang et al.	33 healthy volunteers	Event related potentials (ERP) on EEG associated with auditory attention task during angular and linear acceleration			Selective improvement (shorter latency) during semicircular canal stimulation, selective worsening (longer latency) during otolith stimulation. Vestibular stimulation appears to have an effect on attention
2014 van Elk et al.	18 healthy right handed volunteers	Mental rotation of human figure with and without yaw axis rotation	Reaction times improved when actual body rotation direction was congruent with human figure mental rotation direction		Physical rotation facilitated reaction times on human figure mental rotation in the same direction, suggesting vestibular input primes the cortical network responsible for mental rotation

no effect [42,53,145–147]. Again, these authors suggest these results are due to altered cerebral blood flow in response to vestibular stimulation [145–147]. While signal changes indicative of increased metabolic activity have been seen on fMRI and PET with supra-threshold GVS, to date no functional imaging studies have been performed using sub-threshold GVS, and the specific brain regions activated vary across studies [15,30,46,83,84,126]. The results could be an artifact of small sample sizes or, as Ghaheri et al. suggest, related to inherent learning of the cognitive tasks that is due to repeated measurement and unrelated to stimulation [54].

Supra-threshold GVS, on the other hand, has con-

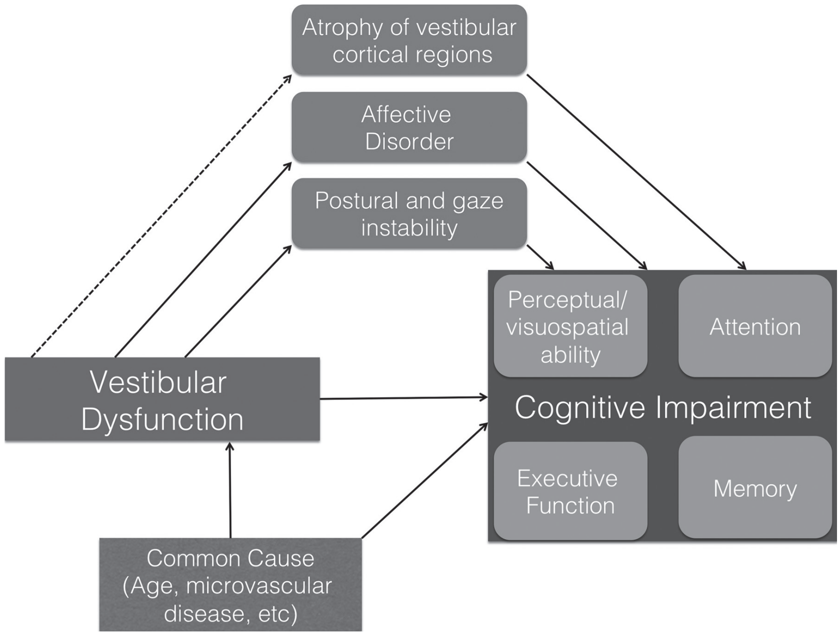

Fig. 1. Conceptual model proposing mechanism of cognitive dysfunction due to the vestibular system.

sistently been shown to have a detrimental effect on visuospatial ability (mental rotation, perspective taking, match to sample) [42,80]. Supra-threshold GVS may worsen cognitive performance indirectly by worsening visual stability, causing nystagmus or oscillopsia. It may also increase cognitive load and use of attentional resources by forcing the brain to reconcile the conflicting vestibular, visual, and proprioceptive sensory inputs in order to maintain orientation.

In case reports and small case series caloric stimulation has been shown to have a diverse range of other cognitive/psychiatric effects, including changes in number generation, purchase decisions, optimism, mood, manic delusions, somatoparaphrenic delusions (denial of ownership of body parts), visual neglect, pain perception, phantom limb and body spatial perception [18,23,24,33,48,49,64,72,73,78,81,85,91–93,112, 113,116,121,148]. These reports suggest that the vestibular system has a broad and sometimes profound effect on cognition and emotion, but the sample sizes are all small and the literature would benefit from more rigorous, larger studies of these reported effects.

These studies on vestibular stimulation, summarized in Table 4, suggest that vestibular stimulation has an effect on cognitive function, but the exact effect differs from study to study. One complicating factor is the different portions of the vestibular system stimulated by the different modalities. The timing of vestibular stimulation may also be important. It is possible that vestibular stimulation during learning may improve later performance as shown by Bächtold et al. [9]. However, stimulation during recall or other cognitive tasks may worsen performance, depending on the type of task performed and side of vestibular activation [42,80,90]. Despite the use of sham and control stimulations, it is also possible that the cognitive changes seen in GVS and CVS are due to some other effect of the stimulation, such as the sensations produced by electrical current or temperature changes. Future research into the cognitive effects (both improvements and impairments) of vestibular stimulation would benefit from careful selection of stimulation modality and cognitive tests used, as suggested by Palla and Lenggenhager [102].

6. Other factors that may influence cognitive – vestibular interactions

Thus far we have reviewed evidence that vestibular function is associated with the cognitive functions of visuospatial ability, attention, executive function, and memory. A substantial body of literature also exists linking vestibular function to emotional states and affective disorders. A thorough review of the topic is beyond the scope of this paper. However,in brief, there appear to be complex bidirectional interactions between vertigo and affective disorders, such that vertigo worsens affective symptoms, and emotional states can have an effect on the perception of vertigo and disequilibrium [16,125,150]. Interested readers are directed to reviews by Balaban et al. from 2011 and Gurvich et al. from 2013 for further reading [10,63].

Another emerging topic that is important for further study is the effect of age-related vestibular decline on cognitive function. Numerous studies have shown vestibular function declines with age, but the impact of this decline on physical and cognitive function has not been well-characterized [2,3,11,12,26,101, 107,108,141,142]. Previc has provocatively hypothesized that vestibular loss may contribute to the development of Alzheimer's disease [114]. Indeed, one of the hallmark features of Alzheimer's disease is impaired topographic memory and wandering behavior, both of which are related to visuospatial function which in turn has been linked to vestibular function [17,40]. Future large-scale longitudinal studies tracking vestibular function, cognitive function, and the development of dementia would help further elucidate this relationship.

7. Conclusions

The studies discussed in this paper suggest that the vestibular system is linked to a variety of cognitive functions, particularly in the domains of visuospatial ability and attention but also in executive function and memory (see attached tables for summary of major papers). The mechanism by which vestibular dysfunction is associated with cognitive dysfunction is still unclear, but the available research suggests several potential pathways, shown in Fig. 1. Vestibular dysfunction may lead to atrophy of areas within the cortical vestibular network as suggested by Brandt and Hüfner, including the hippocampus, which may in turn be responsible for impairments in memory and visuospatial ability [25,68,134]. Increased gaze and postural instability associated with vestibular loss may require increased attentional resources allocated to maintaining balance and decreased resources available for cognitive tasks. The high comorbidity of affective disorders in individuals with vestibular impairment may also contribute to cognitive dysfunction [63].

More research is needed to further elucidate the relationship between vestibular function and cognition. Larger studies with well-matched controls, as well as longitudinal studies tracking the time course of vestibular function and cognitive function would provide valuable insights. As the population ages in the United States and globally, the prevalence of age-related vestibular dysfunction will likely increase. The impact of this sensory decline on cognitive function, activities of daily living, and development of dementia needs to be defined, with the potential goal of developing vestibular rehabilitation or cognitive training programs to limit the functional impact of age-related vestibular loss.

References

[1] B. Abernethy, Dual-task methodology and motor skills research: Some applications and methodological constraints, *Journal of Human Movement Studies* **14**(3) (1988), 101–132.

[2] Y. Agrawal, J.P. Carey, C.C. Della Santina, M.C. Schubert and L.B. Minor, Disorders of balance and vestibular function in US adults: Data from the National Health and Nutrition Examination Survey, 2001–2004, *Archives of Internal Medicine* **169**(10) (2009), 938–944. doi:10.1001/archinternmed.2009.66.

[3] Y. Agrawal, M.G. Zuniga, M. Davalos-Bichara, M.C. Schubert, J.D. Walston, J. Hughes and J.P. Carey, Decline in semicircular canal and otolith function with age. Otology & Neurotology: Official Publication of the American Otological Society, *American Neurotology Society [and] European Academy of Otology and Neurotology* **33**(5) (2012), 832–839. doi:10.1097/MAO.0b013e3182545061.

[4] D. Alway, L.I. Shotland, P. Nichelli, I. Appollonio and J. Grafman, No specific effects of caloric stimulation on the visual-imagery processes of normal subjects, *Perceptual and Motor Skills* **78**(3 Pt 2) (1994), 1147–1152.

[5] G. Andersson, L. Yardley and L. Luxon, A Dual-task Study of Interference Between Mental Activity and Control of Balance, *American Journal of Otology* **19** (1998), 632–637.

[6] R.S. Astur, M.L. Ortiz and R.J. Sutherland, A characterization of performance by men and women in a virtual Morris water task: A large and reliable sex difference, *Behavioural Brain Research* **93**(1-2) (1998), 185–190.

[7] R.S. Astur, L.B. Taylor, A.N. Mamelak, L. Philpott and R.J. Sutherland, Humans with hippocampus damage display severe spatial memory impairments in a virtual Morris water task, *Behavioural Brain Research* **132**(1) (2002), 77–84. doi:10.1016/S0166-4328(01)00399-0.

[8] A.J. Ayres, Learning Disabilities and the Vestibular System, *Journal of Learning Disabilities* **11**(1) (1978).

[9] D. Bächtold, T. Baumann, P.S. Sándor, M. Kritos, M. Regard and P. Brugger, Spatial- and verbal-memory improvement by cold-water caloric stimulation in healthy subjects, *Experimental Brain Research* **136**(1) (2001), 128–132. doi:10.1007/s002210000588.

[10] C.D. Balaban, R.G. Jacob and J.M. Furman, Neurologic bases for comorbidity of balance disorders, anxiety disorders and migraine: Neurotherapeutic implications, *Expert Review of Neurotherapeutics* **11**(3) (2011), 379–94. doi:10.1586/ern.11.19.

[11] R.W. Baloh, J. Enrietto, K.M. Jacobson and A. Lin, Age-related changes in vestibular function: A longitudinal study, *Annals of the New York Academy of Sciences* **942** (2001), 210–219.

[12] R.W. Baloh, S.H. Ying and K.M. Jacobson, A longitudinal study of gait and balance dysfunction in normal older people, *Archives of Neurology* **60**(6) (2003), 835–839. doi:10.1001/archneur.60.6.835.

[13] K. Barin, G.D. Jefferson, P.J. Sparto and M. Parnianpour, Effect of aging on human postural control during cognitive tasks, *Biomedical Sciences Instrumentation* **33** (1997), 388–393.

[14] G. Been, T.T. Ngo, S.M. Miller and P.B. Fitzgerald, The use of tDCS and CVS as methods of non-invasive brain stimulation, *Brain Research Reviews* **56**(2) (2007), 346–361. doi:10.1016/j.brainresrev.2007.08.001.

[15] S. Bense, T. Stephan, T.A. Yousry, T. Brandt and M. Dieterich, Multisensory Cortical Signal Increases and Decreases During Vestibular Galvanic Stimulation (fMRI), *J Neurophysiol* **85**(2) (2001), 886–899.

[16] C. Best, A. Eckhardt-Henn, G. Diener, S. Bense, P. Breuer and M. Dieterich, Interaction of somatoform and vestibular disorders, *Journal of Neurology, Neurosurgery, and Psychiatry* **77**(5) (2006), 658–664. doi:10.1136/jnnp.2005.072934.

[17] L. Birdane, A. Incesulu, M.K. Gurbuz and D. Ozbabalik, Sacculocolic reflex in patients with dementia: Is it possible to use it for early diagnosis? *Neurological Sciences? Official Journal of the Italian Neurological Society and of the Italian Society of Clinical Neurophysiology* **33**(1) (2012), 17–21. doi:10.1007/s10072-011-0595-3.

[18] E. Bisiach, M.L. Rusconi and G. Vallar, Remission of somatoparaphrenic delusion through vestibular stimulation, *Neuropsychologia* **29**(10) (1991), 1029–1031.

[19] F.O. Black, S. Pesznecker and V. Stallings, Permanent gentamicin vestibulotoxicity. Otology & Neurotology: Official Publication of the American Otological Society, *American Neurotology Society [and] European Academy of Otology and Neurotology* **25**(4) (2004), 559–569.

[20] O. Bock, C. Weigelt and J.J. Bloomberg, Cognitive demand of human sensorimotor performance during an extended space mission: A dual-task study, *Aviation, Space, and Environmental Medicine* **81**(9) (2010), 819–824.

[21] L. Borel, F. Harlay, C. Lopez, J. Magnan, A. Chays and M. Lacour, Walking performance of vestibular-defective patients before and after unilateral vestibular neurotomy, *Behavioural Brain Research* **150**(1-2) (2004), 191–200. doi:10.1016/S0166-4328(03)00257-2.

[22] G. Bottini, R. Sterzi, E. Paulesu, G. Vallar, S.F. Cappa, F. Erminio and R.S. Frackowiak, Identification of the central vestibular projections in man, a pet activation study, *Experimental Brain Research* **99** (1994), 164–169.

[23] G. Bottini, E. Paulesu, M. Gandola, S. Loffredo, P. Scarpa, R. Sterzi and G. Vallar, eds, Left caloric vestibular stimulation ameliorates right hemianesthesia, *Neurology* **65**(8) (2005), 1278–1283. doi:10.1212/01.wnl.000018 2398.14088.e8.

[24] G. Bottini, M. Gandola, A. Sedda and E.R. Ferrè, Caloric vestibular stimulation: Interaction between somatosensory system and vestibular apparatus, *Frontiers in Integrative Neuroscience* **7** (2013), 66. doi:10.3389/fnint.2013.00066.

[25] T. Brandt, Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans, *Brain* **128** (2005), 2732–2741.

[26] K. Brantberg, K. Granath and N. Schart, Age-related changes in vestibular evoked myogenic potentials, *Audiology & Neuro-Otology* **12**(4) (2007), 247–253. doi:10.1159/000101332.

[27] J. Braswell and R.M. Rine, Evidence that vestibular hypofunction affects reading acuity in children, *International Journal of Pediatric Otorhinolaryngology* **70**(11) (2006), 1957–1965. doi:10.1016/j.ijporl.2006.07.013.

[28] B. Brown, G. Haegerstrom-Portnoy, C.D. Yingling, J. Herron, D. Galin and M. Marcus, Dyslexic children have normal vestibular responses to rotation, *Archives of Neurology* **40**(6) (1983), 370–373.

[29] L.A. Brown, A. Shumway-Cook and M.H. Woolacott, Attentional demands and postural recovery: The effects of aging, *Journal of Gerontology* **54**(4) (1999), M165–M171.

[30] S.F. Bucher, M. Dieterich, M. Wiesmann, A. Weiss, R. Zink, T.A. Yousry and T. Brandt, Cerebral functional magnetic resonance imaging of vestibular, auditory, and nociceptive areas during galvanic stimulation, *Annals of Neurology* **44**(1) (1998), 120–125. doi:10.1002/ana.410440118.

[31] N.N. Byl, F.M. Byl and J.H. Rosenthal, Interaction of spatial perception, vestibular function, and exercise in young school age boys with learning disabilities, *Perceptual and Motor Skills* **68**(3 Pt 1) (1989), 727–738.

[32] M. Candidi, A. Micarelli, A. Viziano, S.M. Aglioti, I. Minio-Paluello and M. Alessandrini, Impaired mental rotation in benign paroxysmal positional vertigo and acute vestibular neuritis, *Frontiers in Human Neuroscience* **7** (2013), 783. doi:10.3389/fnhum.2013.00783.

[33] S. Cappa, R. Sterzi, G. Vallar and E. Bisiach, Remission of hemineglect and anosognosia during vestibular stimulation, *Neuropsychologia* **25**(5) (1987), 775–782.

[34] J.G. Casler and J.R. Cook, Cognitive Performance in Space and Analogous Environments, *International Journal of Cognitive Ergonomics* **3**(4) (1999), 351–372.

[35] G. Clément, Fundamentals of Space Medicine (2nd ed.). New York: Springer, 2011.

[36] H.S. Cohen, Vestibular disorders and impaired path integration along a linear trajectory, *Journal of Vestibular Research: Equilibrium & Orientation* **10**(1) (2000), 7–15.

[37] H.S. Cohen and K.T. Kimball, Improvements in path integration after vestibular rehabilitation, *Journal of Vestibular Research: Equilibrium & Orientation* **12**(1) (2002), 47–51.

[38] I.S. Curthoys and H.G. Macdougall, What galvanic vestibular stimulation actually activates, *Frontiers in Neurology* **3** (2012), 117. doi:10.3389/fneur.2012.00117.

[39] M. Dalecki, S. Dern and F. Steinberg, Mental rotation of a letter, hand and complex scene in microgravity, *Neuroscience Letters* **533** (2013), 55–59. doi:10.1016/j.neulet.2012.11.002.

[40] C. De Boer, F. Mattace-Raso, J. van der Steen and J.J. Pel, Mini-Mental State Examination subscores indicate visuomotor deficits in Alzheimer's disease patients: A cross-sectional study in a Dutch population, *Geriatrics & Gerontology International*, (2013). doi:10.1111/ggi.12183.

[41] A. Deutschländer, S. Bense, T. Stephan, M. Schwaiger, M. Dieterich and T. Brandt, Rollvection versus linearvection: comparison of brain activations in PET, *Human Brain Mapping* **21**(3) (2004), 143–153. doi:10.1002/hbm.10155.

[42] V. Dilda, H.G. MacDougall, I.S. Curthoys and S.T. Moore, Effects of Galvanic vestibular stimulation on cognitive function, *Experimental Brain Research* **216**(2) (2012), 275–285. doi:10.1007/s00221-011-2929-z.

[43] M. Dieterich and T. Brandt, Functional brain imaging of peripheral and central vestibular disorders, *Brain? A Journal of Neurology* **131**(Pt 10) (2008), 2538–2552. doi:10.1093/brain/awn042.

[44] I. Driscoll, The Aging Hippocampus: Cognitive, Biochemi-

cal and Structural Findings, *Cerebral Cortex* **13**(12) (2003), 1344–1351. doi:10.1093/cercor/bhg081.

[45] I. Driscoll, D.A. Hamilton, R.A. Yeo, W.M. Brooks and R.J. Sutherland, Virtual navigation in humans: The impact of age, sex, and hormones on place learning, *Hormones and Behavior* **47**(3) (2005), 326–335. doi:10.1016/j.yhbeh.2004.11.013.

[46] S.B. Eickhoff, P.H. Weiss, K. Amunts, G.R. Fink and K. Zilles, Identifying human parieto-insular vestibular cortex using fMRI and cytoarchitectonic mapping, *Human Brain Mapping* **27**(7) (2006), 611–621. doi:10.1002/hbm.20205.

[47] C.J. Falconer and F.W. Mast, Balancing the mind: Vestibular induced facilitation of egocentric mental transformations, *Experimental Psychology* **59**(6) (2012), 332–339. doi:10.1027/1618-3169/a000161.

[48] E.R. Ferrè, M.R. Longo, F. Fiori and P. Haggard, Vestibular modulation of spatial perception, *Frontiers in Human Neuroscience* **7** (2013a), 660. doi:10.3389/fnhum.2013.00660.

[49] E.R. Ferrè, E. Vagnoni and P. Haggard, Galvanic vestibular stimulation influences randomness of number generation, *Experimental Brain Research* **224**(2) (2013b), 233–241. doi:10.1007/s00221-012-3302-6

[50] B. Fowler, D. Comfort and O. Bock, A review of cognitive and perceptual-motor performance in space, *Aviation, Space, and Environmental Medicine* **71**(9 Suppl) (2000), A66–8.

[51] E.S. Franco and I. Panhoca, Vestibular function in children underperforming at school, *Brazilian Journal of Otorhinolaryngology* **74**(6) (2008), 815–825.

[52] J.M. Furman, M.L.T.M. Mller, M.S. Redfern and J.R. Jennings, Visual vestibular stimulation interferes with information processing in young and older humans, *Experimental Brain Research* **152**(3) (2003), 383–392. doi:10.1007/s00221-003-1560-z.

[53] A. Graybiel and J. Knepton, Sopite syndrome: A sometimes sole manifestation of motion sickness, *Aviation, Space, and Environmental Medicine* **47**(8) (1976), 873–882.

[54] F. Ghaheri, M.A. Ghahraman, F. Jarollahi and S. Jalaie, Visuo-spatial memory enhancement by galvanic vestibular stimulation: A preliminary report, *Audiology* **23**(1) (2014).

[55] S. Glasauer, M.A. Amorim, E. Vitte and A. Berthoz, Goal-directed linear locomotion in normal and labyrinthine-defective subjects, *Experimental Brain Research* **98**(2) (1994), 323–335.

[56] S. Glasauer, M.-A. Amorim, I. Viaud-Delmon and A. Berthoz, Differential effects of labyrinthine dysfunction on distance and direction during blindfolded walking of a triangular path, *Experimental Brain Research* **145**(4) (2002), 489–497. doi:10.1007/s00221-002-1146-1.

[57] L. Grabherr, F. Karmali, S. Bach, K. Indermaur, S. Metzler and F.W. Mast, Mental own-body and body-part transformations in microgravity, *Journal of Vestibular Research: Equilibrium & Orientation* **17**(5–6) (2007), 279–287.

[58] L. Grabherr and F.W. Mast, Effects of microgravity on cognition: The case of mental imagery, *Journal of Vestibular Research: Equilibrium & Orientation* **20**(1) (2010), 53–60. doi:10.3233/VES-2010-0364.

[59] L. Grabherr, C. Cuffel, J.-P. Guyot and F.W. Mast, Mental transformation abilities in patients with unilateral and bilateral vestibular loss, *Experimental Brain Research* **209**(2) (2011), 205–214. doi:10.1007/s00221-011-2535-0.

[60] M.A. Gresty and J.F. Golding, Impact of vertigo and spatial disorientation on concurrent cognitive tasks, *Annals of the New York Academy of Sciences* **1164** (2009), 263–267. doi:10.1111/j.1749-6632.2008.03744.x.

[61] R.J. Grimm, W.G. Hemenway, P.R. Lebray and F.O. Black, The perilymph fistula syndrome defined in mild head trauma. Acta Oto-Laryngologica, *Supplementum* **464** (1989), 1–40.

[62] G. Guidetti, D. Monzani, M. Trebbi and V. Rovatti, Impaired navigation skills in patients with psychological distress and chronic peripheral vestibular hypofunction without vertigo, *Acta Otorhinolaryngologica Italica: Organo Ufficiale Della Società Italiana Di Otorinolaringologia E Chirurgia Cervico-Facciale* **28**(1) (2008), 21–25.

[63] C. Gurvich, J.J. Maller, B. Lithgow, S. Haghgooie and J. Kulkarni, Vestibular insights into cognition and psychiatry, *Brain Research* **1537** (2013), 244–259. doi:10.1016/j.brainres.2013.08.058.

[64] M. Hartmann, L. Grabherr and F.W. Mast, Moving along the mental number line: Interactions between whole-body motion and numerical cognition, *Journal of Experimental Psychology. Human Perception and Performance* **38**(6) (2012), 1416–1427. doi:10.1037/a0026706.

[65] Healthboards.com. Just diagnosed with Vestibular Imbalance Disorder... after a decade!!! Now what? – Inner Ear Disorders Message Board – HealthBoards. (n.d.). Retrieved June 30, 2014, from http://www.healthboards.com/boards/inner-ear-disorders/728885-just-diagnosed-vestibular-imbalance-disorder-after-decade-now-what.html.

[66] H.C. Hendrie, M.S. Albert, M.A. Butters, S. Gao, D.S. Knopman, L.J. Launer and M.V. Wagster, eds, The NIH Cognitive and Emotional Health Project. Report of the Critical Evaluation Study Committee, *Alzheimer's & Dementia?: The Journal of the Alzheimer's Association* **2**(1) (2006), 12–32. doi:10.1016/j.jalz.2005.11.004.

[67] K. Hüfner, D.A. Hamilton, R. Kalla, T. Stephan, S. Glasauer, J. Ma and T. Brandt, Spatial memory and hippocampal volume in humans with unilateral vestibular deafferentation, *Hippocampus* **17**(6) (2007), 471–485. doi:10.1002/hipo.20283.

[68] K. Hüfner, T. Stephan, D.A. Hamilton, R. Kalla, S. Glasauer, M. Strupp and T. Brandt, Gray-matter atrophy after chronic complete unilateral vestibular deafferentation, *Annals of the New York Academy of Sciences* **1164** (2009), 383–385. doi:10.1111/j.1749-6632.2008.03719.x.

[69] K. Hüfner, C. Binetti, D.A. Hamilton, T. Stephan, V.L. Flanagin, J. Linn and T. Brandt, eds, Structural and functional plasticity of the hippocampal formation in professional dancers and slackliners, *Hippocampus* **21**(8) (2011), 855–865. doi:10.1002/hipo.20801.

[70] I. Iachini, A. Iavarone, V.P. Senese, F. Ruotolo and G. Ruggiero, Visuospatial memory in healthy elderly, AD and MCI: A review, *Current Aging Science* **2**(1) (2009), 43–59.

[71] K. Jahn, A. Naessl, M. Strupp, E. Schneider, T. Brandt and M. Dieterich, Torsional eye movement responses to monaural and binaural galvanic vestibular stimulation: Side-to-side asymmetries, *Annals of the New York Academy of Sciences* **1004** (2003), 485–489.

[72] K. Jáuregui-Renaud, V. Ramon-Toledo, M. Aguilar-Bolanos, B. Montano-Velazques and A. Pliego-Maldonado, Symptoms of detachment from the self or from the environment in patients with an acquired deficiency of the special senses – Journal of Vestibular Research – Volume 18, Number 2–3/2008 – IOS Press, *Journal of Vestibular Research* **18** (2008a), 129–137.

[73] K. Jáuregui-Renaud, F.Y.P. Sang, M.A. Gresty, D.A. Green and A.M. Bronstein, Depersonalisation/derealisation symptoms and updating orientation in patients with vestibular dis-

ease, *Journal of Neurology, Neurosurgery, and Psychiatry* **79**(3) (2008b), 276–283. doi:10.1136/jnnp.2007.122119.

[74] D. Kahneman, Attention and effort. Englewood Cliffs, NJ: Prentice-Hall, 1973.

[75] Kessels, Roy P.C. van Zandvoort, M. J.E. Postma, L. Albert Kappelle and E.H.F. Jaapde Haan, The Corsi Block-Tapping Task: Standardization and Normative Data, *Applied Neuropsychology* **7**(4) (2000), 252–258. 7p. 1 Black and White Photograph.

[76] V. Koppelmans, B. Erdeniz, Y.E. De Dios, S.J. Wood, P.A. Reuter-Lorenz, I. Kofman and R.D. Seidler, eds, Study protocol to examine the effects of spaceflight and a spaceflight analog on neurocognitive performance: Extent, longevity, and neural bases, *BMC Neurology* **13** (2013), 205. doi: 10.1186/1471-2377-13-205.

[77] D.J. Kravitz, K.S. Saleem, C.I. Baker and M. Mishkin, A new neural framework for visuospatial processing, *Nature Reviews. Neuroscience* **12**(4) (2011), 217–230. doi: 10.1038/nrn3008.

[78] B.D. Lawson and A.M. Mead, The sopite syndrome revisited: Drowsiness and mood changes during real or apparent motion, *Acta Astronautica* **43**(3-6) (1998), 181–192.

[79] L. Le Chapelain, J.M. Beis, J. Paysant and J.M. André, Vestibular caloric stimulation evokes phantom limb illusions in patients with paraplegia, *Spinal Cord* **39**(2) (2001), 85–87.

[80] B. Lenggenhager, C. Lopez and O. Blanke, Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations, *Experimental Brain Research* **184**(2) (2008), 211–221. doi:10.1007/s00221-007-1095-9

[81] J. Levine, D. Toder, V. Geller, M. Kraus, T. Gauchman, M. Puterman and N. Grisaru, Beneficial effects of caloric vestibular stimulation on denial of illness and manic delusions in schizoaffective disorder: A case report, *Brain Stimulation* **5**(3) (2012), 267–273. doi:10.1016/j.brs.2011.03.004.

[82] H.N. Levinson, The cerebellar-vestibular basis of learning disabilities in children, adolescents and adults: hypothesis and study, *Perceptual and Motor Skills* **67**(3) (1988), 983–1006.

[83] E. Lobel, J.F. Kleine, D. Le Bihan, A. Leroy-Willig and A. Berthoz, Functional MRI of Galvanic Vestibular Stimulation, *J Neurophysiol* **80**(5) (1998), 2699–2709.

[84] E. Lobel, J.F. Kleine, A. Leroy-Willig, P.-F. Moortele, D. Le Bihan, O.-J. Grusser and A. Berthoz, Cortical Areas Activated by Bilateral Galvanic Vestibular Stimulation, *Annals of the New York Academy of Sciences* **871**(1 OTOLITH FUNCT) (1999), 313–323. doi:10.1111/j.1749-6632.1999.tb09194.x.

[85] C. Lopez, H.-M. Schreyer, N. Preuss and F.W. Mast, Vestibular stimulation modifies the body schema, *Neuropsychologia* **50**(8) (2012), 1830–1837. doi:10.1016/j.neuropsychologia.2012.04.008.

[86] D. Manzey, B. Lorenz, A. Schiewe, G. Finell and G. Thiele, Behavioral aspects of human adaptation to space: analyses of cognitive and psychomotor performance in space during an 8-day space mission, *The Clinical Investigator* **71**(9) (1993), 725–731.

[87] D. Manzey, B. Lorenz, A. Schiewe, G. Finell and G. Thiele, Dual-task performance in space: Results from a single-case study during a short-term space mission, *Human Factors* **37**(4) (1995), 667–681.

[88] D. Manzey, B. Lorenz and V. Poljakov, Mental performance in extreme environments: Results from a performance monitoring study during a 438-day spaceflight, *Ergonomics* **41**(4) (1998a), 537–559. doi:10.1080/001401398186991.

[89] D. Manzey and B. Lorenz, Mental performance during short-term and long-term spaceflight, *Brain Research Brain Research Reviews* **28**(1-2) (1998b), 215–221.

[90] F.W. Mast, D.M. Merfeld and S.M. Kosslyn, Visual mental imagery during caloric vestibular stimulation, *Neuropsychologia* **44**(1) (2006), 101–109. doi:10.1016/j.neuropsychologia.2005.04.005.

[91] P.D. McGeoch and V.S. Ramachandran, Vestibular stimulation can relieve central pain of spinal origin, *Spinal Cord* **46**(11) (2008), 756–757. doi:10.1038/sc.2008.47.

[92] P.D. McGeoch, L.E. Williams, R.R. Lee and V.S. Ramachandran, Behavioural evidence for vestibular stimulation as a treatment for central post-stroke pain, *Journal of Neurology, Neurosurgery, and Psychiatry* **79**(11) (2008), 1298–1301. doi:10.1136/jnnp.2008.146738.

[93] R. McKay, C. Tamagni, A. Palla, P. Krummenacher, S.C.A. Hegemann, D. Straumann and P. Brugger, Vestibular stimulation attenuates unrealistic optimism. Cortex; *A Journal Devoted to the Study of the Nervous System and Behavior* **49**(8) (2013), 2272–2275. doi:10.1016/j.cortex.2013.04.005.

[94] S.D. Moffat and S.M. Resnick, Effects of age on virtual environment place navigation and allocentric cognitive mapping, *Behavioral Neuroscience* **116**(5) (2002), 851–859. doi:10.1037/0735-7044.116.5.851.

[95] S.D. Moffat, W. Elkins and S.M. Resnick, Age differences in the neural systems supporting human allocentric spatial navigation, *Neurobiology of Aging* **27**(7) (2006), 965–972. doi:10.1016/j.neurobiolaging.2005.05.011.

[96] A. Nascimbeni, A. Gaffuri, A. Penno and M. Tavoni, Dual task interference during gait in patients with unilateral vestibular disorders, *Journal of Neuroengineering and Rehabilitation* **7** (2010), 47. doi:10.1186/1743-0003-7-47.

[97] K. Ottenbacher, Identifying vestibular procession dysfunction in learning-disabled children. The American Journal of Occupational Therapy: *Official Publication of the American Occupational Therapy Association* **32**(4) (1978), 217–221.

[98] K. Ottenbacher, P.J. Watson and M.A. Short, Association between nystagmus hyporesponsivity and behavioral problems in learning-disabled children. The American Journal of Occupational Therapy: *Official Publication of the American Occupational Therapy Association* **33**(5) (1979), 317–322.

[99] K. Ottenbacher, Excessive postrotary nystagmus duration in learning-disabled children. The American Journal of Occupational Therapy: *Official Publication of the American Occupational Therapy Association* **34**(1) (1980), 40–44.

[100] Ottenbacher, KennethAbbott, CarmenHaley and P.J. DonnaWatson, Human figure drawing ability and vestibular processing dysfunction in learning-disabled children, *Journal of Clinical Psychology* **40**(4) (1984).

[101] G.D. Paige, Senescence of human visual-vestibular interactions. 1. Vestibulo-ocular reflex and adaptive plasticity with aging, *Journal of Vestibular Research? Equilibrium & Orientation* **2**(2) (1992), 133–151.

[102] A. Palla and B. Lenggenhager, Ways to investigate vestibular contributions to cognitive processes, *Frontiers in Integrative Neuroscience* **8** (2014), 40. doi:10.3389/fnint.2014.00040.

[103] L.M. Parsons, Imagined spatial transformation of one's body, *Journal of Experimental Psychology General* **116**(2) (1987), 172–191.

[104] P. Péruch, L. Borel, F. Gaunet, G. Thinus-Blanc, J. Magnan

and M. Lacour, Spatial performance of unilateral vestibular defective patients in nonvisual versus visual navigation, *Journal of Vestibular Research: Equilibrium & Orientation* **9**(1) (1999), 37–47.

[105] P. Péruch, L. Borel, J. Magnan and M. Lacour, Direction and distance deficits in path integration after unilateral vestibular loss depend on task complexity, *Brain Research. Cognitive Brain Research* **25**(3) (2005), 862–872. doi:10.1016/j.cogbrainres.2005.09.012.

[106] P. Péruch, C. Lopez, C. Redon-Zouiteni, G. Escoffier, A. Zeitoun, M. Sanjuan and L. Borel, eds, Vestibular information is necessary for maintaining metric properties of representational space: Evidence from mental imagery, *Neuropsychologia* **49**(11) (2011), 3136–3144. doi:10.1016/j.neuropsychologia.2011.07.026.

[107] R.J. Peterka, F.O. Black and M.B. Schoenhoff, Age-related changes in human vestibulo-ocular and optokinetic reflexes: Pseudorandom rotation tests, *Journal of Vestibular Research? Equilibrium & Orientation* **1**(1) (1990), 61–71.

[108] R.J. Peterka and P.J. Loughlin, Dynamic regulation of sensorimotor integration in human postural control, *Journal of Neurophysiology* **91**(1) (2004), 410–423. doi:10.1152/jn.00516.2003.

[109] S. Pinker, Visual cognition: An introduction, *Cognition* **18**(1-3) (1984), 1–63. doi:10.1016/0010-0277(84)90021-0.

[110] H.J. Polatajko, A Critical Look at Vestibular Dysfunction in Learning-disabled Children, *Developmental Medicine & Child Neurology* **27**(3) (1985), 283–292. doi:10.1111/j.1469-8749.1985.tb04538.x.

[111] H.J. Polatajko, Visual-Ocular Control of Normal and Learning-disabled Children, *Developmental Medicine & Child Neurology* **29**(4) (1987), 477–485. doi:10.1111/j.1469-8749.1987.tb02507.x.

[112] N. Preuss, G. Hasler and F.W. Mast, Caloric vestibular stimulation modulates affective control and mood, *Brain Stimulation* **7**(1) (2014a), 40. doi:10.1016/j.brs.2013.09.003.

[113] N. Preuss, F.W. Mast and G. Hasler, Purchase decision-making is modulated by vestibular stimulation, *Frontiers in Behavioral Neuroscience* **8** (2014b), 51. doi:10.3389/fnbeh.2014.00051.

[114] F.H. Previc, Vestibular loss as a contributor to Alzheimer's disease, *Medical Hypotheses* **80**(4) (2013), 360–367. doi:10.1016/j.mehy.2012.12.023.

[115] V. Querner, S. Krafczyk, M. Dieterich and T. Brandt, Patients with somatoform phobic postural vertigo: The more difficult the balance task, the better the balance performance, *Neuroscience Letters* **285**(1) (2000), 21–24.

[116] V.S. Ramachandran, P.D. McGeoch, L. Williams and G. Arcilla, Rapid relief of thalamic pain syndrome induced by vestibular caloric stimulation, *Neurocase* **13**(3) (2007), 185–188. doi:10.1080/13554790701450446.

[117] M.S. Redfern, M.L.T.M. Muller, J.R. Jennings and J.M. Furman, Attentional Dynamics in Postural Control During Perturbations in Young and Older Adults, *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences* **57**(8) (2002), B298–B303. doi:10.1093/gerona/57.8.B298.

[118] M.S. Redfern, M.E. Talkowski, J.R. Jennings and J.M. Furman, Cognitive influences in postural control of patients with unilateral vestibular loss, *Gait & Posture* **19**(2) (2004), 105–114. doi:10.1016/S0966-6362(03)00032-8.

[119] J. Risey and W. Briner, Dyscalculia in patients with vertigo, *Journal of Vestibular Research: Equilibrium & Orientation* **1**(1) (1990–1991), 31–37.

[120] J.C. Roberts, H.S. Cohen and H. Sangi-Haghpeykar, Vestibular disorders and dual task performance: Impairment when walking a straight path, *Journal of Vestibular Research: Equilibrium & Orientation* **21**(3) (2011), 167–174. doi:10.3233/VES-2011-0415.

[121] A.B. Rubens, Caloric stimulation and unilateral visual neglect, *Neurology* **35**(7) (1985), 1019–1024.

[122] N.J. Sandstrom, J. Kaufman and S.A. Huettel, Males and females use different distal cues in a virtual environment navigation task, *Brain Research Cognitive Brain Research* **6**(4) (1998), 351–360.

[123] F. Schautzer, Spatial Memory Deficits in Patients with Chronic Bilateral Vestibular Failure, *Annals of the New York Academy of Sciences* **1004**(1) (2003), 316–324. doi:10.1196/annals.1303.029.

[124] P.F. Smith and Y. Zheng, From ear to uncertainty: vestibular contributions to cognitive function, *Frontiers in Integrative Neuroscience* **7** (2013), 84. doi:10.3389/fnint.2013.00084.

[125] J.P. Staab and M.J. Ruckenstein, Which comes first? Psychogenic dizziness versus otogenic anxiety, *The Laryngoscope* **113**(10) (2003), 1714–1718.

[126] T. Stephan, A. Deutschländer, A. Nolte, E. Schneider, M. Wiesmann, T. Brandt and M. Dieterich, Functional MRI of galvanic vestibular stimulation with alternating currents at different frequencies, *NeuroImage* **26**(3) (2005), 721–732. doi:10.1016/j.neuroimage.2005.02.049.

[127] Y. Takei, R. Grasso and A. Berthoz, Quantitative analysis of human walking trajectory on a circular path in darkness, *Brain Research Bulletin* **40**(5-6) (1996), 491–495; discussion 495–496.

[128] M.E. Talkowski, M.S. Redfern, J.R. Jennings and J.M. Furman, Cognitive requirements for vestibular and ocular motor processing in healthy adults and patients with unilateral vestibular lesions, *Journal of Cognitive Neuroscience* **17**(9) (2005), 1432–1441. doi:10.1162/0898929054985419.

[129] N. Teasdale, C. Bard, J. Larue and M. Fleury, On the cognitive penetrability of posture control, *Experimental Aging Research* **19**(1) (1993), 1–13. doi:10.1080/03610739308253919.

[130] E.M. Tucker-Drob, D.A. Briley, J.M. Starr and I.J. Deary, Structure and correlates of cognitive aging in a narrow age cohort, *Psychology and Aging* **29**(2) (2014), 236–249. doi:10.1037/a0036187.

[131] R.M. Umarova, D. Saur, S. Schnell, C.P. Kaller, M.-S. Vry, V. Glauche and C. Weiller, eds, Structural connectivity for visuospatial attention: Significance of ventral pathways, *Cerebral Cortex (New York, N.Y.: 1991)* **20**(1) (2010), 121–129. doi:10.1093/cercor/bhp086.

[132] K.S. Utz, V. Dimova, K. Oppenländer and G. Kerkhoff, Electrified minds: Transcranial direct current stimulation (tDCS) and galvanic vestibular stimulation (GVS) as methods of non-invasive brain stimulation in neuropsychology – a review of current data and future implications, *Neuropsychologia* **48**(10) (2010), 2789–2810. doi:10.1016/j.neuropsychologia.2010.06.002.

[133] M. Van Elk and O. Blanke, Imagined own-body transformations during passive self-motion, *Psychological Research* **78**(1) (2014), 18–27. doi:10.1007/s00426-013-0486-8.

[134] J. Ventre-Dominey, Vestibular function in the temporal and parietal cortex: distinct velocity and inertial processing pathways, *Frontiers in Integrative Neuroscience* **8** (2014), 53. doi:10.3389/fnint.2014.00053.

[135] E. Vitte, C. Derosier, Y. Caritu, A. Berthoz, D. Hasboun and D. Soulié, Activation of the hippocampal formation

by vestibular stimulation: A functional magnetic resonance imaging study, *Experimental Brain Research* **112**(3) (1996), doi:10.1007/BF00227958.

[136] S.B. Wallwork, D.S. Butler and G.L. Moseley, Dizzy people perform no worse at a motor imagery task requiring whole body mental rotation; A case-control comparison, *Frontiers in Human Neuroscience* **7** (2013), 258. doi:10.3389/fnhum.2013.00258.

[137] L.-J. Wang, J.-H. Wei, D. Zhang, W.-J. Dong, J.-P. Guo and M.-Q. Hu, The effects of vestibular stimuli on brain cognitive processing: An ERP study, *Neuroreport* **15**(18) (2004), 2757–2560.

[138] D.L. Wardman and R.C. Fitzpatrick, What does galvanic vestibular stimulation stimulate? *Advances in Experimental Medicine and Biology* **508** (2002), 119–128.

[139] D.G. Watt, Pointing at memorized targets during prolonged microgravity, *Aviation, Space, and Environmental Medicine* **68**(2) (1997), 99–103.

[140] Z.R. Weeks, Effects of the vestibular system on human development, part 2: Effects of vestibular stimulation on mentally retarded, emotionally disturbed, and learning-disabled individuals, *The American Journal of Occupational Therapy: Official Publication of the American Occupational Therapy Association* **33**(7) (1979), 450–457.

[141] M.S. Welgampola and J.G. Colebatch, Vestibulocollic reflexes: normal values and the effect of age, *Clinical Neurophysiology* **112**(11) (2001), 1971–1979. doi:10.1016/S1388-2457(01)00645-9.

[142] M.S. Welgampola and J.G. Colebatch, Selective effects of ageing on vestibular-dependent lower limb responses following galvanic stimulation, *Clinical Neurophysiology?: Official Journal of the International Federation of Clinical Neurophysiology* **113**(4) (2002), 528–534.

[143] R. Wenzel, P. Bartenstein, M. Dieterich, A. Danek, A. Weindl, S. Minoshima and T. Brandt, eds, Deactivation of human visual cortex during involuntary ocular oscillations. A PET activation study, *Brain? A Journal of Neurology* **119**(Pt 1) (1996), 101–110.

[144] S.R. Wiener-Vacher, D.A. Hamilton and S.I. Wiener, Vestibular activity and cognitive development in children: perspectives, *Frontiers in Integrative Neuroscience* **7** (2013), 92. doi:10.3389/fnint.2013.00092.

[145] D. Wilkinson, P. Ko, P. Kilduff, R. McGlinchey and W. Milberg, Improvement of a face perception deficit via subsensory galvanic vestibular stimulation, *Journal of the International Neuropsychological Society: JINS* **11**(7) (2005), 925–929.

[146] D. Wilkinson, S. Nicholls, C. Pattenden, P. Kilduff and W. Milberg, Galvanic vestibular stimulation speeds visual memory recall, *Experimental Brain Research* **189**(2) (2008).

[147] D. Wilkinson, O. Zubko, J. Degutis, W. Milberg and J. Potter, Improvement of a figure copying deficit during subsensory galvanic vestibular stimulation, *Journal of Neuropsychology* **4**(Pt 1) (2010), 107–118. doi:10.1348/174866409X468205.

[148] L. Winter, T.H.C. Kruger, J. Laurens, H. Engler, M. Schedlowski, D. Straumann and M.A. Wollmer, Vestibular stimulation on a motion-simulator impacts on mood States, *Frontiers in Psychology* **3** (2012), 499. doi:10.3389/fpsyg.2012.00499.

[149] L. Yardley, M. Gardner, N. Lavie and M. Gresty, Attentional demands of perception of passive self-motion in darkness, *Neuropsychologia* **37**(11) (1999), 1293–1301.

[150] L. Yardley, Overview of psychologic effects of chronic dizziness and balance disorders, *Otolaryngologic Clinics of North America* **33**(3) (2000), 603–616.

[151] L. Yardley, Interference between postural control and mental task performance in patients with vestibular disorder and healthy controls, *Journal of Neurology, Neurosurgery & Psychiatry* **71**(1) (2001), 48–52. doi:10.1136/jnnp.71.1.48.

[152] L. Yardley, Attentional demands of continuously monitoring orientation using vestibular information, *Neuropsychologia* **40**(4) (2002), 373–383. doi:10.1016/S0028-3932(01)00113-0.

[153] R.M. Yoder and J.S. Taube, The vestibular contribution to the head direction signal and navigation, *Frontiers in Integrative Neuroscience* **8** (2014), 32. doi:10.3389/fnint.2014.00032.